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Regeneration and recovery dynamics of logged forests in the Solomon Islands

ERIC KATOVAI

(MSc. Conservation Biology, University of Queensland, Australia)

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Co-author Affiliations in Alphabetical order

Dawnie, D Katovai;	School of Science and Technology, Pacific Adventist University, 14 Mile, Port Moresby, NCD 111, Papua New Guinea. (Email: dawnie.katovai@pau.ac.pg)
Myknee Sirikolo	National Herbarium and Botanical Gardens, Ministry of Forestry, Honiara, Solomon Islands. (Email: mqusa@mofr.gov.sb)
Susan G Laurance	Centre for Tropical Environmental and Sustainability Science, and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia. (Email: susan.laurance@jcu.edu.au)
Will Edwards	Centre for Tropical Environmental and Sustainability Science, and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia. (Email: will.edwards@jcu.edu.au)
William F Laurance	Centre for Tropical Environmental and Sustainability Science, and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia. (Email: bill.laurance@jcu.edu.au)
Umesh Srinivasan	Program in Science, Technology and Environmental Policy, Woodrow Wilson School for Public and International Affairs, Princeton University, Princeton, NJ 08540, USA. (Email: umesh.srinivasan@gmail.com)

Statement of contribution by authors

Chapter 2 was published as '**Katovai, E., Katovai, D. D., Edwards, W., & Laurance, W. F. (2015). Forest structure, plant diversity and local endemism in a highly varied New Guinea landscape. *Tropical Conservation Science*, 8(2), 284-300.'** The research idea was conceived and developed by EK. Data collection was carried out by EK and DDK. EK did the plant ID with the assistance of Papua New Guinea national herbarium expert. EK and WE did the data analyses. EK wrote the paper. DDK, WE reviewed the paper and provided useful comments. WFL edited the final manuscript. EK did all revisions during the peer review process.

Chapter 3 was published as '**Katovai, E., Katovai, D., 2012. Forest gaps: A blessing in disguise? A review on gap dynamics, human interpolations and interventions. *Science in New Guinea* 32, 40–50.'** EK conceptualized the idea, did the review and wrote the paper. DK reviewed the paper and finalised changes before submission. EK dealt with the review process.

Chapter 4 was published as '**Katovai, E., Edwards, W., & Laurance, W. F. 2015. Dynamics of logging in Solomon Islands: The need for restoration and conservation alternatives. *Tropical Conservation Science*, 8, 718-731.'** EK developed the research idea, and also carried out literature review and writing of this paper. WE critically reviewed the early drafts of this paper. WFL did the final edit on the paper before submission. EK was responsible for all amendments during the review process.

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compositional change across logged forests in the Solomon Islands*. Forest Ecology and Management*, 372, 53-63.' EK conceived the research idea. Data collection was done by EK. Plant identification was done by MS and EK. Data analyses were conducted by EK and US. EK wrote the manuscript. WE and WFL provided useful comments and edited the manuscript. Finally EK and WE revised the manuscript during the review process.

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Statement of contribution by others

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Abstract

Logging is among the major drivers of deforestation and forest degradation in tropical landscapes globally. Its enduring persistence over the past century was driven by the high demand for tropical wood. Tropical forests in the Solomon Islands have been heavily logged over the last century, but very little is known about the recovery dynamics and ecology of logged forests in this region. Furthermore, it is still unknown whether these forests can return to a pre-cut state via natural regeneration processes.

In this thesis, the effects of industrial selective logging on forest floristics, functions and structure are assessed in the Solomon Islands. Furthermore, factors influencing the recovery of these attributes and their implications in forest management and conservation are considered. This thesis initially assesses the rich plant biodiversity in Oceania, in Chapter 2. Results from this study suggest that highly varied landscapes in Papua New Guinea contain high plant endemism and *beta* diversity via intense segregation and establishment of locally varied vegetation communities. Therefore, to effectively conserve biodiversity in such forests, protection must include landscapes that best represent the full range of topographic and edaphic variability throughout the island to account for locally endemic species restricted to specific ecological niches.

Chapter 3 reviews the differences between forest-gap characteristics and gap-phase regeneration in natural and anthropogenically created forest gaps in tropical forests. It also evaluates whether or not forest degradation can provide an opportunity for

generating floral compositions in rainforests that might be better adapted to continually changing environmental conditions.

A review of the dynamics of logging in the Solomon Islands in chapter 4 highlights how the socioeconomic dynamics in this small developing nation promoted excessive logging, resulting in highly degraded forests. The key elements discussed here are the roles of (i) economic interests, (ii) corruption, (iii) poor employment conditions in the logging sector, (iv) high forest accessibility, (v) resource limitations for forest monitoring, (vi) disputes over logging benefits, and (vii) a paucity of information for policy development. The review also suggests that some logged forests in the Solomon Islands may require active restoration—especially those that have been most heavily damaged.

Chapter 5 compares the taxonomic diversity and composition of trees between unlogged forest and sites that were logged 10, 30 and 50 years previously to evaluate the floristic dynamics of these forests following timber harvesting. The results reveal that distance to logging roads and to unlogged forest influenced post-logging recovery, emphasising the importance of edge effects in influencing forest composition. At least in the first 50 years after logging, tree-community composition did not appear to converge over time toward that in unlogged forests. Although species assemblages in previously logged forests generally tend to shift over time from light demanding-pioneers to old-growth species, a long-lived pioneer *Campnosperma brevipetiolata* dominated the forest even 50 years after logging. It was suggested that the persistence of *C. brevipetiolata* may have hindered the recovery of tree communities in logged forests. The removal and harvesting of such persistent, long-lived pioneer trees via careful silviculture techniques could potentially help to accelerate recovery of heavily logged forests.

Chapter 6 explores the influence of light on the occurrence of understory plant functional traits and diversity in logged forests. Plant functional types–growth form, chlorotype and leaf area were used to predict the development of post-logging understory plant communities as such functional types show strong links with disturbance history and capture interspecific variation in strategies that drive plant performance. The response of the plant-trait elements of each plant functional types to changing light levels was determined across post-logging recovery times of 10, 30 and 50 years. The highly varied associations between the influence of light and the occurrence of each plant-trait element across recovery times revealed in the results suggest that plant-trait elements are closely linked to a range of environmental response strategies. Functional diversity can fully recover to pre-cut levels if logged forests are given ample time to regenerate, suggesting that the functional diversity of forests in logged Oceanic forests can be highly resilient under effective management regimes.

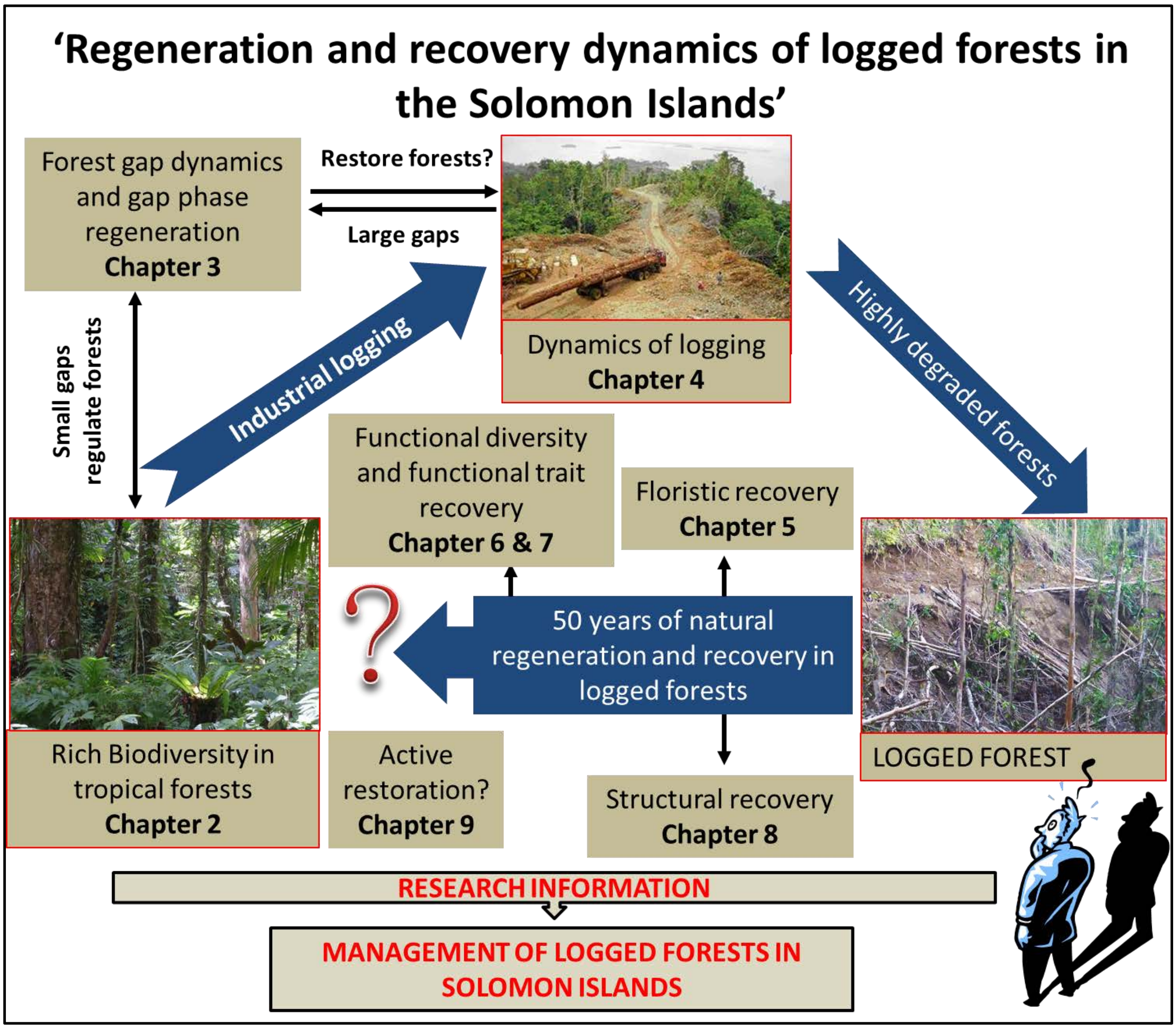
Factors influencing the recovery of tree biomass, wood density and understory tree-specific leaf area (SLA) in logged forests were investigated in Chapter 7. Harvest intensity, tree abundance and liana abundance influenced tree biomass and wood density, whereas elevation and ground litter affected understory tree SLA during post-logging recovery. Tree biomass and wood density did not recover to pre-cut levels after 50 years of post-logging regeneration whereas SLA values were similar among logged-forest time classes and unlogged forests. The full recovery of tree biomass and wood density within 50 years of logging is unlikely in the Solomon Islands. Improving the recovery of wood functional traits in logged forests in this region requires the development and implementation of policies that regulate initial harvest intensity and re-entry harvesting in post-logged forests.

Chapter 8 examines factors that influenced the recovery of several forest 'keystone structures' during 50 years of post-logging regeneration in the rainforests of Kolombangara Island. The results reveal that half a century of post-logging regeneration has been insufficient for full structural recovery of logged forests on Kolombangara. The results also suggest that proxies of logging, soil and tree attributes were more important than topographical factors in influencing the recovery of keystone structures over time. Based on these results, it was concluded that logging practices in the Solomon Islands must be regulated by more rigorous and effective management policies in order to facilitate full structural recovery of forests.

Finally, Chapter 9 presents a 'one–stop shop' for forest-restoration practitioners. This chapter discusses forest-restoration approaches that have been successfully implemented in tropical forests, and recommends an integrative approach whereby forest-restoration techniques are amalgamated for potentially better outcomes in heavily logged forests.

Because of the high intensity of logging on Kolombangara, natural regeneration alone is inadequate to permit full recovery of forests to pre-cut levels within 50 years since logging. The findings presented in this thesis can be used for both precautionary and remedial approaches to manage logged forests in the Solomon Islands. Nevertheless, much more information is required in terms of research and policy development to ensure that these and other logged forests in Oceania are appropriately managed to balance important economic and conservation outcomes.

Concept diagram of thesis



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CHAPTER 1

GENERAL INTRODUCTION

Eric Katovai

1.1 OVERVIEW

Tropical islands of the Solomons comprise of some of the richest and ecologically unique forest biota in the world, yet are also impacted by some of the worst logging practices documented anywhere in the tropics (Shearman et al. 2012; Katovai et al. 2012; 2015a). This thesis attempts to amalgamate research that highlights key aspects of post-logging regeneration and recovery in this region. The succeeding chapters highlight the rich forest biodiversity and structure in the region by using a case study from neighbouring New Guinea conducted by the authors (Chapter 2), followed by a literature review of gap-phase regeneration and its ecological implications (Chapter 3). Although these two chapters are not specifically focused on the Solomons, they present important information about the diversity and structure of tropical forests in Oceania and a general outlook on post-disturbance recovery in tropical forests. A literature review on the dynamics of logging is covered in Chapter 4, followed by empirical studies of key aspects of regeneration and recovery of logged forests in the Solomon Islands (Chapters 5–8). Chapter 9 outlines potential restoration approaches for heavily logged forests. Finally, Chapter 10 includes a general discussion that binds together key aspects of this thesis.

Research findings comprised in this thesis are novel for the studied region and are vital for forest management practices and policy development, particularly for biodiversity conservation and the sustainability of forest bioecological functioning.

1.2 CONTEXT OF RESEARCH

Like much of Oceania, the Solomon Islands have been heavily logged over the last century, mainly through industrial selective logging (Whitmore 1989a; Bennett 2000). Though much of the logged forest has been converted to agricultural land-use or human settlements, vast areas have been regenerating, creating secondary rainforest of unknown value to biodiversity conservation, local product extraction and the provisioning of ecosystem services. However, most research on rainforest regeneration to date has focused on tropical mainland forests or forests on large continental islands in Southeast Asia (e.g. Sax et al. 2002; Denslow 2003; Mayfield et al. 2005; Sax and Gaines 2008; Denslow et al. 2009; Gunawan et al. 2012; Asase et al. 2014; Bongers et al. 2015). Almost nothing is known about the ecology of secondary forests on tropical oceanic islands, or whether regeneration processes differ from those in the mainland tropics given the unique features of such islands. For instance, high-intensity logging in concert with isolation from propagule sources or seed dispersers might slow recovery of biodiversity compared to forests regenerating on continents (D'Orangeville et al. 2008).

Primary forests on Pacific and other oceanic islands are currently being logged at an unsustainable rate (Shearman et al. 2012). In the Solomon Islands, much of the accessible native forests may be logged at least once within this decade (Wairu

2007; Solomon Islands National Forest Resources Assessment [SINFRA] 2011 Update; Katovai et al. 2015a). With industrial logging contributing largely to the country's annual export income (SINFRA 2011; Katovai et al. 2015a), the exhaustion of accessible native forests could well result in increased pressure for re-entry logging in previously logged areas. It is, therefore, crucial to study the regeneration and recovery dynamics of these forests. Based on this information, effective decision-making and policy implementation to balance the competing pressures of conservation and economic growth can be better achieved.

This thesis is an amalgamation of studies that examine the regeneration processes occurring in logged forests of Kolombangara in the Solomon Islands. In these studies we explored the importance of time since logging, logging intensity, proximity from propagule sources in undisturbed old-growth forests, logging road networks, island topography and other important environmental variables on the recovery of plant diversity, key ecological functions and the physiognomic structure of these forests.

1.3 BACKGROUND INFORMATION

The Solomon archipelago has a long history of large-scale logging operations dating back to the early 1900s (Whitmore 1966; Bennett 2000; Katovai et al. 2012). These operations were initiated to diversify the country's economy, which was then solely dependent on copra (Bennett 2000). However, since its establishment, the logging industry has been the main driver of the country's economy, contributing 50–70% of total exports over the last two decades (Bennett 2000; SINFRA 2011). Contemporary logging activities have resulted in the further loss of remnant patches of mature forests on these islands. Kolombangara, in the New Georgia group (Fig. 1.1) presents an ideal location to study the dynamics of post-logging regeneration on tropical oceanic islands for the following reasons:

1. Kolombangara contains substantial patches of remnant forest reserves adjacent to naturally regenerating coupes of selectively logged forests.
2. The logged forests on Kolombangara vary in recovery time (i.e. 10–50 years), isolation from propagule sources and logging history, providing excellent contrast in the parameters thought to be important in forest vegetation recovery.
3. The climate and geological morphology across the island are relatively homogenous and distribution of vegetation types across remnant forests is relatively homogenous around the island (Hansell and Wall 1975; Whitmore 1969, 1989b; Katovai et al. 2012).
4. The island's terrain is relatively hospitable compared to other islands in the group, making accessibility easier.
5. Kolombangara has not experienced any major cyclones for almost half a century. Hence the effect of cyclones across the post-logging regeneration period examined in this study is marginal (Burslem et al. 2000).

Kolombangara Island is an excellent choice for one further reason. Early understanding of rainforest dynamics on oceanic islands came from extensive work conducted by Tim Whitmore and David Burslem on Kolombangara. These studies were mainly focused on documenting patterns of species richness and composition (Whitmore 1966), vegetation types (Whitmore 1969), comparison of tree growth and forest change over 20–30 year time periods, (Whitmore 1989b; Burslem et al. 1998) and forest response to cyclone-induced disturbances (Burslem et al. 2000). Nevertheless, these studies were all conducted within natural, intact forest systems. Less attention was given to the escalating human land-use impacts such as commercialised agriculture, industrial logging and human settlements on these systems (e.g. Denslow 2003; Denslow et al. 2009; Sax et al. 2002; Sax and Gaines 2008, Goldman et al. 2008; Katovai et al. 2012). As a result, there has been little information available to assess the impacts of industrial logging on biodiversity conservation and ecological functioning.

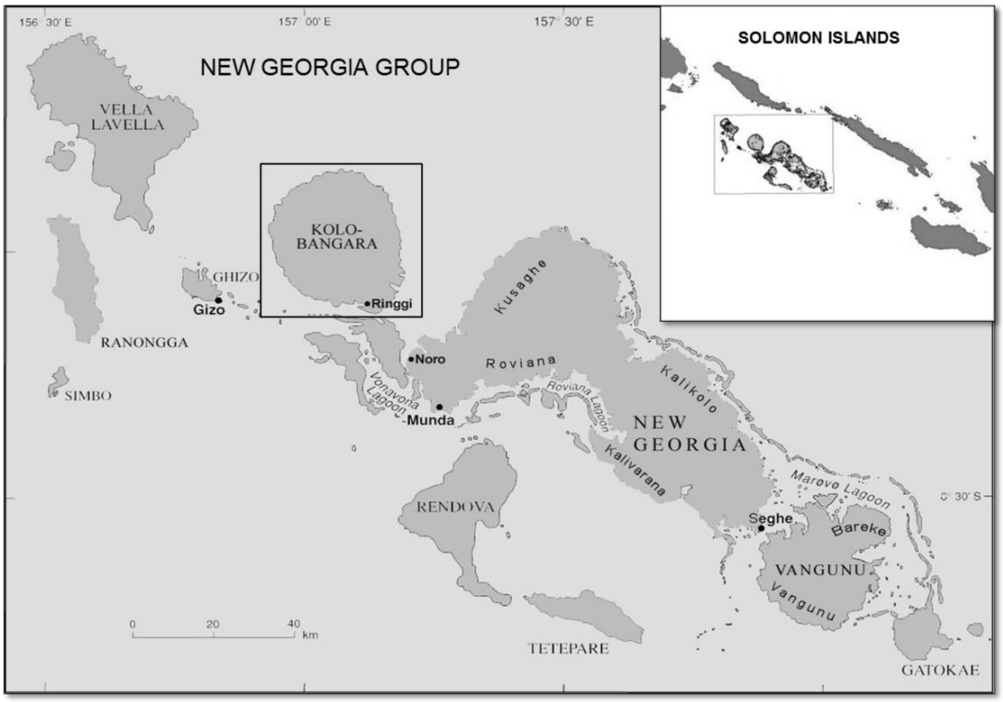


Figure 1.1. Kolombangara Island (delineated) is part of the New Georgia group and one of the highly logged islands in the Solomon Archipelago. (Map adapted from http://westernsolomons.uib.no/)

At a global scale, processes involved in regeneration dynamics in previously logged forests are comparatively poorly studied and thus poorly understood (Sist et al. 2015). Of the numerous studies on forest disturbance and regeneration, 80% of papers in the Web of Science database focussed on naturally-induced disturbances. Studies on human-induced disturbances mostly documented the severity of forest degradation, species loss and invasions by exotic species (e.g. Sax et al. 2002; Denslow 2003; Sax and Gaines 2008; Denslow et al. 2009). Only recently has attention shifted to the intrinsic and potential value of degraded forests and their role in maintaining and preserving biodiversity (Mayfield et al. 2010; Laurance and Edwards 2014; Bongers et al. 2015; Shenkin et al. 2015). On Kolombangara, 30 years (1964–1984) of monitoring old-growth forests by David Burslem and colleagues (Burslem et al. 2000) has provided important ecological information about the temporal and spatial changes in species diversity and forest structure in the context of naturally induced canopy disturbance. However, this long-term study did not assess changes in previously logged forests and thus cannot be reliably used to predict their recovery dynamics (Brewer et al. 2012).

In this thesis, I detail proxies of forest recovery such as patterns of plant species, functioning and community structure, and determine important factors driving these patterns.

1.4 RATIONALE FOR RESEARCH

The Solomon Islands has been dependent on commercial logging since the 1920s to drive and sustain the country's economic growth and development (Bennett 2000). However, with intense harvesting transforming large areas of primary forests into heavily logged forests, it is critical to establish ecologically based information on the regeneration and recovery dynamics of logged forests on these islands. Such information is paramount to form management strategies that will help forest use become more sustainable. The aim of this thesis is to achieve this milestone, which is particularly important for a country like the Solomon Islands where the future challenges for forest sustainability seem daunting.

1.5 OBJECTIVES

The objectives of this thesis are to:

1. Highlight the rich diversity in forest structure and plant communities and the high endemism in tropical Oceania.
2. Discuss forest 'gap-phase' dynamics in the context of natural and human land-use changes.
3. Review the dynamics of logging in the Solomon Islands.
4. Evaluate factors influencing tree diversity and compositional change across logged forests in the Solomon Islands.
5. Examine the influence of light on functional diversity across understory plant communities in logged forests of the Solomon Islands.

6. Assess factors influencing the recovery of wood and leaf traits across logged forests in the Solomon Islands.
7. Identify factors affecting the recovery of forest structure across logged forests on Kolombangara, Solomon Islands.
8. Highlight potential restoration approaches for logged tropical forests.

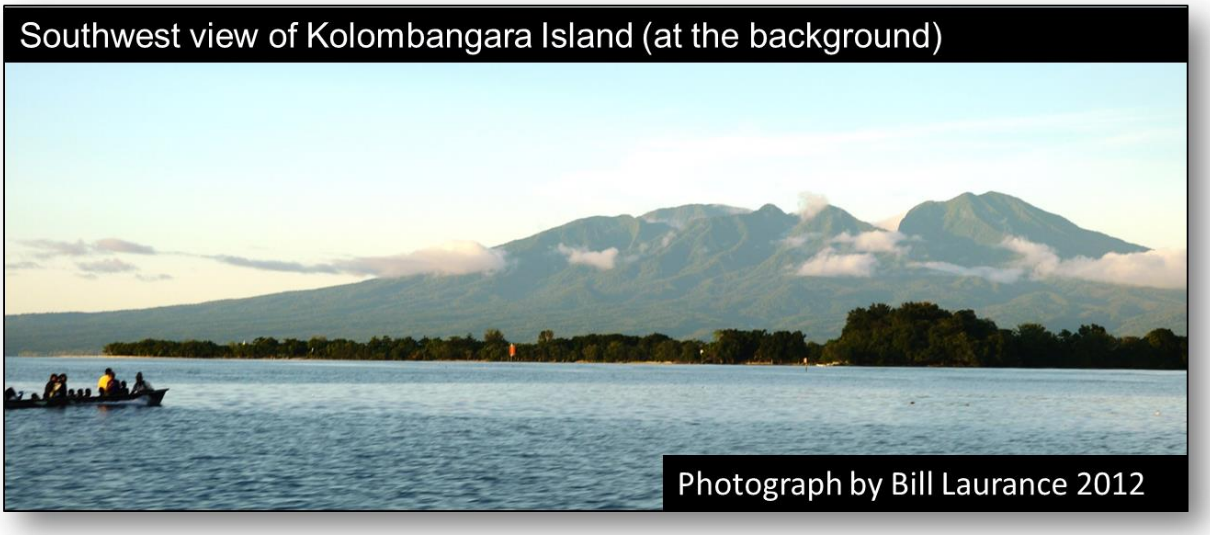
1.6 THESIS STRUCTURE

Each of the aforementioned objectives is covered in a chapter in the sequence outlined in section 1.5.

In Chapter 2, I present results from a study on floristic and structural diversity across forests in New Guinea.This study underscores the rich biodiversity and high endemism found across forests in tropical oceanic island landscapes threatened by logging. For instance, in the Solomon Islands such forest landscapes have been intensively logging since the early 1900s (Katovai et al. 2015a). In Chapter 3 I review differences in forest-gap phase regeneration between natural and anthropogenic treefall gaps. I further examine whether logging on natural tropical forests triggers a succession trajectory that would enhance forest diversity and adaptability to changing the climate. In Chapter 4 I (i) highlight the dynamics for selective logging in the Solomon Islands, (ii) stressing the need for active restoration in logged forests in the country, and (iii) propose several active restoration techniques already employed in tropical islands of Southeast Asia that may potentially aid recovery in heavily logged forests in the Solomon Islands.

In chapter 6, I present results that reveal factors influencing tree diversity and compositional change across logged forests in the Solomon Islands, and their floristic recovery status in the first 50 years after logging. In chapter 7, I assess the influence of light on functional diversity and recovery in understory plant communities in logged forests. Chapter 8 highlights important factors influencing functional recovery of core wood and leaf functional traits, including tree community biomass and wood density, and understory tree-community specific leaf area. This chapter also contrasts the recovery of these traits across 50 years of forest recovery.

In Chapter 9, I examine factors influencing the recovery of forest keystone structures across half a century of post-logging regeneration in the Solomon Islands. Chapter 10 underscores the potential importance of applying restoration measures in heavily logged forests and discusses potential restoration mechanisms. Chapter 11 comprises a general discussion highlighting the significance of key research findings, the need for future research, and major Conclusions and recommendations.


Southwest view of Kolombangara Island (at the background)

Photograph by Bill Laurance 2012

CHAPTER 2

FOREST STRUCTURE, PLANT DIVERSITY AND LOCAL ENDEMISM IN A HIGHLY VARIED NEW GUINEA LANDSCAPE

Eric Katovai, Dawnie D. Katovai, Will Edwards and William F. Laurance

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Chapter overview:

This chapter examines the rich plant diversity, floristic structure and high endemism in tropical Oceania associated with landscape variation and the geographical location of this region.

Contribution to thesis:

This chapter is attempts to address objective No. 1 which is to highlight the rich diversity in forest structure and plant communities, and high endemism in tropical Oceania that is currently under threat from large scale industrial logging and other anthropogenic activities.

2.1 INTRODUCTION

The island of New Guinea is estimated to contain 5-7% of total global biodiversity, making it one of the richest tropical biomes in the world (Haberle 2007; Shearman and Bryan 2011). There are at least two likely explanations for this. First, because of its geographic location, New Guinea is the confluence point for biodiversity from both Australasia and Southeast Asia (Simberloff 1974). Second, high habitat heterogeneity generated by the geological processes (tectonic uplift and volcanism) from which the island originated, have also enhanced diversity (McKnight et al. 2007). A classic example of this is the exceptionally high biodiversity found on Mount Bosavi, an extinct Pleistocene volcano in the Southern Highlands of Papua New Guinea (McGavin 2009). In this area, topographical barriers have restricted species migration, promoting a radiation of new plant and animal species, many of which are locally endemic (McGavin 2009).

Much of the biodiversity in New Guinea is still undescribed scientifically, as evidenced by continued discoveries of new species in remote areas (e.g. Mack 1998; Richards 2007; McGavin 2009; Richards and Gamui 2011). Furthermore, information on species occurrences and the structural dynamics of biodiversity in multiple forest types is still far from adequate (Frodin 1990). The only known published studies of the structural dynamics of biodiversity in New Guinea focused on insect herbivory and trophic interactions between food webs (e.g. Novotny et al. 2007; Novotny 2009; Novotny et al. 2010). In addition, recent publications provide novel information on diversity patterns of forest succession in New Guinea lowland forests (e.g. Trigas et al. 2013; Whitfeld et al. 2014). Despite the biological advances in New Guinea, information on the diversity and composition of plant communities is still scarce.

Previous plant surveys in New Guinea mainly focused on *alpha* diversity, which is the species richness within a localised area (Whittaker 1960; Legendre and De Caceres 2013). These surveys reported tree richness ranging from 98 to 178 species per hectare (e.g. Wright et al. 1997; Weiblen 1998; Harrison 2005; Takeuchi 2007; Keppel et al. 2010), with the highest published estimate of tree and liana diversity (≥ 10cm diameter-at-breast height [DBH]) reaching 228 species per hectare in the Crater Mountain Wildlife Management Area (Weiblen 1998). However, *beta* diversity, the variation in species composition through space (Legendre and De Caceres 2013), remains virtually unstudied in New Guinea. Understanding patterns of *beta* diversity is crucial for guiding conservation efforts in rich tropical biomes such as New Guinea that are being rapidly altered by deforestation and forest degradation (Shearman and Bryan 2011, Legendre and De Caceres 2013).

The relative lack of biodiversity surveys in New Guinea have been attributed to financial constraints, limited availability of experts, and the difficulty of accessing many areas due to highly rugged terrain (Paijmans 1975; Faith et al. 2001; Nicholls 2004; Takeuchi 2007). However, increasing human encroachment into old-growth forests is leading to increasing numbers of environmental impact assessments, which often involve rapid plant surveys. Such surveys could improve the spatial resolution of plant compositional data and thereby allowing *beta* diversity to be better estimated in New Guinea (e.g. Baraloto et al. 2013).

Here we present a study of forest structure and floristics in a rugged New Guinea landscape from such a rapid plant survey. Specifically, we ask: (1) Do forest types within the Naoro-Brown River catchment vary considerably in structure and plant richness? (2) How does *beta* diversity vary among the major forest types? (3) Does local topography influence plant endemism within this catchment?

2.2 METHODS

2.2.1 Study Area

Our study was conducted in July 2010 along a 13-km transect within the Naoro-Brown catchment area in the West Koiari district (S 9° 12.46' E 147° 34.45' and S 9° 10.35' E 147° 27.93'), on the south-eastern region of Papua New Guinea (Fig. 2.1). This rapid assessment was conducted over six days as part of an Environmental Impact Assessment for a proposed mini-dam and hydro-power station (Katovai and Saguba 2010). The study area extends over highly forested riverine plains and foothills to lower montane forests. Rainfall is seasonal, ranging between 1,550 – 2,000 mm yr^{-1} and increases with elevation (Paijmans 1975; World weather and climate 2010–2013). Pristine vegetation dominates most of the study area, although it also includes patches of successional regrowth in old village and garden sites abandoned more than three decades ago.

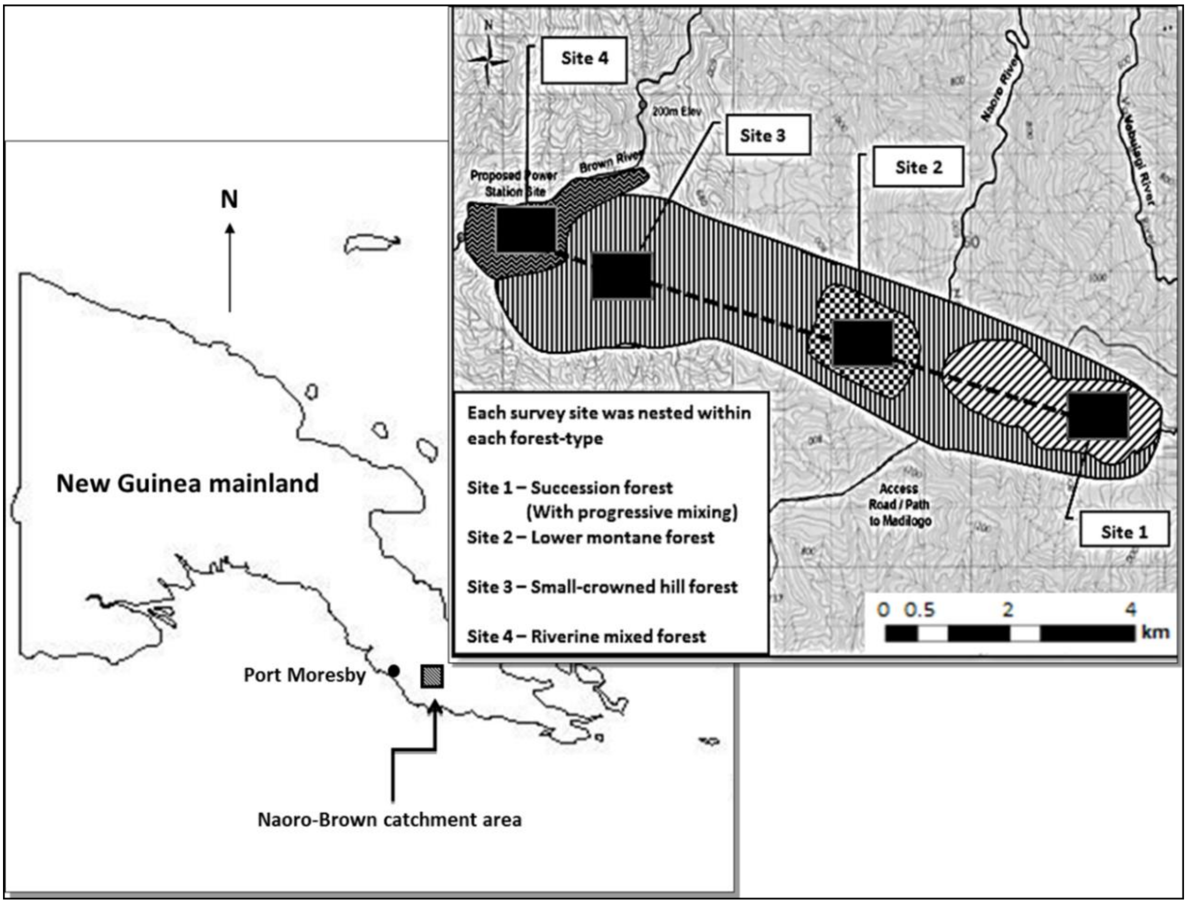


Figure 2.1. Orientation of the study sites showing the four forest types along a 13-km transect. The study area is dominated by small-crown hill forest with tracts of riverine mixed forests and lower montane forests associated with waterways and low mountain peaks, respectively.

2.2.2 Study design

We identified four forest types along the transect, using forest classifications for Papua New Guinea (Paijmans 1975). These were riverine mixed forest (~173 m above sea level [a.s.l]), hill forest (~665 m a.s.l), lower montane forest (~1,174 m a.s.l), and riverine succession forest (~874 m a.s.l). Riverine mixed forest generally extends from riverbanks, through ravines, and along the ascending ridges where it merges with hill forest. Hill forest covers most of the study area (Fig. 2.1), extending along the ascending ridge crest of low mountains where it meets patches of lower montane forest covering the highest crests within the area. Unlike these three forest types, which are currently intact, riverine succession forests are patches of post-disturbance regrowth in abandoned human settlements along the Naoro-Brown river.

The topographical aspects defining each forest type were fairly distinctive. Four 50 x 20 m (0.1 ha) plots were randomly established >0.1 km apart in each forest type. Topography within each plot was measured by elevation, linear distance between plots, and slope, as these have shown to be ecologically meaningful in complex landscapes (Yasuhiro et al. 2004; Apgaua et al. 2014; Arellano and Macía 2014). Elevation above sea level and the distance between each pair of plots were measured in the centre of each plot using a Garmin GPSmap 76Cx (Garmin International, Inc., Kansas City, USA). Slope of each plot was estimated using a clinometer by averaging five slope measurements at randomly selected points along the direction of the greatest slope (Clark and Clark 2000).

2.2.3 Forest structure survey

Forest structure was measured by tree height, stand density, and biomass. For each plot tree height was measured using a Haglöf ECII Electronic Clino / Height Meter. We measured and recorded all living trees ≥10 cm DBH, according to Pearson et al. (2013), and enumerated all measured stems to determine the tree-stand density. Tree biomass was estimated using a generic allometric equation for tropical forests adapted from Chave et al. (2001), and plot-level biomass was generated by summing values for all trees in each plot. Forest height was the average maximum tree height recorded at five random points within each plot.

2.2.4 Plant survey

Plant diversity was estimated via plant species richness and the Shannon-Wiener diversity index (Asase et al. 2014). Compositional similarity among forest types was used as a proxy for *beta* diversity (Legendre and De Caceres 2013). We collected voucher specimens of all tree morphospecies and tagged each tree for identification purposes. Voucher specimens were also collected for non-tree species (herbs, shrubs, climbers, creepers, and ferns) and treelets in each plot. All non-tree plants were sampled using twenty 1 x 1 m quadrats randomly placed within each plot (after Katovai et al. (2012)). Flowers and fruiting bodies were collected where possible to assist with identification. Vouchers were taken to Pacific Adventist University, Port Moresby, for further taxonomical sorting and then to the National Herbarium at the Forest Research Institute in Lae for expert verification. All voucher specimens were keyed to genus and to species level where possible. A species list for each plot was then generated (Appendix 1) and used to compare species compositional similarity among forest types. Saplings were excluded from the survey due to challenges in taxonomical sorting.

2.2.5 Statistical Analysis

A one-way analysis of variance (ANOVA) was used to test whether forest structure and species diversity variables differed among forest types, followed by Tukey's HSD tests to assess pair-wise differences. All analyses were run in SPSS (IBM Corp. Released. 2013).

We ran an analysis of similarity (ANOSIM) based on Bray–Curtis similarity matrices of species occurrence to determine how plant community composition varied among forest types (Bray and Curtis 1957; Clarke and Gorley 2006). We then used non-metric multi-dimensional scaling (NMDS) to identify major gradients in species composition. These analyses were carried out using PRIMER V6 (Clarke and Gorley 2006).

To examine the effect of topography on plant endemism in the forest types, we categorised all species found in each plot into tree and non-tree categories. Using these categories, we estimated local endemism, the proportions of trees and non-trees occurring uniquely in a single forest type. Pearson correlations were used to test for associations among the arcsine-transformed endemism levels and log-transformed values of slope and elevation. Based on the correlation outputs, we selected highly associated predictor-response combinations ($r>0.70$), and used linear regressions to examine how topography influenced variation in local plant endemism within the Naoro-Brown landscape.

2.3 RESULTS

In total, we sampled 1.6 ha in the Naoro-Brown catchment area and identified 163 species (87 non-tree and 76 tree species) from 60 families, of which 93 were identified to species level (Appendix 1). We also counted 754 trees with DBH ≥10 cm across the forest types. The estimated mean (±SD) of tree biomass for the entire area was 537± 356 tonnes/ha.

2.3.1 Forest structure and diversity

Forest structure differed among forest types, although results varied among response variables (Table 2.1). For example, while there were overall significant differences in mean tree height ($F_{3, 12} = 68.8$, $p < 0.0001$), tree stand density ($F_{3, 12} = 43$, $p < 0.0001$), and tree biomass ($F_{3, 12} = 110$, $p < 0.0001$), Tukey's tests showed different groupings of forest types associated with each measure (Table 1.1). Tree height, for instance, showed two homogenous groups. One group consisted of riverine mixed forest (31.6±1.4 m) and hill forest (25.9±0.7m), and the other consisted of riverine succession (22.8±0.6 m) and lower montane forest (21.2±1.4 m). Mean tree density in riverine succession forest was significantly higher than in the three primary forests (Table 2.1). Riverine mixed forest had the highest mean biomass (1,113±141 tonnes/ha), followed by homogenous groups hill forest (442±32 tonnes/ha) and lower montane forest (315±24 tonnes/ha). Mean biomass of riverine succession forests was lowest (277±27 tonnes/ha), and differed significantly from all others (Table 2.1).

Table 2.1 Details of landscape, floristics and forest structure variables across forest types in the Naoro-Brown catchment. Mean values ±SD of four 0.1ha plots per forest type are given for each variable except for biomass which is extrapolated to tonnes per hactare. Superscript letters beside mean numbers of variables indicate significant pair-wise differences across forest types and elevation bands using Tukey's HSD tests. Means with different superscript letters are significantly different. Forest type acronyms explained: RSF = Riverine succession forest, LMF = Lower montane forest, HF = Hill forest and RMF = Riverine mixed forest.

Forest-type	**Mean Species richness**	**Shannon Index**	**Est. Forest height (m)**	**Tree stand density**	**Est. Mean biomass (tonnes/ha)**
RSF	31±2.2^{D}	2.60±0.09^{B}	22.8±0.6^{C}	62.3±4.6^{A}	277.4±26.8^{C}
LMF	44.8±1.0^{C}	2.73±0.15^{B}	21.2±1.4^{C}	41.3±1.5^{B}	314.9±24.3^{BC}
HF	50.3±2.6^{B}	3.07±0.04^{A}	25.9±0.7^{B}	47±1.8^{B}	441.5±31.9^{B}
RMF	55.3±1.9^{A}	3.24±0.09^{A}	31.6±1.4^{A}	41.5±3.1^{B}	1113.2±141^{A}

Plant diversity also differed among forest types (Table 2.1). Mean species richness differed significantly among forest types ($F_{3,\,12} = 69.3$, $p < 0.0001$), with all pairwise comparisons being considerably different (Table 2.1). Riverine mixed forest had the highest mean richness (55.3±1.9 species), followed by hill (50.3±2.6 species), lower montane (44±1.0 species), and riverine succession forests (31±2.1 species). Shannon diversity indices also differed significantly among the forest types ($F_{3,\,12} = 38.1$, $p < 0.000$), with Tukey's tests revealing two homogeneous subsets: riverine mixed forests (3.24±0.09) and hill forests (3.07±0.04); and lower montane forests (2.73±0.15) and riverine succession forests (2.60±0.09).

2.3.2 *Beta* diversity

ANOSIM and pairwise comparisons revealed that species composition differed significantly among forest types (*P* < 0.001; Fig. 2.2). As expected, species compositional similarity was highest between hill forest and riverine mixed forest, albeit still with a relatively low similarity of 17.86%. Compositional similarity was lowest between riverine mixed forest and lower montane forest, with 3.70% similarity (Fig. 2.2).

2.3.3 Topography and local endemism

Tree species endemism was strongly negatively associated with slope ($r = -0.82$, $p < 0.001$), but its association with elevation was non-significant ($r = 0.20$, $p > 0.05$). In contrast, non-tree endemism was highly negatively associated with elevation ($r = -0.87$, $p < 0.001$) but not with slope ($r = -0.15$, $p > 0.05$; all Pearson correlations).

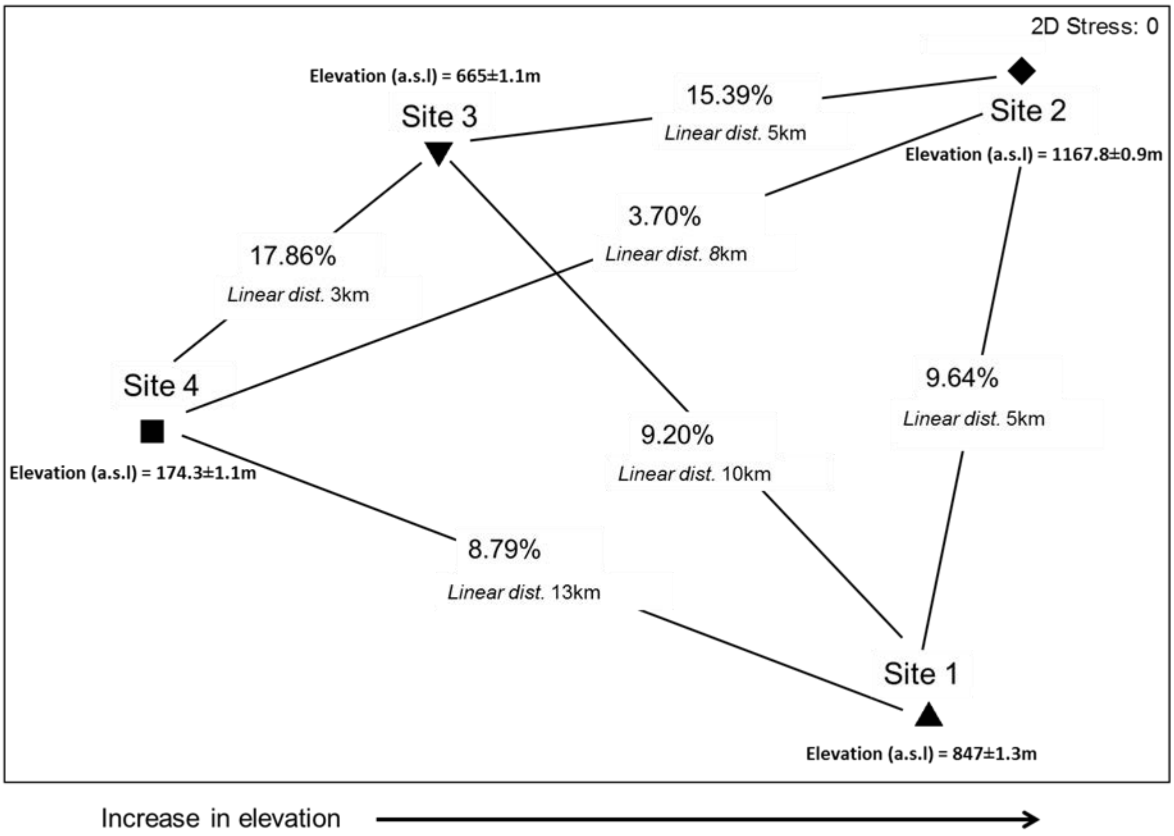


Figure 2.2. Multidimensional Scaling (MDS) for similarity in species composition between Riverine successional forest (▲), Lower montane forest (◆), Hill forest (▼) and Riverine mixed forest (■). MDS is based on Bray–Curtis similarity indices. Also displayed are the species compositional similarity percentage and linear geographic distance (in km) between each forest type. The elevation gradient along the horizontal axis shows how forest types are positioned with respect to topographical elevation within the landscape.

Linear regressions showed that elevation was a good predictor of local endemism for non-tree species ($F_{1,\,14}$ = 102.7, $p < 0.001$), explaining 87% of the variability in non-tree endemism among forest types (Fig. 2.3c). Local endemism in trees was predicted by slope ($F_{1,\,14}$ = 28.92, $p < 0.001$), explaining 65% of the total variation among forest types (Fig. 2.3b).

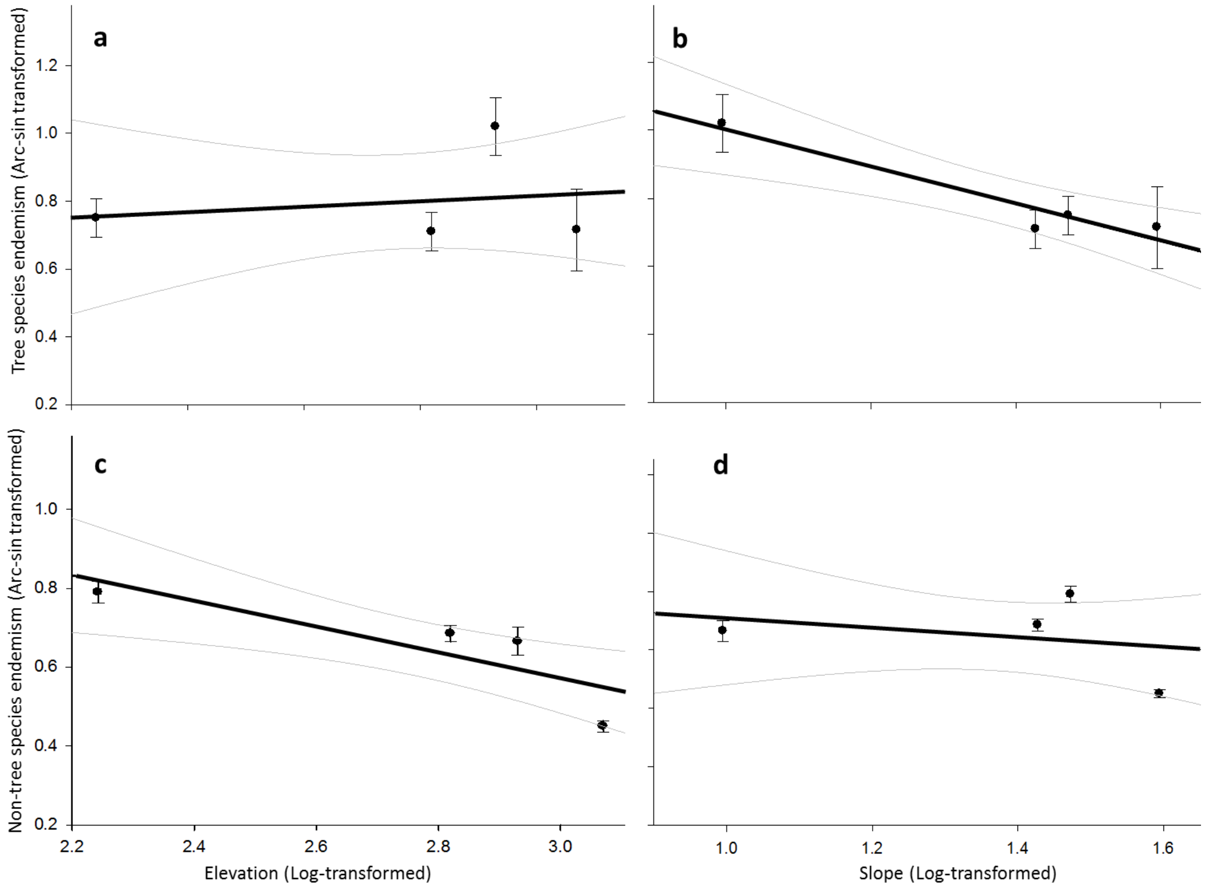


Figure 2.3. The regression plots (with 95% Confidence Intervals – in grey) displaying relationships between tree and non-tree local endemism across elevation and slope in the Naoro-Brown catchment area in Papua New Guinea. Solid lines in 'b' and 'c' indicate the strong effects of elevation and slope on non-tree species and tree species endemism respectively. In contrast, solid lines in 'a' and 'd' indicate non-significant relationships between the compared variables.

2.4 DISCUSSION

2.4.1 Forest structure and diversity across forest types

Forest structure and plant diversity were highly variable in our study transect (Table 2.1, Fig. 2.2). Such high spatial variation could result from both local environmental factors, such as varying precipitation, temperature, and topographical features (Clark and Clark 2000; Apgaua et al. 2014), as well as from different dynamics and disturbance histories throughout the study area (Pukkala and Gadow 2012; Sheil 2016). Below we consider key attributes of each of these four major forest types.

2.4.2 Riverine mixed forest

In riverine mixed forest, canopy trees are relatively uniform in height, averaging 31 m. This forest has large tree crowns that significantly reduce the amount of light penetrating into the understory and forest floor. Common trees are mainly from the genera *Syzigium*, *Litsea*, *Aglaia*, *Harpullia* (Tulipwood), and *Acalypha* (Copperleaf), with no evidence of single-species dominance. The dense canopy cover and leaf litter on the forest floor help to maintain surface moisture (Xiong et al. 2003), which supports moss growth covering the base of trees and a high abundance of herbaceous forms. Large woody vines throughout the forest column are also apparent, which may indicate a mature forest system (Putz 1983, 1984; Allen et al. 2005; DeWalt et al. 2006).

We observed a low density of treefall gaps in this forest type, which suggests only sporadic disturbance from wind or tree death. Treefall gaps displayed a range of seral stages, augmenting plant species diversity (Denslow 1995; Letcher and Chazdon 2009a). Perhaps a more substantial form of disturbance is triggered by huge volumes of run-off channelled through ravines that flood the forest floor during monsoonal rains between October and January. These ravines develop microtopographical formations on the forest floor that could help diversify microhabitats within the forest (Wright et al. 1997; Wright 2002).

2.4.3 Hill forest

Hill forests mainly contain small-crowned deciduous trees, thus having a relatively open canopy with tree heights rarely exceeding 28 m. Understory trees are abundant because understory light levels are relatively high (Letcher and Chazdon 2009b). Common deciduous trees include *Bombax ceiba* (Bombax), *Gordonia papuana* (Gordiana), *Pterocarpus* spp. (Makua or Nara) and *Terminalia spp.* (Terminalia). The shrub layer is dominated by scrambled bamboo, *Maniltoa psilogyne*, and a variety of lianas and palm species that may be maintained by relatively high light and semi-dry conditions of the understory (Schnitzer and Bongers 2002; Cintra et al. 2005). The rarity of herbaceous forms may also be related to such dry environmental conditions.

2.4.4 Lower montane forest

In lower montane forests the trees exhibit smaller crowns than those at lower elevations. Mean canopy tree height was ~21 m with a few scattered *Syzygium* trees over 25 m high. Due to the small crowns and high variance in canopy height, light penetration into the understory and forest floor is irregular, creating large variability in the structure of the undergrowth. Trees dominating the canopy and sub-canopy mostly belong to the genera *Garcinia*, *Harpullia* (Tulipwood), *Cryptocarya*, *Macaranga* (Euphorbs), and *Syzygium*. The understory mainly includes a few genera of palms (*Calamus, Caryota, Hydriastile*), pandanas (*Freycinetia*) and a number of ground orchids in the genera *Tropidia* and *Bulbophylum*.

2.4.5 Riverine successional forest

After fallow decades, riverine successional forest mainly exhibited a high abundance of thin trees dominated by *Terminalia, Glochidion, Cryptocarya*, and a few *Ficus* species. Also present were multi-phase successional trees (*Litsea timoriana, Annesijoa novoguineensis, Dysoxylum* [Rose Mahogany], *Xylopia papuana*), ferns, herbaceous creepers and shade-tolerant understory species, such as epiphytes and non-woody climbers. These varied groups indicate a mixing of plant life forms and successional stages in this forest (Jakovac et al. 2016).

2.4.6 *Beta* diversity and endemism

The low species compositional similarity among these forests suggests high *beta* diversity in the Naoro-Brown catchment area (Fig. 2.2). However, other tropical studies at comparable geographical distance (0-13km) reported lower species turnover of ~50% (e.g. Condit et al. 2002; Pennington et al. 2009; Toledo et al. 2011; Apgaua et al. 2014; Arellano and Macía 2014). The high *beta* diversity in our study area may have been overestimated due to limited sampling, restricted to trees ≥10 cm DBH only. The large gradient in elevation along our transect (~1,000 m) would likely have enhanced *beta* diversity relative to the aforementioned studies, which were conducted over less topographically variable areas.

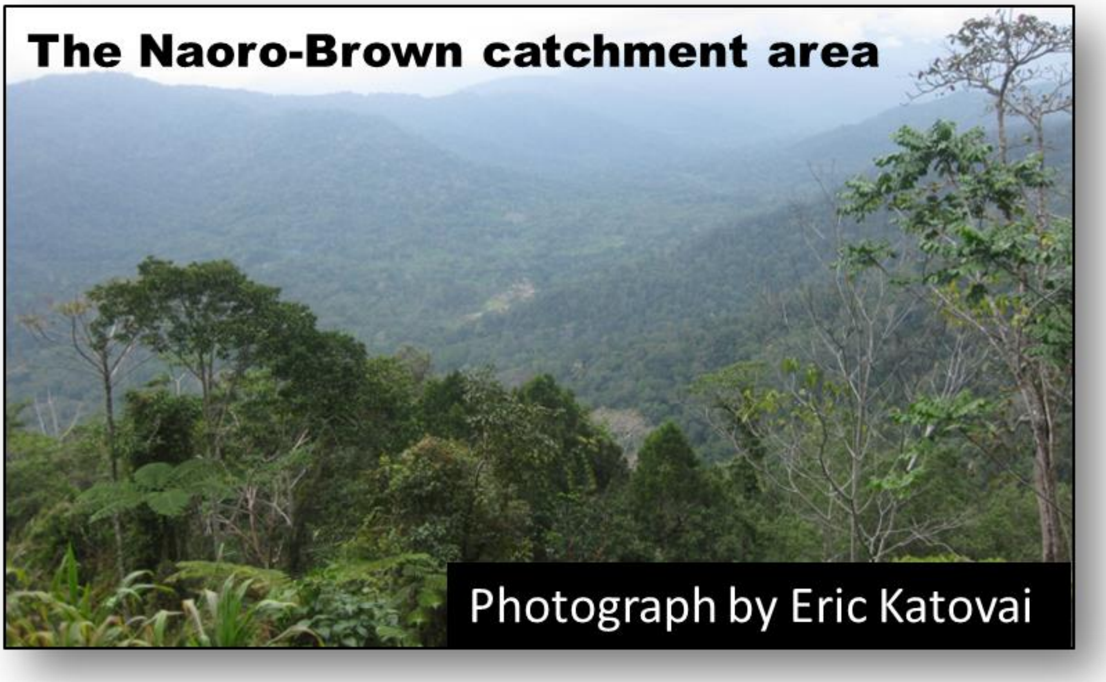
Our results also suggest that topography strongly influences local endemism of plant species. Such responses are generally regulated by microclimate and soil attributes along topographical gradients (e.g. Chen et al. 2011; Malhi et al. 2013; Lippok et al. 2014). However, consistent trends of plant endemism have been reported on larger spatial scales. For example, studies on oceanic islands have revealed a unimodal response to elevation whereby endemism peaks at mid-elevation and then gradually decreases at high elevations (Kessler 2002; Trigas et al. 2013). Relatively low diversification and speciation at high elevations on recently uplifted mountains may have caused these patterns (Kessler 2002). Our results cannot account for this because of the relatively small spatial extent of our study and its location. We suggest that the ecological mechanisms driving shifts in plant endemism vary at any given time and space due to complex interactions among environmental variables throughout the studied landscape (Warren 2008; Bonetti and Wiens 2014).

2.4.7 Implications for conservation

Our findings suggest that to conserve biological and structural diversity in New Guinea, protected areas must at least include landscapes that best represent the topographical variability throughout the island (Faith et al. 2001; Shearman and Bryan 2011; Katovai et al. 2012). Immediate efforts should focus on forests that are most vulnerable to deforestation and degradation (see Nicholls 2004; Shearman and Bryan 2011). Rapid plant surveys can be used opportunistically to document vital information on spatial vegetation patterns of uncharted landscapes in New Guinea. In the absence of such information, a focus on maximizing the conservation of gradients spanning topographic, geological, and climatic gradients should be a priority. For an island rich in locally endemic species that is being rapidly altered by a range of human land uses, such simple surrogate variables can help to guide near-term conservation efforts.

2.5 CHAPTER SUMMARY

- We surveyed forest plant communities in the poorly studied Naoro-Brown catchment of the West Koiari region of Papua New Guinea and examined forest structure (tree height, stand density, and biomass) and tree species diversity (species richness, Shannon-Wiener diversity index, and composition) in these forest types. We also assessed the effect of local topography on floristic patterns.
- Forest structure and species diversity varied greatly among the forest types, with topography strongly affecting species assemblages.
- These results suggest that highly varied landscapes may contain high *beta* diversity via intense segregation and establishment of varied vegetation communities. *Beta* diversity in New Guinea may be higher than expected as such highly varied landscapes are common, yet poorly studied.
- To effectively conserve biodiversity in New Guinea’s forests, protection must include forested landscapes that best represent the topographical variability throughout the island to account for locally endemic species restricted to specific ecological niches.


The Naoro-Brown catchment area
Photograph by Eric Katovai

CHAPTER 3

A REVIEW ON FOREST GAP DYNAMICS AND GAP-PHASE REGENERATION

Eric Katovai and Dawnie D. Katovai

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Chapter overview:

This chapter is part of my literature review which aims to provide background information on forest gap dynamics and gap-phase regeneration pathways across natural and human-induced treefall gaps in tropical forests.

Contribution to thesis:

This chapter addresses objective No. 2, which is to discuss forest ‘gap-phase’ dynamics in the context of natural and human land-use changes.

3.1 INTRODUCTION

Forest gaps and their impact on forest ecosystems have been widely studied since the early 1970s (Yamamoto 2000), as they play a driving role in the spatial and temporal changes in forest structure and dynamics (Whitmore 1975; Halle et al. 1978; van der Sande et al. 2016). This, subsequently, alters the uniformity of forest communities and hence determines the composition of the forest for a few decades and even sometimes up to centuries after gap formation (Whitmore 1991). This phenomenon is termed “gap dynamics” and varies throughout different forest types as a function of climate-type, biodiversity and disturbance factors (Brokaw 1985; Yamamoto 2000; Denslow et al. 2001; Sheil 2016). The great deal of the historical interest in gap dynamics was associated with a desire to forecast practical forest applications such as forest conservation practice, natural regeneration methods and as a test of basic ecological theories including niche partitioning, species adaptation and latitudinal gradients of species diversity (Yamamoto 2000).

Gaps associated with anthropogenic activities have surely created a whole new dimension in the understanding of forest regeneration. Various studies have shown that a significant amount of biodiversity can be lost in anthropogenic treefall gaps and clearings (e.g. Denslow et al. 2001; Schnitzer and Carson 2001; Lamb et al. 2005). This conclusion was derived by comparing species richness and composition between the initial pristine diversity and regenerating gap diversity.

This review aims to provide background information on forest gap dynamics and gap-phase regeneration pathways across natural and human-induced treefall gaps in tropical forests.

3.2 FOREST GAP DYNAMICS

Due to the exceptionally high floral diversity in tropical forest stands (Gentry 1990), the complexities of forest structure in gap regeneration may be equally intricate. Swaine and Whitmore (1988) proposed a discrete division of tree species into two groups or guilds: pioneer (non-climax) and non-pioneer (or climax), based on seed germination and seedling establishment characteristics. These definitions have been widely used in the recent literature (e.g. Brown 1993; Brokaw and Busing 2000; Dietze and Clark 2008). Pioneer species are shade-intolerant plants that do best in well-lit conditions (Whitmore 1989a). Their seeds are dispersed by animal vectors, water and wind movements (Keane and Finney 2006). The seeds lie dormant on the forest floor until enough light is available to germinate, with seeds of some species capable of surviving in dormancy for very long periods (Lamb 1998).

Non-pioneers are shade-tolerant species that favour moist conditions (Popma et al. 1988; Lamb et al 2005). They continue the successional process by germinating under the cover of pioneer growth that provides a low-light and moist microclimate at ground level (Hubble et al. 1999). Non-pioneers may also regenerate from existing plant parts, particularly roots, bulbs and other self-generative plant parts (Dietze and Clark 2008).

Forest gaps can be created in a variety of ways. Some of these result from natural causes such as tree death due to old age (Eysenrode et al. 2000), local pathogenic attacks (Runkle 1981; McCune et al. 1988), windthrow (Whitmore 1975; Yamamoto 1992), volcanic flows or landslides (Hugget 2004), and vine entrapment (Swayne and Whitmore 1988). These natural disturbances create gaps on a relatively small scale, and their occurrences are generally randomly distributed throughout the forest stand. Prior research has shown that naturally-caused gaps rarely exceed 100m^2 in area (Arévalo and Fernández-Palacios 2007). The study of treefall gaps can provide insights into species regeneration (Hartshorn 1989), survival (Hubbel et al. 1999) and many other aspects of the structure of a viable forest (Runkle 1981).

Human-induced gaps differ from natural gaps in various aspects, although they are also broadly defined as forest gaps. Such gaps can be created by all forms of logging; land clearing for agricultural, mining and urban development; and slashing and burning for various purposes (Bruner et al. 2001; Gondard and Deconchat 2003; Schwartz et al. 2016). Topsoil erosion and compaction, such as often occurs from bulldozer and other heavy-vehicle use in logged forests, can also kill trees and thereby create treefall gaps; these changes also have negative impacts on the gap-regeneration phase, as most naturally dispersed seeds are located within the topsoil and hence are lost in the process. In addition, soil erosion reduces the fertility of affected areas because most nutrients for plant growth in rainforests are in the upper topsoil as a result of rapid turnover of nutrients through continuous decomposition of organic matter on the forest floor (Moran et al. 2000; Peña-Claros et al. 2012).

Gaps resulting from natural canopy perforation caused by death of one or few trees are the kernel of rainforest regeneration (Eysenrode et al. 2000). Seedlings already present in the undergrowth form a building-phase forest as a result of the sharply increased understorey light levels (Whitmore 1998). Natural gaps also promote heterogeneity within forest stands, and may help to promote high species richness in rainforests (Brandani et al. 1988). The latter has been described as the “intermediate disturbance hypothesis” suggesting that the highest diversity is maintained at intermediate scales of disturbance (Connell 1978; Dietze and Clark

2008; Sheil and Burslem 2013; Sheil 2016). However, this hypothesis remains largely untested for highly diverse rainforest communities, and for the most prevalent patch-size disturbances in such communities, as well as for canopy light gaps (Brokaw and Busing 2000). Testing this hypothesis rigorously is challenging because of:

(i) The longevity of many forest tree species. Large data sets covering temporal and spatial variation of tree species richness and their relationships with disturbances are limited and inconclusive (Gentry 1990; Leopard and Salazar 2008).
(ii) The mechanisms through which light gaps influence tree regeneration are still not fully elucidated (Brokaw and Busing 2000). However, recent studies have shown that altering light conditions in wind-throw canopy gaps by removing shrub growth resulted in a two-fold increase in seed growth and species diversity of trees in gaps (Arihafa and Mack 2013; Royo et al. 2016). This provides evidence that natural gaps could potentially enhance tree diversity given the right microclimatic conditions.

Relatively large gaps are mostly associated with anthropogenic activities (Delegue et al. 2000; Peña-Claros et al. 2008) and other infrequent natural causes such as multiple windthrows (Whitmore 1975; Yamamoto 1992), earthquakes and plate-tectonic movements (Kobayashi 2001), lightning, landslides, volcanism, fire (which is very rare for rainforest) and cyclones (Whitmore 1991; McCune et al. 1988). These large openings tend to promote a rather different tragectory of gap regeneration due to a distinct shift in microclimatic conditions near and below the ground as a result in higher influx of solar radiation (Whitmore 1991). It is this that drives the key disparity in the dynamics of regeneration between “small” and “large” gaps.

Although light is a universally accepted cue for regeneration, large gaps have the propensity to do poorly in terms of species richness (Lamb et al. 2005; 2012). Two common factors driving poor regeneration in larger gaps are (i) the lack of ground moisture needed for seed germination and above-ground moisture to maintain seedlings (Xiong et al. 2003), and (ii) seed death caused by soil disturbances (Pugnaire and Lozano 1997). The former is strongly associated with higher temperatures in large gaps. The latter is caused by factors such as (i) the use of machinery in logging activities and land-clearing that may affect the soil through excavation, trenching and skidding on topsoil, and soil compaction by heavy equipment (Marsden 1998; Zimmerman and Kormos 2012), (ii) spillage of chemicals, such as lubricants from heavy logging machinery, (iii) topsoil erosion and landslides caused by flooding, earthquakes and volcanism (Whitmore 1991; Yamamoto 1992).

3.3 SUCCESSION IN FOREST GAPS

The process of gap succession has been widely discussed (e.g. Whitmore 1991; Zou et al. 1995; Zipperer 2005; Dietze and Clark 2008) in the context of understanding how human disturbances can affect forest regeneration. Understanding how such disturbances affect forests would allow for proper actions to be taken to assist the restoration process in extremely degraded gaps and maximise unaided natural regeneration and restoration in such gaps (Sheil 2016). However, a forest community’s value in maintaining ecological relationships and functions is generally considered far greater than the cost of recovering from large disturbance such as deforestation. Lu et al. (2002) proposed that large-scale deforestation leads to losses in biological diversity, alteration of the hydrological cycle, increase soil erosion and loss of productivity. In tropical rainforests, most soils are heavily weathered and infertile with a low content of nutrients such as cations and phosphorus, making nutrient cycling an important mechanism in maintaining the ecosystem (Villela et al. 2006; Peña-Claros 2012). When the process is disturbed, nutrients can be rapidly lost, and the greater the disturbance on a mature forest, the longer it takes to recover. An extreme situation is when disturbance produces intense nutrient loss and soil degradation with no chance for recovery (Lu et al. 2002).

Restoration in gaps is important for the sustainability of the forest, but how superior will the restored forest be to the initial stand? There is no universal answer to this question because forest and gap dynamics vary spatially and temporally, and forest stands are typically far from homogeneous. However, to achieve a good qualitative understanding on how gap dynamics steer the process of regeneration, let us consider four chief sources that, when put together, determine the quality of regeneration in gaps. Each of these four factors varies in their role in gap regeneration.

The first factor is the regeneration of pre-existing forest species that have survived following the mechanical phase of disturbance and hence continue to utilize the abundance of light, which often is barely sufficient to facilitate growth in the absence of any gaps. These may be smaller trees of climax species that dominated the canopy prior to disturbance, or understorey species (Denslow et al. 1998; Zipperer 2003) waiting for the appropriate environment to flourish. Obviously, gap species represent an amalgamation of shade-intolerant pioneers and shade-tolerant advanced regeneration. Yet, due to the complexities of vegetation responses and the lack of quantified information, non-seed regenerations (e.g. advanced regeneration and species that grow vegetatively into gaps) are typically avoided in the theoretical discussions of gap dynamics (Clark 1991, Loehle 2000; Bond and Midgly 2001).

Secondly, the germination from the soil seed bank is vital for gap regeneration and diversification. Studies have shown that this natural process is spurred by an increased availability of light (Brokaw and Busing 2001; Tiansawat et al. 2014).However it is clear that not all forest species seeds are capable of dormancy. Evidence of this has been reported by Augspurger (1984), who found that none of the 18 climax species in Barro Colorado Island had seeds capable of dormancy. The lack of pioneers in the Bornean heath forest is another classic example of species lacking seed dormancy (Whitmore 1991). It is also important to note that by definition forest gap dynamics would not be applicable to all forest stands, as the concept revolves around sapling growth from seed banks. Much is still unknown about the temporal and spatial scale of seed-banks in rain forest.

Thirdly, sprouting from cut or crushed roots and stems also play an important contribution in gap regeneration (Dietze and Clark 2008). In such cases where seed bank regeneration does not occur, sprouting re-growth will dominate the gap restoration phase. Therefore, it is very likely that species composition at the early stages of gap-phase regeneration will resemble the pre-existing flora, but have a lower overall diversity as not all pre-disturbance species would survive through the disturbance regime. Numerous studies have documented the high rate of damaged flora being a significant part of gap regeneration (see Dietze and Clark 2008 and references therein).

The fourth source of regeneration is termed ‘seed rain,’ which is a practical description of how seeds disperse into a gap via biotic vectors such as frugivorous birds, bats and terrestrial mammals as well as wind, water and other abiotic vectors. Pejchar et al. (2008) discussed the impact of birds as a natural means of forest restoration. It was determined that birds use tall trees on gap edges for perching, and that by increasing artificial perches over gaps, bird colonization has increased and so has the seed-rain population and plant species diversity, particularly under the perches.

Although forest gaps play an important role in the maintenance of tree species richness in forest communities, or may diversify the forest stand (Tabarelli 1999; Franklin et al. 2002), the mechanism maintaining richness of tree species would largely depend on the sources of regeneration as mentioned earlier, the quality and richness of soil, climate conduciveness and other abiotic and biotic factors (Xiong et al. 2003; Peña-Claros et al. 2012). Hulst (1992) delineated six possible groups of factors that influence future vegetation through the succession process. These are: (i) Present vegetation, (ii) Present vegetation in surrounding areas or immigration of propagules, (iii) Past vegetation (dormant seeds), (iv) Present resource levels (light humidity and soil mineral levels), (vi) Disturbance level including herbivory, and (vii) Stochastic factors such as climate variability and fluctuating supplies of resources. It is rare for a single factor to determine the species diversity and dispersal within gaps, as forest dynamics result from a complex array of ecological relationships and determininstic and chance factors. However, in comparison with crop-plant regeneration in agricultural clearings, forest-gap-successional vegetation emerges to be better adapted to poor nutrient soils (Lu et al. 2002; Peña-Claros et al. 2012).

3.4 GAP REGENERATION PATHWAYS AND CHALLENGES

Mechanisms that enhance species diversity in tree-fall gaps are yet to be determined and are an ongoing focus in forest ecology (Arihafa and Mack 2013; Dechnik-Vazquez et al. 2016; Royo et al. 2016). Most reviewed literature has agreed with the general notion that tree densities within gaps increase initially, but begin to decline sometime into the gap-phase regeneration process. Some literature has quantified this further, by suggesting that a species decline occurs within 3 to 6 years of gap formation as the trees increase in size (Brokaw 1985; Hubbell and Foster 1986; Runkle and Yetter 1987). The competitive abilities of tree species to partition heterogeneous resources rests on the assumption that forest gaps provide spatially and temporally varying environmental conditions driven by abiotic factors (i.e. light, nutrients and space). However, empirical support for this notion is still poor (Sapkota and Oden 2009; Arihafa and Mack 2013; Dechnik-Vazquez et al. 2016) and some studies even suggest otherwise (e.g. Hubbell and Foster1986; Uhl et al. 1988, Lieberman et al. 1995).

Although some studies have proposed that gaps do maintain plant species diversity when reaching climax, most of these did not make comparisons between gap diversity and the undamaged forest stand (Hubbell and Foster 1986, Uhl et al. 1988, Lieberman et al. 1995, Hubbell et al. 1999). Moreover, in many Neotropical forests, the early aggressive dominance of lianas may have paved an alternative pathway in gap regeneration, thus stalling tree regeneration in liana-dominated gaps at a low canopy height for an extensive period (Tang et al. 2011; Campbell 2015). The eventual advancement of regeneration after a long halt has been known to result in low species richness of trees in the secondary forest (Schnitzer et al. 2000, 2011). The paucity of trees in this pathway is revealed to be a function of liana density. A study on gap-phase regeneration in an old-growth tropical forest on Barro Colorado Island in Panama supported these conclusions (Schnitzer et al. 2000).

Forest gap-phase recovery is stalled when the system has crossed an ecological threshold thus inhibiting the perseverance of forest species (Hobbs et al. 2006). Regeneration at this point can be described as reaching a new steady state condition (Lamb et al. 2005). A common example is when degradation via logging leads to topsoil loss and a reduction in soil fertility, complicating recolonisation of these sites for many of the original species. Logged forests are also prone to liana invasion (Dawkins 1961; Neil 1984). Subsequent to logging, lianas from the crowns of felled trees can grow rapidly in the gap environment, where they are able to blanket regenerating vegetation and colonize surrounding trees (Gerwing et al. 2009). Hence, due to the high prevalence of lianas in tropical forests (Clark and Clark 1990; Schnitzer et al. 2000), the impact of lianas on gap-phase regeneration may be highly pervasive. Nevertheless relatively little study has focused on the role of lianas in gap-phase regeneration.

Another threshold is commonly crossed when sites become occupied by grasses and other invasive non-forest species. This increases the risk and severity of wildfires, particularly in the seasonal tropics, which then reduces woody plant recruitment and favours the further spread of grasslands (Lamb et al. 2005). There are many examples throughout the tropics of extensive grasslands that persist over time despite being entirely surrounded by forests (Maeto et al. 2009; Lamb et al. 2012). Forest gaps created by logging are usually highly degraded and therefore may have a reduced restoration potential. The alteration of topsoil in these gaps often results in the loss of seeds and nutrients, and other physical, chemical and biological changes (Wunderle 1997). In this situation, forest succession may be greatly stalled. If unaided by human assistance, succession would even be incomplete and therefore result in a possible change in the biome structure from forest to non-forest species, such as grass and shrubs. Natural gaps of very large size (i.e. over several hectares in area), though encountering moderate disturbances and retaining a relatively intact soil seed bank, might parallel changes in logging-induced gaps due to similar changes in soil and surface moisture (Breshears and Barnes 1999).

Post-disturbance-recovery of anthropogenically degraded tropical forests can be enhanced by strategically protecting areas in close proximity to forest fragments, particularly undisturbed forests (Margules et al. 2002; Laurance et al. 2002; Lamb 2012). Forest fragments are capable of producing seeds that can be vectored into adjacently cleared areas by animals or natural dispersal processes. Nonetheless, without proper protection applied to such landscape, further land-uses, such as human-lit fires or livestock grazing, may inhibit the effectiveness of this natural re-vegetation process.

3.5 CONCLUSIONS

Forest gaps (despite their varying sizes) are all results of various forms of disturbances to the forest canopy and stand. Naturally caused gaps are most likely to recover through the gap-dynamic processes that not only rely on regeneration through seedlings but also through regrowth of damaged and pre-existing flora. This has been the natural process that has allowed forest structures to evolve over time, hence tolerating climatic shifts over large temporal scales.

Self-restoration is not always possible, especially in relatively large anthropogenically-induced gaps. Nonetheless, these gaps can still undergo ample regeneration via different pathways if human efforts ensure that the process does not stall or lead to alternative states of degraded, fire-prone vegetation. A huge potential lies ahead in converting degraded land into new forest stands via human-assisted restoration.

3.6 CHAPTER SUMMARY

- This chapter provides background information on plant succession in forest gaps and gap-phase regeneration pathways across natural and human-induced treefall gaps in tropical forests.
- It also highlights important factors that drive gap-phase regeneration and recovery in degraded forests.
- This review concludes that natural gaps stand a better chance of recovering than human-induced gaps. However, the latter can recover well if assisted by well-designed human interventions.
- A huge potential lies ahead in converting degraded land into new forest stands via human-assisted restoration, or via halting degrading processes such as fire or grazing so that forests can recover naturally over time.

Photographs by Eric Katovai 2013

CHAPTER 4

DYNAMICS OF LOGGING IN SOLOMON ISLANDS: THE NEED FOR RESTORATION AND CONSERVATION ALTERNATIVES

Eric Katovai, Will Edwards, William F. Laurance

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Chapter overview:

This chapter is an integral part of my literature review that examines important factors driving high intensity logging in the Solomon Islands. This chapter also highlights the need for restoration and conservation alternatives across logged forests in the region.

Contribution to thesis:

This chapter attempts to address objective No. 3 which is to review the dynamics of logging in the Solomon Islands.

4.1 INTRODUCTION

Worldwide, tropical forests are highly vulnerable to industrial exploitation. During the past century, tropical Asia-Pacific islands, ranging from Malaysia to the Solomon Islands and westward across the equatorial Pacific, have experienced severe forest loss and degradation, exacerbated by some of the worst-known land-use practices, including heavy industrial logging (e.g., Fig. 4.1A-B) (Houghton 2012; Page et al. 2013; Miettinen et al. 2014). Sustainable forest management strategies have achieved some success by reducing forest damage and maintaining biodiversity and ecological functions needed for spatio-temporal recovery through natural regeneration (Lamb et al. 2005; Meijaard and Sheil 2008; Putz et al. 2008; 2012; Wilcov et al. 2013). However, logging practices in this region are usually unsustainable, leaving little chance for natural regeneration processes to restore forest stands to pre-cut levels of biodiversity, carbon storage, and ecological functioning (e.g., Fig. 4.1C-D) (Berry et al. 2010; Shearman et al. 2012).

Some studies have suggested that natural regeneration in logged forests is capable of achieving nearly complete recovery of biodiversity (e.g., Clark and Covey 2012; Katovai et al. 2012; Wilcove et al. 2013). Nonetheless, without adequate protection, previously logged forests are usually vulnerable to unsustainable repeated logging or complete deforestation (Katovai et al. 2012; Putz et al. 2012; Page et al. 2013). Further, it is unclear whether excessively logged and highly degraded forests will naturally recover their original species composition and ecological functioning if protected indefinitely without intervention. Active restoration could therefore become necessary for tropical Asia-Pacific islands, because large areas of once-forested landscapes on these islands either have been permanently altered or have plant species compositions that are largely novel and of unknown value for biodiversity conservation.

Figure 4.1. A-B show damage associated with excessive logging in the Solomon Islands. Non-compliance with logging legislation has exacerbated such damage. C-D show post-logging natural regeneration. This process alone may not be adequate to sustain floristic diversity in extensively damaged forests in Solomon Islands.

Selective logging has been practiced globally as a preferred alternative to clear felling (Laurance and Edwards 2014). It is defined as the felling of selected trees based on species preference and/or cut-size limitations (e.g., 50-60 cm diameter at breast height [DBH] (Putz et al. 2012)). Selective logging is normally initiated in the most accessible and fertile areas within logging concession boundaries, and gradually shifts towards lower-fertility forests that are commonly associated with unfavourable topography, such as higher elevations, steep ridges, and ravines (Pearce et al. 2003). If properly managed, this approach can achieve healthy economic gains with minimal forest damage, after which the forest stand is left unmanaged to recover through processes of natural regeneration (Pearce et al. 2003). However, the overly broad definition of “selective logging” has resulted in highly varied logging practices throughout the tropics, some of which fail to achieve their conservation goals.

While selective logging attempts to minimise overall impacts of forest degradation, some studies have reported excessive and highly detrimental effects to the forest environment. When felling is based entirely on tree size, all tree species above the cut-size limit are usually harvested (Villela et al. 2006). Harvest intensity per se depends on the quantity of timber trees above the cut-size limit, averaging 10 – 17 trees per hectare in densely wooded forests (Sist et al. 1998; Putz et al. 2012). When felling is species-based, all individuals of target tree species are frequently harvested (Sasaki et al. 2011). This usually includes trees well below the conventional cut-size limits (Bennett 2000; Katovai et al. 2012). Both species and cut-size restrictions may be violated due to the relentless demand for tropical hardwood (Sasaki et al. 2011; Budiharta et al. 2014). In this case, harvest intensity is extremely high, often reaching 30 cut trees per hectare, leaving behind a residual stand of severely damaged or killed immature trees. If not properly monitored by forest authorities, this strategy frequently violates legislation restricting export of timber species that are protected for cultural, biological, and conservational reasons (Elevitch et al. 2006).

Excessively heavy selective logging practises are widespread in most of the tropical Asia-Pacific islands, despite legislation to curtail such practices (Kabutaulaka 2000; Berch et al. 2012). The Solomon Islands present an ideal case for exploring the dynamics of these excessive practices because research on logging and its ecological outcomes in the country is poorly reported (Fig. 4.1). In this review we (i) highlight the dynamics for selective logging in the Solomon Islands, (ii) stress the need for active restoration in logged forests in the country, and (iii) propose several active restoration techniques already employed in tropical Islands of Southeast Asia that could aid recovery in excessively logged forests in the Solomons.

4.2 THE DYNAMICS OF LOGGING PRACTICES IN THE SOLOMON ISLANDS.

The Solomon Islands are a group of tropical oceanic islands east of Papua New Guinea with a modest forest estate. Logging began in the Solomons in the early 1920s, first on state-owned land, and eventually encroaching into native-owned lands in the 1980s (Bennett 1995; 2000). Logging practices in this country are mainly driven by synergisms among i) economic interests; ii) corruption; iii) poor employment conditions in the logging sector; iv) high forest accessibility; v) resource limitations for forest monitoring; vi) contention over logging benefits; and vii) paucity of information for policy development.

4.2.1 Economic interests

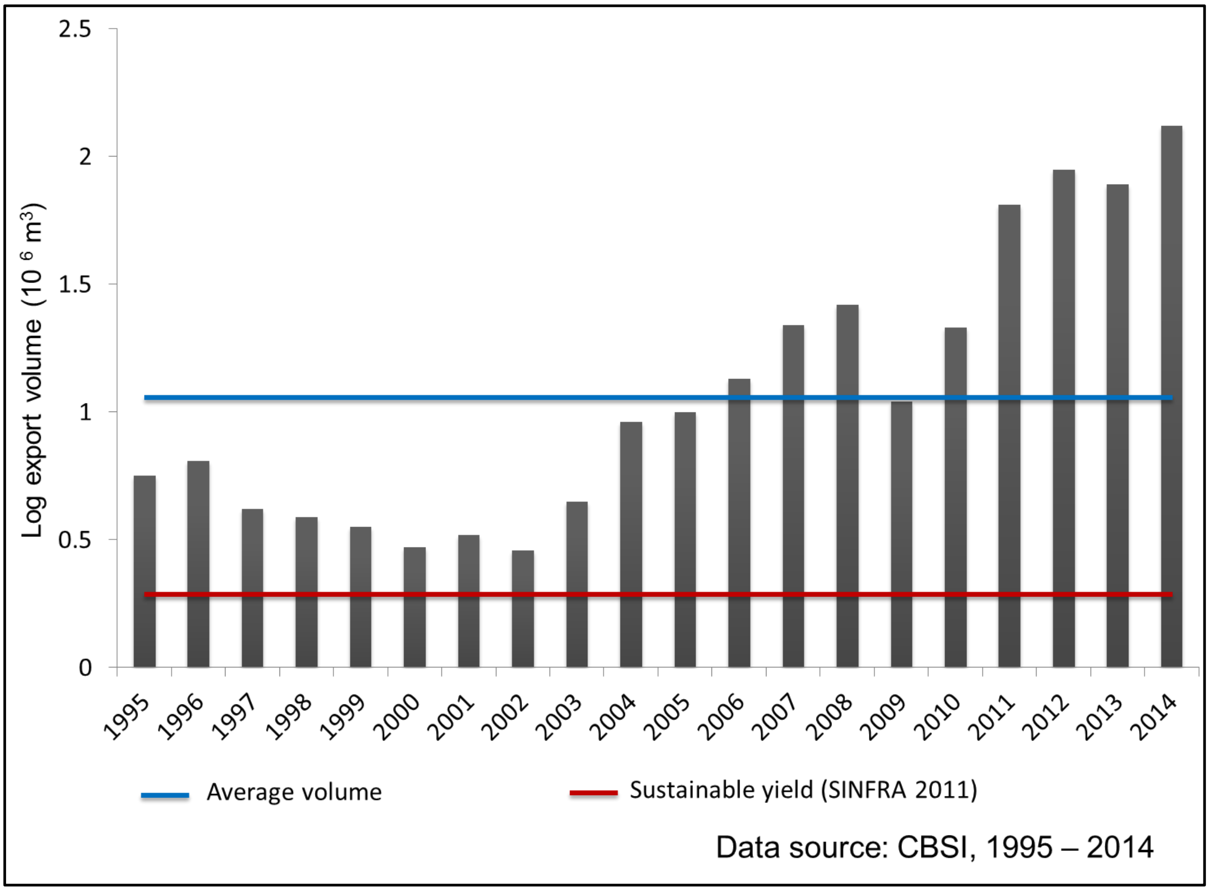
Logging has been a major contributor to the Solomon Islands' national and rural economies for several decades. Log exports alone contribute between 50 - 70% of the country's annual export revenue (Solomon Islands Forest Resource Assessment Update (SINFRA) 2011; Shearman et al. 2012). Timber stocks in the country have been severely over-harvested during the last two decades. Harvesting within this time period revealed an average yearly increase of 68,500 m^3yr^{-1}, reaching seven times the estimated sustainable level of 250,000 m^3yr^{-1} within the last five years (CBSI, 1995 - 2014. Annual Reports, Central Bank of Solomon Islands). Moreover, log production still continues to increase despite earlier assertions that peak production was reached in 2009 (Fig. 4.2) (Shearman et al. 2012).

Native landowners receive smaller returns from their logs than the national government. Nevertheless, they usually perceive logging as a lucrative means of quick financial gain through royalty spin-offs, and therefore ensure requirements are met for logging to commence in their area (Kabutaulaka 2000). This practice is likely to continue until all commercially viable wood stock in accessible forest estates is depleted, unless alternative viable economic opportunities become available to resource owners.

4.2.2 Corruption

Corruption among logging companies and various sectors of society has also contributed to excessive logging in the Solomon Islands (Kabutaulaka 2000; Dinnen and Firth 2008). This involves opportunists (i.e., influential groups or individuals who cunningly pursue any foreseeable logging opportunities to make financial gains), mostly through illegal transactions (Kabutaulaka 2000; Dinnen and Firth 2008; Larmour et al. 2012). Such transactions are usually bounded by ambiguous agreements between the logging companies and the receiver. For instance, over the past three decades successive governments have been infiltrated by a political culture driven by logging money (Birch et al. 2012). Such engagements undermine government policies and environmental protections pertaining to logging. Politicians and government officials benefiting from such illegal deals enable and protect logging interests, even compromising national interests by overstepping any resistance to logging (Frazer 1997; Dinneth and Firth 2008). Several high-profile politicians, prominent government officers, and opportunistic individuals and groups have allegedly been associated with such illegal practices and been charged with illegal conduct (Bennett 2000; Dinnen and Firth 2008).

Logging companies have also been exposed for fraudulent conduct, including tax evasion through illegal logging, under-reporting of export volumes, transfer pricing, informal agreements between buyers, altering species names (using species names with low market value), and bribery (Duncan 1994; Price Waterhouse, 1995; Dauvergne 1997; Kabutaulaka 2000; Dinnen and Firth 2008. The regularity of such fraud reveals the unprecedented levels of logging-driven corruption in Solomon Islands. For instance, in 1993 it was estimated that more than US$12 million of logging revenue was evaded through under-reporting (Duncan 1994). During the ethnic tension in Solomon Islands (1998 – 2003), logging was the least-affected industry, with operations progressively expanding to new areas (CBSI, 1995 – 2014). Surprisingly, log export volumes appeared to drop over these years (Fig. 4.2). While socio-political factors may have been blamed for low export levels, it is likely that opportunistic under-reporting of exported logs also contributed to this downturn. Government employees, particularly those in the forest sector, are usually implicated in such high-profile bribery and money-laundering activities (See examples in Dinnen and Firth 2008).



Data source: CBSI, 1995 – 2014

Figure 4.2. Log export volume for the Solomon Islands between 1995 and 2014. The rapid increase in logging licences issued during this period has resulted in a steep increase in logging activities in the country, with harvest quadrupling the sustainable yield.

4.2.3 Poor employment condition in the logging sector

When in operation, most logging companies employ their field workforces on a contract basis whereby employees are paid according to volume of wood harvested

(Ketily Gideon 2013, pers.comm). Because salary rates are generally low and working benefits such as medical insurance and life-insurance policies, housing allowance, and risk allowance are almost non-existent, employees are obliged to maximize harvests to sustain their livelihoods (Ketily Gideon 2013, pers.comm). This trade-off has contributed to high-intensity harvesting.

4.2.4 High forest accessibility

Forests in the Solomon Islands are easily accessed due to the islands' geographical layout and land tenure system. Islands in the group are relatively small, with lower mean population density than the islands of New Guinea and Southeast Asia, and are in close proximity to each other (Fig. 4.3). This makes it more economical for logging companies to establish concurrent operations on multiple islands across the country than in larger countries in the tropical Asia-Pacific region. Land tenure in Solomon Islands is based on traditional arrangements whereby a large swath of land (usually extending inland from the coastline) is owned by a particular native tribe (Bayliss-Smith et al. 2003). Logging concessions are usually demarcated within such tribal land, particularly in areas lacking human settlements (Bennett 2000; Bayliss-Smith et al. 2003).

Where road access is required through non-concession areas, loggers offer cash payments to the primary landowners of the intended road-access area. In most instances this arrangement works in favour of the loggers, because opportunities to make money are sporadic and therefore welcomed by traditional landowners. This is particularly true as a cash economy rapidly replaces traditional non-cash practices (Kabutaulaka 2000). Having roads through non-concession forests creates avenues for both legal and illegal logging, as well as for other human encroachment (Laurance et al. 2014).

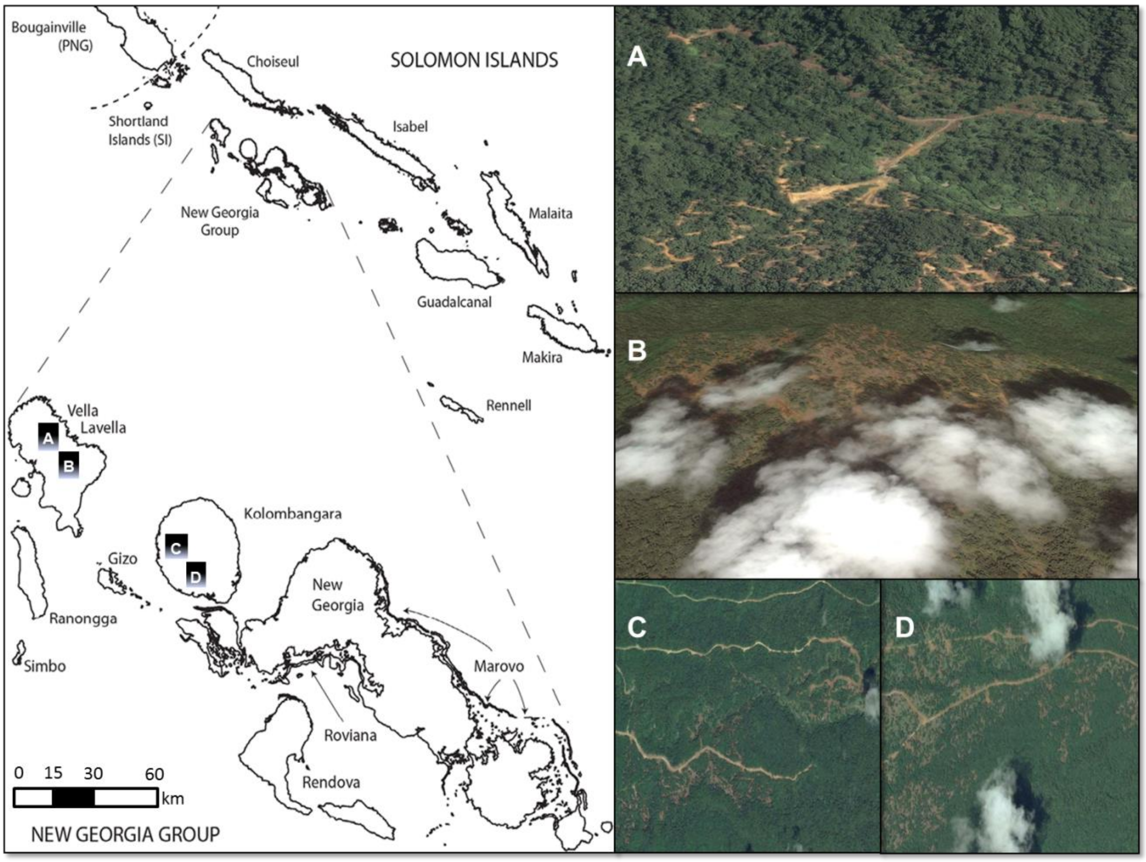


Figure 4.3. Natural forests in the Solomon Islands have been excessively logged within the last two decades. Inserts A-D show recent excessively logged forests on Kolombangara and Vella Lavela within the New Georgia group. Such logging operations are rarely monitored due to lack of funds and trained human resources in the country.

4.2.5 Resource limitations for forest monitoring

Poor monitoring of logging activities in Solomon Islands has resulted in excessive logging subtly carried out over several decades (e.g., Fig. 4.3 A-D). Forest authorities have insufficient funds and human resources to conduct effective monitoring (SINFRA 2011). Furthermore, remote areas are often difficult to access due to lack of transportation, and therefore are frequently neglected by authorities (Schloenhardt 2008). Yet these areas contain some of the largest timber stocks in the country (Whitmore 1969; Bennett 2000). Resource owners may work alongside loggers by providing support to the logging operations, and their lack of knowledge of logging codes-of-practice may limit their ability to identify illegal practices.

4.2.6 Contention over landownership and logging benefits

The logging industry in Solomon Islands is undergoing a critical period as the last tracts of accessible unlogged forests in the country are being exploited (Shearman et al. 2012). Realizing that a plunge in the logging industry is inevitable, stakeholders are currently focusing on what remains of the once highly wooded forests. While the government and logging companies are ensuring that all remaining unlogged accessible forests are exploited, resource owners are also contesting for benefits. Nonetheless, unlike the recent past, when logging was a matter of disagreement among pro- and anti-logging factions within tribal communities, it is increasingly becoming a land-grabbing race (Kabutaulaka 2000), whereby who logs first becomes the winner of the modest benefits the loggers have to offer. Apparently, traditional landowners who have previously maintained sustainable forest use instead of industrial logging have realized that they are continuously fighting a losing battle against the logging industry and its inherent corruption (Dauvergne 1997; Bennett 2000). Therefore, they too have become facilitators of logging in order to reap benefits from what is left of their forests.

4.2.7 Paucity of information for policy development

In the last two decades, numerous logging licences were issued for concessions throughout the Solomon Islands (Dinnen and Firth 2008; SINFRA 2011), causing the near-complete depletion of unlogged forests, as well as prompting re-entry logging which is now increasingly common (Fig. 4.4) (Usa 2009). Logging companies are gradually diverting their focus to previously logged forests, where residual wood stocks are still profitable. Such practices inflict severe damage on the forest stand (Putz et al. 2012). For example, re-entry harvesting in the Western and Isabel provinces in the Solomons have been extremely excessive, with cut-size limitation reaching as low as 15 cm DBH.

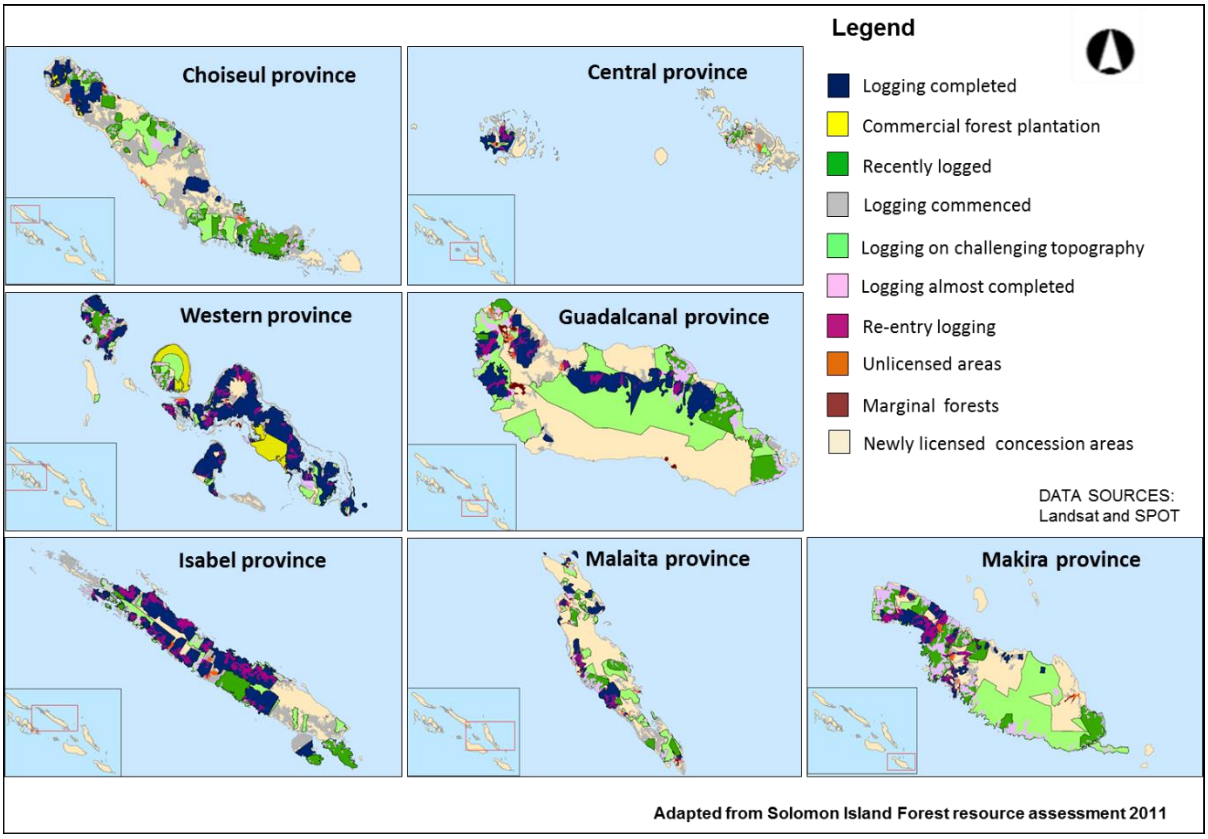
The impacts of logging on natural regeneration and biodiversity are still poorly understood in the Solomon Islands. Lack of such information makes it difficult to implement restoration and conservation efforts where needed (Cook et al. 2014). In addition, there are no policies pertaining to re-entry logging in the country. This has prompted premature re-entry harvesting, most of which is unregulated and excessive (Usa 2009). Consequently, natural regeneration alone may not be adequate for full forest recovery. Active restoration may also be required (Kammesheidt et al. 2001; Brienen and Zuidema 2007; Putz et al. 2012).

4.3 ACTIVE RESTORATION IN LOGGED FORESTS OF SOLOMON ISLANDS

Although wet tropical forests in Southeast Asia demonstrate strong recovery potential in post-logging regeneration (Berry et al. 2010; Wilcove et al. 2013), this may not be the case for the Solomon Islands. Forests throughout these islands are increasingly vulnerable to highly destructive logging practices with harvesting intensity often reaching 30 trees per hectare. Nearly all of the commercially viable forests in the country have been impacted by logging (Fig. 4.4). The commercial depletion of round logs in the Solomon Islands is likely to occur very soon (SINFRA 2011; Katovai et al. 2012).

Highly degraded forests in the Solomons may not achieve full recovery by natural regeneration (e.g., Fig. 4.3). In the 1960s and 1970s, tree planting projects were undertaken by the British Solomon Island Protectorate in order to restock highly degraded forests with commercial species (Bennett 1995), because the rate of forest-stock depletion apparently could not be compensated via natural regeneration alone (British Solomon Islands Protectorate [BSIP] 1960-1970). Preliminary results from a current study on Kolombagara Island, in the New Georgia group (Fig. 4.3), revealed that tree community composition differed significantly from the pre-logged state even after 50 years of post-logging regeneration, suggesting a slow recovery (Katovai et al. 2016).

Research findings from Southeast Asia may also have implications for forest restoration efforts in the Solomon Islands. However, it must be noted that variability in forest formation and ecological and biodiversity structure among regions may affect outcomes in different and unique ways (Whitmore 1989b; Burslem and Whitmore1999; Keppel et al. 2009; 2010; Malhi et al. 2013; 2014). It is therefore essential to determine the ecological factors that govern forest responses to logging in Solomon Islands. Furthermore, a comprehensive re-assessment is urgently needed to determine how much timber remains in the country's forest estates. This information is vital for making strategic decisions about the fate of forest estates and to determine precautionary and remedial measures to address forest crises in Solomon Islands.



Adapted from Solomon Island Forest resource assessment 2011

Figure 4.4. The spatial extent of logging on accessible forests in the Solomon Islands. It is estimated that all accessible forests in the Solomon Islands will be logged within the next decade.

4.4 RESTORATION ALTERNATIVES FOR LOGGED FORESTS IN THE SOLOMON ISLANDS

Regeneration studies in Southeast Asia have urged active restoration of severely over-logged forests (Brown and Lugo 1994; Lamb 1998; Lamb et al. 2005; Chazdon et al. 2009), and several of their proposals have been implemented in that region. In cases where unaided recovery is not possible in the Solomon Islands, a number of restoration strategies have been proposed.

4.4.1 Enrichment planting

Enrichment planting involves the introduction of ecologically valuable pioneer species to degraded landscapes (Karam et al. 2012). Though an expensive exercise, enrichment planting has proven successful in many instances (e.g., Lamb 1998; Parrotta and Knowles 2001; Lamb et al. 2005; Chazdon 2008; Cole et al. 2010; Karam et al. 2012). These studies highlighted two distinct phases by which floral diversity can be restored through enrichment planting. The first phase includes planting a small number of light-demanding, short-lived nurse trees. These trees serve as pioneer species that overshade non-forest species such as grasses and other possible unwanted competitors. Such a process provides a microclimate conducive for the establishment of newly introduced or pre-existing secondary species that lie dormant, awaiting the right conditions for germination and growth (Lamb et al. 2005; Chazdon et al. 2009).

The second phase involves planting a large number of secondary species, thereby increasing the chance to generate the highest possible diversity in the climax stand. In situations where seed banks do not contain secondary species, this method ensures that the later-successional stages are reached. However, in this circumstance the climax stand would be mostly determined by artificially disseminated seedlings that may or may not resemble the pre-existing forest stand, depending on the selection of seed sources. Where seeds are collected near the disturbed landscape, local knowledge is important for selecting native species for re-seeding (Sheil et al. 2006; Suárez et al. 2012). This may produce strong resemblances between old growth and recovering vegetation, and also ensure that the restored vegetation contains species of high cultural, economic, and ecological value to native communities, who depend on the forest for their livelihood (Suárez et al. 2012).

Planting commercial tree species has proven to be an effective approach on very degraded and deforested landscapes (Holl et al. 2011; Katovai et al. 2012; Lindell et al. 2013). Studies have shown that monoculture tree plantations provide a favourable environment for restoration of native understory vegetation (Guariguata et al. 1995; Parrotta 1995; Parrotta and Knowles 2001; Gunawan et al. 2012, Lindell et al. 2013). Tree plantations are also less expensive and less challenging to implement compared to mixed-species planting regimes (Bennett 2000; Cobin and Holl 2012; Gunawan et al. 2012; Karam et al. 2012). In the latter part of their growth and development, plantation trees often shade out light-demanding pioneer competitors such as lianas and woody shrubs, and allow the germination and establishment of late-successional species (Guariguata and Ostertag 2001). At this stage, the soil may have also accumulated nutrients from decomposed vegetation such as fallen branches and leaves, as well as decomposed biomass of the outgrown pioneer stand. Earlier studies have also shown that tree plantations attract a range of seed dispersers that aid soil seedbank recovery (Parrotta 1995; Parrotta and Knowles 2001).

Plantations are commonly established for economic gains. Large areas previously cleared for agriculture and cattle ranching are converted into commercial tree plantations (Chazdon 2008). The fate of such efforts depends on future management strategies for these restored landscapes. Regrettably, the worst-case scenario, where cyclic clear-cutting and replanting strategies have been used for many years, still predominates in many tropical regions (Thornley and Cannell 2000). It is still unclear how this process affects the regeneration ability of native vegetation in the tropics. However, repeated mechanical disturbances during log harvesting and extraction, and soil clearing during preparation for replanting, can cause further loss of soil seed banks.

A more recent approach, termed nucleation, involves planting selected tree species in strategic locations within heavily disturbed sites (Cobin and Holl 2012). The planted trees develop into vegetation patches that attract seed dispersers, subsequently increasing seed rain into the disturbed landscape (Cobin and Holl 2012; Lindell et al. 2013). This approach, however, does not work well for large-bodied dispersers such as forest-dwelling mammals, since they prefer to forage under continuous forests (Lindell et al. 2013). Nevertheless, nucleation is relatively inexpensive to implement and can be highly practical in large scale restoration efforts (Cobin and Holl 2012). Although information on the impact of design and long-term viability of this approach is still lacking, the success of nucleation in an array of habitat types and species guilds seems possible (Cobin and Holl 2012; Lindell et al. 2013).

4.4.2 Direct seeding

In direct seeding, seeds are directly scattered throughout disturbed landscapes (Cole et al. 2011). Seeding is usually undertaken at high densities (e.g., 92,500 seeds per hectare; Parrotta 1995), and requires copious shade-tolerant species to increase chances of a full recovery (Lamb et al. 2005). Mature forest developing from direct seeding is a function of the competitive interaction between the seedlings in later succession (Bonilla-Moheno et al. 2010). Direct seeding can be used to initiate reforestation in open fields under appropriate conditions, but may be most useful to enhance diversity once tree cover is already established (Lamb et al. 2005; Cole et al. 2011). This approach is not as versatile as enrichment tree planting, because eco-physiological conditions needed for initial germination are narrowly specific for most species.

Direct seeding with multiple native species has shown some success and great potential in the Solomon Islands (Bennett 2000; Blakesley et al. 2002; Shono et al. 2007; Kettle 2012). However, there are also challenges. First, seed collection can be time-consuming and difficult on a broad scale. When phenological information on forest types is lacking, biased selection of seeds may limit genetic variability and increase the homogeneity of the regenerated stands (Shono et al. 2007). Several studies have shown that shifting seeds from old-growth forests to disturbed landscapes can improve genetic variability in degraded landscapes (e.g., (Pither et al. 2003; Rodrigues et al. 2009; Sebbenn et al. 2011; Ratnam et al. 2014)). However, the germination and establishment of native tree seeds may be generally poor, perhaps due to the sudden shift in microclimatic and soil conditions (Kettle et al.

2012). To overcome this challenge, much more information is needed on the germination and establishment ecology of individual species (Blakesley et al. 2002).

4.4.3 Artificial perches

Deforested landscapes in Southeast Asia have benefited significantly from seed rain brought in by birds lured to artificial perches (e.g., McClanahan et al. 1993; Metcalfe et al. 1995; Holl 1999; Huth and Tietjen 2007; Sritongchuay et al. 2014). This is particularly true for small, deforested landscapes surrounded by forests. In degraded landscapes such as selectively logged forests, artificial perches are usually not as effective, because dispersers (mostly birds) have many natural perching sites to choose from, such as residual trees (Graham and Page 2012). Studies have shown that birds prefer natural over artificial perches if both alternatives are available (McDonnell and Tiles 1983; Holl 1999; Slocum and Horvitz 2000; Graham and Page 2012). Also, bird activity is mostly concentrated around the forest edge, decreasing with distance into cleared landscape despite the erection of artificial perches throughout the open landscape (Slocum and Horvitz 2002; Graham and Page 2012).

4.5 CONSERVATION CONCESSION MODEL – A PROMISING MECHANISM

We recognise that the previously mentioned efforts may only be successful if government policies on re-entry logging and forest restoration are implemented to boost investor confidence in such a cause (Ferraro and Kiss 2002). It is equally important that landowning communities be an integral part of this initiative (Hviding and Baines 1994; Kabutaulaka 2000; Govan et al. 2013). Several models of natural resource management in Solomon Islands have proven successful within the last two decades (e.g., Hviding and Baines 1994; Filardi and Pikacha 2007; Keppel et al. 2012). The ‘conservation concession’ model has been highly effective (Filardi and Pikacha 2007). Conservation concession allocates endowment funds to landowning communities in return for carefully outlined conservation outcomes (Filardi and Pikacha 2007; Govan et al. 2013). Such efforts have earned much community respect and ownership, harnessed a wealth of ethno-biological information needed to achieve conservation outcomes, and reduced labour costs through regular, voluntary community involvement (Hviding and Baines 1994; Kabutaulaka 2000; Bayliss-Smith et al. 2003; Vermeulen and Sheil 2007; Suárez et al. 2012).

The Kolombangara Island Biodiversity Conservation Association (KIBCA), established in 2008, is a classic example of this model (Filardi and Pikacha 2007). The endowment funds awarded to KIBCA are generally used to benefit its community through fee payments for school-aged children, establishing small, self-sustainable businesses, organizing life-skills workshops and training, building relevant community infra-structures (e.g., schools and churches), and financing the operation of the association. We see potential in using such a model to initiate forest restoration efforts in Solomon Islands where required.

4.6 SUMMARY AND CONCLUSIONS

We describe the dynamics of selective logging in Solomon Islands and the potential need for aided restoration in the country. At the outset, we highlight the unsustainable practices of selective logging in tropical Asia-Pacific Islands and the regeneration potential of these forests. Though studies in Southeast Asia have revealed that natural regeneration alone can restore degraded forests to near pre-logging levels, we suggest that comparative research is needed in Pacific Island countries to verify such claims. This will provide critical information for implementing the measures required for effective restoration. For the Solomon Islands, research is immediately required as multiple re-entry logging practices continue to further degrade already-logged forests and reduce their regenerative potential. We also suggest several restoration alternatives tested in Southeast Asia that may be effectively implemented in the Solomons. Finally, we highlight community-based restoration concessions as a potential mechanism whereby intensively logged forests of the Solomon Islands can be restored.

Based on evidence discussed in this review, we conclude that the impact of logging on lowland forests of Solomon Islands have been exceptionally damaging and must be addressed immediately. However, without appropriate political, economic and social remedies to curtail the current dynamics of logging in the country, restoration efforts may not succeed.

4.7 CHAPTER SUMMARY

- Forests of Asia-Pacific islands have undergone degradation by some of the worst known selective logging practices in the tropics. It is unclear whether severely damaged forests can return to a pre-logging state via natural regeneration, or whether active restoration is required. In this review, we highlight how the socioeconomic dynamics in the Solomon Islands promote excessive logging, resulting in highly degraded forests.
- We detail seven key elements currently promoting excessive logging in this region: (i) economic interests, (ii) corruption, (iii) poor employment conditions in the logging sector, (iv) high forest accessibility, (v) resource limitations for forest monitoring, (vi) contention over logging benefits, and (vii) a paucity of information for policy development.
- Though research on the regeneration capacity of logged forests in the Solomon Islands remains extremely limited, we suggest that some logged forests in the country may require active restoration—especially those that have been most heavily damaged. Our argument is based on previous tree planting initiatives in logged forest in the 1970s and 1980s. We propose three broad restoration techniques—enrichment planting, direct seeding, and the use of artificial perches—as viable options to help restore logged forests in the Solomon Islands.
- Lastly, we recommend the conservation-concession model to aid forest restoration, given its recent success in the region.

A recently logged forest in Kolombangara, Solomon Islands

Photograph by Eric Katovai 2013

CHAPTER 5

FACTORS INFLUENCING TREE DIVERSITY AND COMPOSITIONAL CHANGE ACROSS LOGGED FORESTS IN THE SOLOMON ISLANDS

Eric Katovai, Myknee Sirikolo, Umesh Srinivasan, Will Edwards, William F. Laurance.

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Chapter overview:

This chapter presents data on tree regeneration in logged forest of Kolombangara, Solomon Islands. We examined tree species communities and assessed the dynamics of recovery of tree diversity and species composition in previously logged forests, with a particular focus on determining whether a halfof a century was sufficient to allow forests to recover to pre-logging conditions.

Contribution to thesis:

This chapter attempts to address objective No. 4 of this thesis, which is to determine factors influencing tree diversity and compositional change across logged forests in the Solomon Islands.

5.1 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 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.

5.2 METHODS

5.2.1 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. 6.1). 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. 6.1). 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.

5.2.2 Study design

From January to November 2013, we sampled 144 0.1-ha (50 m x 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. 5.1). 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).

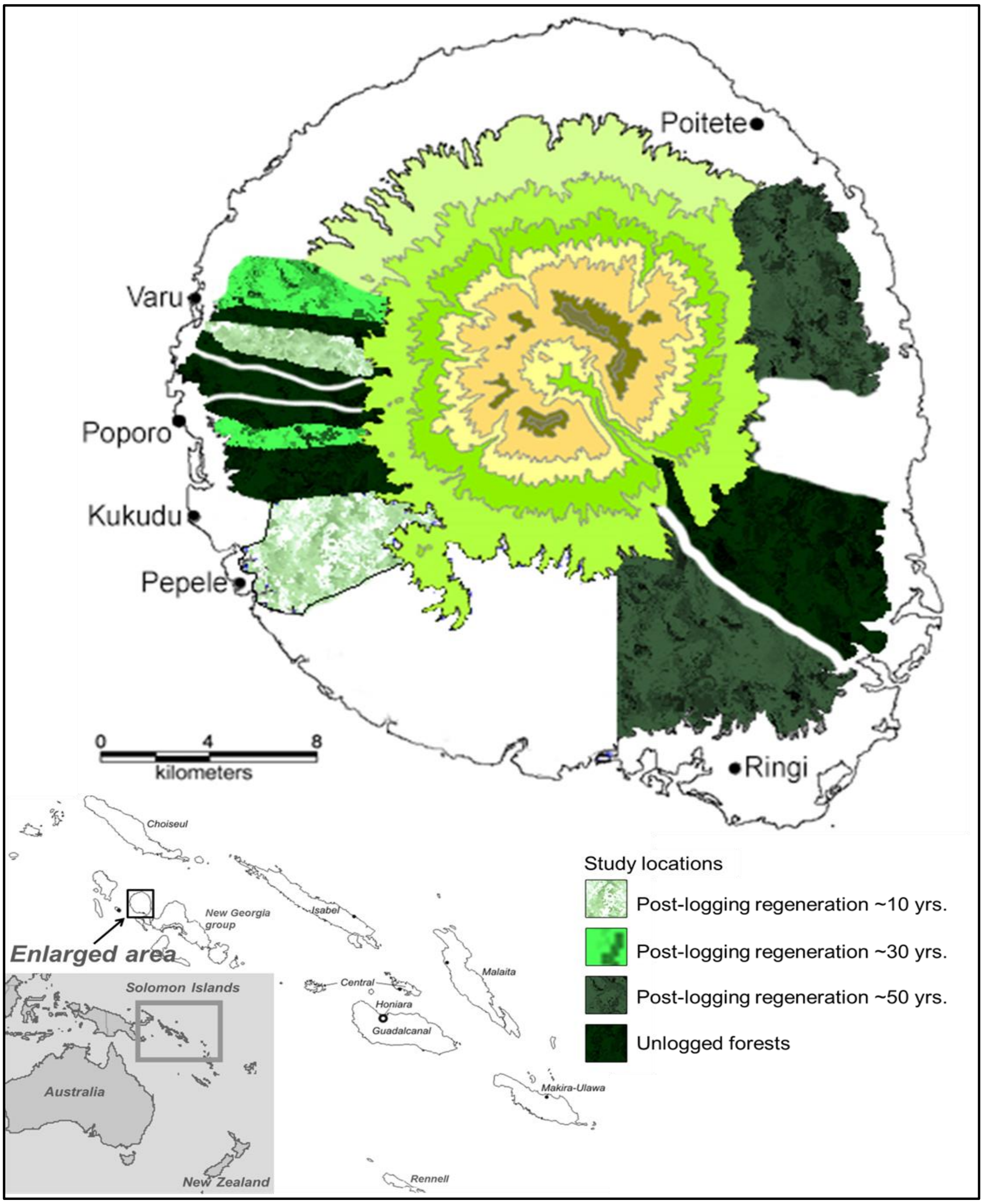


Figure 5.1. Kolombangara is part of the New Georgia group of islands in the Solomon archipelago located in the northwest Pacific. Logged forest sites were demarcated according to regeneration times of 10, 30 and 50 years. Two forest coupes were selected for each timeframe. Unlogged forests were demarcated to topographically match logged forests.

The 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 50m x 70m 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 [1.3m] (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 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).

5.2.3 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/homeoriginal) and published floras (e.g. Whitmore, 1967, 1969; Peekel, 1984; Hancock and Henderson, 1988) were also used to aid the identification of morphospecies.

5.2.4 Statistical analyses

5.2.4.1 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).

5.2.4.2 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).

5.2.4.3 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).

5.2.4.4 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).

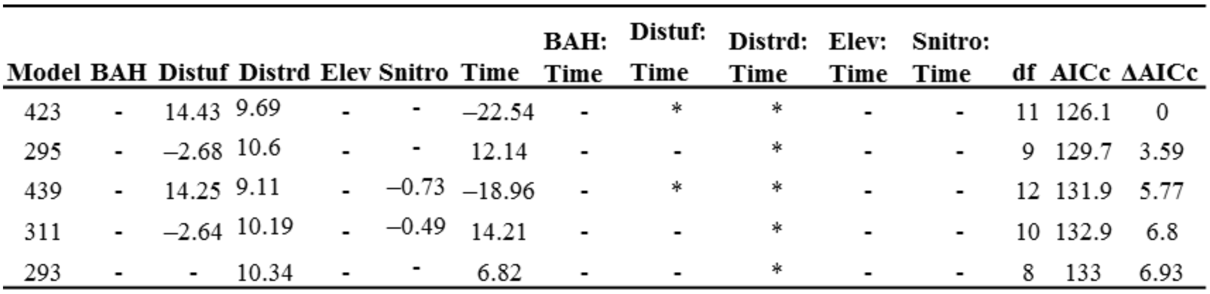
5.3 RESULTS

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 (Appendix 2). Fifty seven species were found only in unlogged forest as compared to 54 in logged forests, while 65 occurred in both forest categories (Appendix 3).

5.3.1 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 5.1).

Table 5.1. The species richness candidate model set (only with ΔAICc < 7) used in the linear mixed model (LMM) analyses, with associated effect degrees of freedom, AICc and ΔAICc 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 thatpredictors or their interactions with time were not included in the corresponding model.



Model	BAH	Distuf	Distrd	Elev	Snitro	Time	BAH: Time	Distuf: Time	Distrd: Time	Elev: Time	Snitro: Time	df	AICc	ΔAICc
423	-	14.43	9.69	-	-	–22.54	-	*	*	-	-	11	126.1	0
295	-	–2.68	10.6	-	-	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	6.8
293	-	-	10.34	-	-	6.82	-	-	*	-	-	8	133	6.93

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

Final averaged model results indicated that two effects were particular important: distance to raod, distance to forest and the interactions of these effects with time. 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. 5.2a) and negative effects at 30 years post-logging (slope = –14.71; 95% CI = –22.66, –6.75) (Fig. 5.2b). The effect for 50 years post-logging was weakly negative (slope = –11.2; 95% CI = –19.41, –2.95) (Fig. 5.2c). Distance to unlogged forest had no effect on species richness at 10 years post logging (slope = –11.27; 95% CL = –1.64, 25.0) (Fig. 5.2d). 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. 5.2e 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 5.1).

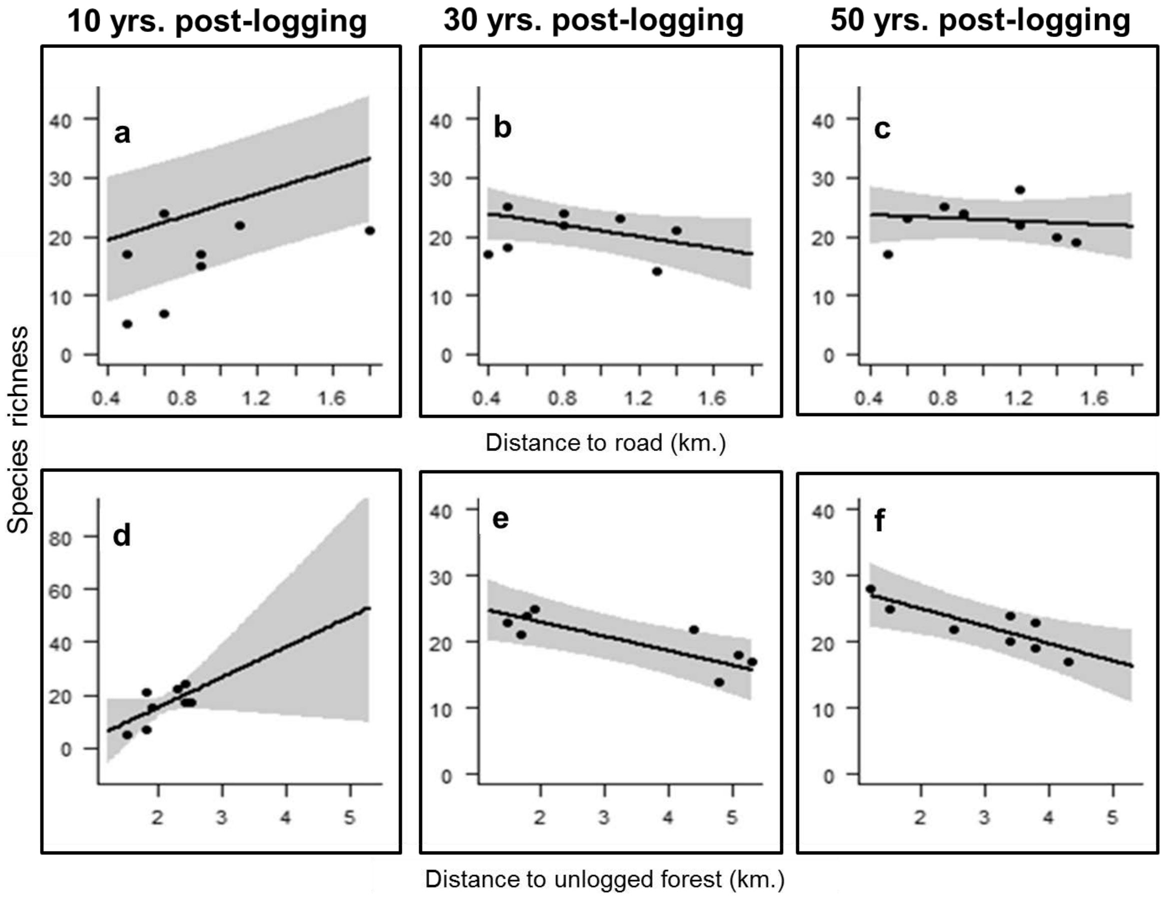


Figure 5.2. The relationship between tree species richness and distance to road and distance to unlogged forest across recovery time. Solid lines represent fit (predicted) values from the LMM, and the grey polygons, the 95% CI associated with the modelled predictions. Both distance to road and distance 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 years (a and d), and negatively influenced forests undergoing regeneration at 30 and 50 years post-logging (b, c, e and f). Distance to unlogged forest (fig d) however had no pronounced effect on species richness in recently logged forests. In fig d the prediction appears strongly positive due to the relative proximity of recently logged forests to propagule sources (d).

5.3.2 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 unlogged forest. However, harvest intensity and soil N had no important effect on *H'* diversity across recovery time (Table 5.2).

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. 5.3a). The effect of distance to road was weakly negative for 30 years post-logging (slope = –0.96, CI = –1.25, –0.67) (Fig. 5.3b). In 50 years post-logging, the effect of distance to road was weakly positive (slope = 0.79, CI = 1.11, 0.47) (Fig. 5.3c). 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. 5.3d–f).

Table 5.2. The Shannon diversity candidate model set (only with ΔAICc < 7) used in the LMM analyses, with associated effect degrees of freedom, AICc and DAICc values. Columns 2–12 represent the predictors used in the model (with columns 8–12 indicating interactions between each predictor and time). A slope coefficient for each predictor is 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.

Model	BAH	Distuf	Distrd	Elev	Snitro	Time	BAH: Time	Distuf: Time	Distrd: Time	Elev: Time	Snitro: Time	df	AICc	ΔAICc
423	-	2.16	0.78	-	-	–4.58	-	*	*	-	-	11	28.5	0
1	-	-	-	-	-	-	-	-	-	-	-	3	28.8	0.36
5	-	-	0.33	-	-	-	-	-	-	-	-	4	30	1.53
17	-	-	-	-	–0.21	-	-	-	-	-	-	4	31.2	2.72
21	-	-	0.31	-	–0.2	-	-	-	-	-	-	5	32.8	4.32
2	–0.09	-	-	-	-	-	-	-	-	-	-	4	33	4.51
33	-	-	-	-	-	0.58	-	-	-	-	-	5	33.8	5.36
3	-	0.02	-	-	-	-	-	-	-	-	-	4	34.8	6.39
293	-	-	0.89	-	-	–0.2	-	-	*	-	-	8	35	6.51

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

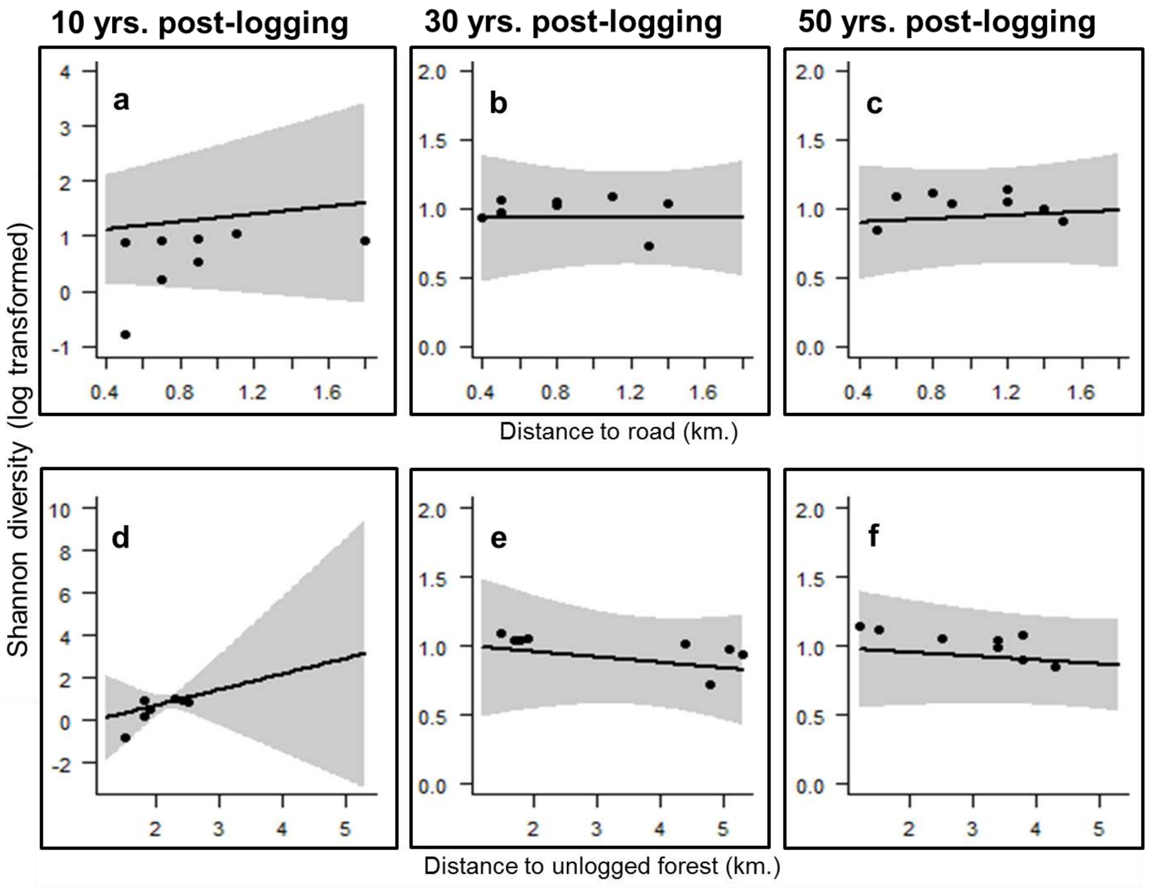


Figure 5.3. The relationship between Shannon–Weiner diversity index (*H'*) and distance to road and distance to unlogged forest across recovery time. Solid lines represent fitted (predicted) values from the LMM, and the grey polygons, the 95% confidence intervals associated with the modelled predictions. 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 years (a and d). In Fig. d the prediction appears strongly positive due to the relative proximity of recently logged forests to propagule sources (d). Effects of distance to road on *H'* diversity was relatively weak for logged forests at 30 and 50 years of recovery (b and c). Distance to unlogged forest, however, had a marked negative effect on *H'* diversity in these forests (e and f).

5.3.3 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, mean est8imates of Shannon diversity 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 years post-logged forests was significantly lower than those of older logged and unlogged forests (Appendix 5.2).

5.3.4 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. 5.4a). 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 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 50% and 20%, respectively. Mean similarities across logged and unlogged forest forests were 32.8% and 29.9%, respectively.

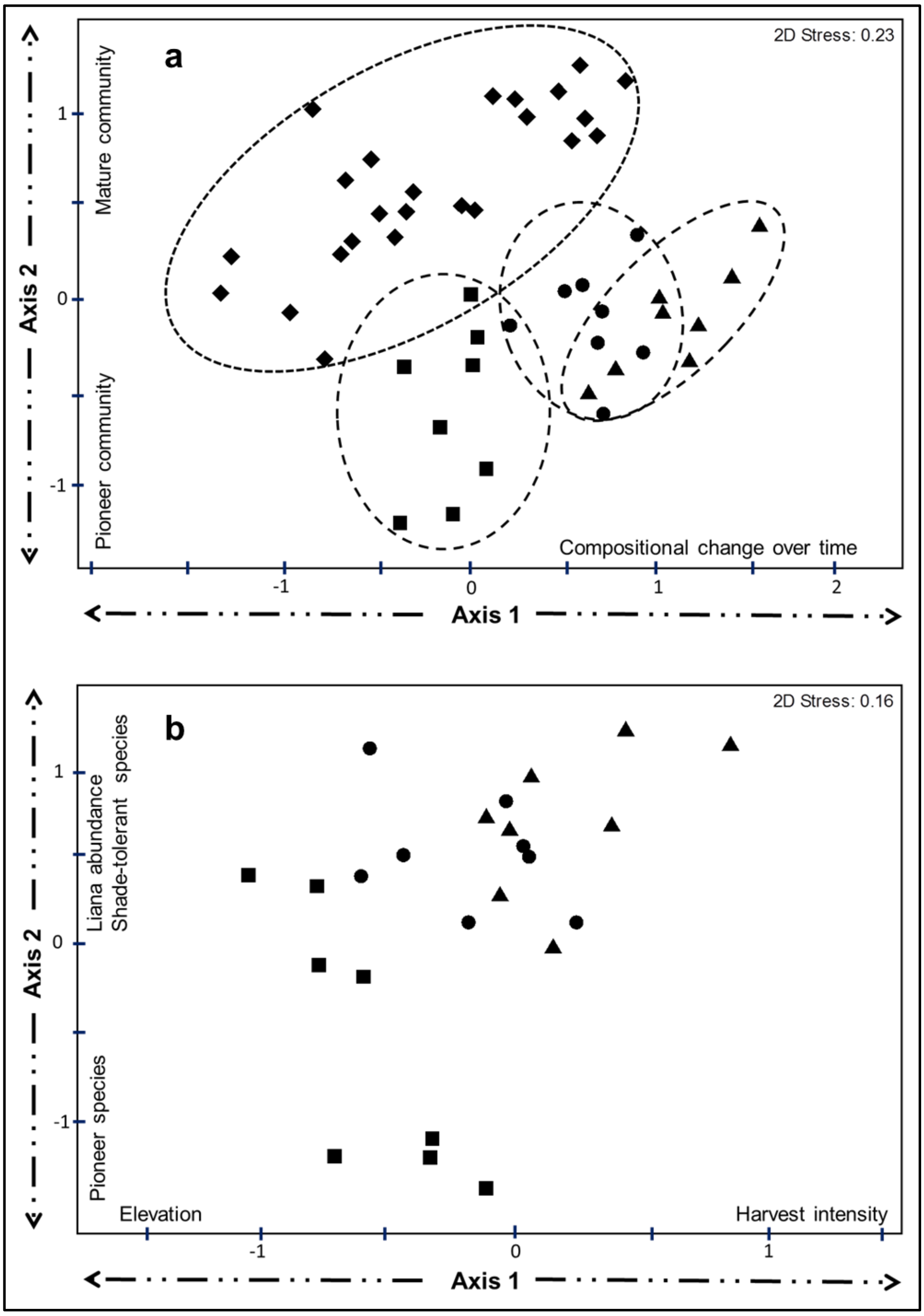


Figure 5.4. Non-metric multi-dimensional scaling (MDS) for similarity of tree species composition between logged forests at 10 years of regeneration (■), 30 years of regeneration (●), 50 years of regeneration (▲) and unlogged forests (◆). MDS is based on Bray–Curtis similarity indices. Species compositions 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).

A two-dimensional MDS ordination showed strong associations with several ecological gradients (Fig. 5.4b). 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. 5.5). Only *Campnosperma brevipetiolata* and *Teijsmanniodendron ahernianum* were relatively important across all logged forest classes, of which *C. brevipetiolata* was the most important species (Fig. 5.5). The relative importance of *T. ahernianum* decreased from 10 to 30 years postlogging and then increased between 30 and 50 years post-logging. *T. ahernianum* was the most important species in unlogged forests.

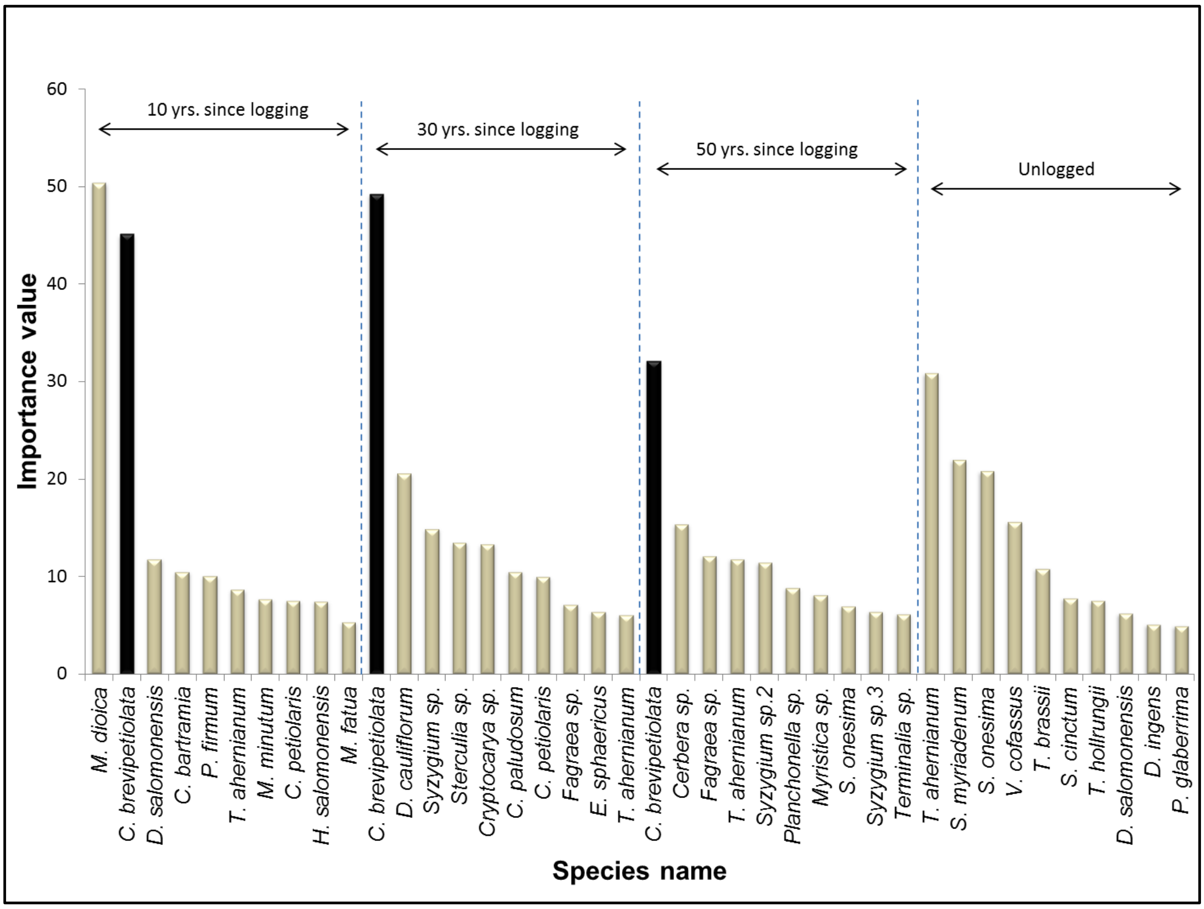


Figure 5.5. Importance values of the top 10 dominant tree species in logged forest time classes and unlogged forests. *Campnosperma brevipetiolata* (in black) was highly dominant in logged forests.

5.4 DISCUSSION

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

Although being part of the average models, soil nitrogen (Tables 5.1 and 5.2), and basal-area harvest (Table 5.2) 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.

5.4.1.1 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. 5.2a and 5.3a). This might result both from topographic effects 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., Calophylum spp.* and *Dilenia spp.* remained an integral part of the forest stand along with several recently established mid-succession species such as *Dosyxylum, Syzigium, Sterculia, Cryptocarya* and *Callophylum spp.* (Bayliss-Smith et al., 2003).

5.4.1.2 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. 5.2d–f and 5.3d–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).

5.4.2 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 years 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 years 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 years 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).

5.4.3 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. 5.4a). 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; Jakovac et al. 2016), 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; Putz et al., 2012; Cazzolla Gatti et al., 2015).

Post-logging regeneration across wet topical 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 m^2), 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. dioica* and *C. brevipetiolata* among others (Fig. 5.5). *Macaranga* dominance subsided within two decades of regeneration, whereas *C. brevipetiolata* 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. brevipetiolata* may have stalled succession in logged forests by delaying growth and development of late-successional species (Fig. 5.6). The frequent occurrence of important late succession species such as *Dellinia spp., Callophylum spp.* and *Terminalia spp.* in the understory and sub canopy layer of *C. brevipetiolata*-dominated forests on Kolombangara supports this view (e.g. Whitmore, 1989; Katovai et al., 2012). Although the importance of *C. brevipetiolata* declined between 30 and 50 years post-logging, the turnover between *C. brevipetiolata* 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).

Figure 5.6. A 50 year old logged forest highly dominated by *Campnosperma brevipetiolata* trees that have naturally regenerated post logging. Climax forest species are mostly restricted in the understory of these forests, awaiting the chance to re-occupy the canopy level.

Silviculture experiments involving post-logging thinning of *C. brevipetiolata* could potentially shed more light on its impact on floristic recovery. Since *C. brevipetiolata* 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 (Ouédraogo et al., 2011; Gourlet-Fleury et al., 2013). However, the success of such efforts relies on well-regulated forest management policies (Meijaard and Sheil 2008; 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 (Meijaard and Sheil 2008; 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.).

5.5 CONCLUSIONS

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. brevipetiolata* 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.

5.6 CHAPTER SUMMARY

- 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 *Campnosperma 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.

Campnosperma brevipetiolata, a highly vigorous tree that dominated logged forests across Kolombangara. This tree is bent as a result of logging damages early in its growth.

Photograph by Eric Katovai 2013

CHAPTER 6

THE INFLUENCE OF LIGHT ON THE OCCURRENCE OF PLANT-TRAIT ELEMENTS AND PLANT FUNCTIONAL DIVERSITY ACROSS LOGGED FOREST UNDERSTORY PLANT COMMUNITIES IN THE SOLOMON ISLANDS

Eric Katovai, Umesh Srinivasan, Susan G. Laurance, Will Edwards, William F. Laurance

This manuscript is in preparation for submission in *Functional Ecology*.

Chapter overview:

This chapter presents data on the influence of light on plant function in logged forests across three different recovery stages on Kolombangara, Solomon Islands. Three easily measured plant functional types and their plant trait elements were used to quantify functional diversity.

Contribution to thesis:

This chapter attempts to address objective No. 5 of this thesis, which is to examine the effect of light on functional diversity across understory vegetation communities in logged forests on Kolombangara, Solomon Islands.

6.1 INTRODUCTION

Disturbance to natural vegetation causes restructuring of plant community composition in forest communities. On a global scale this process is becoming more pronounced as a result of persistent human land-use activities, such as selective logging, encroaching into pristine forest areas (Baraloto et al. 2012; Schwartz et al. 2013; Cole et al. 2015). For instance, approximately one third of the world's remaining tropical forests have been degraded through selective logging (Zimmerman and Kormos 2012), and this will certainly increase because of the high global demand for tropical hardwood products (Miettinen et al. 2014). Such a trend poses an immediate challenge for conservation and restoration in tropical forests, and finding effective solutions to these challenges is critical (Baraloto et al. 2012; Schwartz et al. 2013; Lamb 2014). Predicting vegetation patterns emerging in logged forests is vital for implementing effective management strategies through the integration of conservation and restoration practices (Lamb 2012, 2014; Schwartz et al. 2013; Cole et al. 2015).

Disturbance caused by logging can cause a wide array of biotic and abiotic changes to tropical forests that will influence their floristic recovery and ecosystem function (Lavorel and Garnier 2002; Wright et al. 2005; Carreño-Rocabado et al. 2012). Observed changes in logged forests include altered community composition and structure (Katovai et al. 2015b; 2016), and modification to soil drainage, and nutrient cycling (Bernhardt-Romermann et al. 2011; Katovai et al. 2012; Mayfield et al. 2013). However, it is often difficult to quantify alterations in post-logging vegetation development based entirely on taxonomic identity because of the high degree of overlap in plant tolerance limits and response to environmental factors

(Mayfield et al. 2009; Bernhardt-Romermann et al. 2011). For example, in tropical forests, certain tree species can tolerate large variations in light levels and also respond uniformly to the decline in light levels over the course of post-disturbance forest recovery (Whitmore 1996; Yamamoto 2000; Katovai and Katovai 2012).

Attention has recently shifted from taxonomical identity to plant function as an alternative proxy to explain successional changes and species co-existence, as well as specific ecosystem processes and services (e.g., Lebrija-Trejos et al. 2010; Bernhardt-Romermann et al. 2011; Katovai et al. 2012; Mayfield et al. 2013; Fortunel et al. 2014; Sakschewski et al. 2016). There is a growing consensus that plant functions appear to better explain the environmental dynamics influencing spatial and temporal changes in forest community composition than taxonomic identity (Geovana et al. 2012; Gillison et al. 2013; Flores et al. 2014; Lasky et al. 2014). For instance, plant functional types (PFTs) capture interspecific variation in plant strategies that may determine species persistence and/or occurrence under a given set of conditions (Westoby et al. 1998; McGill et al. 2006).

Changes in a single PFT can be detected and quantified using a generic set of easily measured morphological or behavioural characteristics termed plant-trait elements (PTEs) (Gillison et al. 2013). For example, growth form is a PFT which include PTEs such as epiphyte, fern, grass, herb, palm, shrub, seedling and vine (Katovai et al. 2012). Change in levels of each PTE in any vegetation community over time can provide vital information on plant strategy in response to environmental gradients. The response of plant-trait elements is independent of species and can be detected in either natural or human-driven environmental change across various spatial scales (Gillison and Carpenter 1997; Gillisson et al. 2013). Plant-trait elements can potentially be measured across plant history thus allowing for comprehensive analyses of how plant functions respond to changing environments (Lavorel and Garnier 2002; Sakschewski et al. 2016). However, applying this avenue have not been realised until very recently (Gillison et al. 2013; Franks et al. 2014).

Although plant functional traits have been widely used to quantify post-disturbance recovery in forest communities, most of these efforts have been conducted on tree species occupying the forest canopy (e.g. Westoby et al. 1998; McGill et al. 2006; Geovana et al. 2012; Flores et al. 2014; Lasky et al. 2014). Response strategies to disturbances of other growth forms, especially those occupying the forest understory, remain poorly studied to date (Mayfield et al. 2005; Katovai et al. 2012).

Research interest in understory vegetation developed in recognition of the vital role this stratum plays in forest structure and driving forest dynamics (Huo et al. 2014). Understory plant communities facilitate energy flow and nutrient cycling, and drive succession in disturbed forests (Messier et al. 1998; Katovai et al. 2012; Huo et al. 2014). These communities also contribute greatly to floristic diversity and structural complexity in forests (D’Amato et al. 2009; Katovai et al. 2012; Huo et al. 2014), providing habitat and ecological niches for other biotic groups (Bartels et al. 2010; Huo et al. 2014). Furthermore, understory vegetation may sustain species that can be used as bio-indicators of environmental change, as multiple species across each of the growth forms (i.e. epiphyte, grass, herb, palm, seedling, shrub, tree and vines) are usually highly sensitive to disturbance (Mataji et al. 2010).

Light is a heterogeneous resource that changes continuously within the forest environment across spatial and temporal scales (Chazdon 1988; Rozendaal et al.

2006). In intact tropical forests, only about 1% of available light reaches the forest floor (Corlett and Primack 2011). However, damage to the forest canopy results in an influx of light into the understory. This change in light levels–quantity and wavelengths–quality apparently prompts the change of understory plant composition from shade-tolerant to light demanding species (Sorek and Levy 2012; Batista et al. 2014). Treefall gaps not only increase light quantity, but they change the light quality (Sorek and Levy 2012). In general, canopy foliage tends to absorb the shorter, more energetic wavelengths and let longer wavelengths filter through. When a gap is created, both the quantity and quality of light reaching the forests floor changes (Capers and Chazdon 2004). Plant physiological responses to such changing light may occur within minutes, commencing with photosynthesis induction and adjustment, followed by ATP expenditure and storage several hours later (Rijkerset al. 2000; Rijkers and Bongers 2005; Rozendaal et al. 2006). Morphological changes take place within several weeks or months (Ackerly 1997; Rozendaal et al. 2006; Mao et al. 2014), whereas forest architectural changes may take months or years to occur (Rozendaal et al. 2006; Batista et al. 2014). However, despite this knowledge, understanding the processes controlling plant species' occurrences and distributions across environmental gradients, particularly in highly diverse tropical forests, is still a daunting challenge to ecologists (Geovana et al. 2012; Fortunel et al. 2014).

In the wet tropics, light is generally considered one of the most important factors influencing the post-disturbance regeneration in forest understory plant communities (Yamamoto 2000; Chazdon 2003; Hardwick et al. 2004; Sundqvist et al. 2013). The influence of light at PTE level can potentially provide vital details of how these communities recovery across time (Gillison et al. 2013). We tested this hypothesis through measuring the effect of light on PTEs of three PFTs, chlorotype, growth form and leaf-area classes, across understory plant communities in logged forests of Kolombangara, Solomon Islands. We hypothesised that changes in each PTE across post-logging recovery highly depends on the ability of these communities to adapt to changing light levels.

This study aims to (i) examine how understory light vary across a recovery gradient of post-logging forest regeneration, (ii) determine how light influence PTE occurrence during post-logging forest regeneration (iii) estimate whether functional diversity across understory plant communities in logged forest regain pre-logging levels entirely through natural regeneration. Achieving these objectives can advance our understanding of how light and recovery time influence plant functional diversity over the course of post-logging forest regeneration. This study also represents a step towards forecasting the general responses of understory plant communities to landscape-scale disturbances.

6.2 METHODS

6.2.1 Study area

The island of Kolombangara (157° E and 5° S) in the western part of the Solomon Islands was selected for this study due to its long history of logging and post-logging regeneration (Fig. 6.1). The island is volcanic in origin, and last erupted during the Pleistocene (Burslem et al. 2000; Katovai et al. 2012). What remains of this now-extinct volcano is a near-perfect circular island ~32 km in diameter; the island is relatively flat along the coastline, with elevation steadily increasing inland to

~400–500 m above sea level (a.s.l.). An increase in topographical variation then follows, with elevation increasing exponentially from the base of the volcanic cone to the crater rim, which is ~1700 m a.s.l. and ~6.5 km in diameter. The relatively steep crater wall descends into the highly rugged crater floor, which lies at ~600 m a.s.l. and is covered with dense mixed forest.

Rainfall on Kolombangara is relatively uniform on all sides of the island, and increases with elevation (based on unpublished data obtained from the island-wide weather stations of Kolombangara Forest Products Ltd [KFPL]). Mean rainfall is high, exceeding 3000 mm yr^{-1} (Aldrick 1993, Katovai et al., 2012a), which is common for high islands in Oceania where precipitation results from orographic convection (Granger et al. 1998). Kolombangara experiences bi-annual wet seasons from November to March and from July to August (Aldrick 1993). Regular rainfall is also experienced in dry months, presumably due to both orographic precipitation and ocean storm cell blow-over (Rhodes et al. 2006; Katovai et al. 2012).

Kolombangara like other large oceanic islands within the Bismarck-Solomon archipelago is less diverse than the New Guinea mainland and the Islands of Southeast Asia but has high endemism (Whitmore 1966; Woinarski et al. 2010; Katovai et al. 2016). However, much of the island’s lowland forest (~90%) has been either degraded through logging and is undergoing regeneration, or has been converted to other land-use activities (Katovai et al. 2012). Early anthropogenic disturbances on the island were linked to nomadic settlers in the pre-20th century era, when patches of forests were cleared for subsistence agriculture and settlements across the island (Baylis-Smith and Whitmore 2003), followed by early European settlers who introduced the concept of commercial plantations on the Island (Bennet 2000).

Logging commenced on Kolombangara in 1964 and its continued persistence has exacerbated degradation of a large expanse of lowland forests from the coastline to 400–500 m a.s.l covering an area exceeding 45000 hectares. Harvest intensity was extremely high across the island, often reaching 30 trees per hectare (Katovai et al. 2015a). Logging began in the SE region of the island, and progressed into the NE and NW within 21 years (Katovai et al. 2016). Although much of the post-logging landscape was converted into commercial tree plantations in the mid-to-late 1980s (Bennett 2000), sizable patches of regenerating forests still exist between plantations. These secondary forests are generally contiguous with intact upland forests, and radiate towards the coast, mainly along watersheds. Logging in the SW region of Kolombangara started in the early 80s and is still active in some areas.

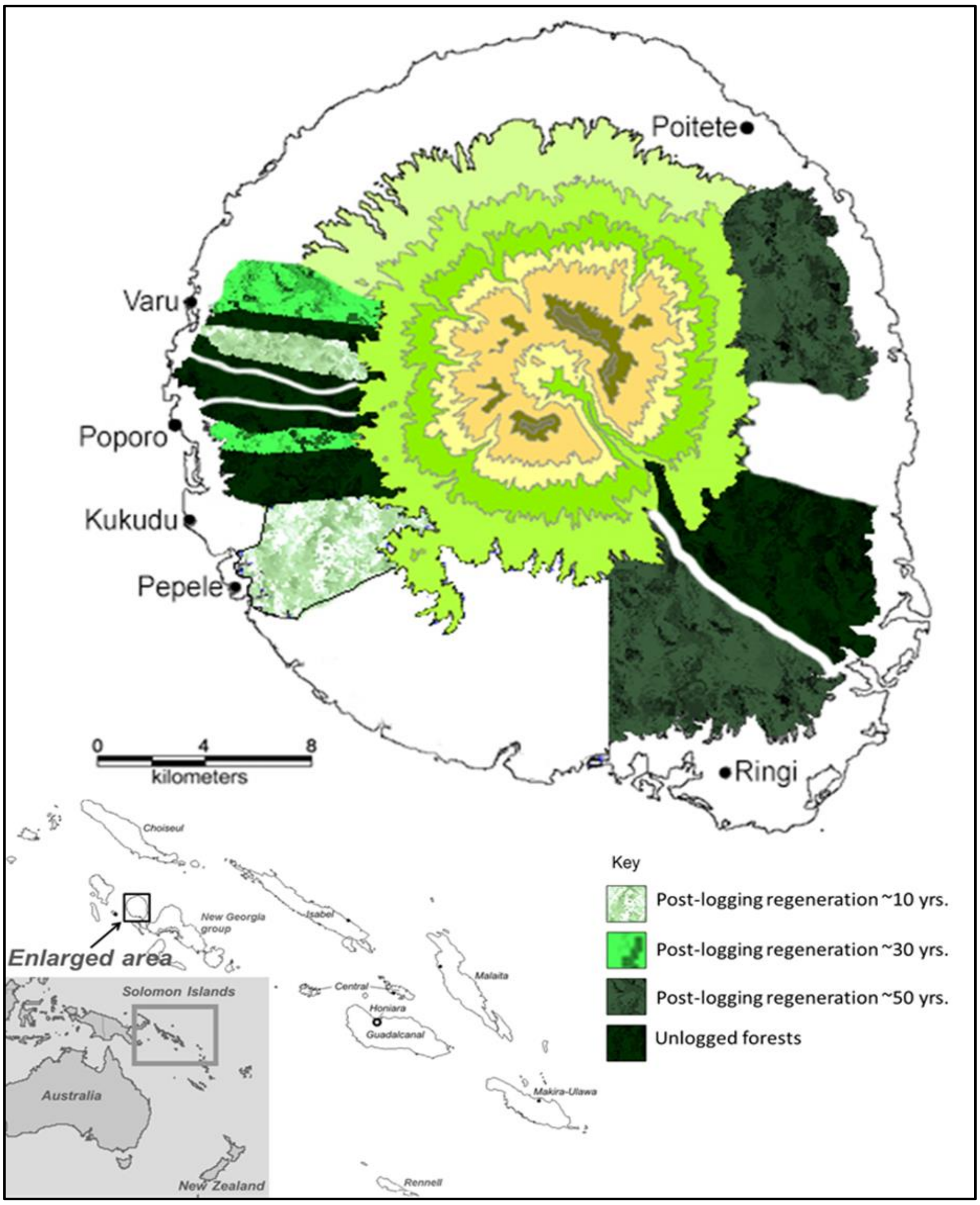


Figure 6.1. Logging history and study locations on Kolombangara, a high volcanic island in the Solomon Islands.

6.2.2 Study design

The mosaic of secondary forests at various stages of regeneration on Kolombangara presents an ideal setting to examine changes in PFTs as a function of recovery time. Regeneration times of logged forests were estimated using the available literature, combined with firsthand information from former logging employees, several of whom have worked for a succession of logging operations on Kolombangara. Logged forests were categorised into randomly selected coupes (i.e. ~350–800 ha areas) representing forests regenerating 50, 30, and 10 years after logging. Two coupes were chosen for each forest class, for a total of six logged coupes. An equivalent number (six) unlogged forest patches adjacent to selected logged coupes were also demarcated. Twelve 0.1 ha (50m × 20m) plots were randomly located within each logged coupe and unlogged forest patch (a total of 144 plots). While the logging coupes and unlogged forest patches came from all over the island, it is unlikely that topography or weather patterns were different between sites, since both features are fairly homogenous across the island (Katovai et al. 2012).

6.2.3 Data collection

6.2.3.1 Light measurement

Light intensity (lux) was measured using digital LI-COR® LI-250A light meters (LI-COR Inc., Lincoln, Nebraska, USA). Light readings were collected at two meters above ground level in 10 randomly selected points across each plot. These readings were averaged and divided by ambient light intensity to determine the relative light intensity (RLI). Both understory and ambient light were measured simultaneously for accurate relative comparisons.

6.2.3.2 Plant function survey

Floristic surveys were conducted using integrative methods based on the Modified-Whittaker nested vegetation sampling method (e.g. Stohlgren et al. 1995; Mayfield et al. 2005; Katovai et al. 2012). Easily-measured PTEs were assigned to three PFTs—growth form, chlorotype, and leaf-area class—and used as proxies for functional diversity (see Table 6.1). These PTEs were selected based on their potential use in dynamic vegetation description and analysis (Gillison and Carpenter 1997; Weiher et al., 1999).

Within each plot, sixteen 1 × 1 m sampling units were randomly selected. In these sampling units, we recorded the occurrence of PTEs within each PFT of understory plants (except for mosses) that were < 2 m in height at the time of survey (Gillison and Carpenter 1997; Weiher et al., 1999). Binary classification was used to quantify the occurrence of PTEs, with 1 or 0 used to specify presence or absence, respectively. To determine the proportion of occurrence of each PTE, we counted the number of sampling units in which the PTE was present and divided it by 16. We then used the proportion of occurrence indices as our proxy for functional diversity.

Table 6.1. Plant functional types examined in this study and their corresponding plant-trait elements.

Plant Functional Type (PFT)	Plant Trait Elements (PTE)
Growth Form	Epiphyte (ep)
Specific growth structures.	Fern (fe)
	Herb (he)
	Liana (li)
	Non-woody climber (nc)
	Palm (pa)
	Seedling (se)
	Shrub (sh)
	Treelet (tr)
Chlorotype	Dorsoventral (do) – Chlorophyll mainly on the upper side of a flat leaf.
	Isobilateral (is) – Chlorophyll equally distributed on both sides of the leaf.
The distribution of chlorophyll tissue.	Deciduous (de) – Plants that lose all their leaves either completely or almost completely at one or more times per year.
	Cortic (co) – Chlorophyll is contained in the cortex.
	Achlorophyllous (ac) – Without chlorophyll.
Leaf-area classes	No repeating leaf units (nr)
Leaf sizes based on ventral area.	Picophyll <2 mm^2 (pi)
	Leptophyll 2-25 mm^2 (le)
	Nanophyll 25-225 mm^2 (na)
	Microphyll 225-2025 mm^2 (mi)
	Notophyll 2025-4500 mm^2 (no)
	Mesophyll 4500-18200 mm^2 (me)
	Platyphyll 18200-36400 mm^2 (pl)
	Macrophyll 36400-18x 104 mm^2 (ma)
	Megaphyll >18x 104 mm^2 (mega)

6.2.4 Statistical analysis

6.2.4.1 Comparing light levels and plant-trait element occurrence

We examined changes in RLI and each PTE amongst forest classes using mixed modelling. Since plots were nested within coupes within forest classes, we generated analyses of variance (ANOVA) using the mixed model function in the lme4 package in R to examine the difference in means between RLI and each PTEs (Bates 2015). We then used Satterthwaite’s approximation to calculate degrees of freedom in the mixed models (with ‘coupe’ as a random effect and time as a fixed effect) using the lmeTest package in R (Kuznetsova et al. 2015). Finally, the multcomp package in R was used to generate post-hoc tests on models that revealed significant difference in the response mean between forest classes.

6.2.4.2 Determining the influence of light on functional occurrence

We used generalised linear mixed models (GLMMs) with a binomial link function and coupe as a random effect to explore the relationship between functional diversity and light attenuation and recovery time. Prior to modelling, we checked for potential correlations in our predictor variables by plotting pairs of variables, calculating correlation coefficients for every pair of the predictor variables, and by examining variance inflation factors (VIF) in the package *usdm* in R (Naimi 2013). Global models were built with growth form, chlorotype, and leaf-area class each as a function of PTE, time since logging, and RLI.

We expected the occurrence of individual growth forms to vary across each predictor variable. Seedlings, treelets, lianas, shrubs, and epiphytes are highly likely to occur in recently logged and high-light environments, making these growth forms likely to decrease with time since logging (Hazlett et al. 2007; Santiago et al. 2012; Hartmann et al. 2014); the opposite pattern was expected for palm, fern, herb, and non-woody climber forms (Yamamoto 2000; Chazdon 2003; Chazdon et al. 2007). For chlorotype and leaf-area class, we expected to find a high occurrence of relatively small-leafed dorsiventral and isobilateral plant forms in recently logged forests. We anticipated a gradual increase in chlorotype and leaf-area class diversity with increasing time since logging, as time since logging changes the understory light availability as the forest canopy recovers (Gillison and Carpenter 1997; Wright et al. 2004; Xu et al. 2009; Donovan et al. 2011). Finally, we included the interaction of all predictors in the models with time since logging.

The dredge function in the R package *MuMIn* was used to create a candidate model set containing possible simpler subsets of each global model (Barton 2013). We selected models for inference based on a small sample-size corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002; Mazerolle 2014). Using AICc trade off model complexity for model fit, identifying the best simplest model(s) for which ΔAICc <7 (Burnham and Anderson 2002; Mazerolle 2014). We then averaged the parameters from these models based on model weight (Burnham and Anderson 2002). Averaged parameter estimates were used for interpretations based on effect sizes and on whether their 95% confidence intervals overlapped zero. Finally, to visualise the effect sizes and confidence intervals, we used the predictSE function in R package *MuMIn* to generate predicted values from the average models. All statistical analyses were executed using R (R Core Team 2014).

6.3 RESULTS

6.3.1 Light levels and plant-trait element occurrence across forest sites

6.3.1.1 Light levels at different stages of forest recovery

Mean RLI differed significantly between the forest classes ($F_{3,140} = 141$, $p < 0.0001$) with the Tukey's post-hoc test revealing three homogenous groups: 10 years since logging, 30 & 50 years since logging, and unlogged forests (Fig. 6.2). There was a large reduction in understory RLI between 10 years and older plots of 30 & 50 years since logging. The older logged forests had low RLI levels but were still significantly higher than unlogged forest.

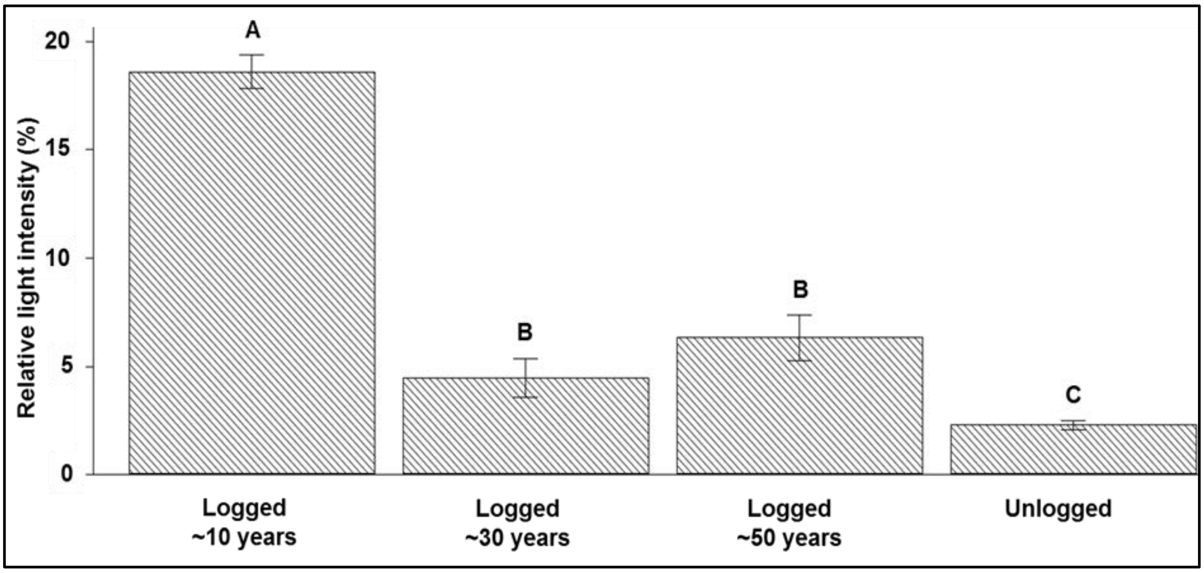


Figure 6.2. Mean relative light intensity across logged forest classes and unlogged forests in the Solomon Islands. Error bars represent ±1 standard error and letters A, B, and C indicate significant pairwise differences across forest classes using Tukey's honest significant difference (HSD) post hoc tests. Bars with the same letter above them do not differ significantly based on post-hoc tests.

6.3.1.2 Occurrence of plant-trait elements

Over 70% of all PTEs examined differed in occurrence between forest classes, with chlorotype PTEs varying the least (Table 6.3). For chlorotype PTEs, mean cortic occurrence significantly increased between 10 and 30 years post logging, 10 and 50 years post logging, and 50 years post logging and unlogged forests respectively ($F_{3, 143}$ = 9.9, p<0.0001). Mean cortic occurrence levels between 30 and 50 years post logging, 30 years post logging and unlogged forests and 10 years post logging and unlogged forests were relatively homogenous. In contrast, Isobilateral mean occurrence decreased between 10 and 30 years post logging to levels comparable to 50 years post logging and unlogged forests ($F_{3, 143}$ = 17.5, p< 0.0001). The mean occurrence for dorsiventral, deciduous, and achlorophyllous PTEs remained unchanged over the course of forest recovery, and was comparable to the associated means of unlogged forests (Table 6.2).

Mean occurrence for most growth form PTEs varied to some degree across forest recovery times, except for herbaceous forms and non-woody climbers (Table 6.2). Seedling and liana mean occurrence at 10 years post logging was significantly higher than in older logged forest classes, in which their mean levels were comparable. Mean occurrence of seedlings and lianas in unlogged forests was significantly lower than for all logged forest classes – seedling ($F_{3, 143}$ = 101, p < 0.0001) and liana ($F_{3, 143}$ = 51.1, p <0.0001). Mean palm occurrence significantly increased between 10 and 50 years post logging, even exceeding that of unlogged forests ($F_{3, 143}$ = 8.47, p <0.0001). Mean occurrence for ferns was significantly higher at 10 years post logging compared to 30 years post logging, 50 years post-logging, and unlogged forests ($F_{3,\,143}$ = 27.2, *p* <0.0001). Mean occurrence of epiphytes, non-woody climbers, and shrubs was relatively consistent across all forest classes.

Table 6.2. Results of one-way ANOVA for comparisons of mean functional diversity of plant-trait elements (PTEs) within their respective plant functional types (PFTs) for logged and unlogged forest classes in the Solomon Islands. *p*-values > 0.05 (bolded) indicate homogenous PTE mean functional diversity across forest classes. Superscript letters (A, B, C) represent Tukey's post-hoc groupings within each PTE across the forest classes.

PFT	PTE	*F*-stat	*P* value	10 yrs. post-logging	30yrs. Post-logging	50yrs. Post-logging	Unlogged forests
Chlorotype	Dorsiventral	2.57	**>0.05**	1.5708	1.5301	1.5560	1.570
	Isobilateral	17.5	<0.0001	0.2112^{B}	0.1667^{A}	0.1824^{A}	0.3221^{A}
	Decidious	1.25	**>0.05**	0.0235	0.3086	0.2834	0.2810
	Cortic	9.9	<0.0001	0.0522^{C}	$0.1156^{A,\,B}$	0.1581^{A}	$0.0823^{B,\,C}$
	Achlorophyllous	3.77	**>0.05**	Absent	0.00261	0.00261	0.0204
Growth form	Seedling	101	<0.0001	1.2875^{A}	0.5633^{B}	0.3962^{B}	0.2241^{C}
	Palm	8.47	<0.0001	$0.4969^{B,\,C}$	$0.6442^{A,\,B}$	0.6764^{A}	0.4425^{C}
	Treelet	4.46	**>0.05**	1.4800	1.2222	1.4843	1.2878
	Liana	55.1	<0.0001	0.8110^{A}	0.4985^{B}	0.6008^{B}	0.2565^{C}
	Fern	23.7	<0.0001	1.1070^{A}	0.4836^{B}	0.6844^{B}	0.5741^{B}
	Shrub	27.2	<0.0001	0.6641^{A}	0.3800^{C}	0.5289^{B}	0.3202^{C}
	Herbaceous	0.22	**>0.05**	0.4275	0.4588	0.4521	0.4411
	Epiphyte	3.06	<0.05	0.3108^{A}	$0.2663^{A,\,B}$	0.1807^{B}	$0.2300^{A,\,B}$
	Nonwoody climber	3.01	<0.05	$0.3108^{A,\,B}$	0.2663^{A}	0.1807^{B}	$0.2300^{A,\,B}$
Leaf area class	No repeating leaf	2.66	**>0.05**	0.1398	0.1632	0.2170	0.1415
	Picophyll	29.2	<0.0001	0.7372^{A}	0.3820^{B}	0.3816^{B}	0.2099^{C}
	Leptophyll	3.61	<0.05	0.3985^{A}	$0.312^{A,\,B}$	$0.3227^{A,\,B}$	0.2663^{B}
	Nanaphyll	2.15	**>0.05**	0.4205	0.6161	0.4560	0.4808
	Microphyll	4.07	<0.001	0.4541^{B}	0.7711^{A}	$0.5516^{A,\,B}$	$0.6530^{A,\,B}$
	Notophyll	1.93	**>0.05**	0.8671	0.9430	0.7356	0.8405
	Mesophyll	10.7	<0.001	0.4026^{B}	0.6923^{A}	0.3739^{B}	0.4137^{B}
	Platophyll	11.9	<0.001	0.3539^{B}	0.5918^{A}	0.2459^{B}	0.3200^{B}
	Macrophyll	3.42	<0.05	$0.1261^{A,\,B}$	0.2235^{A}	0.0992^{B}	$0.1790^{A,\,B}$
	Megaphyll	3	<0.05	0.00786^{B}	0.0867^{A}	0.00783^{B}	0.0592^{A}

Mean occurrence for leaf area classes, no repeating leaf units, nanophyll, and notophyll was similar across all four forest classes. Picophyll and leptophyll mean occurrence declined significantly as recovery time increased *(*$F_{3,\,143}$ = 29.2, *p*

<0.0001, $F_{3, 143} = 3.61$, $p < 0.005$), with picophyll exhibiting a more pronounced decline. Mean occurrence of microphyll, mesophyll, and platophyll increased significantly between 10 and 30 years post logging ($F_{3, 143} = 4.07$, $p < 0.001$, $F_{3, 143} = 10.7$, $p < 0.001$, $F_{3, 143} = 11.9$, $p < 0.001$), but declined between 30 and 50 years post logging; the mean occurrence of these three PTEs were comparable to unlogged forests at 50 years post logging (Table 6.2).

6.3.2 Influence of understory light on the occurrence of plant-trait elements of plant functions

Relative light intensity and time were not collinear (VIF of RLI for growth form = 1.31, chlorotype = 2.29, and leaf-area class = 2.29), with all three global models showing homoscedasticity. The averaged model for each PFT fit the data well, with Pearson's R between observed and model-fitted values for the growth-form averaged model (0.79), chlorotype averaged model (0.95), and leaf-size class averaged model (0.90). Plant-trait element, time, RLI and time: PTE and time: RLI interactions were important predictors in each average model (Table 6.3).

Table 6.3. The influence of light on plant-trait elements (PTEs) in each plant functional type (PFT) across forest classes on Kolombangara, Solomon Islands.

		The influence of light		
Plant funtional type	**Plant trait element**	**Slope**	**95%Confidence interval**	
Chlorotype				
10 yrs post-logging	Achlorophyllous (ac)	-	-	-
	Cortic (co)	21.39	—2.12E+04	2.13E+04
	Deciduous (de)	23.75	—2.12E+04	2.13E+04
	Dorsoventral (do)	48.85	—3.01E+04	3.02E+04
	Isobilateral (is)	19.55	—2.12E+04	2.13E+04
30 yrs post-logging	Achlorophyllous (ac)	-	-	-
	Cortic (co)	0.99	—3.07E+04	3.07E+04
	Deciduous (de)	—0.22	—3.07E+04	3.07E+04
	Dorsoventral (do)	—20.9	—3.74E+04	3.73E+04
	Isobilateral (is)	4.2	—3.07E+04	3.07E+04
50 yrs post-logging	Achlorophyllous (ac)	-	-	-
	Cortic (co)	1.54	—3.04E+04	3.01E+04
	Deciduous (de)	—0.06	—3.04E+04	3.01E+04
	Dorsoventral (do)	0.07	—4.30E+04	4.30E+04
	Isobilateral (is)	4.06	—3.04E+04	3.04E+04
Growth form				
10 yrs post-logging	Epiphyte (ep)	-	-	-
	Fern (fe)	3.41	2.72	4.11
	Herb (he)	1.02	0.45	1.59
	Liana (li)	2.01	1.44	2.59
	Non-woody climber (nc)	1.24	0.68	1.82
	Palm (pa)	1.27	0.71	1.85
	Seedling (se)	2.79	2.17	3.41
	Shrub (sh)	1.09	0.51	1.66
	Treelet (tr)	4.48	3.54	5.42
30 yrs post-logging	Epiphyte (ep)	-	-	-
	Fern (fe)	—3.55	—4.42	—2.68
	Herb (he)	—0.49	—2.26	0.27
	Liana (li)	—0.49	—2.45	—0.9
	Non-woody climber (nc)	—0.44	—0.35	1.22
	Palm (pa)	—0.11	—0.88	0.66
	Seedling (se)	—0.98	—1.81	—0.15
	Shrub (sh)	—1.91	—2.7	—1.1
	Treelet (tr)	—3.17	—4.24	—2.69
50 yrs post-logging	Epiphyte (ep)	-	-	-
	Fern (fe)	—1.6	—2.52	—0.67
	Herb (he)	0.48	—0.36	1.31
	Liana (li)	0.49	—0.36	1.34
	Non-woody climber (nc)	1.08	0.24	1.29
	Palm (pa)	0.32	—0.52	1.15
	Seedling (se)	—0.84	—1.72	0.03
	Shrub (sh)	0.48	—0.36	1.32
	Treelet (tr)	0.32	—0.85	1.94
Leaf area class				
10 yrs post-logging	No repeating leaf units (nr)	—1.86	—2.58	—1.13
	Picophyll <2 mm^2 (pi)	1.53	0.99	2.07
	Leptophyll 2-25 mm^2(le)	-	-	-
	Nanophyll 25-225 mm^2 (na)	0.1	—0.41	0.62
	Microphyll 225-2025 mm^2 (mi)	0.24	—0.27	0.75
	Notophyll 2025-4500 mm^2 (no)	1.53	0.99	2.07
	Mesophyll 4500-18200 mm^2 (me)	0.63	0.12	1.14
	Platyphyll 18200-36400 mm^2 (pl)	0.4	—0.11	0.91
	Macrophyll 36400-18x 10^4 mm^2 (ma)	—1.23	—1.84	—0.61
	Megaphyll >18x 104 mm^2 (mega)	—18.97	—272.51	234.57
30 yrs post-logging	No repeating leaf units (nr)	1.32	0.37	2.26
	Picophyll <2 mm2 (pi)	—2.24	—3.06	—1.42
	Leptophyll 2-25 mm2 (le)	-	-	-
	Nanophyll 25-225 mm2 (na)	1.52	0.78	2.27
	Microphyll 225-2025 mm2 (mi)	2.12	1.34	2.91
	Notophyll 2025-4500 mm2 (no)	1.15	0.33	1.98
	Mesophyll 4500-18200 mm2 (me)	1.5	0.74	2.27
	Platyphyll 18200-36400 mm2 (pl)	1.41	0.66	2.16
	Macrophyll 36400-18x 104 mm2 (ma)	1.77	0.95	2.59
	Megaphyll >18x 104 mm2 (mega)	18.48	—235.06	272.02
50 yrs post-logging	No repeating leaf units (nr)	1.23	0.25	2.2
	Picophyll <2 mm2 (pi)	—1.32	—2.11	—0.54
	Leptophyll 2-25 mm2 (le)	-	-	-
	Nanophyll 25-225 mm2 (na)	0.48	—0.28	1.23
	Microphyll 225-2025 mm2 (mi)	0.8	0.06	1.55
	Notophyll 2025-4500 mm2 (no)	0.22	—0.55	0.99
	Mesophyll 4500-18200 mm2 (me)	0.38	—0.37	1.13
	Platyphyll 18200-36400 mm2 (pl)	0.04	—0.72	0.79
	Macrophyll 36400-18x 104 mm2 (ma)	0.67	—0.22	1.55
	Megaphyll >18x 104 mm2 (mega)	16.41	—237.13	269.96

6.3.2.1 Chlorotype

The influence of light on each chlorotype PTE across logged forest classes was generally trivial (Table 6.3). The probability of occurrence of each PTE was relatively homogenous across time since logging; the only exception was isobilateral leaves, which had a very low occurrence 10 years post logging as compared to 30 and 50 years post logging. Dorsiventral leaves occurred most frequently, followed by isobilateral, deciduous, and cortic leaves, all of which exhibited similar levels of occurrence across all post-logging forest classes. Achlorophyllous plants were rare across all logged forests (Fig. 6.3).

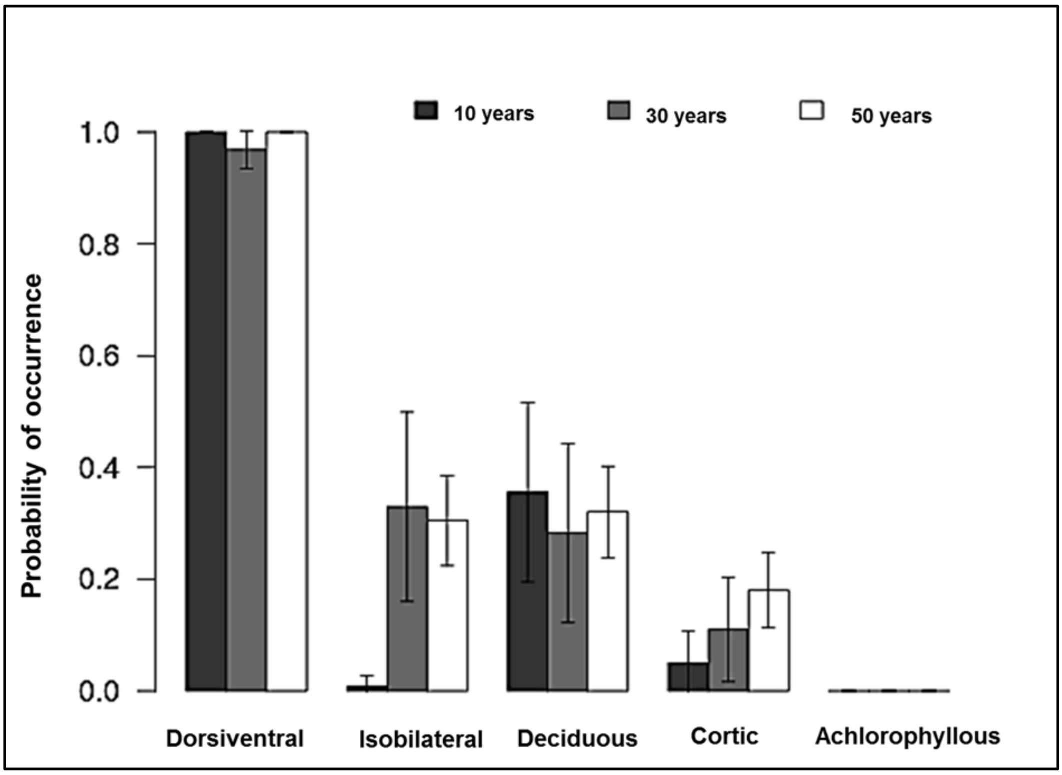


Figure 6.3. The probability of occurrence of each chlorotype plant-trait element (PTE) across the logged forest classes. The bar plots represent predicted fit values from the generalized linear mixed-effects models (GLMMs), and error bars represent the 95%

confidence interval associated with the modelled predictions. None of the chlorotype PTEs was influenced by light across the post-logging recovery gradient.

6.3.2.2 Growth form

The effects of understory light on the probability of occurrence of growth forms varied with time since logging (Table 6.3, Fig. 6.4). At 10 years post logging, understory light had a positive effect on the occurrence on fern (slope = 3.42; 95% CI = 2.72), herb (slope = 1.02; 95% CI = 0.45, 1.59), liana (slope = 2.01; 95% CI = 1.44, 2.59), non-woody climber (slope = 1.25; 95% CI = 0.68, 1.82), palm (slope = 1.28; 95% CI =0.71, 1.85), seedling (slope = 2.79; 95% CI = 2.12, 3.41), shrub (slope = 1.09; 95% CI = 0.51, 1.66) and treelet (slope = 4.48; 95% CI = 3.54, 5.42). Epiphytes were not influenced by light in this forest class.

At 30 years post logging, the influence of understory light was mostly negative across the PTEs – fern (slope = –3.58; 95% CI = –4.43, –2.69), liana (slope = –1.68; 95% CI = –2.45, –0.91), seedling (slope = –0.98; 95% CI = –1.81, –0.15), shrub (slope = –1.92; 95% CI = –2.73, –1.10) and treelet (slope = –3.17; 95% CI = –4.25, –2.10). Epiphyte, non-woody climber and palm were not influenced by light in this forest class.

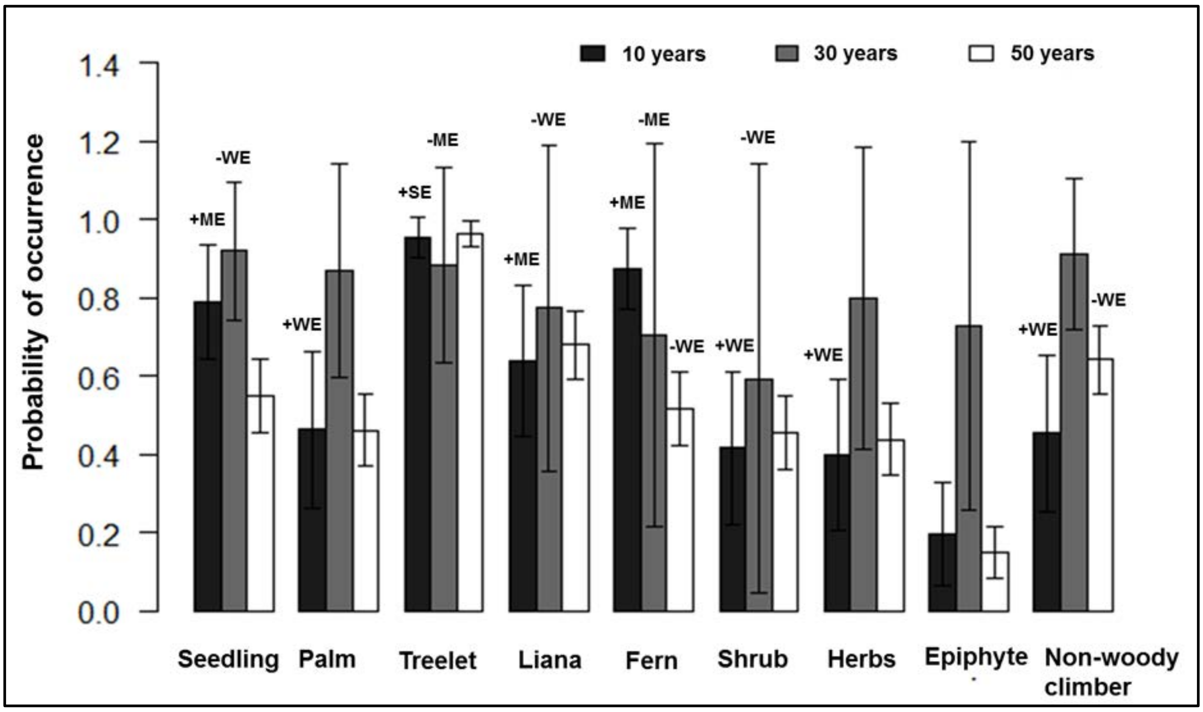


Figure 6.4. The probability of occurrence of each growth form PTE across the logged forest classes. The bar plots represent predicted fit values from the GLMM, and error bars represent the 95% confidence interval associated with the modelled predictions. Light had a varied effect on growth form PTEs across the post-logging recovery gradient. The effect of light is given at the top of each bar. These effects were coded as follows: +SE = strong positive effect, +ME = moderate positive effect, +WE = weak positive effect, -WE = weak negative effect and -ME = moderate negative effect. The absence of a code signifies a trivial effect.

The influence of understory light on growth form PTEs was generally weak at 50 years post logging compare to 10 and 30 years (Fig. 6.4). Only fern and non-woody climber forms were negatively influenced by light (slope = –1.60; 95% CI = –2.51, –0.67; slope = –1.08; 95% CI = 0.24, 1.92, respectively).

6.3.2.3 Leaf-area class

The influence of light on leaf-area class PTEs was generally weak across all time classes (Table 6.3, Fig. 6.5). At 10 years post logging, only ‘no repeating leaf units’ was influenced by light, and negatively so (slope = –1.86; 95% CI = –2.58, –1.13). The influence of light on other PTEs was weak in this forest class. At 30 years post logging understory light had a weak positive influence on the occurrence of ‘no repeating leaf units’ (slope = 1.32; 95% CI = 0.38, 2.26), as well as on the nanophyll (slope = 1.52; 95% CI = 0.78, 2.27), microphyll (slope = 2.12; 95% CI = 1.34, 2.91) , notophyll (slope = 1.15; 95% CI = 0.333, 1.98), mesophyll (slope = 1.50; 95% CI = 0.74, 2.27), platyphyll (slope = 1.41; 95% CI = 0.66, 2.16), and macrophyll (slope = 1.77; 95% CI = 0.96, 2.59) classes. The influence of light on picophyll was weakly negative (slope = 18.48; 95% CI = –3.06, –1.42). At 50 years post logging, only the no repeating leaf units, picophyll, and microphyll classes were influenced at all by understory light (slope = 1.23; 95% CI = 0.25, 2.20; slope = 0.8; 95% CI = 0.05, 1.55; slope = –1.32; 95% CI = –2.11, –0.54, respectively).

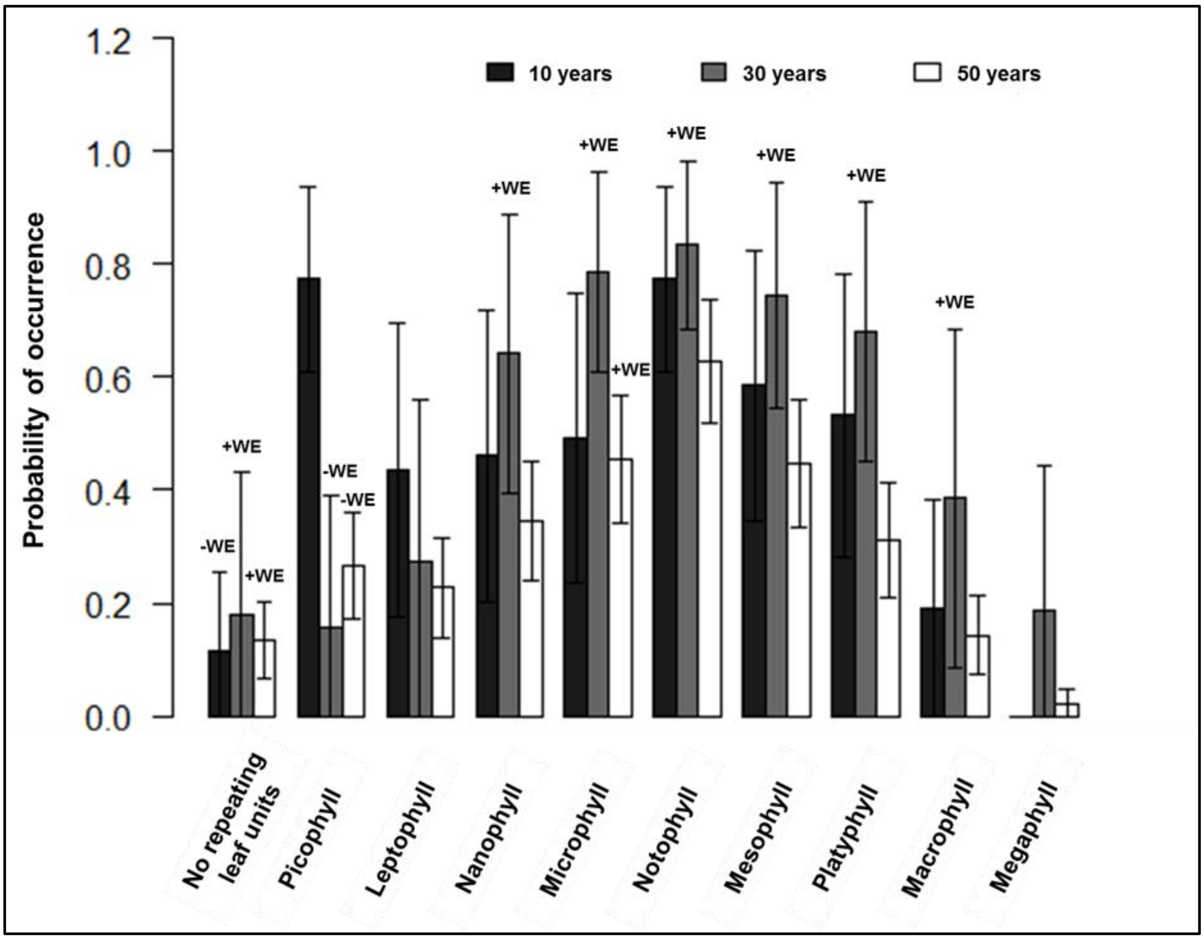


Figure 6.5. The probability of occurrence of each leaf-area class PTE across the logged forest classes. The bar plots represent predicted fit values from the GLMM, and the error bars represent the 95% confidence interval associated with the modelled predictions. Light had a varied effect on leaf-area class PTEs across the post-logging recovery gradient. Above each bar plot, the corresponding light effect is given: +WE = weak positive effect and –WE = weak negative effect. The absence of a code signifies a trivial effect.

There was a general increase in the mean probability that all leaf-area class PTEs would occur between 10 and 30 years after logging; followed by a decrease for all leaf-area class PTEs between 30 and 50 years post logging, except for picophyll and leptophyll (Fig. 6.5). The probability that picophyll would occur was considerably higher at 10 years post logging compared to 30 and 50 years post logging. The probability that leptophyll would occur, however, decreased with time since logging. Notophyll had the highest mean probability of occurrence as predicted by time and RLI, and the probability of megaphyll at 10 years post logging was extremely low.

6.3.3 Functional diversity across forest recovery

Mean functional diversity of each PFT significantly differed between logged and unlogged forest classes: growth form ($F_{3,\ 140} = 89.1$, $p < 0.0001$), chlorotype (F3, 140 = 10.6, p < 0.0001), and leaf-area class ($F_{3,\ 140} = 6.8$, $p = 0.003$). Tukey's tests, however, showed different groupings of forest classes associated with each PFT (Fig 6.6). Mean chlorotype diversity at 10 years post logging was significantly lower than at 30 years post logging, at 50 years post-logging, and for unlogged forest. Mean growth form diversity fell into three homogenous groups: 10 years post logging had the highest mean functional diversity, followed by 30 and 50 years post logging (as a single group), and unlogged forests. Two homogenous groups emerged for leaf-area class diversity, with forests that were 10 and 30 years post logging exhibiting higher functional diversities than 50 years post logging and unlogged forests.

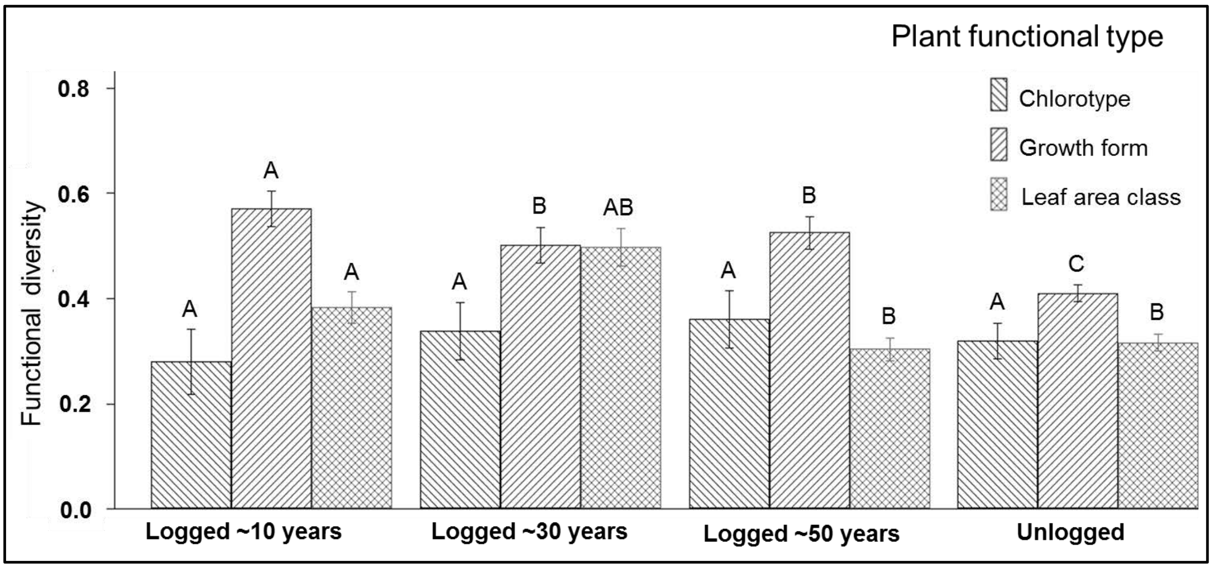


Figure 6.6. Functional diversity of each plant functional type across logged and unlogged forest classes. Error bars represent ±1 standard error and letters above bars denote significant pairwise differences across forest classes using Tukey's HSD post hoc tests. Bars with the same letter and subscript above them do not differ significantly based on post hoc tests.

6.4 DISCUSSION

6.4.1 Light levels at different stages of post-logging recovery and unlogged forests

This study demonstrated that logging significantly altered understory light regimes across the forests of Kolombangara. As expected, understory light intensity was highest in recently logged forests and decreased significantly within 30 years of post-logging regeneration (Fig 6.6). This pattern is due to the establishment and growth of light-demanding trees, which fuels forest architectural complexity, eventually closing off the canopy gaps created by logging (Rozendaal et al. 2006; Batista et al. 2014). Although understory light levels at 30 and 50 years post logging did not differ statistically the latter had a slightly higher mean. Such light re-intensification suggest that understory light dynamics 50 years after logging are regulated by new forest gaps possibly due to the senescence of pioneer species (e.g. Yamamoto 2000; Katovai and Katovai 2012).

The extremely low understory light levels of unlogged forests indicate that logged forests on Kolombangara are still recovering after 50 years of natural regeneration and have yet to reach the level of canopy closure of typical unlogged forests. Achieving pre-cut levels of architectural complexity in human-disturbed forests can be very slow, particularly in intensively logged forests such as those on Kolombangara (Burslem et al. 2000; Katovai et al. 2012). The fact that there were only slight variations in light levels within unlogged forests on Kolombangara may suggest that the dynamics of natural disturbance across the island are relatively homogenous, as proposed in previous studies (Bayliss-Smith et al 2003; Katovai et al. 2012). The fact that cyclones have only had a trivial impact on forest recovery on Kolombangara over the past five decades (Burslem et al. 2000) has been another likely reason that the patches of undisturbed forests on the island remain intact.

6.4.2 Plant functional occurrences over the course of forest recovery

The influence of light on different PTEs varied in this study. Growth form and leaf-area class, in particular, were highly influenced (Figs 6.3–6.5). The distribution of chlorophyll in plant communities across stages of post-logging recovery was relatively consistent. The diversity of growth forms appeared to peak at 30 years post logging and then decreased thereafter, whereas leaf size tended to shift from small to large classes during forest recovery.

6.4.2.1 Chlorotype

The results indicated that chlorotype diversity was not influenced by light over the course of post-logging regeneration, although light has previously been strongly linked to plant growth and development (Offord et al. 2014). Despite an attenuation of understorey light levels over 50 years of post-logging forest structural recovery (Fig. 6.2), it is possible that the intensity of light at shorter wavelengths was still elevated relative to unlogged forests, which might account for the observed trends in the distribution of chlorotype diversity. The low chlorotype diversity suggests that chlorotype plasticity was limited across successional stages in logged forests on Kolombangara. Related studies have suggested that chlorotype plasticity is an evolution-driven process triggered by genetic variability, causing hybridization and phenotypic changes over several generations (Adler et al. 2014; Lamy et al. 2014). Although our results would not allow us to make such a comparison, they indicate that mean chlorotype plasticity across plant life history in understory communities in wet tropical forests is trivial. In that case, chlorotype diversity over 50 years of post-logging regeneration in the present study may have been driven by other factors, such seed availability, favourable habitat, and environmental conditions affecting seed germination and the course of ontogenic development (Katovai et al. 2012; Adler et al. 2014; Katovai et al. 2015b).

6.4.2.2 Growth form

The strong influence of light on treelets at 10 years since logging may have resulted from the high proliferation of light-demanding pioneers. Light-demanding pioneers either occupy the soil seed bank prior to logging, or are introduced through the post-logging influx of seeds via dispersal mechanisms (Tiansawat et al. 2014). A recent study on Kolomabangara reported that anemochory (the dispersal of diaspores by wind), hydrochory (the dispersal of diaspores by water), and zoochory (the dispersal of diaspores by animals, particularly birds and insects) are highly effective on the island (e.g. Katovai et al. 2012). The high occurrence of pioneer treelets in the present study may have also functioned as an ecological filter that determined the establishment and occurrence levels of other growth forms (Gadolfi et al. 2007). For example, the influence of understory light on seedlings, lianas, and ferns may have declined due to light attenuation prompted by forest restructuring and overshading by small to intermediate-sized trees (Lochhead and Comeau 2012). Nonetheless, the relatively high occurrence of seedlings was probably due to progressive mixing between early light-demanding pioneers and newly established shade-tolerant mid-succession species (Katovai et al. 2015b). The high occurrence of tree ferns (*Cyanthea spp.*) in the 10 years since logging may have also attributed to further light attenuation in this forest class (E. Katovai, personal observation). The influence of light on the occurrence of seedling, fern, liana, and treelet growth forms 10 years since logging evidently helps to explain why early successional plant communities in logged forests were dominated by the aforementioned forms.

The negative effect of understory light on growth forms in older logged sites (>30 years post-logging) suggests a species compositional shift from light- to shade-tolerant species (Katovai et al. 2015b). This change is most evident in trees, ferns, and seedlings, as the species of these forms respond divergently to relatively high and low light conditions, and therefore can easily be categorised into light-tolerant and shade-tolerant groups (Whitmore 1989a). For instance, in the present study, understory treelets in these forest classes were mainly shade-tolerant species such as *Callophylum spp., Dillenia spp., and Terminalia spp.* (Katovai et al. 2012). The weak negative influence of light on lianas, shrubs, ferns, and non-woody climbers at >30 years after logging may suggest weak compositional shifts between light- and shade-tolerant species within these four growth forms.

Although species in these growth forms possess specific light requirements for growth and maturity, their occurrence and persistence may be controlled by other bottom up and top down processes. For instance, it has been widely maintained that water availability has a superior influence on epiphytic ontogeny than light or even nutrient availability (Zotz and Hietz 2001; Lobel and Rydin 2010). Epiphytes generally proliferate when secondary forests reach maturity (Laube and Zotz 2006), and epiphytic establishment per se is generally stimulated by enhanced habitat diversity, greater tree surface area for colonisation and seed interception, and temporal accumulation of organic soil and moisture on host trees, which facilitates epiphytic ontogeny (Zotz and Vollrath 2003; Laube and Zotz 2006; Wagner and Zots 2015). Therefore, the relatively high occurrence of epiphytes at 30 years after logging indicate that the Kolombangara forest has attained some level of maturity; accordingly, the later deaths of many long-lived pioneer hosts may explain the decrease in epiphyte occurrence at 50 years since logging.

6.4.2.3 Leaf-area class

A number of studies have confirmed that leaf-area plasticity is generally low for short-lived pioneers when exposed to high light conditions, for the reason that energy requirements are met through the optimisation of photosynthesis (Popma et al. 1992; Rozendaal et al. 2006; Markestijn et al. 2007; Souza et al. 2010). Under such conditions, short-lived pioneers invest highly in seed production to ensure the proliferation and trans-generation survival of the species (Markestijn et al. 2007). The trivial influence of light on leaf-area classes at 10 years post logging may therefore indicate low plasticity across understory plant communities, as short-lived pioneer species are common in these forests (Katovai et al. 2012). In contrast, under relatively low light conditions, understory plant communities will resort to leaf-area plasticity, as indicated by the widespread positive influence of light at 30 years post logging. Such a strategy allows plants to sustain essential energy, mostly for growth and maintenance (Osunkura et al. 1994; Markestijn et al. 2007).

Apart from being highly prolific, short-lived pioneers may persist unusually longer, forming dense understory vegetation under prime light conditions (Kammesheidt et al. 2000; Markestijn et al. 2007). Short-lived pioneers can also tolerate large variations in light levels after reaching maturity, and can therefore tolerate declines in light levels resulting from canopy closure (Rozendaal et al. 2006). In the present study, the overall increase in occurrence across leaf-area classes between 10 and 30 years post logging may have been due to the high proliferation and persistence of short-lived pioneers, along with a gradual increase in shade-tolerant species. The transition from the dense understory vegetation of pioneers to the comparatively lighter distributions of climax species may have occurred thereafter, resulting in the decline in occurrences across leaf area classes at 50 years post logging (Moreira et al. 2014). The trivial influence of light across these forests may suggest that post-logging succession in understory plant communities has climaxed before 50 years

6.4.3 Functional diversity

Functional diversity of understory plant communities was generally similar between logged and unlogged forest classes (Table 6.2 and Fig. 6.6). This finding suggests that with respect to the plant functional traits examined here that functional diversity in the logged forests of Kolombangara can be restored to pre-cut levels entirely through natural regeneration. The return of chlorotype and leaf-area class diversity to pre-cut levels within 50 years of post-logging recovery may have been prompted by compositional alteration of species across forest successional stages (see Table 6.2), as reported in Katovai et al. (2012 and 2015b). This explanation supports the assertion that some mid-to-late succession species utilise morphological PTEs to increase light capture under low light levels (Valladares and Niinemets 2008; Sakschewski et al. 2016). It appears that these species take over from light-demanding species, colonising the understory in the later stages of succession (Whitmore 1989a; Fortunel et al. 2014). The resilience of PFTs observed in the present study—despite the species loss and compositional alterations—may indicate that logged forests (as is the case for other forested land-use types) have reduced functional redundancy (Laliberté et al., 2010; Mayfield et al., 2010; Katovai et al. 2012).

6.5 CONCLUSIONS

The results of this study present information on the understory light conditions and their influence on the functional diversity in the logged forests of Kolombangara, Solomon Islands. Light attenuation across recovery time in logged forests was highly statistically significant. However, relatively lower light levels in unlogged forests may suggest that 50 years is an inadequate length of time for forests to make a structural recovery to pre-cut levels. Understory light can be used as a proxy to examine how disturbances associated with logging influence post-logging structural recovery across understory communities.

The highly varied associations between the influence of light and the occurrence of each PTE across recovery times may suggest that the studied PTEs are closely linked to a range of environmental response strategies (Mayfield et al. 2013; Sakschewski et al. 2016). Our results revealed that, while the effect of light on understory plant communities is better evaluated at the PFT level, only growth form and leaf-area class were potential indicators of the effect of light on the post-logging recovery of understory plant communities.

Finally, functional diversity can fully recover to pre-cut levels if logged forests are given ample time to regenerate. This may suggest that functional diversity is more resilient than species diversity in logged tropical forests.

6.6 CHAPTER SUMMARY

- Disturbance caused by logging has been an important factor in changing vegetation patterns whereby plant development and restructuring are often left to natural regeneration processes, facilitated by both biotic and abiotic factors.
- We used plant functional types (PFTs) to predict post-logging understory plant community development as they show strong links with disturbance history and capture interspecific variation in strategies that drive plant performance. We determined the response of the plant-trait elements (PTEs) of selected PFTs to changing light levels across post-logging recovery times of 10, 30 and 50 years in the Solomon Islands.
- Our results indicated that understory light in logged forests declined significantly across 50 years of recovery, but did not returned to pre-cut levels. Our results also revealed that PTEs of selected PFTs responded similarly to light within different stages of regeneration. However, these responses varied among different stages for recovery.
- Highly varied associations between the influence of light and the occurrence of each PTE across recovery times suggest that the studied PTEs are closely linked to a range of environmental response strategies. While the effect of light on understory plant communities is better evaluated at the PFT level, only growth form and leaf-area class were potential indicators of the effect of light on the post-logging recovery of understory plant communities.
- Finally, we show that functional diversity can fully recover to pre-cut levels if logged forests are given ample time to regenerate, signifying the high resilience of functional diversity in human-altered landscapes.

Light is an important factor in forest recovery after disturbance.

Photograph by Eric Katovai 2013

CHAPTER 7

FACTORS AFFECTING TEMPORAL CHANGES OF TREE BIOMASS, WOOD DENSITY AND SPECIFIC LEAF AREA ACROSS LOGGED FORESTS IN THE SOLOMON ISLANDS

Eric Katovai, Will Edwards, William F. Laurance

This manuscript is being prepared for submission to *Forest Ecology and Management*.

Chapter overview:

This chapter presents data on wood and leaf traits in logged forests at three different temporal stages of regeneration (i.e. 10, 30 and 50 years) on Kolombangara, Solomon Islands. Possible factors influencing these changes were also assessed using ecological modelling protocols.

Contribution to thesis:

This chapter attempts to address objective No.6, which is to determine factors influencing the recovery of wood and leaf traits across logged forests in the Solomon Islands.

7.1 INTRODUCTION

Much of the world’s tropical forests have been degraded by an array of economics-driven land-use activities, including industrial logging (Houghton 2012). Industrial logging typically results in the loss of biodiversity and ecosystem function and provisioning in tropical forests (Houghton 2012; Carreño-Rocabado et al. 2012; Arcilla et al. 2015). It also has adverse long-term effects on forest plant recovery processes (Lavorel and Garnier 2002; Katovai et al. 2016). In most tropical regions, logged forests are left to recover through natural regeneration (Katovai et al. 2015a). However, in the absence of clear policies to safeguard this process, logged forests are often highly vulnerable to further anthropogenic impacts (Laurance at al. 2012; Zimmerman and Kormos 2012; Katovai et al. 2015a). Inadequate policies on post-logging regeneration in the tropics mainly result from a lack of information on the dynamics of forest recovery. Although recent studies have shown that the recovery to pre-cut levels of several taxonomic and functional groups can occur entirely through natural post-logging regeneration (e.g., Berry et al. 2010; Katovai et al. 2012; Wilcove et al. 2013; Asase et al. 2014), the ecological dynamics of this process have rarely been investigated.

Any form of disturbance, whether natural or anthropogenic, can alter the environmental state of forests (Sheil 2016). The forest recovery that subsequently follows is an environment-dependent mechanism in which ecosystem processes and functions respond to a combination of environmental conditions through space and time (Carreño-Rocabado et al. 2012; Dwyer et al. 2014; Xiao et al. 2015). Many physical factors (including topographical and meteorological conditions) and biological factors (including seed availability, residual vegetation, and animal dispersers and pollinators) have been shown to independently influence the process of floristic recovery (Schnitzer et al. 2000; Yamamoto 2000; Schliemann and Bockheim 2011; Lavorel 2013; Allan et al. 2015; Katovai et al. 2015a). Several studies have also shown that environmental influences trigger changes in plant traits due to changes in plant community composition or phenotypic changes within species, both of which influence ecosystem function (Lavorel 2013; Budiharta et al. 2014). Although very informative, recent work has mainly focused on plant traits in grasslands (Lavorel 2013), and comparable studies of other ecosystems remain scarce.

Because taxonomic information alone is insufficient, forest ecologists have increasingly explored the impacts of land-use changes on forest recovery using both taxonomic and functional identities (Mayfield et al. 2005). Numerous studies have investigated the use of functional diversity as a proxy for post-disturbance recovery in tropical forests (e.g., Mayfield et al. 2005, 2013; Katovai et al. 2012), and these have shown trends in the recovery of functional diversity in disturbed forests. However, such trends are usually more conspicuous than trends in the recovery of taxonomic diversity, because species within particular taxonomic groups tend to be functionally similar, and therefore respond similarly to environmental gradients across land-use types (Mayfield et al. 2010; Katovai et al. 2012; Brown et al. 2013). These findings suggest that taxonomic and functional diversity respond to the environmental alterations caused by land-use changes in broadly similar ways, and may be complementary when describing forest change.

Plant attributes that influence fitness and ecosystem function (plant traits) are increasingly used as proxies to investigate how human-modified forests respond to environmental change (Weiher et al. 1999; Baraloto et al. 2012; Carreño-Rocabado et al. 2012; Lu et al. 2015). Plant traits are well-defined plant properties that can be measured and compared at the species and community levels (Baraloto et al. 2012; Katovai et al. 2012; Brown et al. 2013). Plant trait patterns across environmental gradients can provide vital information on ecosystem provisioning, environmental stress, and ecological and physiological wellbeing, and can be used to predict important trends in forest recovery, allowing the development of better management strategies (Laliberté et al. 2010; Butterfield et al. 2013; Mayfield et al. 2013; Katovai et al. 2016). However, studies of human-modified forests have revealed that comparisons of plant traits across uniform land-use types are highly indicative of the dynamics driving trait changes, unlike comparisons across multiple land uses (Katovai et al. 2012; Butterfield et al. 2013; Mayfield et al. 2013). Furthermore, the selected traits must be closely linked to the disturbance regime of interest and its impact on environmental conditions.

Industrial logging abruptly alters the bio-ecological environment of tropical forests. The response of plant traits to environmental shifts as logged forests recover through natural regeneration can be quantified using a set of easily measured traits. Weiher et al. (1999) proposed a set of easily measured core traits that capture the structural, anatomical, and physiological variations in plant dispersal, development, and persistence in response to environmental pressures. For instance, biomass and wood density are core plant traits of the fecundity, growth, and mortality of large trees, whereas the specific leaf area has been shown to be an important trait in the performance of understory plants (Pearson et al. 2003; Poorter et al. 2006; Katovai et al. 2012; Woodal et al. 2015). These plant traits can potentially be used to investigate the recovery of plant communities from the impacts of logging. Changes in these traits during recovery may also indicate whether forest recovery to the pre-logged state entirely through natural regeneration is viable, or whether some form of human intervention is required (Katovai et al. 2015a).

Tropical oceanic islands in the Solomon Islands archipelago are ideal locations for such studies. Firstly, the environment and biology of each island is relatively homogeneous (Whitmore 1969; Katovai et al. 2012), and secondly, several islands in this group have a long history of logging, which has resulted in large areas of naturally regenerating forest. This study is among the first to use wood and leaf plant traits to quantify post-logging forest recovery in tropical Pacific islands. Tree biomass, wood density and specific leaf area (SLA) were the traits selected for this study, because they have been shown to vary markedly in response to human modification of forests, and are closely linked to ecosystem function and provisioning (e.g. Weiher et al. 1999; Brown et al. 2013; Dwyer et al. 2014; Katovai et al. 2015b). In this chapter, we assess the factors influencing the recovery of the aforementioned traits in logged forests in the Solomon Islands. We also determine whether 50 years was sufficient to allow these traits to recover to their pre-logging state.

7.2 METHODS

7.2.1 Site description

The study was conducted in lowland wet tropical forests on Kolombangara Island (157°E, 5°S), a volcanic island 32 km in diameter, situated in the western part of the Solomon Islands archipelago. The island has a cone-like near-perfect circular shape with a central volcanic crater, which is presumed to have erupted in the late Pleistocene era (Katovai et al. 2012). Kolombangara Island has the second highest peak among islands in the archipelago, with a crater rim reaching approximately 1700 m above sea level (a.s.l). The island's coastline area is relatively flat, but gradually steepens inland towards the base of the central volcanic cone. Although rainfall on Kolombangara Island is biannual, with wet seasons from November to March and July to August, the orographic condensation of moist air from the surrounding sea sustains regular rainfall, even during the dry season. As a result, the mean annual rainfall is relatively high, exceeding 3000 mm (Kolombangara Forest Products Limited, unpublished data). As a consequence of the island's topography, rainfall is presumably higher at the upper inland elevations than in the lowland coastal area (Burslem and Whitmore 1999; Katovai et al. 2012).

Kolombangara Island's old growth forests are biologically and structurally diverse, and contain high levels of endemic species (Whitmore 1966; Burslem and Whitmore 1999; Katovai et al. 2016). However, commercial logging and other land use activities that followed (i.e., commercial tree plantations and human settlements) have modified much of the island's lowland forests (Katovai et al. 2012). Land use activities are more extensive in the southeast, northeast, and northwest regions of Kolombangara than in the southwest. Large areas in the former regions were clear-felled and converted to commercial tree plantations in the early 1980s. Nonetheless, patches of natural forests, both logged and unlogged, are still present among these plantations. The southwest area is mostly covered by natural forests, mainly logged forests and, to a lesser extent, intertwining patches of unlogged forests (Fig. 7.1).

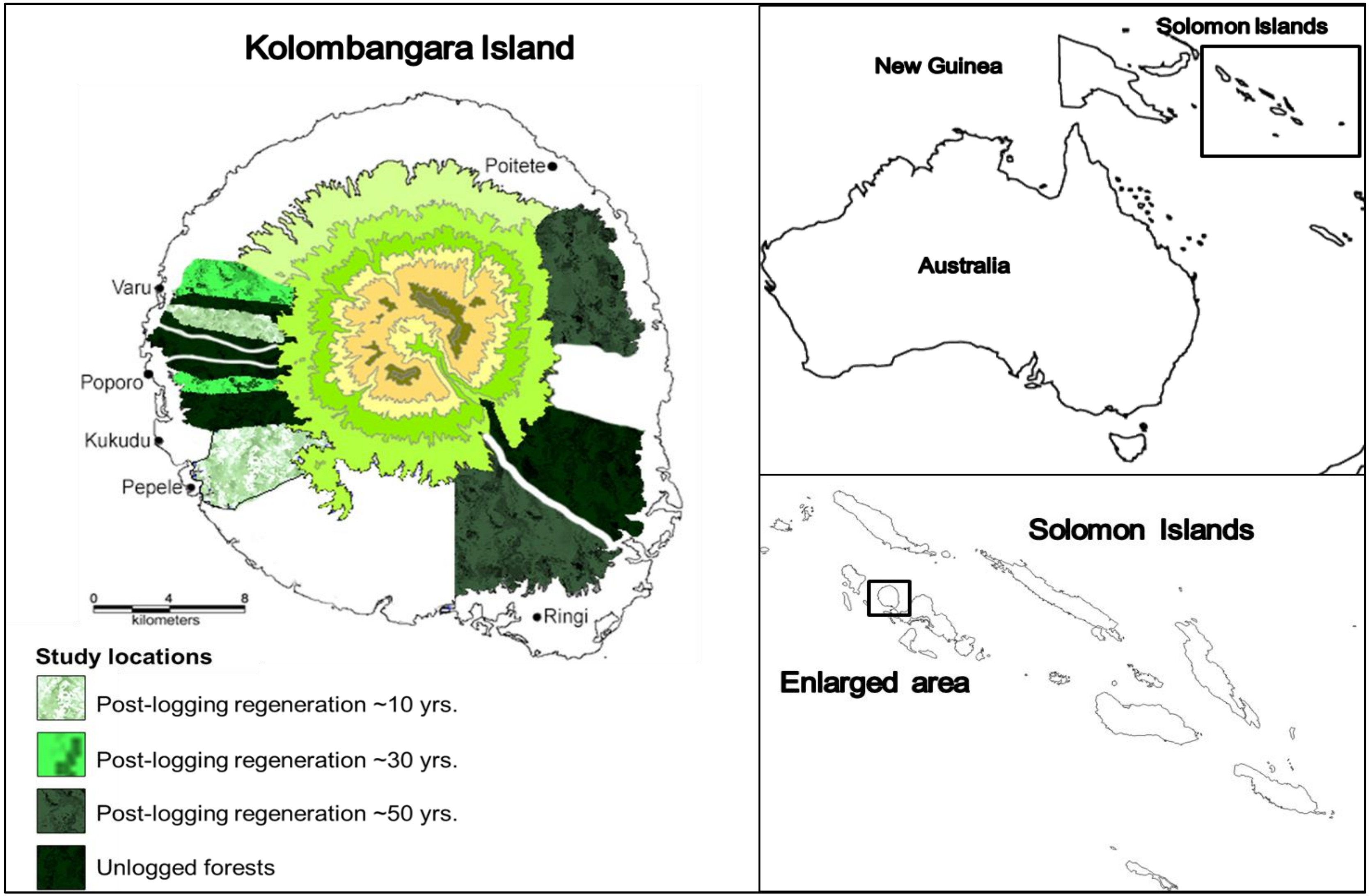


Figure 7.1. Location of study sites on Kolombangara Island (New Georgia group, Solomon Islands).

Logging activities on Kolombangara began in the early 1960s, and since then have been the main cause of forest degradation on the island (Bennett 2000). Although logging on the island involved multiple companies over several decades, their logging practices were very similar (Katovai et al. 2015a), with operations typically extending from coastline areas to approximately 400 m a.s.l. (Katovai et al. 2016). In this study, the study sites were located in both logged and unlogged forest patches situated around the island (Fig. 7.1). All sites were topographically similar and showed no indication of current anthropogenic disturbance.

7.2.2 Study design

From January to November 2013, plant trait surveys were conducted in 144 plots of 0.1 ha (50m × 20 m), located in both logged and unlogged forests. The plots in logged forests were within logged coupes, which are large tracts of forest logged within a fixed period of time. Twelve plots were randomly located in each coupe to ensure sampling at both the coupe edges and internally (Katovai et al. 2016). To compare the changes in plant trait diversity during forest recovery, two logged coupes were selected that represented recovery time frames of 50, 30, and 10 years post-logging (Fig. 7.1). The distances from each plot in the logged coupes to the nearest logging road and unlogged forest were determined with a Garmin 76Cx GPS (Garmin International, Inc., Kansas City, USA). To determine the harvest intensity in each plot, the plot size was increased to 0.28 ha (70 × 40 m^2), by extending the 0.1 ha plot area outwards by 10 m on all sides. This was necessary to improve the resolution of the data, because harvesting is usually not spatially uniform, but rather focused in timber-rich forest patches. The cut stumps in each plot were identified and the diameter of each stump was measured. The diameter at breast height (DBH) was calculated for each cut stump using the protocol described by Katovai et al. (2016). The total basal area harvested was then estimated for each plot.

Six patches of unlogged forests were selected to allow trait comparisons between logged and unlogged forests to be made. Each patch included 12 × 0.1 ha plots, to provide a balanced experimental design. All plots were randomly located and all established more than 100 m from the forest edge, to minimize edge effects (Laurance et al. 2002; Katovai et al. 2016).

For each plot, the parameters of topographic elevation and slope, ground litter, relative light intensity (RIL), tree abundance, liana abundance, and soil nitrogen (N) were measured, because these variables can have marked effects on the functional changes in forest communities (e.g., Tang et al. 2011; Katovai et al. 2015b; Nottingham et al. 2015). Elevation was measured at the center of each plot, using the Garmin 76Cx GPS instrument. The slope was measured using a Haglöf ECII electronic clinometer (Haglöf, Inc., Mississippi, USA) by averaging 10 slope measurements randomly made within each plot (e.g. Katovai et al. 2015b). The ground litter in each plot was estimated by averaging the litter thickness (cm) measured at 10 sampling points stratified across the plot. To estimate RIL, the understory and open light intensities were measured simultaneously across 10 randomly selected points using digital Li-Cor® LI-250A light meters (LI-COR, Inc., Nebraska USA).The mean understory light intensity value for each plot was divided by the mean open light intensity value, and the result multiplied by 100 to obtain the RLI. All trees with a DBH > 10 cm were counted in each plot to estimate tree abundance. The numbers of lianas (all sizes) were counted in four 10 × 10 m^2 nested subplots, and the liana abundance was extrapolated to the standard plot size.

To estimate the soil N level in each plot, soil samples to a depth of 30 cm were extracted at four randomly selected points in each plot, using a cylindrical soil extractor. The samples for each plot were air-dried, thoroughly mixed, and sieved through a 2 mm mesh to remove residuals (Asese et al. 2014; Katovai et al. 2016). An element analysis (Costech Elemental Analyzer; Analytical Technologies, Inc., CA, USA) and continuous-flow isotope ratio mass spectrometry were used to estimate the N weight percentage (N%) (Bay et al. 2015; Katovai et al. 2016).

The time since logging, soil N, tree abundance, and the distance to the nearest logging road were expected to positively affect tree biomass and wood density (Unger et al. 2012; Katovai et al. 2016). In contrast, the effects of elevation, slope, basal area harvested (harvest intensity), liana abundance, and distance to unlogged forest were expected to have negative effects on tree biomass and wood density (Asase et al. 2014; Mohamed et al. 2014; Katovai et al. 2015a; 2015b). The effect of time since logging on the specific leaf area was expected to be positive, whereas the effects of elevation, RLI, ground litter, and soil N were expected to be negative (James and Bell 2000; Wang et al. 2012). The responses were also expected to vary among coupes,_and it was anticipated that time would have an interactive effect on each selected variable (Asase et al. 2014).

7.2.3 Plant trait survey

7.2.3.1 Estimating aboveground tree biomass

The DBH was recorded for all trees with a DBH ≥ 10 cm. To estimate the aboveground tree biomass, generic allometric models for wet tropical forests (Chave et al. (2001, 2005) were used, because no specific allometric model for the studied region was available.

$$Biomass_{Est.} = \exp(-2 + (2.42\, x \ln(DBH)) \qquad \textit{Equation 1}$$

$$Biomass_{Est.} = 0.0776\ \times\ (\rho(DBH)^2\ H)^{0.940} \qquad \textit{Equation 2}$$

Equation 1, which is based on DBH data, was only used for trees with a DBH of 10–40 cm because it overestimates biomass for larger trees (Chave et al. 2001; Feldpausch et al. 2012). Equation 2 was used for larger trees because it also incorporates wood density (ρ) and tree height (H), which gives a better biomass estimate for large trees (Chave et al. 2005). The plot biomass was estimated by summing the values for all trees in each plot (Katovai et al. 2015b).

7.2.3.2 Tree wood density

Tree wood density was estimated for each heartwood sample collected using the protocol described by Chave (2005). Wood samples were removed from 10 randomly selected trees in each plot with a Haglöf increment borer (Haglöf, Inc., Mississippi, USA). Each sample was placed in water for at least 30 min to ensure the wood was fully hydrated before the core length (L) and diameter (D) were measured. Based on the assumption that the wood cores were cylindrical, the volume of each core was calculated using the geometric method (Equation 3) (Chave 2005).

$$Volume = \frac{\pi}{4} D^2 L \qquad \textit{Equation 3}$$

To determine its dry mass (M), each wood core was oven-dried to a constant mass, then weighed to the nearest 0.01 g with an electronic balance. The wood density for each core was calculated by dividing the core dry mass by its volume, using Equation 5, and the mean wood density was then determined for each plot.

$$Wood\ density = \frac{m}{\frac{\pi}{4}D^2L} \qquad \text{Equation 4}$$

7.2.3.3 Specific leaf area

Forty understory trees < 2 m in height were randomly selected within each plot to estimate the plot-SLA. A mature leaf was removed from each plant, and the leaf area was determined using a CI-202 portable laser area meter (Li-Cor, Inc.). The leaf was oven-dried at 65 °C for 72 h, then weighed to determine the dry mass (Ackerly et al. 2002; Kadell et al. 2010). The SLA ($cm^2\ g^{-1}$) for each leaf was calculated separately, and the mean SLA for each plot was determined (Kadell et al. 2010).

7.3.4 Statistical analyses

Descriptive statistics summarizing the mean (± SD) values for tree biomass, wood density, and SLA for the logged and unlogged forests were generated. To determine the patterns of change during the course of regeneration, the rates of change for each of the abovementioned traits within the various logged forest time classes were also calculated.

7.3.4.1 Dynamics of plant traits

Linear mixed models (LMMs) were used to investigate the responses of tree biomass and wood density, and SLA to several ecologically important predictors. ‘Coupe’ was included in the models as a random effect because the plots were nested within coupes, and therefore highly dependent on each other and reliant on the coupe effect. The collinearity in all possible paired combinations of selected predictor variables was assessed by visualizing the paired plots, and examining the correlation coefficients and variance inflation factors using the *usdm* package in the program R (Naimi 2013; R Development Team 2014). The final predictors for the models were selected based in these collinearity analyses.

A global model that included the most important predictor variables was built for each plant trait. Tree biomass and wood density were modelled as functions of time, elevation, slope, soil N, distance to the nearest road, distance to the nearest unlogged forest, liana abundance, harvest intensity, and tree abundance. Understory tree SLA was modeled against time, elevation, ground litter, soil N, and RLI. The interactions of time with other predictor variables were also included in the respective models. A candidate model set with all possible simpler subsets of each global model was then generated using the dredge function in the *MuMIn* package in R (Barton 2015). The models for interpretation were selected based on sample-size-corrected Akaike’s information criterion (AICc), which trades off model fit and complexity (Burnham and Anderson 2004; Mazerolle 2015) and identifies the “best simplest model(s)”. This included all models having ∆AICc < 7. The parameters from these models were then averaged based on the model weights (Burnham and Anderson 2004). Inferences were drawn from averaged parameter estimates based on the effect sizes, and whether their 95% confidence limits overlapped zero. The *predictSE* function in the R package *MuMIn* was used to generate the predicted values from the averaged models for visualization. All statistical analyses were performed with R (R Development Team 2014).

7.3.4.2 Comparison of plant trait values between forest time classes

Nested ANOVA was used to compare the differences in the mean values for tree biomass, wood density, and SLA among the forest time classes (plots were nested within coupes within forest time classes), using the mixed model function in the lme4 package in R (Bates 2015). Although the distances between the plots were sufficient to assume independence, logging practices are normally homogeneous within each coupe, thus increasing the pseudoreplication (Katovai et al. 2015a). The degrees of freedom in the mixed models were calculated with Satterthwaite’s approximation, using the lmerTest package in R, where ‘coupe’ was treated as a random effect and ‘time’ as a fixed effect (Kuznetsova 2015). The random effects were also analyzed to test the influence of random effects in each model. All models were then checked using standard residual diagnostics

7.3 RESULTS

A total of 7515 trees were sampled during the study, of which 53% and 47% were from logged and unlogged forests, respectively. The estimated mean tree biomass (± SD) across all the study sites was 409 ± 197 tonnes ha^{-1}, and for the logged and unlogged forests were 252 ± 106 and 566 ± 132 tonnes ha^{-1}, respectively. The estimated annual mean tree biomass (± SD) for the time increments from 10 to 30 years and from 30–50 years post-logging were 11 ± 3.6 and 5 ± 1.4 tonnes ha^{-1}, respectively.

Approximately 19% (1440) of the trees in this study were cored to determine the wood density. The overall mean wood density (± SD) in the forests across Kolombangara Island was 0.545 ± 0.095 g cm^{-3}, and those for logged and unlogged forests were 0.481 ± 0.044 and 0.597 ± 0.055 g cm^{-3}, respectively. The estimated annual mean wood density (± SD) for the time increments from 10–30 years and from 30–50 year post-logging regeneration were $6.4 \times 10^{-3} \pm 7.0 \times 10^{-4}$ and $-3.0 \times 10^{-4} \pm 3.0 \times 10^{-5}$ g cm^{-3}, respectively.

The estimated mean SLA (± SD) for the entire study was 221 ± 44 cm^2 g^{-1}. This mean was determined from 5760 understory trees representing approximately 12% of the understory trees counted within the study area. The mean SLA (± SD) values for logged and unlogged forests were 223 ± 50 cm^2 g^{-1} and 218 ± 38 cm^2 g^{-1}, respectively.

7.3.1 Recovery dynamics of the selected plant traits

Collinearity was trivial among the predictors for each LMM. The variance inflation factor for all the paired comparisons was < 1.3, and the correlation coefficient ranged from –0.01 to 0.3.

7.3.2.1 Tree biomass

The averaged model for tree biomass was based on 23 models and fitted the data well (Pearson's R between the observed and model-fitted values = 0.89) (Table

7.1). The averaged model contained distance to unlogged forest, distance to the nearest road, elevation, harvest intensity, liana abundance, slope, soil N, tree abundance, and time.

Table 7.1. Tree-biomass candidate model set (only for ΔAICc < 7) used in the LMM analyses, showing predictor effects, degrees of freedom, and AICc and ΔAICc values. Columns 2–18 include all the predictors used in the model and their interactions with time. The slope coefficient is shown for the numerical predictors included in each model. An "*" indicate that time and/or predictor–time interactions were included in the corresponding model. "-", implies that predictors and their interactions with time were not included in the corresponding model.

Model	Distuf	Distrd	Elev	Harv	Liab	Slop	Snitro	Stab	Time	Distuf: Time	Distrd: Time	Elev: Time	Harv: Time	Liab: Time	Slop: Time	Snitro: Time	Stab: Time	df	AICc	ΔAICc
38860	43.8	44.8	-	–0.7	-	-	–15.8	0.2	*	*	*	-	*	-	-	*	-	18	724.1	0
38892	41.7	43.6	-	–0.7	-	1.2	–18.9	0.2	*	*	*	-	*	-	-	*	-	19	724.3	0.29
38876	-0.2	59.4	-	–0.5	–0.1	–	–46.9	0.2	*	*	*	-	*	-	-	*	-	19	724.4	0.31
55276	38.3	43.8	-	–0.7	-	2.6	–21.0	0.2	*	*	*	-	*	-	*	*	-	21	724.9	0.82
38908	–1.4	58.3	-	–0.5	–0.1	1.1	–48.7	0.2	*	*	*	-	*	-	-	*	-	20	725	0.96
104396	30.9	61.9	-	–0.7	-	-	3.9	–0.03	*	*	*	-	*	-	-	*	*	20	725.9	1.85
104428	28.6	60.9	-	–0.7	-	1.2	0.4	-	*	*	*	-	*	-	-	*	*	21	726.3	2.22
55292	–3.0	58.4	-	–0.5	–0.1	1.8	–49.2	0.2	*	*	*	-	*	-	*	*	-	22	726.3	2.28
120812	30.5	61.7	-	–0.7	-	0.2	3.1	–0.02	*	*	*	-	*	-	*	*	*	23	727.6	3.58
104412	–5.6	71.1	-	–0.6	–0.1	-	–29.1	0.02	*	*	*	-	*	-	-	*	*	21	728.1	4.04
38732	32.1	51.4	-	–0.8	-	-	–1.3	-	*	*	*	-	*	-	-	*	-	17	728.6	4.53
51180	32.3	31.4	-	–0.7	-	3.1	–35.6	0.3	*	*	*	-	-	-	*	*	-	19	728.7	4.65
104444	–6.8	70.1	-	–0.5	-	1.1	–30.7	0.04	*	*	*	-	*	-	-	*	*	22	728.9	4.82
34764	39.1	28.3	-	–0.8	-	-	–37.8	0.2	*	*	*	-	-	-	-	*	-	16	729.5	5.45
38864	39.4	54.0	0.1	–0.7	-	-	6.8	0.2	*	*	*	-	*	-	-	*	-	19	729.6	5.6
55148	30.7	59.3	-	–0.7	-	0.5	–2.8	-	*	*	*	-	*	-	*	*	-	20	730.2	6.19
38748	–11.9	73.5	-	–0.5	–0.1	-	–34.1	-	*	*	*	-	*	-	-	*	-	18	730.3	6.22
38764	31.4	59.3	-	–0.7	-	0.2	–2.1	-	*	*	*	-	*	-	-	*	-	18	730.3	6.26
38896	38.8	50.7	0.1	–0.7	-	1.1	–1.5	0.2	*	*	*	-	*	-	-	*	-	20	730.5	6.49
34796	37.9	26.9	-	–0.8	-	0.6	–40.1	0.3	*	*	*	-	-	-	-	*	-	17	730.8	6.7
38880	–2.2	64.9	0.1	–0.5	–0.1	-	–37.1	0.2	*	*	*	-	*	-	-	*	-	20	730.8	6.71
120828	–4.7	70.9	-	–0.6	–0.1	-0.02	–28.2	0.02	*	*	*	-	*	-	*	*	*	24	730.8	6.75
55280	32.7	53.5	0.1	–0.7	-	2.9	2.1	0.3	*	*	*	-	*	-	*	*	-	22	730.9	6.89

Distuf = distance to nearest unlogged forest; **Distrd** = distance to nearest logging road; **Elev** = elevation; **Harv**= harvest intensity; **Liab** = liana abundance; **Slop** = slope; **Snitro** = soil N; **Stab** = tree abundance. **AICc** = Akaike's information criterion corrected. **ΔAICc** = Change in Akaike's information criterion corrected.

The overall influence of the predictors in the tree biomass model was greatest at 50 years post-logging (slope = 387.94, CL 95% = 55.07, 720.83). Harvest intensity negatively influenced tree biomass recovery at 10 and 50 years post-logging (slope =

–0.64, 95% CL = –1.1, –0.18; and slope = –1.69, 95% CL = –2.61, –0.77, respectively) (Fig. 7.2a and 7.2c). At 50 years post-logging, tree abundance positively influenced tree biomass (slope = 0.19, 95% CL = 0.15, 0.68) (Fig. 7.2f). Liana abundance at 10 years post-logging had a weak negative effect on tree biomass (slope = –0.06, 95% CL = –0.10, –0.02) (Fig. 7.2g).

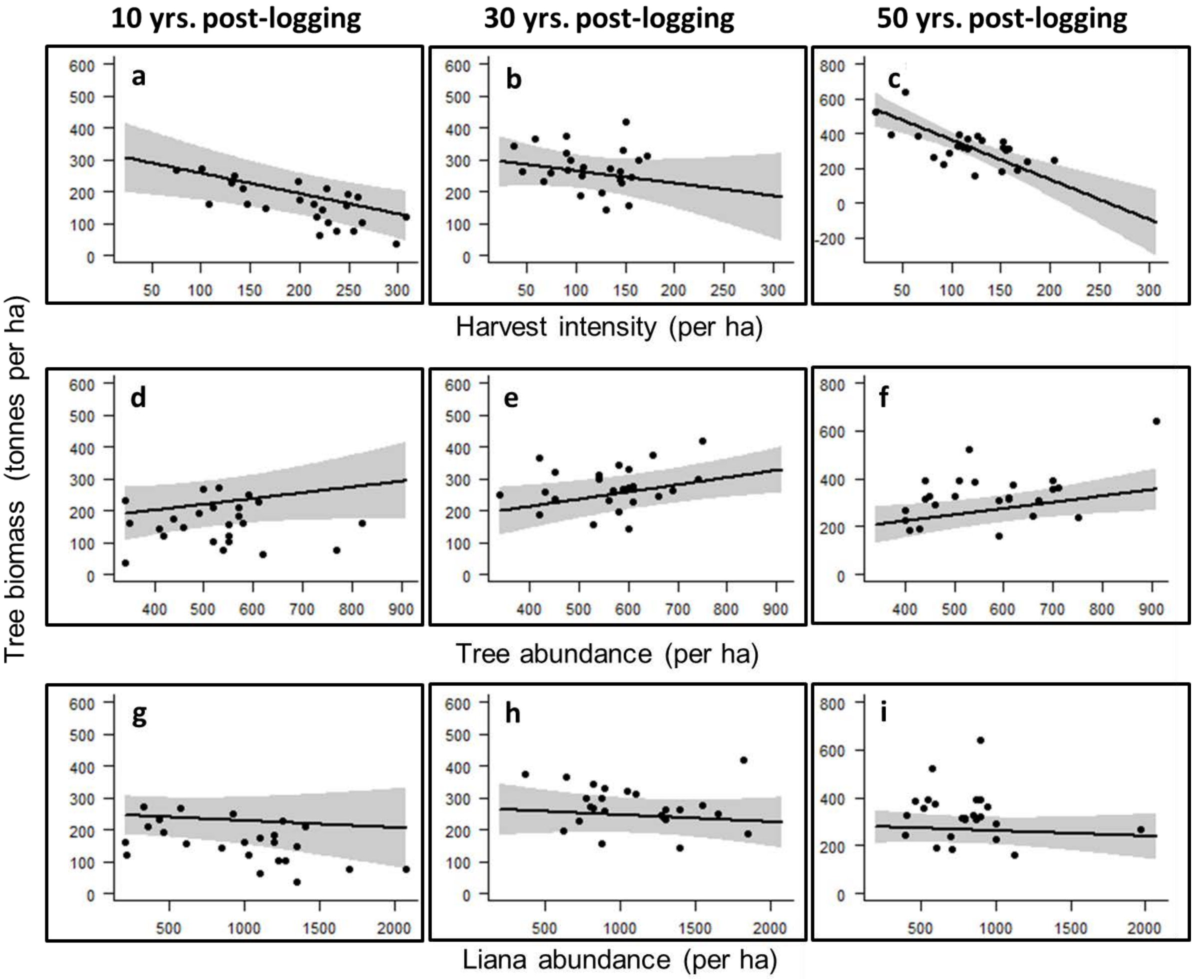


Figure 7.2. Relationships between tree biomass and influential predictors in the logged forests of Kolombangara Island. The linear mixed model fit (predicted) values and the 95% CIs linked to the modeled predictions are shown by the solid lines and the areas within the gray polygons, respectively. Each predictor appeared to vary in its influence on tree biomass during the recovery period, indicated by significance of the interaction effects with time. Harvest intensity and tree abundance both had negative effects on tree biomass at 10 and 50 years post-logging (Fig. 7.2a, 7.2c, and 7.2g), whereas liana abundance positively influenced tree biomass at 50 years post-logging (Fig. 7.2f).

7.3.2.2 Tree wood density

The averaged wood density model (based on 23 models) fitted the data moderately well (Pearson's *R* between the observed and model-fitted values = 0.59). It included the distance to nearest unlogged forest, distance to the nearest road, elevation, harvest intensity, liana abundance, slope, soil N, tree abundance, and time (Table 7.2).

Table 7.2. Tree wood density candidate model set (only for AICc < 7) used in the LMM analyses, showing predictor effects, degrees of freedom, and AICc and ΔAICc values. Columns 2–18 include all predictors used in the model and their interactions with time. The slope coefficient is shown for the numerical predictors included in each model. A "*" sign indicates that time and/or predictor–time interactions were included in the corresponding model. A "-"implies that predictors or their interactions with time were not included in the corresponding model.

Model	Distuf	Distrd	Elev	Harv	Liab	Slop	Snitro	Stab	Time	Distuf: Time	Distrd: Time	Elev: Time	Harv: Time	Liab: Time	Slop: Time	Snitro: Time	Stab: Time	df	AICc	ΔAICc
51044	19.8	7.48	-	-	-	–2.5	145	-	*	*	*	-	-	-	*	*	-	17	715.9	0.00
34628	13.2	9.24	-	-	-	-	145	-	*	*	*	-	-	-	-	*	-	14	715.0	0.10
34636	6.09	–5.68	-	0.36	-	-	150	-	*	*	*	-	-	-	-	*	-	15	715.0	0.16
51052	11.5	–8.61	-	0.35	-	–2.3	146	-	*	*	*	-	-	-	*	*	-	18	715.6	0.70
34660	15.3	8.60	-	-	-	–0.8	145	-	*	*	*	-	-	-	-	*	-	15	715.6	0.86
34668	7.87	–6.17	-	–0.35	-	–0.7	149	-	*	*	*	-	-	-	-	*	-	16	715.7	1.31
34652	39.4	–18.3	-	–0.44	0.1	-	162	-	*	*	*	-	-	-	-	*	-	16	716.2	4.14
38732	4.36	–9.40	-	–0.43	-	-	150	-	*	*	*	-	*	-	-	*	-	17	719.0	4.79
51172	16.2	11.50	-	-	-	–3.2	146	–0.1	*	*	*	-	-	-	*	*	-	18	719.7	5.32
38764	6.87	–10.5	-	–0.43	-	–1.0	148	-	*	*	*	-	*	-	-	*	-	18	720.2	5.52
51068	42.1	–20.00	-	–0.44	0.1	–1.6	159	-	*	*	*	-	-	-	*	*	-	19	720.4	5.58
34684	40.9	–18.8	-	–0.44	0.1	–0.6	162	-	*	*	*	-	-	-	-	*	-	17	720.5	5.65
55148	9.88	11.79	-	–0.04	-	–2.2	146	-	*	*	*	-	*	-	*	*	-	20	720.5	5.74
34756	10.1	14.32	-	-	-	-	150	–0.1	*	*	*	-	-	-	-	*	-	15	720.8	5.97
34788	11.6	13.94	-	-	-	–1.1	149	–0.1	*	*	*	-	-	-	-	*	-	16	721.0	6.12
34644	40.2	3.94	-	-	0.01	-	158	-	*	*	*	-	-	-	-	*	-	15	721.1	6.21
34632	13.3	8.45	-	-	-	-	143	-	*	*	*	-	-	-	-	*	-	15	721.1	6.23
51048	20.1	6.84	-	-	-	–2.5	143	-	*	*	*	-	-	-	*	*	-	18	721.2	6.35
34764	3.19	–2.34	-	–0.04	-	-	151	–0.1	*	*	*	-	-	-	-	*	-	16	721.3	6.41
34640	5.74	–4.90	0.01	–0.04	-	-	152	-	*	*	*	-	-	-	-	*	-	16	721.3	6.47
51180	8.92	–4.34	-	–0.04	-	–2.8	147	–0.1	*	*	*	-	-	-	*	*	-	19	721.5	6.67
51060	43.5	1.60	-	-	0.01	–2	154	-	*	*	*	-	-	-	*	*	-	18	721.8	6.89
34664	13.6	9.17	0.03	-	-	–0.9	147	-	*	*	*	-	-	-	-	*	-	16	721.9	6.99

Distuf = distance to nearest unlogged forest; **Distrd** = distance to nearest logging road; **Elev** = elevation; **Harv**= harvest intensity; **Liab** = liana abundance; **Slop** = slope; **Snitro** = soil N; **Stab** = tree abundance. **AICc** = Akaike's information criterion corrected. **ΔAICc** = Change in Akaike's information criterion corrected.

Wood density was positively influenced by time at 10 and 50 years post-logging (slope = 0.036, 95% CI = 1.55, 561.01; and slope = 0.029, 95% CI = 5.53, 531.09, respectively). Harvest intensity negatively influenced wood density at 10 years post-logging (slope = –0.36, 95% CI = –6.99, –0.03) (Fig. 7.3a). Liana abundance also had a slight positive effect on wood density at 10 years post-logging (slope = 0.05, 95% CI = 0.02, 0.10) (Fig. 7.3d).

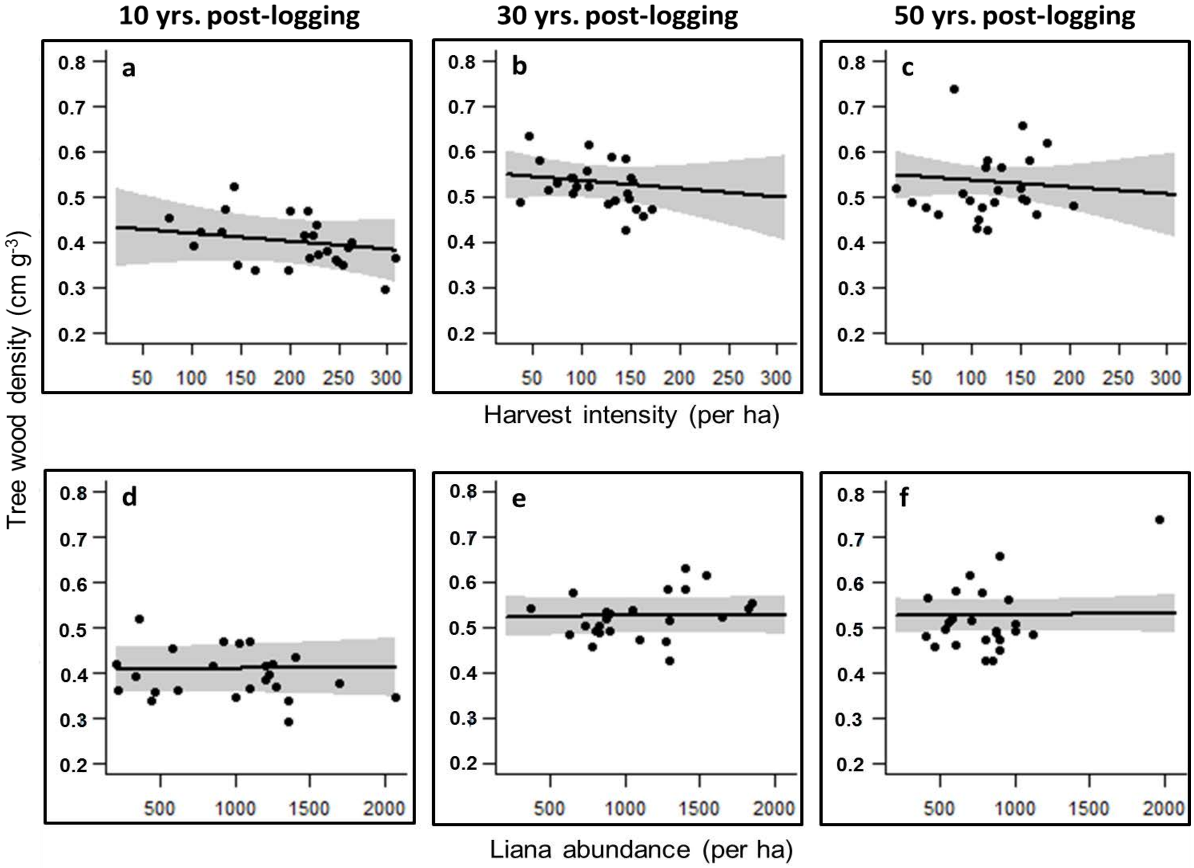


Figure 7.3. Relationships between tree wood density and influential predictors in the logged forests on Kolombangara Island. The linear mixed model fit (predicted) values and the 95% CIs linked to the modeled predictions are shown by the solid lines and the areas within the gray polygons, respectively. Each predictor appeared to vary in its influence on wood density during the recovery period, as indicated by significance of the interaction effects with time. Harvest intensity had a negative effect on wood density at 10 years post-logging (Fig. 7.3a), whereas liana abundance positively influenced wood density at 10 years post-logging (Fig. 7.3d).

7.3.2.3 Understory tree specific leaf area

The averaged model for SLA fitted the data well (Pearson’s R between the observed and model-fitted values = 0.75), and included elevation, ground litter, RLI, soil N, and time. Only three models were used for the averaged model (Table 7.3).

Table 7.3. Understory tree SLA candidate model set (only for AICc < 7) used in the LMM analyses, showing predictor effects, degrees of freedom, and AICc and ΔAICc values. Columns 2–10 include all the predictors used in the model and their interactions with time. The slope coefficients are shown for the numerical predictors included in each model. A “*” indicates that time and/or predictor–time interactions were included in the corresponding model. A “–“implies that predictors or their interactions with time were not included in the corresponding model.

Model	Elev	Litter	RLI	Snitro	Time	Elev: Time	Litter: Time	RLI: Time	Snitro: Time	df	AICc	ΔAICc
512	0.09	–44.6	–2.7	37.07	*	*	*	*	*	17	679	0.00
380	–0.01	–6.62	-	37.5	*	*	*	-	*	14	680	1.12
384	-	–8.66	–0.2	37.49	*	*	*	-	*	15	681	2.00

Elev = elevation; **Litter** = ground litter; **RLI** = relative light intensity; **Snitro** = soil N. **AICc** = Akaike’s information criterion corrected. **ΔAICc** = Change in Akaike’s information criterion corrected.

Only elevation and ground litter had some effect on SLA within the logged forest time classes. Elevation had a strong positive effect on the UTSLA at 50 years post-logging (slope = 13.5, 95% CI= 0.84, 1.86) (Fig. 7.4c), whereas ground litter had a strong negative effect on SLA at 50 years post-logging (slope = –97.09, 95% CI = –172.92, –21.26) (Fig. 7.4f).

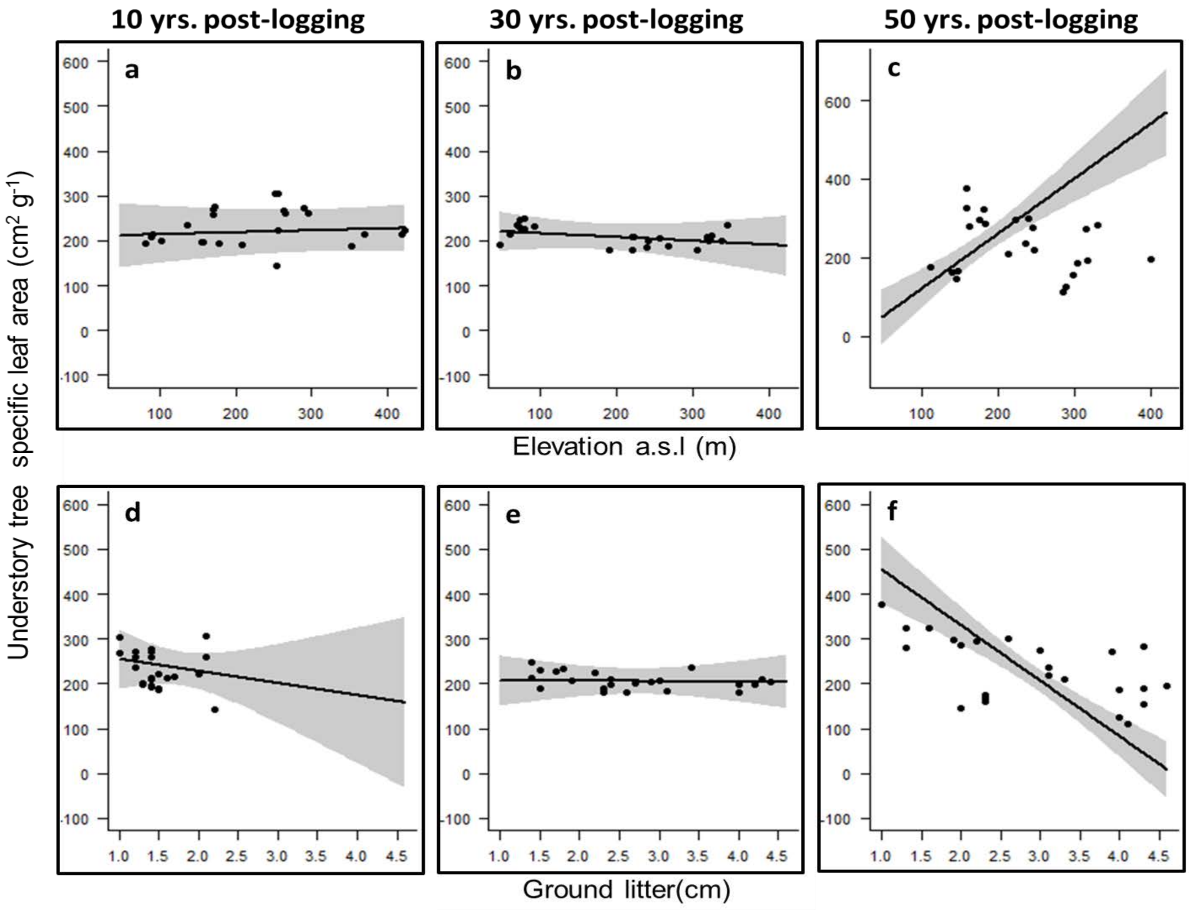


Figure 7.4. Relationships between SLA and influential predictors in the logged forests on Kolombangara Island. The linear mixed model fit (predicted) values and the 95% CIs linked to the modeled predictions are shown by the solid lines and the areas within the gray polygons, respectively. Each predictor appeared to vary in its influence on the SLA during the recovery period. Elevation had a positive effect on SLA at 50 years post-logging (Fig. 7.4c), whereas ground litter had a strong negative effect at 50 years post-logging (Fig. 7.4f).

7.3.2 Post-logging recovery patterns for the selected plants traits

All the models showed approximate normality and homoscedasticity. Nested ANOVA, using Satterthwaite's approximation of degrees of freedom, showed that the mean tree biomass and wood density values differed significantly between the forest time classes ($F_{3,8}$= 107.34, p < 0.0001; and $F_{3,8}$ = 61.76, p < 0.0001). Tukey's post hoc test showed similar groupings in for tree biomass and wood density (Fig. 7.5a and 7.5b). Unlogged forests had the highest mean values, followed by the 30- and 50-year post-logged forests (which were similar), and then the 10-year post-logged forests. The coupe variations for both tree biomass and wood density within each forest time class were fairly low and homogeneous (χ^2 (1, *N = 144*) = 2.27e^{-13}, *p* = 1; and χ^2 (1, *N = 144*) = 0.501, *p* = 0.5, respectively). Mean SLA did not differ significantly among the forest time classes or among the coupes within each class ($F_{3,\,8}$ = 0.85, *p* = 0.50; and χ^2 (1, *N = 144*) = 2.23, *p* = 0.50, respectively.

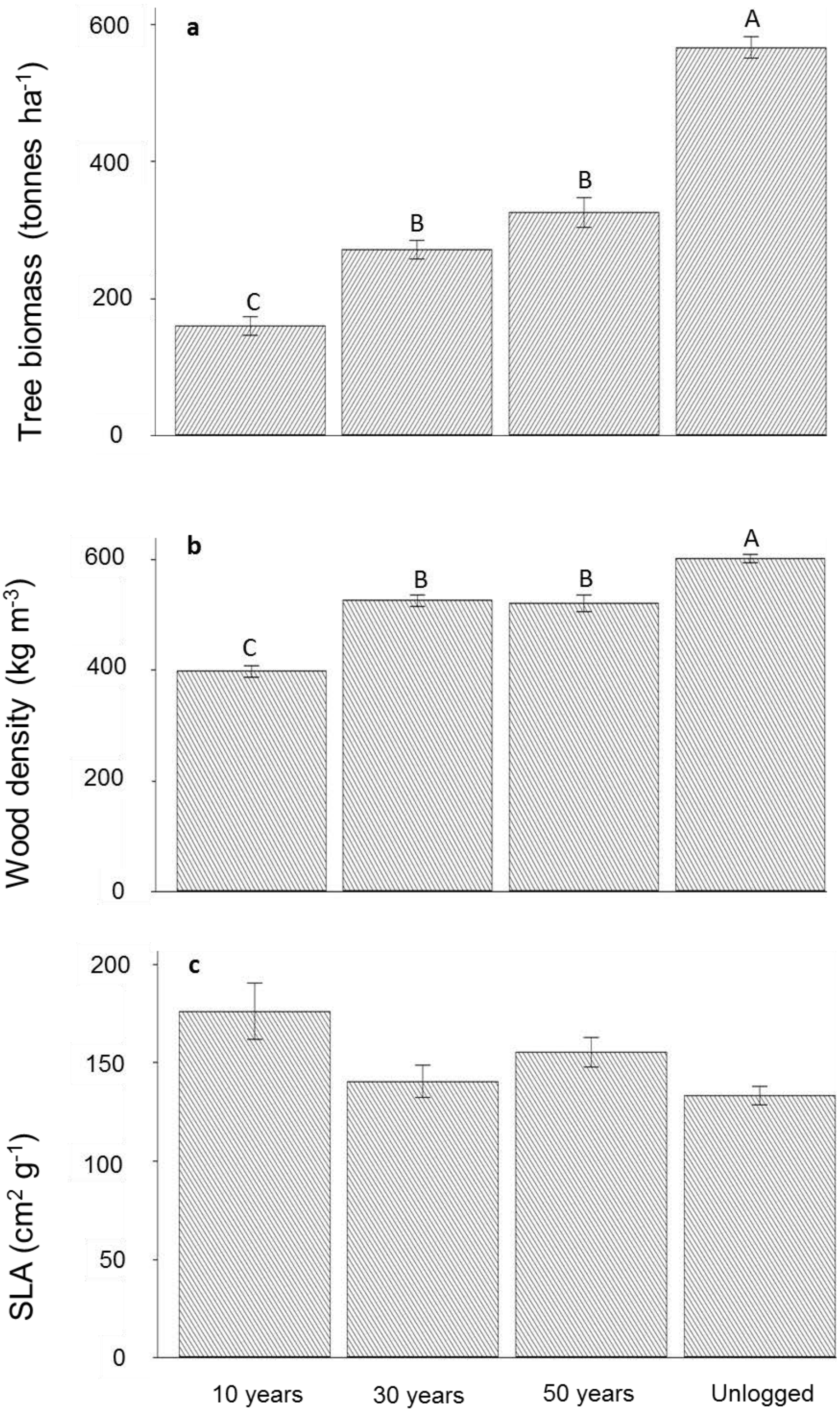


Figure 7.5. Mean values for the selected plant traits (a) biomass, (b) wood density, and (c) SLA for logged forests at 10, 30 and 50 years post-logging, and for unlogged forests. Error bars represent ± SE. The letters above the error bars represent homogeneous groups across each measure where appropriate.

7.4 DISCUSSION

7.4.1 Factors affecting plant trait recovery

The results of this study show that damage associated with logging practices in the forests of Kolombangara, and the floristic succession that followed, influenced the biomass and wood density of tree during their post-logging regeneration. Site productivity and topography were also important predictors, but had no pronounced effect on the patterns of these plant traits (Tables 7.1 and 7.2). In contrast, specific leaf area was influenced by site productivity and topography, but not by logging damage (Table 7.3).

7.4.1.1 Harvest intensity

Our results show that intense logging negatively affected the recovery of plant traits across logged forests on Kolombangara. The negative influence of harvest intensity on tree biomass at 10 and 50 years post-logging and on wood density at 50 years showed that harvest intensity has a long-term impact on growth recovery in logged forests. Recent studies in Amazonian and African tropical forests have shown similar trends and have attributed the rate of tree biomass recovery in logged forests to harvest intensity and associated logging practices (Zimmerman and Kormos 2012; Asase et al. 2014; West et al. 2014; Valverde-Barrantes and Rocha 2014). The low tree biomass value for highly logged forests on Kolombangara at 10 years post-logging is possibly attributable to the extremely high level of loss of large trees, felled during logging, coupled with the high level of mortality in trees damaged during the logging operations (Valverde-Barrantes and Rocha 2014). At 30 years post-logging, tree biomass was relatively similar among the logged forests, regardless of their harvest history. In intensively logged forests, the rapid accumulation of tree biomass results from the rapid proliferation, establishment, and growth of light-demanding long-lived pioneer species (Chazdon et al. 2007; Selaya et al. 2007; Katovai et al. 2016). Nonetheless, a high level of compositional turnover between long-lived pioneer species and climax tree species in intensively logged forests clearly occurred between 30 and 50 years post-logging (Katovai et al. 2016). This may have led to the similar levels in tree biomass across this time interval (Fig. 7.5a), which could explain the influence of harvest intensity on tree biomass at 50 years post-logging.

The negative influence of harvest intensity on wood density at 10 years post-logging may have been associated with the proliferation of light-demanding pioneer trees early in the succession. Low-intensity-logged forests tend to retain trees of high wood density, derived from the old growth forests (Osazuwa-Peters et al. 2015), and therefore have relatively higher wood density than do intensively logged forests. As pioneer trees decline and non-pioneer trees with higher wood density become progressively more dominant in the forest stand, the effect of past harvest intensity apparently declines to a point where it is no longer discernible.

7.4.1.2 Tree abundance

The positive influence of tree abundance on tree biomass at 50 years post-logging indicates that tree biomass is directly linked to the forest tree stand density of climax tree communities (Sist et al. 2014; West et al. 2014). It was evident in the present study that climax trees were highly abundant in 30- and 50-year logged forests, particularly among forest-edge communities, where forest damage at the time of logging was extreme. These climax communities generally form a sub-canopy layer under *Campnosperma brevipetiolata,* a long lived pioneer species that dominated logged forests after logging (Baylis Smith et al. 2003; Katovai et al. 2012). The declining dominance of *C. brevipetiolata* between 30 and 50 years post-logging may have enhanced the growth and structural modification of the climax tree communities as they gradually achieved canopy supremacy (Katovai et al. 2015b). This progressive succession may result in a short-term decline in tree biomass followed by a grander recovery as climax species grow and develop to reclaim dominance across all forest strata. Such a change in tree biomass is perhaps more substantial at forest edges because longed lived pioneers are more abundant at edges than interiors of logged forests.

7.4.1.3 Liana abundance

The negative influence of liana abundance on tree biomass and wood density at 10 years post-logging on Kolombangara Island suggests that liana proliferation following logging inhibited early successional tree growth and development. Several studies have shown that lianas compete with trees for resources including moisture, nutrients, and light (Putz 1984; Schnitzer and Bongers 2002; 2011; Tang et al. 2011), which can increase the physiological stress that individual trees experience and alter the ecological dynamics of affected tree communities (Chao et al. 2008). For example, trees under stress usually trade off growth attributes for survival strategies such as investing in chemical defense and mutualistic relationship with a range of insects that feed on lianas (van Gelder et al. 2006; Chao et al. 2008;

Schnitzer et al. 2012). The involvement of such strategies could have possibly contributed to the relatively low tree biomass in liana-affected forests (Schnitzer et al. 2011).

The slight positive effect of liana abundance on wood density during early succession suggests that even fast-growing pioneer trees can decrease growth and invest in structural attributes in response to environmental stresses (Mao et al. 2014). The reduction in growth rate may have been caused by an increase in wood density (Martinez-Cabrera et al. 2011). Previous studies have shown that variability in wood density is usually attributable to changes in the species composition of plant assemblages over time (Chave et al. 2006; Genet et al. 2012). Nonetheless, this study underscores the apparent importance of liana abundance in influencing the observed changes in wood density, via growth plasticity in pioneer-dominated logged forest communities. The influence of liana abundance on wood density was very weak at later age classes, although older logged forest classes in this study had higher overall abundances of lianas (See chapter five). This suggests that mature trees tolerate the negative impact of lianas, and so may be better hosts than young developing trees.

7.4.1.4 Elevation

Topographical factors have a marked effect on microhabitat environments on high oceanic islands (Gillespie et al. 2008; Keppel et al 2011). Oceanic islands have similar biological communities to continental islands and mainland areas (Katovai et al. 2012; 2015b; Ostertag et al. 2014); however, on oceanic islands changes in microclimate are associated with changes in elevation over short geographical distances (mass elevation effect; Han et al. 2012) and vegetation communities are relatively compressed because of this. For example, montane forests on high oceanic islands in the Solomon Islands occur at relatively low elevations (approximately 700 m a.s.l.) compared with those in mainland tropical areas and continental islands, because of the high level of orographic condensation carried inland from nearby seas (Katovai et al. 2012; 2015b). In support of this, there is strong evidence that microclimatic changes associated with elevational gradients influence the understory plant assemblages on Kolombangara (Katovai et al. 2012).

The positive effect of elevation on SLA in 50-year post-logged forests in this study may have resulted from the increasing soil productivity along the elevation gradient. Our data showed strong associations between ground litter levels and soil N with elevation in this forest class. This notion is also supported by recent studies in the equatorial Andes that have shown that soil productivity (i.e., nitrogen and phosphorus concentrations) increased with elevation within lowland forests (Girardin et al. 2010; Unger et al. 2012; Nottingham et al. 2015). The trivial influence of elevation on SLA in 10- and 30-year post-logged forests may indicate that primary productivity patterns in these forests were altered by logging-related damage. These changes can have a major impact on the regeneration of understory tree communities in recently logged forests (Katovai et al. 2012). Because logging practices are usually more intensive at low elevations (Katovai et al. 2015a), our results also suggest that understory tree communities in low-elevation forests are subject to greater ecological stress than those at high elevations

7.4.1.5 Ground litter

The negative influence of ground litter on SLA in the 50-year post-logged forests suggests that soil fertility in these forests is highly heterogeneous. Low levels of ground litter may indicate high rates of mineralization, with the subsequent release of nutrients for plant use (Kaspari and Yanoviak 2008; Nottingham 2015). In contrast, high levels of ground litter can signify low rates of decomposition, resulting in poor soil productivity (Bakker et al. 2011). Ground litter is a fundamental indicator of soil productivity, and in tropical forests, it is mainly controlled by the rate of nutrient mineralization in the decomposing litter (Kaspari and Yanoviak 2008; Notingham 2015). There is increasing agreement that the primary productivity in lowland tropical forests is mainly limited by phosphorous (Kaspari and Yanoviak 2008; Nadeau and Sullivan 2015). The soils in these forests are usually highly weathered, and therefore contain limited amounts of biologically available phosphorous (Nottingham et al. 2015). Nevertheless, it was commonly observed in the current study that there was more litter in the natural tree-fall gaps than in the closed forests. This observation supports the notion that forest turnover strongly influences soil fertility in tropical forests (Toberman et al. 2011), and implies that excessive harvesting can potentially cause long-term loss of soil productivity, which can hinder plant recovery in logged forests (Toledo et al. 2011; Katovai et al. 2015a, b).

The negative influence of ground litter on SLA at 50 years post-logging also suggests that soil productivity limits ecological functioning in understory plant communities at later stages of forest recovery. The soil productivity in mature forests is usually low, because most of the available nutrients have been absorbed and stored in living plant tissues (Nadeau and Sullivan 2015). This reduction in soil productivity can stress plant communities, and consequently affect plant growth and function (Heineman et al. 2015). Understory plant communities are more likely to show major responses to environmental stress than tree communities, because their nutrient requirements for growth and development are greater, and they are highly sensitive to environmental change (Kaspari and Yanoviak 2008; Toledo et al. 2011; Nadeau and Sullivan 2015). The results of this study indicate that SLA can potentially be used as a proxy for changes in soil productivity in human-degraded tropical forests.

7.4.2 Recovery of plant traits

Results from this study show the recovery potentials of tree biomass, wood density and SLA in logged forests on Kolombangara. The lower community-weighted mean values for tree biomass and wood density in the logged forests relative to those in the unlogged forests suggest that the effects of logging are still present, even after 50 years of recovery. It has been widely recognized in recent studies that the impact of logging on tree demography contributes substantially to the post-logging recovery patterns (Putz et al. 2012; Osazuwa-Peters et al. 2015; van der Sande et al. 2016). The effects of logging are mainly measured by harvest intensity (the number of logs felled per area) and the damage associated with the logging operations (Katovai et al. 2015a). The regeneration responses of forests to these impacts are strongly influenced by post-logging coppicing, seed dispersal and germination, and plant growth and development (Katovai et al. 2012, Katovai and Katovai 2012; 2015a, b).

The harvest intensity in logged forests throughout the Solomon Islands has been relatively high, averaging approximately 17 trees ha^{-1} (and often reaching 30 ha^{-1}), compared with approximately 10 trees ha^{-1} in southeast Asia (Sist et al. 2003; Forshed et al. 2008; Katovai et al. 2015a). Such high-intensity logging commonly results in > 50% loss of the forest canopy, high levels of damage to the remaining trees, and the loss of soil seed banks caused by mechanized harvesting techniques (Sist et al. 2003; Forshed et al. 2008; Katovai et al. 2015a). Predicting plant trait recovery to pre-cut levels entirely through natural regeneration is a significant challenge, because there is a lack of long-term experimental data within the region (Zou et al. 2014). However, comparing different stages of post-logging regeneration in small insular forest systems, such as Kolombangara Island, provides an alternative solution to this challenge (Whitmore 1969; Katovai et al. 2012; Takayama et al. 2015).

Recent studies on Kolombangara Island suggest that forest recovery may have been hindered by several ecological constraints associated with low rates of coppicing, limited seed production and dispersal, and inability of propagules seed sources from unlogged forests (Katovai et al. 2012, 2015a; Katovai et al. 2016). The relatively low coppicing in logged forests on Kolombangara Island suggests that most logged tree species on the island are shade tolerant because coppicing is usually associated with shade intolerance (Burslem and Whitmore 1999; Paciorek et al. 2000). Wet conditions on Kolombangara may have triggered rapid growth and the subsequent establishment of light-demanding pioneers, which overgrew and shaded the coppice shoots, causing their eventually die off (Katovai et al. 2016). Furthermore, observations from this study revealed that proliferation of fungal growth evident on cut stumps in recently logged forests also appears to have triggered the rapid degeneration of the cambium layer on the logged stumps, which has the effect of stalling coppicing, or even preventing it from occurring in some species (Arhipova et al. 2011). The large trees that once dominated the primary lowland forests on Kolombangara Island produce larger but fewer seeds than the small-to-medium and small trees that currently dominate the logged forests. However, most of these seeds are highly recalcitrant (i.e. desiccation-intolerant), and may easily die from desiccation when the forest canopy is strongly reduced by logging (Daws et al. 2006; Lan et al. 2014; Katovai et al. 2016). Large tropical seeds are usually dispersed by animals (zoochory), but in the absence of large mammals on Kolombangara Island, seed dispersal is usually by birds and small mammals, including bats, as well as a few species of marsupials and introduced ungulates. However, seed dispersal into logged forests from unlogged forests only influences the recovery of tree diversity in the later stages of succession (Katovai et al. 2016).

The comparable levels of mean SLA across the examined forest time classes indicate that the range and frequency distribution of SLA values for understory tree species across all forest classes are relatively similar. Understory tree performance may have rebounded to pre-cut levels within several years of recovery as that is usually when microclimatic shifts in logged forests are the greatest (Yong et al. 2012). Related studies have shown that physiological changes linked to photosynthesis and ATP storage in leaves of 38 tropical plants can prompt changes to SLA within several hours (Rozendaal et al. 2006). Such rapid responses may have generated the high variability in SLA within each forest time class resulting in overlapping SLA levels between them. This study therefore confirms that long temporal comparisons of SLA can be challenging and therefore not applicable for examining functional changes in logged forest recovery.

7.5 CONCLUSIONS

The full recovery of tree biomass and wood density within 50 years of the cessation of logging is unlikely in the Solomon Islands. Improving the recovery of wood traits in logged forests in this region requires the development of policies that regulate harvest intensity under current logging practices and re-entry harvesting in post-logged forests (Katovai et al. 2015a). Restoration through the silvicultural thinning of long-lived pioneers may improve plant trait recovery in intensively logged forests over time (Schwartz et al. 2013; Lamb 2014; Cao et al. 2015). The tree biomass and wood density indices may be useful proxies for assessing post-logging recovery in tropical forests, and for providing information that facilitates improved forest management strategies in the future (Bastin et al. 2015; van der Sande et al. 2016). It is also evident from this study that SLA is not a good proxy to distinguish environmental changes across post-logging recovery (Castellanos-Castro and Newton 2015). Nonetheless the similarity of the mean SLA values across the examined forest classes suggests that the physiological functions controlling the energy economics in understory trees is resilient to the impacts of logging.

Understanding key factors influencing the recovery of core plant traits in logged forests may provide new insights for novel applications to enhance the restoration and management of intensively logged forests in the tropics.

7.6 CHAPTER SUMMARY

- Industrial logging sharply alters the bio-ecological environment of tropical forests. The response of plant traits as logged forests recover through natural regeneration can be quantified using a set of easily measured traits.

- We assessed the factors influencing the recovery of the tree biomass and wood density, and understory tree SLA in forests that had undergone 10, 30 and 50 years of post-logging regeneration on Kolombangara, Solomon Islands. We also determine whether 50 years was sufficient to allow these plant traits to recover to their pre-logging state.
- Harvest intensity, tree abundance and liana abundance were influential in tree biomass and wood density, whereas elevation and ground litter affected understory tree SLA. Tree biomass and wood density did not recover to pre-cut levels after 50 years of post-logging regeneration. Understory tree SLA was similar across the logged forest time classes and unlogged forests.
- The full recovery of tree biomass and wood density within 50 years of the cessation of logging is unlikely in the Solomon Islands. Improving the recovery of wood traits in logged forests in this region requires the development of policies that regulate harvest intensity under current logging practices and re-entry harvesting in post-logged forests. Restoration through the silvicultural thinning of long-lived pioneers may improve plant trait recovery in intensively logged forests over time.
- Understanding key factors influencing the recovery of core plant traits in logged forests may provide new insights to enhance the restoration and management of intensively logged forests in the tropics.

Kolombangara and other volcanic islands in the New Georgia group are known for their gigantic trees, most of which have been removed by previous logging.

Photographs by Eric Katovai 2013

CHAPTER 8

FACTORS AFFECTING THE RECOVERY OF KEYSTONE STRUCTURES IN LOGGED FORESTS OF THE SOLOMON ISLANDS

Eric Katovai, Dawnie D. Katovai, Susan G. Laurance, Will Edwards, William F. Laurance

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Chapter overview:

This chapter examines factors influencing the recovery of “keystone structures” in logged forests on Kolombangara, Solomon Islands. The chapter attempts to consider possible reasons for the patterns observed for each keystone across recovery time.

Contribution to thesis:

This chapter attempts to address objective No. 7 of this thesis, which is to determine factors affecting the recovery of forest structure across logged forests on Kolombangara, Solomon Islands.

8.1 INTRODUCTION

Industrial logging is widely known to degrade forest structure (Fisher et al. 2011; Katovai et al. 2015a). In the tropics, studies investigating the degradation of the forest structure in logged forests have typically been conducted within two decades of logging cessation because structural changes can be generally assessed within this period (Marsden 1998; Berry et al. 2010; Gibson et al. 2011; Osazuwa-Peters et al. 2015). These relatively immediate impacts of logging can result in a range of structural changes. For example, damage initiated by tree felling mostly involves the crushing of nearby trees (Forshed et al. 2008; Shenkin et al. 2015). This collateral damage to adjacent plants can be exacerbated by liana networks that link neighbouring trees so that when a tree is felled neighbouring trees or their branches are pulled down with it (Schnitzer et al. 2000; Wright et al. 2015). The extraction of felled logs also requires forest clearing for the construction of logging roads, skidding trails, and log storage areas. These activities usually create large gaps (>90 m^2) in the forest (Katovai and Katovai 2012; Katovai et al. 2015a). The recovery of natural vegetation in these large gaps can be impeded by top-soil removal and compaction and invasive plants (Williamson and Neilsen 2000; Harrison and Swinfield 2015).

Reduced-impact logging, by comparison, causes minor damage to forest structure that not only benefits regeneration but may increase their resilience to anthropogenic fires and to climate change (Cochrane and Barber 2009; Zimmerman and Kormos 2012; Cole et al. 2015; Sakschewski et al. 2016). Unfortunately, logging practices in the tropics are typically unregulated, resulting in widespread damage to forest structure and biodiversity (Marsden 1998; Asner et al. 2004; Katovai et al. 2015a). For example, much of Southeast Asia and the neighboring Pacific Islands were so extensively logged during the 20th century (Harrison and Swinfield 2015;

Katovai et al. 2015a; Sist et al. 2015), that natural regeneration alone may be insufficient to ensure full structural recovery of these forests (Peña-Claros et al. 2008; Harrison and Swinfield 2015; Katovai et al. 2015a;). Consequently, the research focus has now shifted to investigating restoration approaches that will enhance biodiversity and functional recovery in badly degraded forests in the region (Lamb 2014; Harrison and Swinfield 2015; Sist et al. 2015).

Forest structure is fundamental to the regulation of ecosystem functions because it fosters biophysical interactions and biodiversity at various spatial scales (Peña-Claros et al. 2012; Gadow et al. 2012; Arcilla et al. 2015). It can be measured in distinct physiognomies that provide resources, shelter, and ecosystem goods and services crucial for species' survival; these are referred to as 'keystone structures' (Tews et al. 2004).

In addition to regulating primary productivity, gas exchange, and evapotranspiration, forest structure also influences the influx of solar energy to the understory (Ozanne et al. 2003; Wedeux and Coomes 2015). High radiation influx occurs in canopy gaps, and this increases the rate of photosynthesis in exposed understory areas, enhancing tree growth and structural development (Katovai and Katovai 2012). Ecophysiological functions of forest structure also provide goods and services to forest communities, and contributes to niche specializations that can result in in distinct community assemblages among the forest strata (Buchmann et al. 2002; Brauman et al. 2007; Layman et al. 2015). Several studies have suggested that forest canopies alone contain 40% of global biodiversity, 10% of which are canopy specialists (Ozanne et al. 2003). More than 25% of herbivorous insects and 10% of vascular epiphytes are canopy specialists (Basset et al. 2003; Ozanne et al. 2003; Wagner et al. 2015). Several contemporary ecologists have suggested that the levels of ecosystem function and biodiversity in tropical forests are strongly linked to the dimensions and life histories of forest keystone structures (Tews et al. 2004; Poorter et al. 2006; Thompson et al. 2012). For example, keystone structures of a single tree, including the canopy, number or size of cavities, tree height, and tree size show positive correlations with the levels of ecosystem provisioning and resident biodiversity (Ozanne et al. 2003; Poorter et al. 2006; Remm and Lõhmus 2011). At the community level, large old-growth trees contribute extensively to ecosystem functioning, and also provide key habitat for biodiversity (Manning et al. 2006; Almeida-Gomes et al. 2016; Lindenmayer and Laurance 2016a, 2016b).

Damages to tropical forests can have a strong impact on forest structure. Damage caused by natural disturbances, including strong winds, alters forest structure; however, this is usually a short-term impact, with full recovery attainable within a decade (Burslem et al. 2000). In contrast, logging tends to have a longer-term impact on forest structure in terms of the recovery of canopy architecture (Asase et al. 2014; Shenkin et al. 2015), although little is known about the factors affecting post-logging recovery (Wedeux and Coomes 2015) especially in Oceania. Forest recovery in Oceania may differ from other tropical regions (Whitmore 1989b; Gillespie et al. 2008; Katovai et al. 2016), because this region has relatively young soils, a small regional species pool, higher endemism, and is subject to severe weather events including cyclones and hurricanes (Burslem et al. 2000; Keppel et al. 2009; 2010; Katovai et al. 2015a; Osazuwa-Peters et al. 2015). Furthermore, human land-use intensity has probably been lower prior to logging, in Oceania because of the low population density and modest intensity of subsistence-type practices across the region (Baylis-Smith et al. 2003).

In this study we (i) assessed the factors influencing recovery of forest structure in previously logged forests and (ii) determined whether a half century was sufficient to allow forest structure to recover to pre-logging conditions.

8.2 METHODS

8.2.1 Site description

This study was conducted on Kolombangara Island (157° E and 5° S) in the New Georgia group, Solomon Islands. Kolombangara is a volcanic island having a near-perfect circular shape, and comprising a land area of approximately 80,000 ha. Topsoils on the island are generally haplotyorx and acidic (pH < 5), and have a high organic content (Wairiu and Lal 2003; Katovai et al. 2012). The underlying rocks are predominantly olivine basalt breccias and lavas (Burslem et al. 2000). The exceptionally high annual rainfall on the island (~3000 mm/yr) supports wet tropical forests that stretch from the relatively flat coastline to the rim of the volcanic cone (1700 m a.s.l.), which is in the center of the island (Katovai et al. 2016).

The forests on Kolombangara Island have been categorized as lowland mixed evergreen forests (< 400 m a.s.l), hill forests (400–800 m a.s.l.) and montane forests (~800–1700 m a.s.l) (Burslem and Whitmore 1999; Burslem et al. 2000; Katova et al. 2012). Much of the island is covered by lowland forests that are very dense, and rich in endemic plant species (Hancock and Henderson 1988; Katovai et al. 2016). Although the forest structure is comparable to the neighboring New Guinea islands, tree diversity on Kolombangara Island is lower than in New Guinea (Burslem et al. 2000; Katovai et al. 2012). However, the primary lowland forests on Kolombangara

Island are known for their gigantic trees, which often exceed 100 cm in diameter at breast height (DBH), and contribute significantly to the stand biomass of the island (discussed in Chapter 8).

Industrial logging practices in the Solomon Islands are generally similar to those in Southeast Asia (Katovai et al. 2015a). Following tree felling the logs are typically removed using bulldozers and excavators along skidding trails, which are usually constructed perpendicular to the main logging road at intervals of 100–150 m (Marsden 1998). Where skidding is impossible because of the topography, cables are used to pull logs to the main logging road (Bennet 2000). From the early 1960s to the present, large-scale industrial logging has degraded much of the island's lowland forests. Trees ≥ 30 cm DBH were typically harvested for timber and other wood products (Katovai et al. 2012). The high harvest intensity (17–30 trees/hectare) makes Kolombangara Island one of the most intensively logged islands in the Solomon archipelago (Katovai et al. 2015a).

Much of the logged forests on Kolombangara's southeast, northeast, and northwest quadrants were either converted to commercial tree plantations or to pastures for grazing (Katovai et al. 2012). These land use activities were absent in the southwest quadrant of the island thus allowing uninterrupted regeneration in logged forests. There are also patches of of unlogged lowland forest on Kolombangara Island that form a mosaic with logged forests at different stages of recovery (Fig. 8.1). These unlogged forests, however, are vulnerable to future logging, as they are not legally protected (Katovai et al. 2012; 2015a).

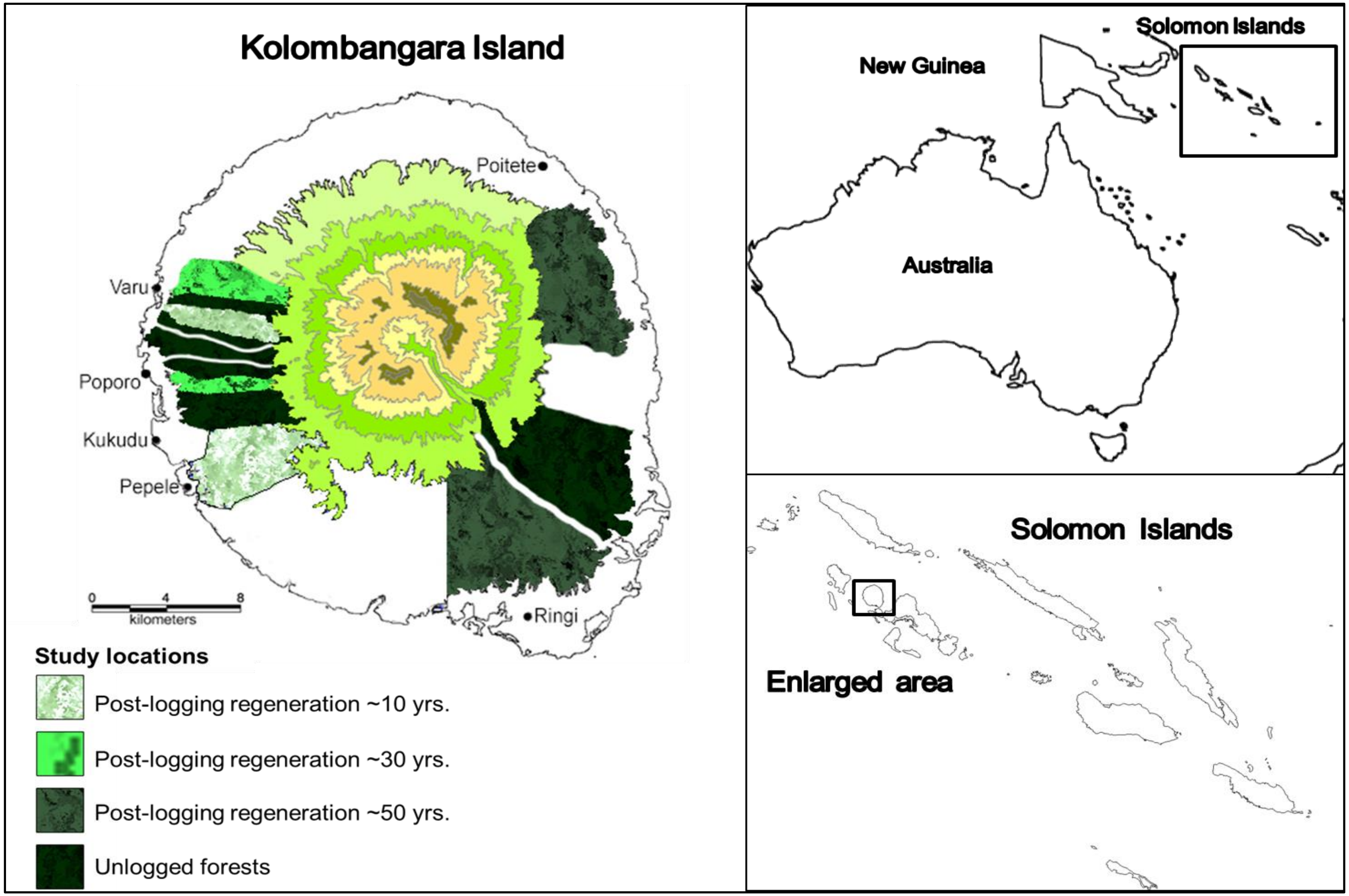

Figure 8.1. Logging history and study sites on Kolombangara, Solomon Islands.

8.2.2 Study design

From January to December 2013, keystone structures, proxies of logging impact, topography, tree architecture and soil attributes were surveyed in 144 sites of 0.1 ha (50 m × 20 m) established in both logged and unlogged forests. To exclude the effects of past land use, traditional and published information were used to avoid past human settlements (Burlsem et al. 2000; Baylis-Smith et al. 2003; Katovai et al. 2016). To investigate structural change during post-logging recovery, the study was restricted to forests logged 10, 30, and 50 years previously. For each time class, two forest coupes logged within the same time frame were selected. In each coupe 12 plots were established, giving a combined total of 72 plots for the three time classes. An additional 72 plots were also established in unlogged forests within the study area, to enable comparison of the structural differences between logged and unlogged areas. Care was taken to ensure that the plots installed within each logged coupe and patch of unlogged forest captured the variations between forest interiors and edges (Katovai et al. 2016).

8.2.3 Predictors

Distance to the nearest unlogged forest, harvest intensity and the liana abundance were used as proxies for logging. The distance between each logged forest plot and the nearest unlogged forest was determined using a GPS (Garmin 76cx GPS; Garmin International, Inc., Kansas City, USA). Harvest intensity was estimated using the protocol outlined in Chapter 6. Lianas of all sizes were tallied to determine liana abundance in four nested subplots, each of 0.01 ha (10 m x 10 m) in size; liana abundance was then extrapolated to 0.1 ha.

Topographical elevation and slope measurements followed the sampling protocol outlined in Chapter 7. We used height of first major branching and stem abundance of canopy trees as proxies for tree architecture. Mean height of major branching was generated per plot from the height of major branching was measured for 10 randomly-picked trees with a Leica laser distance measurer (Leica Disto D5; Geosystems Inc., Heerbrugg, Switzerland). All canopy trees within each plot were counted to determine stem abundance. Soil and surface attributes included measures of litter depth calculated from 10 random-picked points per plot and soil nitrogen (N) estimated using the protocols outlined in Chapter 6.

Table 8.1. Keystone structures and the set of predictors included in the linear mixed models. Each keystone structure was modeled against corresponding predictors (●). Based on sound biological reasoning, canopy openness was included as a predictor for ground vegetation cover.

	Predictors											
Keystone structures	Distance to nearest unlogged forests (Logging)	Harvest intensity (Logging)	Liana abundance (Logging)	Site elevation (Topography)	Site slope (Topography)	Canopy openness (Tree architecture)	Height of major branching (Tree architecture)	Stem abundance of canopy trees (Tree architecture)	Leaf litter (Soil)	Soil nitrogen (Soil)	Soil pH (soil)	Post-logging regeneration (time)
Canopy openness	●	●			●		●	●	●	●	●	●
Ground vegetation cover	●	●			●	●	●		●	●	●	●
Canopy height	●	●	●	●	●				●	●		●
Tree abundance (DBH > 10cm)	●	●	●	●	●				●	●		●
Treelet abundance (DBH 1cm - 10cm)	●	●	●	●	●				●	●		●

8.2.4 Keystone structure survey

The keystone structures include canopy cover, ground vegetation cover, canopy height, and stem abundance for two tree size classes. To identify important factors that have affected the recovery patterns of the keystone structures, each keystone structure was modeled as a function of recovery time, and proxies for logging, topography, tree architecture, and soil attributes (Table 8.1). The influence of each predictor in the respective models was then assessed, and reported in relation to how it affected the pattern of forest structural recovery in the logged forests.

Surveys of canopy cover, canopy height, and ground vegetation cover were conducted at 16 random points within each 0.1 ha plot. The canopy cover (expressed as a fraction of 1) above each survey point was estimated visually within a radius of 2 m from the sampling point, and the mean canopy cover was then calculated for each plot. Canopy height was measured at the sampling points using a Leica laser, and mean values for each plot were then calculated. The ground vegetation cover was estimated at each sampling point using a 1 m^2 quadrat divided into equal-sized square grids The mean plot ground cover fraction was then determined. Stem abundance was measured for large trees (DBH > 30 cm) in 20 x 50 m plots and treelets (DBH 1–10 cm) in 4 subplots of 5 x 5 m (DBH>5cm) and 4 subplots of 10 x 10 m (DBH 5–10 cm) and extrapolated to 1 ha estimates.

8.2.5 Statistical analyses

8.2.5.1 Factors affecting keystone structural recovery

Linear mixed models (LMMs) were used to investigate the relationships between keystone structures and the 12 ecological predictors. Coupe was treated as a random effect in the models, as the plots nested in each coupe were not independent of each other (Katovai et al. 2016). Before generating a global model and candidate model sets for each selected response, potential variables were investigated by plotting pairs of variables, calculating correlation coefficients for each pair, and examining the variance inflation factors (VIFs) using the package *usdm* in R (Naimi 2013). Global models were generated, in which each selected keystone structure was modeled as a function of ecologically important predictors (Table 8.1). Interactions between time since logging and all predictor variables were also included in the models as time–predictor interactions; these are highly important in explaining post-logging forest regeneration (Katovai et al. 2016). A candidate model set having all possible simpler subsets of each global model was then created using the dredge function in the R package *MuMln* (Barton and Barton 2015). Models for inference were selected based on Akaike’s Information Criterion (AICc; corrected for sample size), which trades off model fit and model complexity (Burnham and Anderson 2002; Mazerolle 2014) and identifies the ‘best simplest model(s)’. This included all models having a delta AICc value < 7. The parameters from these models were then averaged, based on model weights (Burnham and Anderson 2002). Inferences from averaged parameter estimates were drawn based on effect sizes, and whether their 95% confidence intervals (CI) overlapped zero. All analyses were generated using R (R Core Team 2014).

8.2.5.2 Keystone structural recovery

We compared the means of canopy height and cover, ground cover and stem abundances across logging ages using nested analysis of variance (ANOVA) generated in the mixed model function in the *lme4* R package (Bates 2015). Satterthwaite's approximation in the *lmerTest* R package was used to determine the degrees of freedom in the analyses, as 'coupe' and 'time' were treated as random and fixed effects, respectively (Kuznetsova 2015). The *multcomp* package in R was then used to generate post hoc comparison tests for keystone structures that showed significant mean differences among forest time classes (Horthon et al. 2015). Graphical visualization of these analyses was generated in Statistix 8 (Tallahassee FL 32317, USA).

8.3 RESULTS

8.3.1 Predictors during the recovery time

Harvest intensity (measured as the loss of stand basal area) was comparable in the 30- and 50-year post-logged forests, but was ~40% higher in the recently logged forests (10-year post-logging). The older logged forests (30- and 50-year) were also further from intact forests than the 10 year logged forests (Table 8.2). The elevational gradient did not differ between the logging treatments but litter reached intact forest depths in older logged forests (>30 years). Liana abundance was lowest in unlogged forests, increased from 10 to 30 years post-logging, but was lower in the 50-years post-logging forests. Site slope was highly variable within and among all forest classes. The soil N content was relatively constant among all forest classes, but the mean soil pH was higher in the 10-year post-logging forests than in the other forest classes, which had similar pH levels.

Table 8.2. Mean values (± 1 SD) for each predictor among forest time classes.

Predictor	Forest class			
	10 yrs post-logging	30 yrs post-logging	50 yrs post-logging	Unlogged
Basal area harvest (m^2 per hectare)	14±2.4	10.5±2	10.6±2.3	-
Distance to nearest unlogged forests (km)	1.8±0.5	3±1.4	2.9±1	-
Elevation (m)	225.3±99.8	209.3±108.2	229.6±75.1	221.1±116.2
Height of major branching (m)	7.2±0.9	16.6±1.2	18.5±1	21.3±2.4
Litter depth (cm)	1.5±0.3	2.6±1	2.9±1.1	2.7±1.3
Liana abundance (per hectare)	966.5±485.4	1088.6±393.4	802.3±319.2	575.4±179.8
Slope (degrees)	6.7±5.3	11.9±10.5	15.8±10.8	14±11.3
Soil nitrogen (%)	0.4±0.1	0.3±0.1	0.4±0.2	0.3±0.1
Soil pH	5.1±0.4	4.5±0.4	4.7±0.5	4.7±0.8

8.3.2 Factors affecting keystone structures

The relatively low VIFs (< 6.42) and range for paired correlation coefficients (R = –0.42 to 0.44) indicated the absence of significant collinearity among the selected predictors.

8.3.2.1 Canopy cover

The average LMM for canopy cover fitted the data well (Pearson's R between observed and model-fitted values = 0.91), and comprised 7 models that included time, height of major branching, litter depth, and soil N (Table 8.3a). Time influenced canopy cover in all three post-logging forest time classes. The time effect for the 10-year post-logging time class was positive (slope = 0.37; 95% CI = 0.2, 0.55), but was negative and of similar in scale for the 30-year (slope = –0.32; 95% CI = –0.41, –0.22) and the 50-year (slope = –0.32; 95% CI = –0.41, –0.22) post-logging time classes. Canopy cover was also weakly influenced by the height of major branching (slope = –0.2; 95% CI = –0.3, –0.2) and litter depth (slope = 0.2; 95% CI = 0.1, 0.4). Although soil N was an important predictor in the averaged model, its effect on canopy covert was trivial (Table 8.4).

Table 8.3. Candidate model set for each keystone structure (only for ΔAICc < 7) used in the LMM analyses. Each row in the table shows a model with a set of corresponding predictors, degrees of freedom (df), Akaike's information criterion corrected (AICc), and the change in corrected Akaike's information criterion (ΔAICc). An "*" indicate that time and/or predictor–time interactions were included in the corresponding model. "-", implies that predictors and their interactions with time were not included in the corresponding model.

a. Canopy cover

Model	BAH	Distuf	Brht	Litter	StAb	Slope	Snitro	SpH	Time	BAH: Time	Distuf: Time	Brht: Time	Litter: Time	Time: StAb	Slope: Time	Snitro: Time	SpH: Time	df	AICc	ΔAICc
257	-	-	-	-	-	-	-	-	0.38	-	-	-	-	-	-	-	-	5	–152	0
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	–150.7	1.36
321	-	-	-	-	-	-	–0.13	-	0.43	-	-	-	-	-	-	-	-	6	–149.2	2.86
5	-	-	–0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	–148.4	3.62
65	-	-	-	-	-	-	–0.14	-	-	-	-	-	-	-	-	-	-	4	–148.3	3.77
265	-	-	-	0.02	-	-	-	-	0.34	-	-	-	-	-	-	-	-	6	–148.1	3.9
9	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	4	–145.8	6.19

b. Ground vegetation cover

Model	BAH	Copen	Distuf	Brht	Litter	Slope	Snitro	SpH	Time	BAH: Time	Distuf: Time	Brht: Time	Litter: Time	Slope: Time	Snitro: Time	SpH: Time	df	AICc	ΔAICc
19	-	0.6	-	-	–0.1	-	-	-	0.5	-	-	-	-	-	-	-	5	63.8	0
83	-	0.61	-	-	–0.1	-	0.15	-	0.4	-	-	-	-	-	-	-	6	63.7	2.62
20	0	0.5	-	-	–0.1	-	-	-	0.4	-	-	-	-	-	-	-	6	61.7	6.62
147	-	0.63	-	-	–0.1	-	-	–0.01	0.6	-	-	-	-	-	-	-	6	61.6	6.73

c. Canopy height

Model	BAH	Distuf	Elev	Liab	Litter	Snitro	Slope	Time	BAH: Time	Distuf: Time	Elev: Time	Liab: Time	Litter: Time	Slope: Time	Smitro: Time	df	AICc	ΔAICc
129	-	-	-	-	-	-	-	2.56	-	-	-	-	-	-	-	5	–125	0
193	-	-	-	-	-	0.07	-	2.54	-	-	-	-	-	-	-	6	–120.2	4.76
137	-	-	-	0.01	-	-	-	2.68	-	-	-	-	-	-	-	6	–118.1	6.9

d. Large tree abundance

Model	Bah	Distuf	Elev	Liab	Litter	Slope	Snitro	Time	Bah: Time	Distuf: Time	Elev: Time	Liab: Time	Litter: Time	Slope: Time	Snitro: Time	df	AICc	ΔAICc
23516	–12.61	–0.2	-	–1.92	–8	-	–52.48	353.7	*	*	-	*	*	-	*	20	683.5	0
21468	–11.93	–10.18	-	–2.67	–6.28	-	–58.31	384.3	*	*	-	-	*	-	*	18	684.8	1.35
23548	–12.47	–0.44	-	–1.84	–4.81	0.36	–50.31	341.6	*	*	-	*	*	-	*	21	685.8	2.32
21500	11.63	–12.15	-	–2.69	–1.94	0.46	–57.32	374.5	*	*	-	-	*	-	*	19	686.8	3.33
31740	–12.73	–0.15	-	–1.99	–10.7	–0.31	–53.84	363.9	*	*	-	*	*	*	*	23	687.4	3.96
29692	–12.15	–9.77	-	–2.78	–10.97	–0.53	–60.55	401.3	*	*	-	-	*	*	*	21	687.8	4.28
21460	–14.36	25.12	-	-	–12.39	-	–37.51	275.3	*	*	-	-	*	-	*	17	688.2	4.77
23520	–14.02	1.21	-	-	–17.8	-	–34.12	356.1	*	*	-	*	*	-	*	21	689.8	6.35
21492	–14.12	23.71	-	-	–8.71	0.39	–36.49	266.0	*	*	-	-	*	-	*	18	690.1	6.64

e. Treelet abundance

Model	BAH	Distuf	Elev	Liab	Litter	Slope	Snitro	Time	BAH: Time	Distuf: Time	Elev: Time	Liab: Time	Litter: Time	Slope: Time	Snitro: Time	df	AICc	ΔAICc
2	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	48.70	0.00
129	-	-	-	-	-	-	-	8.69	-	-	-	-	-	-	-	5	49.70	0.99
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	50.70	2.00
66	0.1	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	5	51.40	2.70
16577	-	-	-	-	-	-	0.06	8.81	-	-	-	-	-	-	*	6	52.60	3.81
193	-	-	-	-	-	-	–0.32	7.99	-	-	-	-	-	-	-	8	52.60	3.86
18	0.1	-	-	-	–0.1		-	-	-	-	-	-	-	-	-	5	53.00	4.23
65	-	-	-	-	-	-	–0.02	-	-	-	-	-	-	-	-	4	53.20	4.46
130	0	-	-	-	-	-	-	8.20	-	-	-	-	-	-	-	6	54.40	5.65

8.3.2.2 Ground vegetation cover

The ground vegetation cover averaged model fitted the data fairly well (R = 0.85). The averaged model contained four models that included time, harvest intensity, height of major branching, litter depth, soil N, and soil pH (Table 8.3b). Time influenced ground vegetation cover in all post-logging forest time classes. Time positively influenced ground vegetation cover in the 10-year post-logging forest time class (slope = 0.58; CI = 0.31, 0.86), but had a negative influence in the 30- and 50-year post-logging forest time classes (slope = –0.22; CI = –0.3, –0.22, and slope = –0.24; CI = –0.33, –0.16, respectively). The influence of harvest intensity and leaf litter on ground vegetation cover was weakly positive and negative, respectively (slope = 0.02; CI = 0.01, 0.03, and slope = –0.05; CI = –0.08, –0.02). Despite their importance in the averaged model, height of major branching, soil N, and soil pH did not influence ground vegetation (Table 8.4).

8.3.2.3 Canopy height

The averaged model for CH had an exceptionally high fit to the data (R = 0.96), and contained three models that included time, liana abundance, and soil N (Table 8.3c). The influence of time was positive for all logged forest classes. The influence of time on CH was greatest for the 10-year post-logging forest time class (slope = 2.56; CI = 0.25, 0.26) and less for the 30- and 50-year post-logging forest time classes (slope = 0.68; CI = 0.63, 0.73, and slope = 0.74; CI = 0.69, 0.79, respectively). The influence of liana abundance on CH was negative and very weak (slope = 0.03; CI = –0.01, 0.0). Although an important component of the averaged model, soil N had no influence on CH (Table 8.4).

8.3.2.4 Large tree abundance

The tree abundance averaged model showed a strong fit to the data (R = 0.74), and comprised nine models that included time, harvest intensity, distance to nearest unlogged forest, liana abundance, litter depth, slope and soil N (Table 8.3d). However large tree abundance was only strongly influenced at 10 years post-logging (slope = 358.81; CI =10.33, 707.31) (Table 8.4).

8.3.2.5 Treelet abundance

The average LMM for treelet abundance fitted the data reasonably well (R = 0.60), and included nine models. The averaged model included time, harvest intensity, litter depth, and soil N (Table 8.3e). Harvest intensity was the most important predictor in the averaged model, having a positive influence on treelet abundance (slope = 0.5; CI = 0.02, 0.09). Litter depth also had a slightly negative influence on treelet abundance (slope = –0.07; CI = –0.14, –0.01). The influence of time on treelet abundance varied, having a positive influence for the 10-year post-logging forest time class, but a negative influence for the 30- and 50-year post-logging forest time classes (slope = 8.18; CI = 7.27, 9.09, and slope = –0.38; CI = –6.42, –7.25, respectively). Although soil N and the interaction between time and soil N were important predictors in the averaged model, they had no influence on treelet abundance (Table 8.4).

Table 8.4. Summary of important predictors and their influence on keystone structures among logged forests on Kolombangara Island.

Keystone structure	Important predictor	Relative importance	Slope	95%Confidence interval	
Canopy cover	Height of major branching	0.07	-0.02	-0.03	-0.02
	Litter depth	0.08	0.02	0.01	0.04
	Soil nitrogen	0.17	-	-	-
	Time~10 yrs	0.61	0.37	0.2	0.55
	Time~30 yrs	0.61	-0.32	-0.41	-0.22
	Time~50 yrs	0.61	-0.32	-0.41	-0.22
Ground vegetation cover	Basal area harvest	0.16	0.02	0.01	0.03
	Height of major branching	0.01	-	-	-
	Litter depth	0.85	-0.05	-0.08	-0.02
	Soil nitrogen	0.23	-	-	-
	Soil pH	0.02	-	-	-
	Time~10 yrs	0.61	0.58	0.31	0.86
	Time~30 yrs	0.61	-0.22	-0.3	-0.22
	Time~50 yrs	0.61	-0.24	-0.33	-0.16
Canopy height	Liana abundance	0.03	-0.01	-0.01	0
	Soil nitrogen	0.08	-	-	-
	Time~10 yrs	1	2.56	2.5	2.6
	Time~30 yrs	1	0.68	0.63	0.73
	Time~50 yrs	1	0.74	0.69	0.79
Large tree abundance (DBH > 30cm)	Liana abundance	0.53	-0.6	-0.47	-0.05
Treelet abundance (DBH >1cm - 10cm)	Basal area harvest	0.51	0.5	0.02	0.09
	Litter depth	0.04	-0.07	-0.14	0
	Soil nitrogen	0.23	-	-	-
	Soil nitrogen:time	0.05	-	-	-
	Time~10 yrs	0.34	8.18	7.27	9.09
	Time~50 yrs	0.34	-0.38	-6.42	-7.25

8.3.3 Keystone structures during the recovery time

8.3.3.1 Canopy cover

Although the mean canopy cover among forest time classes was highly significant ($F_{3,\,8} = 51.1$; $p < 0.0001$), the post hoc comparisons test revealed only two homogenous groups: (i) the 10-year post-logging forest time class; and (ii) all other forest time classes (Fig. 8.2a). The variation in canopy cover between coupes in each forest time class was relatively low (χ^2 (1, $N = 144$) = 0.763; $p = 0.4$).

8.3.3.2 Ground vegetation cover

ANOVA and Tukey's pairwise tests identified three homogenous groups among which the ground vegetation cover means were highly different ($F_{3,\,8} = 101.7$; $p < 0.0001$): (i) the 10-years post-logging forest time class; (ii) the 30- and 50-years post-logging forest time classes; and (iii) unlogged forests. The ground vegetation cover decreased substantially between the 10- and 30-year post-logging forest time classes, but the decrease thereafter was less (Fig. 8.2b). Coupe variation for ground vegetation cover between coupes of each forest time class was not significant (χ^2 (1, $N = 144$) = 1.9; $p = 0.2$).

8.3.3.3 Canopy height

The mean canopy height significantly differed among all forest time classes ($F_{3,\,8} = 471.6$; $p < 0.0001$). The largest difference occurred between the 10- and 30-year post-logging forest time classes. The differences in means between the 30- and 50-year post-logging forests, and between the latter and unlogged forests, were much smaller but still significantly different (Fig. 8.2c). Canopy height variations among coupes in the same forest time class were not significant (χ^2 (1, $N = 144$) = 1.14e^{-13}; $p = 1$).

8.3.3.4 Large tree abundance

The mean for large tree abundance differed among the various forest time classes ($F_{3,\,8} = 14.9$; $p < 0.0001$). However post hoc test revealed only two homogenous groups between which large tree abundance differed (Fig. 8.2d).

Coupe variation for large tree abundance within each forest time class was relatively higher than mean variation among forest classes (χ^2 (1, *N = 144*) = 2.97; *p* = 0.08).

8.3.3.5 Treelet abundance

There were highly significant differences for the mean treelet abundance among the forest time classes ($F_{3,\,8}$ = 50.9; *p* > 0.0001). The post hoc test revealed three homogenous groups among which means differed (Fig. 8.2e). The 10-year post-logging forest time class had the highest mean (6212.5 stems ha^{-1}), followed by the 30-year (4291.7 stems ha^{-1}) and 50-year (4328.1 stem ha^{-1}) post-logging forest time classes, which had similar means. Unlogged forests had the lowest mean (2798.6 stems ha^{-1}). Variations in treelet abundance between coupes in the same forest time class were fairly low (χ^2 (1, *N = 144*) = 0.06; *p* = 0.8).

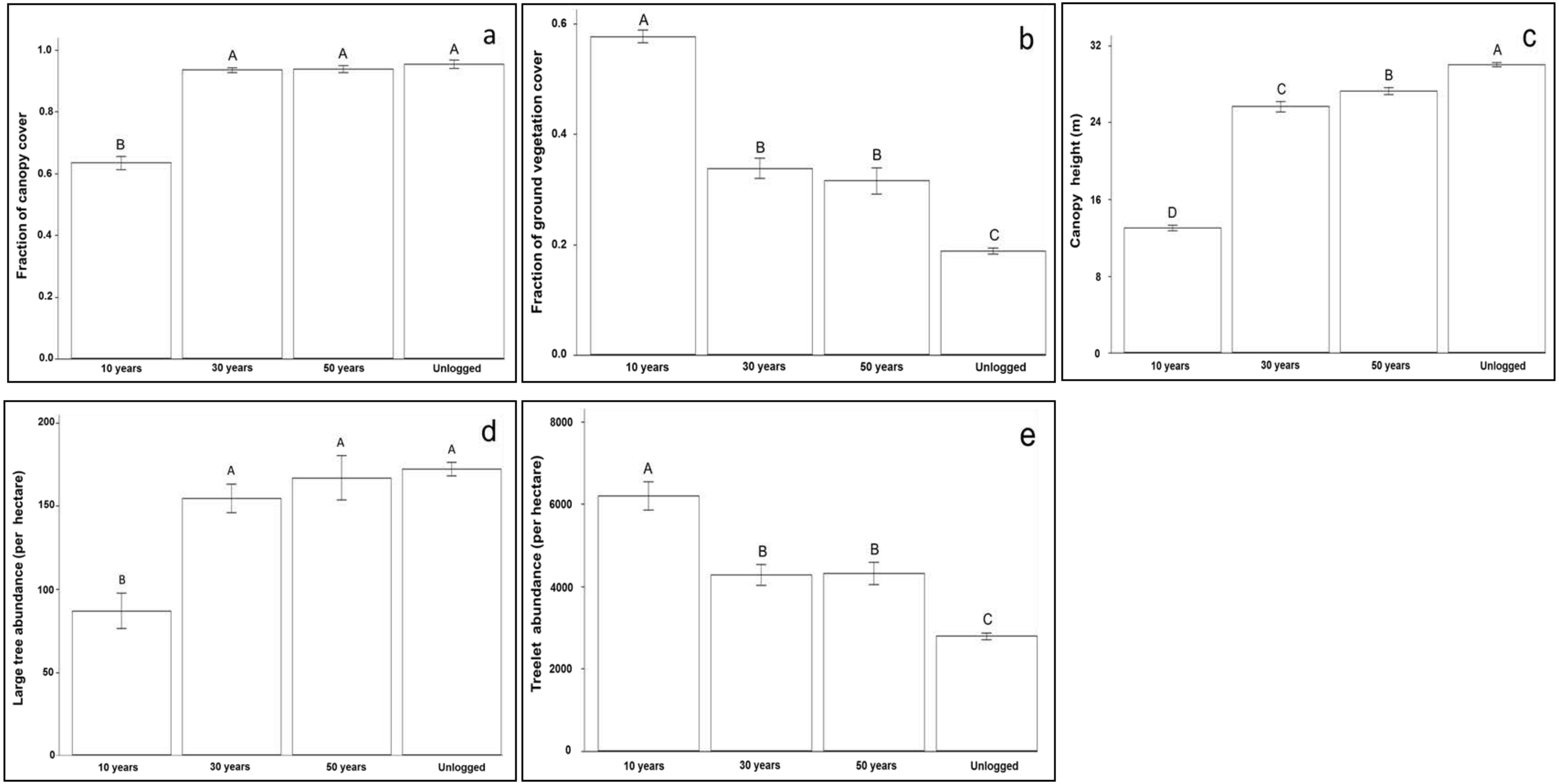

Figure 8.2. Differences in keystone structures among forest time classes. Mean canopy cover and large tree abundance (8.2a & 8.2d) recovered to pre-logging levels between 10 and 30 years post-logging. Ground vegetation cover (8.2b) was much higher in early age classes than unlogged, while canopy height (8.2c), and treelet abundance (8.2e) did not recover to pre-logging levels within 50 years of post-logging regeneration.

8.4 DISCUSSION

In the lowland forests of Kolombangara Island, we discovered that three keystone structures had not recovered within 50 years since the cessation of logging. Our results also revealed that harvest intensity, liana abundance, soil and tree attributes were more important than topographical factors in influencing the recovery of keystone structures over time (Table 8.4).

8.4.1 Canopy cover

Based on our estimates of canopy cover, logged forests on Kolombangara Island appear to return to pre-logging levels of canopy cover after 30 years of natural regeneration (Fig. 8.2a). The effects of logging on the forest canopy structure, however, can be long term as demonstrated in Gola Rainforest National Park, Sierra Leone, West Africa, where logged forests maintained a high percentage of canopy cover despite decades of post-logging regeneration (Kent et al. 2015). The most likely explanation for these disparate regeneration results is differences in species composition, the level of tree recruitment and mortality during succession, and climate (Clark et al. 2015). For example, the recovery of canopy cover to pre-logging levels in this study was largely because of high levels of tree recruitment in logging gaps (Shenkin et al. 2015). The proliferation and long-term dominance of large-crown species including *Campnosperma brevipetiolata* contributed strongly to the recovery of the logged forest canopy (Katovai et al. 2016). Lateral branching and crown extension of adjacent trees also contributed to canopy closure (Meng et al. 2006).There were distinct temporal patterns in canopy recovery post logging. The positive influence on canopy cover at 10 years post-logging was largely because of the turnover between fast growing short-lived pioneers and mid-succession species (Katovai et al. 2016). The marked negative change in canopy cover across 30 and 50 years post-logging suggests that the establishment and growth of long-lived pioneers and late succession species was supplemented by only minimal forest turnover (Weduex et al. 2015; Katovai et al. 2016). It also suggests that the impact of natural disturbances, including extreme weather, was similar in the two forest classes during the intervening 20-year time period. Cyclonic events more than four decades ago caused major damage to the canopy structure on Kolombangara Island (Burslem et al. 2000). The absence of cyclones affecting the island since 1970 has enabled the canopy structure to recover in logged forests.

As logged forests recover, the height of major branching changes due to species recruitment which subsequently influences canopy cover (Katovai et al. 2016). The early stages of succession in the logged forests on Kolombangara Island are largely dominated by *Macaranga dioica* and *C. brevipetiolata* (Katovai et al. 2016). *M. dioica* is a fast growing pioneer that typically colonizes logged forests within a few years post-logging, and remains dominant for > 10 years (Sancayaningsih and Bait 2015; Katovai et al. 2016). This species is shorter than later succession specialists, with major branching occurring at a mean height of ~7 m. Canopy cover in *M. dioica*-dominated stands is usually high because each tree has a narrow irregular crown that produces a relatively thin canopy cover (Silvestrini and Santos 2015). It was also observed that canopy gaps between the crowns of adjacent trees in these forests were fairly high, hence contributing to high canopy cover values.

C. brevipetiolata is a long-lived pioneer, but has similar tree architecture to that of *M. dioica* within the first 10 years post logging (Sheely and Meagher 1996;

Bayliss-Smith et al. 2003). However, its canopy size increases with tree height, leading to adult trees having large spreading crowns, thereby reducing the canopy cover between trees in 30- and 50-year post-logging forests, in which *C. brevipetiolata* is very dominant (Sheely and Meagher 1996; Shenkin et al. 2015; Katovai et al. 2016). The mean height of major branching in adult *C. brevipetiolata* was approximately 17 m above ground level. Therefore, marked variation in tree architecture and the time to dominance of these two species during succession explain how their height of major branching affects canopy cover.

The positive effect of litter depth on canopy cover suggests that an influx secondary forest species in logged forests on Kolombangara have resulted in an increased leaf exchange. This is particularly true for pioneer species in wet environments to ensure their leaves are in full light (Zhang et al. 2015). Prior to logging, the primary forests on the island were classified as mixed evergreen (Whitmore 1969). Seasonal loss of leaves by occasional deciduous trees within these forests would have a trivial effect on the canopy structure (Parthasarathy et al. 2008). However, environmental changes caused by logging in these forests have enabled the establishment of fast growing pioneers and secondary forest specialists (Aoyagi et al. 2013; Katovai et al. 2016). Litter fall from the dominant pioneer species, including *M. dioica and C. brevipetiolata*, may have largely contributed to the positive effect.

Although soil N did not have a marked influence on canopy cover in regenerating forests on Kolombangara Island, its inclusion in the model highlights the importance of soil macronutrients to plant growth and structural development during post-logging succession (Sancayaningsih and Bait 2015). However, several studies have shown that the levels of macronutrients (including soil N) are usually reduced by fast-growing pioneer trees (Olander et al. 2005; Aoyagi et al. 2013; Sancayaningsih and Bait 2015). Therefore, the results of this study suggest that the influence of soil N on canopy cover may have been confounded by the increased leaf turnover (Aoyagi et al. 2013). Furthermore, soil compaction associated with logging may have reduced soil microbial activities, and so lowered macronutrient turnover rates (Hartmann et al. 2014; Spake et al. 2015). The influence of soil N may become more pronounced as the forest composition progressively returns to evergreen species, as the atmospheric deposition of N is usually high in mature evergreen forests (Liu et al. 2014; Rennenberg and Dannenmann 2015). Furthermore, the fluctuation of soil N levels in logged forests during early succession may be a potential indicator of post-logging recovery.

8.4.2 Ground vegetation cover

Post-logging recovery for 50 years was insufficient for the cover of ground vegetation to decline to pre-logging levels (Fig. 8.2b). Extensive increases in the light levels reaching the forest floor during logging favors the proliferation of light-demanding shrubs and trees (Frederickson and Putz 2003; Katovai et al. 2012). This is a natural phenomenon in gap phase regeneration, and strongly influences ground vegetation cover (Sapkota and Oden 2009; Katovai and Katovai 2012). The positive influence of harvest intensity in the average model for ground-vegetation cover suggests that soil compaction may have not limited ground vegetation cover. The negative influence of litter depth on ground vegetation cover however suggests that the litter depth may have prevented the emergence and establishment of pioneer seedlings in the logged forests (Kostel-Hughes et al. 2005). The inclusion of canopy openness, soil N, and soil pH in the ground vegetation cover model indicates the importance of soil and canopy structure in vegetation recovery in logged forests (Peña-Claros et al., 2012). For instance, their positive influence on ground vegetation cover in the 10-year post-logging forests evidently resulted from high levels of radiation reaching the forest floor because of the high canopy openness (Katovai and Katovai 2012), whereas the high levels of macronutrients (Kostel-Hughes et al. 2005; Sancayaningsih and Bait 2015) and shallow litter depth facilitated the emergence and establishment of early pioneer species. Their negative influence in the 30- and 50-year post-logging forests may indicate significant recovery of the forest canopy, and a reduction in macronutrients by early colonizers (Olander et al. 2005).

8.4.3 Canopy height

Even after 50 years post-logging canopy height has not recovered in the logged forests of Kolombangara Island (Fig. 8.2c). Studies in Brazil and Malaysia have reported similar findings, and concluded that canopy structural development in logged forests is a very gradual process (Okuda et al. 2003; Villela et al. 2006). The finding in this study that canopy height increases with time since logging suggests that recovery to pre-logging levels is possible if these forests are protected from further logging. However, with re-entry logging seemingly inevitable in the Solomon Islands, the chance of full recovery is very slim (Katovai et al. 2015a). While the canopy height averaged model revealed that the growth rate of trees was higher in the 10-year post-logging forests than in the other post-logging time classes, it also highlights the negative impact of liana abundance on canopy height. Liana abundance is remarkably high in logged forests in the Solomon Islands. A previous study on Kolombangara Island concluded that high levels of canopy loss resulting from high intensity harvesting on the island led to a hyper-abundance of *Convolvulus* spp. climbers, which may arrest forest regrowth (Neil 1984). However, mounting evidence suggests that lianas play a vital role in the cycling and relocation of nutrients in tropical forests (Tang et al. 2011; Campbell et al. 2015). Although the influence of soil N on canopy height cannot be determined from the model output, its inclusion may indicate the importance of liana abundance in nutrient cycling within logged forests.

8.4.4 Large tree abundance (DBH > 30 cm)

The homogeneity in mean large tree abundance in the 30 years, 50 years and unlogged forest classes suggests that on Kolombangara Island the tree stand density in these forests reached saturation levels during the early stages of recovery (Fig. 8.2d). The consistently high abundance of large trees among the post-logging forest time classes may also indicate a relatively rapid turnover time between pioneers and late succession specialists (Katovai et al. 2016); the high level of recruitment of climax species in the understory of these forests may have facilitated this rapid turnover (Katovai et al. 2012). Although the predictors included in the large tree averaged *LMM* model did not show a pronounced effect on large-tree abundance, these predictors were vital for determining growth, particularly in early stages of regeneration (Table 8.3d).

8.4.5 Treelet abundance (DBH = 1–10cm)

Logging has had an important effect on the community composition of small trees on Kolombangara Island. Treelet abundance doubled in recently logged forests and remained at elevated levels in forest 50 years post logging. Because of the high intensity harvesting that occurred on the island (Katovai et al. 2015a), numerous large forest gaps were created in the logged landscape, which enabled high light intensities to reach the understory (Katovai and Katovai 2012). Light enhancement subsequently triggered the proliferation of fast growing, short-lived pioneers during early succession, particularly *M. dioica* (Sheely and Meagher 1996; Katovai et al. 2016). The high level of mortality of this species that occurred between 10 and 30 years in the post-logging forests occurred because of decreasing light levels associated with the progressive recovery of the forest canopy (discussed in chapter 6). The decline in treelet abundance was also affected by the low rates of recruitment of climax species (Katovai et al. 2012; Pessoa and Araujo 2014).

The similar mean values for treelet abundance in the 30- and 50-year post-logging forest time classes may indicate that the natural thinning is very slow. The process may take more than a century to reach a state of dynamic equilibrium (Pessoa and Araujo 2014). Treelet abundance in these forests was significantly higher than in logged forests because of the persistence of long-lived pioneers during succession (Katovai et al. 2016). This pattern of species co-existence usually occurs in forests subject to ongoing disturbance because of geological volatility and extreme weather (Whitmore 1989b; Burslem et al. 2000). The occurrence of regular strong winds, sporadic earthquakes, and landslides on Kolombangara Island may have resulted in a succession whereby long-lived pioneers can persist (Whitmore 1989b; Katovai et al. 2012; 2016). Nevertheless, the low treelet abundance value in unlogged forests suggests that long-lived pioneer stands will continue to decline over time as the gradual shift in understory microclimate increasingly favors climax species (Scheffer and Carpenter 2003). Indeed treelet abundance may never return to pre-logging levels because of the increasing frequency and intensity of severe weather across Oceania, as a result of global warming. Regardless of which successional trajectory pattern plays out on Kolombangara Island, the results of this study indicate that the legacy of logging on small understory trees is long term in nature.

8.5 CONCLUSIONS

Half of a century of post-logging regeneration has been insufficient for full structural recovery of logged forests on Kolombangara Island, Solomon Islands. Nevertheless, the structural attributes in the regenerating forests may support high levels of biodiversity. Recovery of the canopy structure to pre-logging levels within 50 years post-logging may have facilitated the restoration of biodiversity to levels similar to that in unlogged forests (Gao et al. 2014). Similarly, the comparable levels of large tree abundance in logged and unlogged forests suggest that tree recruitment and mortality patterns in logged forest landscapes might maintain ecological functions able to sustain high levels of biodiversity (Manning et al. 2006). The high levels of ground vegetation cover and treelet abundance in regenerating post-logging forests may favor ground dwelling animals and the recruitment of climax plant species, and so increase understory biodiversity (Katovai et al. 2012). Although the mean canopy height level was lower in the post-logging forests, its large increase with time after logging suggests that biodiversity levels may eventually recover to pre-logging levels (Gillison et al. 2013), provided that further logging or other intensive land-use activities do not occur.

This study also showed that only soil attributes, harvest intensity, and tree architecture influenced post-logging changes among the regenerating post-logging forests. This finding is critical to both preemptive and remedial measures aimed at ensuring that the structural integrity of logged forests is restored, either through natural regeneration or human-assisted restoration. However, unlike harvest intensity and soil attributes, tree architectural attributes are influenced by several complex environmental and genetic factors, the individual effects of which are difficult to distinguish (Ishii et al. 2007; Zytynska et al. 2011). Therefore, the manipulation of tree architecture to aid restoration remains challenging.

8.6 CHAPTER SUMMARY

- This chapter examined factors that influenced recovery of several forest keystone structures across 50 years of post-logging regeneration in wet tropical forests of Kolombangara, Solomon Islands.
- The impacts of logging on forest structure can persist for extensive periods, especially in heavily logged forests. However, little is known about the legacy of logging on structural recovery in tropical forests, especially in Oceania.
- The results revealed that half a century of post-logging regeneration has been insufficient for full structural recovery of logged forests on Kolombangara Island. The results also revealed that proxies of logging, soil and tree attributes were more important than topographical factors in influencing the recovery of keystone structures over time.

- Based on these results, it can be concluded that selective logging practices in the Solomon Islands must be regulated much more carefully than they have been in the past. Otherwise, logged forests will never achieve anything approaching full structural recovery.

The impacts of logging on forest structure in the Solomon Islands are long-term in nature.

Photograph by Eric Katovai 2013

CHAPTER 9

POTENTIAL RESTORATION APPROACHES FOR HEAVILY LOGGED TROPICAL FORESTS: A ‘ONE–STOP SHOP’ FOR RESTORATION PRACTITIONERS

Eric Katovai, Dawnie D. Katovai, William F. Laurance

This manuscript is in preparation for submission to *Restoration Ecology*:

Chapter overview:

This chapter presents restoration approaches that can potentially be used to assist the regeneration of heavily logged tropical forests.

Contribution to thesis:

This chapter attempts to address objective No. 8 of this thesis, which is to highlight potential restoration approaches for logged tropical forests.

9.1 INTRODUCTION

Tropical countries are mostly of low socio-economic status and are often heavily reliant on export earnings from industrial logging (Fig. 9.1). In the tropics logging practices are mostly selective whereby trees are harvested based on tree-size and species preferences (Katovai et al. 2015). However, unregulated logging practices in poor tropical countries have contributed immensely to the degradation of tropical forests within the last century (FAO 2015; Katovai et al. 2015; Sloan and Sawyer 2015). This may have also led to the deforestation of large forest patches within logging concessions that result from the establishment of log, machinery and fuel storage, logging camps and dense networks of roads and skidding trails (Johns et al. 1996; Marsden 1998; Katovai et al. 2016). In heavily or repeatedly logged forests, damage incurred from tree harvest and the aforementioned land-uses can be so intense that natural regeneration may not allow for floristic and functional recovery to pre–cut levels. In spite of many concerns about past and current logging practices, and proposals to address this problem through remedial and preventative actions, little has been achieved in this frontier (Terborgh 2000; Corlett, 2012; Laurance et al. 2011, 2012).

In the last two decades, restoration efforts have transitioned from the experimental stage whereby numerous ideas were tested for their practicality on relatively small patches of disturbed area (Lamb et al. 2005; Barry et al. 2010) to full scale implementations in degraded landscapes (Chazdon 2008; Schwartz et al. 2013). Although large-scale reforestation in such landscapes has increased forest cover in some tropical countries, it is uncertain that restored forests can resemble pre-disturbed conditions (Chazdon 2008; Lamb et al. 2012; Katovai et al. 2015a). This chapter provides a ‘one-stop shop’ for forest restoration practitioners. Here we outline restoration approaches that have been successfully implemented in degraded tropical landscapes that can potentially assist the recovery of intensively logged forests.

Source: https://www.flickr.com

Source: Katovai et al. 2015

Figure 9.1. (A) Logged forest (left) and unlogged forest (far right) in Eastern Kalimantan, Indonesia, and (B) Logged forest in Vella la vella, Solomon Islands.

9.2 A 'ONE–STOP SHOP' FOR TROPICAL FOREST RESTORATION

Forest restoration activities have been broadly categorised into passive and active restoration. Passive restoration involves the elimination of environmental stressors (e.g. industrial logging, agriculture and human-lit fires) that may hamper natural restoration process, thereby allowing natural regeneration to proceed. Although passive restoration has been widely practised in past forest management efforts, prior studies have suggested that intense human disturbances frequently result in loss of species diversity, particularly species of the late successional stage (Chazdon 2003; Meijaard and Sheil 2008). In contrast, active restoration strategies (see Fig. 9.2.) seek to promote recovery particularly in heavily degraded forests or lands (Morrison and Lindell 2011). To obtain optimum results, restoration efforts must include a combination of strategies based upon careful consideration of prevailing environmental conditions, as well as the eco-physiological needs of the recovering vegetation (Cooke and Suski 2008).

9.2.1 Natural regeneration

Restoration in forest gaps is vital for the sustainability and livelihood of the forest. However, the question remains, how comparable will the restored forest be to the pre-disturbed stand in terms of its ecological and biological values? There is no universal answer to this question as forest and gap dynamics vary spatially and temporally (Wright 2005). A recent study by Chazdon et al. (2016) argued that natural unaided regeneration is often the most realistic and cost-effective method to promote forest regeneration across much of the tropics. To understand how gap dynamics influence the process of regeneration, let us consider the synergies of four primary sources that determine the quality of natural regeneration in gaps. Each of these factors varies in their role in gap regeneration.

9.2.1.1 Regeneration of pre-existing forest vegetation

Regeneration of pre-existing forest species that have survived following a disturbance may benefit from the influx of light penetrating through treefall gaps. These species may include juveniles of climax species that dominate the canopy prior to disturbance, which are in dormancy in the undergrowth awaiting an appropriate environment to flourish (Denslow and Hartshorn 1994; Denslow et al. 2001). Gap re-growth represents an amalgamation of shade-intolerant pioneers and shade-tolerant plants. Yet due to the complexities of vegetation responses and the lack of detailed information, regeneration of pre-existing forest vegetation (termed "advanced regeneration") remains excluded from gap dynamic models (Loehle 2000; Dietze and Clark 2008).

9.2.1.2 Germination from the soil seed bank

Germination from the soil seed bank is important for gap regeneration and diversification. Prior studies have shown that this natural process occurs in forests in response to availability of light, with seed germination triggered by certain light wavelengths that result from direct sunlight (Brokaw and Busing 2000; Ru¨ger et al. 2011). On the contrary, not all forest stands possess seed banks capable of dormancy for extended periods of time. For instance, a study of 18 climax species on Barro Colorado Island showed no dormancy capability (Augspurger 1984). The lack of pioneers in the Bornian heath forest is another classic example (Whitmore and Hadley 1991). It is also important to note that by definition forest gap dynamics is not applicable to all forest stands as the concept revolves around sapling growth from seed banks. Much is still unknown about the temporal and spatial scale of seed-banks in tropical forests.

9.2.1.3 Sprouting from cut or crushed roots and stems

Sprouting from cut or crushed roots and stems also plays an important role in gap regeneration (Dietze and Clark 2008). In cases where seed bank regeneration does not occur, sprouting re-growth will dominate the gap restoration phase. Therefore, it is very likely that species composition at the early gap phase regeneration will resemble the pre-existing flora, but having a lower floral diversity as not all pre-disturbance species would survive through the disturbance regime (Dietze and Clark 2008).

9.2.1.4 Seed rain

The fourth source of regeneration is termed ‘seed rain,’ which is a practical description of how seeds disperse into a gap via vectors such as animals, particularly frugivorous birds and bats (Ceccon and Hernández 2009) but also including some scansorial animals such as mammals and ants. The role of birds in re-seeding degraded forests in the tropics has been well documented (Pejchar et al. 2008; Graham and Page 2012; Reid et al. 2012). A widely anticipated challenge in tropical forest regeneration, particularly in heavily degraded landscapes, is the lack of seed diversity to permit the latter stages of regeneration and succession (Chazdon 2008; Budiharta et al. 2014). Numerous studies have since focused on ways to actively restore degraded forests through appropriate reseeding approaches (e.g. Chazdon 2008; Cole et al. 2010; Graham and Page 2012). Through these efforts, a range of approaches have been developed and trialled, some of which have shown considerable success (Fig. 9.2).

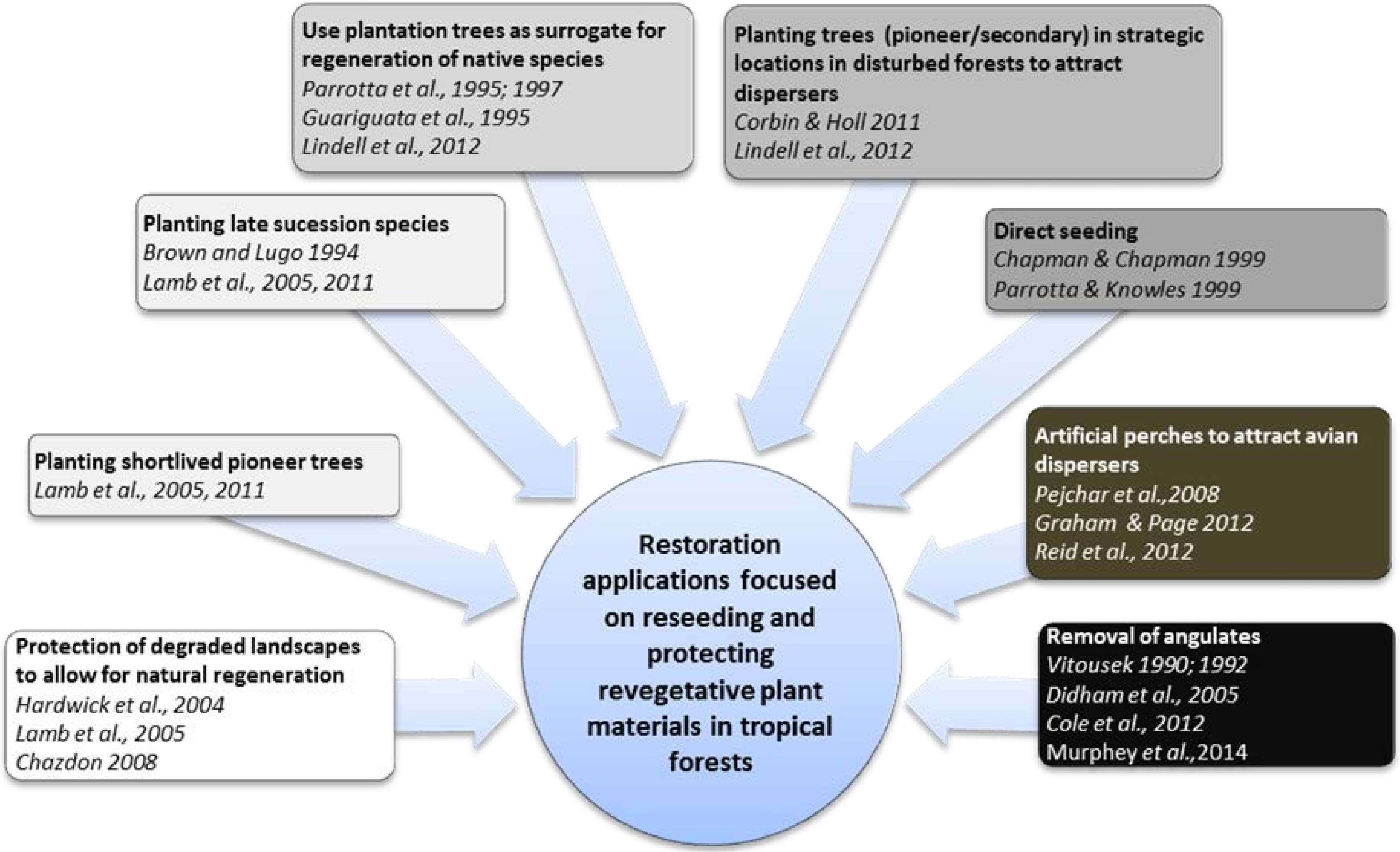

Figure 9.2. Ecological restoration approaches widely used in tropical forests. An integrated approach whereby several techniques are implemented concurrently can potentially aid success in highly degraded forests.

9.2.2 Protection of logged forest landscapes to enhance natural regeneration

It is evident that forest restoration through natural regeneration can be improved by protecting previously logged forests (Margules et al. 2000, 2002; Chazdon 2008; Laurance and Edwards 2014; Chazdon et al. 2016). The inclusion of adjacent undisturbed forest in these protected zones is important for provisioning an influx of seeds and faunal seed dispersers (Chazdon 2008). This strategy is feasible for areas where forests are not entirely cleared; hence leaving fragmented patches of forests capable of producing seeds that would then be vectored into forest gaps by animals or natural dispersal processes (Lamb et al. 2005). Nevertheless, forest recovery through this approach may fail in heavily logged landscapes if the system has crossed an ecological threshold that inhibits the perseverance and proliferation of forest species (Hobbs et al. 2006), or if logged forests are severely hunted or burned leading to defaunation or further forest degradation. Exceeding this ecological threshold limits natural regeneration to an altered climax state, generally associated with light-demanding vegetation (Lamb et al. 2005). For example, the loss of topsoil and/or increased soil compaction associated with heavy logging equipment hinders the establishment and growth of late successional vegetation resulting in the high influx of non-tree and other invasive non-forest species (Vieira and Scariot 2006). Such floristic change increases the risk of wildfires, consequently reducing woody plant recruitment and favouring the proliferation of grasses and other fire-tolerant vegetation (Lamb et al. 2005; 2011). Many examples of extensive grasslands that persist over time despite being entirely surrounded by forests are evident throughout the tropics (e.g. Connell 1978; Zanne and Chapman 2001; Maeto et al. 2009).

9.2.3 Restoration approaches for highly degraded forests

9.2.3.1 Tree planting approaches

In cases where unaided recovery is not possible for logged forest landscapes, several restoration strategies have been proposed. Most studies on tropical forest restoration have highlighted three broad approaches by which floral diversity can be actively restored. These are centred on the concept of restoration through planting. Though an expensive and in most cases an extensive exercise, restoration planting has been proven successful in a enumber of empirical studies (e.g. Parrotta et al. 1999; Chazdon 2008; Cole et al. 2010; Lamb et al. 2011).

The first approach includes restoration plantings using several pioneer ephemeral nurse trees. The early establishment and rapid growth of nurse trees usually shade off light-demanding non-tree vegetation including grasses and other undesirable alien species (Lamb et al. 2005). This effect creates a favourable environment for the regeneration of secondary forest species, some of which lay dormant in the topsoil awaiting the right conditions for germination (Gómez-Aparicio et al. 2004; Lamb et al. 2005).

A second approach involves planting a range of species from later successional stages that improves the chances for a species-rich climax stand (Aerts and Honnay 2011; Cole et al. 2011). This approach is particularly useful in the event where the soil seedbank has few live seeds of late successional species. The resultant species and structural assemblage of the restored community heavily depends on the variety and viability of the introduced seeds, and therefore can be pre-determined to a certain extant (Cole et al. 2011). Where seed collection is done within the proximity of the logged forests, local knowledge is vital when selecting native species for re-seeding as this ensures that the restored forest has high value for forest-dependent communities (Suárez et al. 2012).

The third approach involves planting commercial tree species on deforested landscapes. Tree plantations can offer restoration values for native understory vegetation (Parrotta et al. 1995; 1999; Guariguata et al. 1995; Lindell et al. 2012). For instance, the germination and establishment of late successional species are potentially enhanced by planting commercial trees, as they shade off light-demanding pioneer competitors such as lianas and woody shrubs (Guariguata and Ostertag 2001). The soil may also aid restoration via high nutrient levels retained from the decomposition of pre-existing vegetation. The range of seed dispersers attracted to tree plantations may also aid in the rejuvenation in the topsoil, enhancing successful restoration of understory native vegetation (Parrotta et al. 1995, 1999; Katovai et al. 2012).

Despite the restoration values that tree plantations offer, the development of many tree plantations in the tropics is influenced solely by economic considerations. Many commercial plantations have been converted from large forest areas that had previously been cleared for agriculture and cattle ranching (Chazdon 2008). Successful efforts in restoring heavily degrading landscapes by tree plantations depend entirely on future management strategies. Current strategies such as cyclic clearfelling and replanting strategies prevailing in many tropical regions need to be re-assessed. The effects of this process on the regeneration of native vegetation are still unknown. However, it may be suggested that further degradation of soil seedbanks may result from repeated mechanical disturbances during the process of harvesting and extraction of logs, and soil clearing during preparation for replanting.

Nucleation may be an alternative approach in restoring heavily degraded landscapes. This strategy involves planting small clusters of selected tree species (sometimes termed “framework tree species”; Goosem and Tucker 2014) within the degraded site and allowing them to disperse as well as attract seed dispersers, subsequently increasing seed rain into the disturbed landscape (Corbin and Holl 2012; Lindell et al. 2012; Goosem and Tucker 2014). This approach was successful with bird dispersers but not for larger mammalian seed dispersers (Corbin and Holl 2012). Although implementation of this approach is relatively inexpensive, restoration efforts may be impractical or too expensive at large spatial scales (Corbin and Holl 2012). However, there are still gaps in our understanding of the optimal design and long-term viability of such approaches (Corbin and Holl 2012; Lindell et al. 2012).

9.2.3.2 Direct seeding

Direct seeding is an approach that involves dispersing seeds directly within disturbed landscapes. Such an approach requires a greater number of seed species of more mature successional stages (Lamb et al. 2005). Planting usually requires high densities (e.g. 92,500 seeds per hectare; Parrotta 1995). The climax forest stand depicted in this approach is practically a function of the competitive interactions among the seedlings as they grow and mature. Ideally, this approach resembles a degraded forestland with an initial seed bank that, given the appropriate conditions, will undergo successful regeneration. The number of species that can be successfully established by direct seedling is limited by seed supply, although establishment costs may be lower than other approaches. Reforestation of open fields under appropriate conditions is possible (e.g. with the control of grasses or other competing species); however, it may be most useful in enhancing diversity where some tree cover is already present (Lamb et al. 2005). This approach is not as versatile as those previously discussed as ecophysiological conditions needed for initial germination are often narrowly specific because most seeds of climax species only germinate and dominate in the late successional stages.

9.2.3.3 Artificial perches

The most important seed dispersers in tropical forests are birds, which are responsible for dispersing >50% of trees across forested landscapes (Corlett 2007; Graham and Page 2012). Hence, an approach that is widely used to maximise seed dispersal into degraded sites is the erection of artificial perches. Birds are known to use tall trees on gap edges for perching; by increasing artificial perches in gaps, bird colonization, and seed populations and diversity are increased, particularly under the perches (Pejchar et al. 2008). Although seed recruitment has been enhanced through artificial perches, the composition of seed rain largely depends on the foraging sites of visiting dispersers, which may include degraded forest sites, as evident in a recent study in Indonesian peat swamp forests (e.g. Graham and Page 2012). Studies have also shown that seed recruitment into degraded forests is coupled with the structural complexity within a given degraded environment, whereby simple environs such as abandoned grazed pastures usually have lower zoochorous recruitment than more complex environs (Pejchar et al. 2008; Graham and Page 2012; Reid et al. 2012).

9.2.3.4 Removal of ungulates

Removal of ungulates from restoration sites is complimentary to both natural and assisted regeneration. Studies have shown that non-native ungulates can supress regeneration in the forest understory through rooting, trampling and browsing of plant materials above and within the topsoil (Ickes et al. 2001; Didham et al. 2005; Cole et al. 2012). Areas with a high population density of native ungulates may also produce the same effect (Cole et al. 2012). In contrast, the absence of ungulates may result in the high proliferation of invasive non-native plants, subsequently changing the vegetation structure of restored forests (Cole et al. 2012). Before embracing this approach, it is necessary to take into account the ecological importance of ungulates within the ecosystem.

9.3 CONCLUSIONS

We have outlined various restoration approaches that have been successfully trialed in tropical landscapes. When anticipating a restoration action plan, the choice of restoration approaches must be strongly influenced by the intensity and spatial extent of forest damage. Physiological metrics (e.g., gas exchange, energy transfer and metabolism, stress response, nutritional condition) can potentially provide ecological information to help guide the development and execution of these action plans (Cooke and Suski 2008). Although some stand-alone practices have been successful, we strongly suggest that an amalgamation of carefully selected approaches is applied to any restoration effort. Such an integrative approach may achieve better outcomes and perhaps be more economically viable than stand-alone efforts. With increasing land-use intensification across the tropics, the need for landscape-scale restoration will certainly grow. It is therefore critical that forest restoration models and policies pertaining to their implementations be developed, particularly for poorer tropical countries where the impacts of anthropogenic land use on forest landscapes are colossal (Chazdon et al. 2016). Establishing these mechanisms may potentially assist in the successful restoration of tropical forest threatened by escalating anthropogenic encroachment.

9.4 CHAPTER SUMMARY

- Forest restoration in poor tropical regions is becoming nearly inevitable because economic pressures have driven forest degradation to extreme levels. Damage caused by industrial logging on tropical forests is reaching threshold levels whereby natural regeneration may be insufficient to aid full recovery of biological and functional diversity to pre–cut levels.
- This paper presents a ‘one–stop shop’ for forest restoration practitioners. Here forest restoration approaches that have been successfully implemented in tropical forests are highlighted.
- An integrative approach is recommended whereby forest restoration techniques are amalgamated for potentially better outcomes in intensively logged forests.

Intensively logged forests are likely to require human assistance to aid the recovery of ecological functions and biodiversity

Photograph by Eric Katovai 2013

CHAPTER 10

GENERAL DISCUSSION

Eric Katovai

Chapter overview:

This chapter presents a general discussion summarising key findings in chapters 2–9. It describes the extent to which logged forests on Kolombangara in the Solomon Islands have recovered via natural regeneration. It then highlights logging research in Melanesia in light of findings from this study, and ends with conclusions and recommendations to more effectively manage logged forests in the Solomon Islands and beyond.

Contribution to thesis:

This chapter provides a general summary of work covered in this thesis and its key implications for forest management.

10.1 SIGNIFICANCE OF THIS THESIS TO LOGGING RESEARCH IN MELANESIA

Oceanic islands of Melanesia, particularly New Guinea and the Bismarck-Solomon Archipelago, are known for their exceptionally rich biodiversity and highly varied forests. This region sustains about 7% of global biodiversity while spanning 1% of the global land area (Shearman and Bryan 2011; Katovai et al. 2015b). This rich biodiversity conceivably stemmed from high levels of local endemism prompted by isolation via (i) the geographical distribution and remoteness of these islands from mainland tropical areas (Gillespie et al. 2008) and (ii) highly varied landscapes due to past geological activities, as discussed in Chapter 2. Published research conducted in the Solomon Islands revealed a mean endemic plant biodiversity of about 50% in the archipelago (e.g. Hancock and Henderson 1988; Flannery 1995; Mayr and Diamond 2001; Pikacha et al. 2008; Katovai et al. 2016). Yet much of the Solomon Islands are still understudied, thereby suggesting that endemism estimates in this region will potentially increase as more information on biodiversity becomes available.

The remoteness of islands across the Solomons made accessibility fairly challenging, costly and time-consuming in the past (Whitmore 1989b; Bayllis-Smith et al. 2003). Nevertheless, improved infrastructures aiding better communication and transportation to remote locations has resulted in a marked increase in recent biological research. Much of these research efforts were focused on biodiversity discovery (Marinov and Pikacha 2013; Keith et al. 2016), the cultural value of biodiversity (Morrison and Lindell 2008; Pollard et al. 2014) and invasive species (Pikacha et al. 2015) to aid pre-emptive approaches for conserving pristine environments in the region. Such efforts are crucial to save the remaining patches of accessible forests untouched by decades of heavy logging.

Research on remedial approaches to forest conservation and management are equally important given that most of the accessible forests in the Solomons were severely degraded by logging (Katovai et al. 2015). However, the only remedial effort initiated in the Solomons to date is agroforestry. Agroforestry research has long been conducted in the region, particularly in heavily logged or cleared landscapes to restore forest cover and provide economic and social benefits for local residents through harvesting timber and non-timber forest products (Katovai et al. 2015; Walters and Lyons 2016). However, recurrent harvesting in agroforestry landscapes does not usually facilitate ecological and biological recovery (Asase et al. 2014; Katovai et al. 2016). For this reason, understanding the dynamics of regeneration and recovery in logged forests is crucial for designing appropriate remedial measures for the region. Prior to this thesis, almost nothing had been has been documented on the natural regeneration and recovery of logged forests in the Solomon Islands. In particular, it was unclear whether logged forests in the Solomons could regenerate under natural conditions, or would require management interventions in order to recover their original structure, biodiversity, ecological functioning and carbon storage.

10.2 LOGGING IN THE SOLOMON ISLANDS: A DAUNTING REALITY

This review documents gap-phase regeneration theory as a generic process and how various factors can affect regeneration of logged forest gaps. It is clear that the regeneration process varies among forest types across the tropics. These variations are linked to the type of disturbance mechanism, its intensity and frequency.

In Chapter 3, differences in gap-phase regeneration between natural and human disturbance were assessed and it was concluded that naturally induced forest gaps can fully recover their original floristic diversity within several years. Human-induced gaps, however, are more variable in size and the extent of soil disturbance than natural gaps. If gaps are large and/or soils and their seed banks are heavily damaged, forest recovery may require much longer periods of time. In some cases, silvicultural or reforestation efforts could be needed to facilitate forest recovery. In Chapter 4, logging practices in the Solomons are discussed and it is argued that such practices have, on the whole, been unsustainable in terms of timber supplies and forest damage. With the current dynamics of logging in the Solomon Islands, timber stocks in the country could be depleted within the next decade as logging operations encroach into the last tracts of accessible forest.

10.3 DYNAMICS OF POST-LOGGING REGENERATION AND RECOVERY IN SOLOMON ISLANDS

Chapters 5–8 of this thesis contained the first detailed studies of the dynamics of post-logging regeneration and recovery in Solomon Islands and even within Melanesia. Results from this work suggests that many logged forests in the Solomon Islands have been heavily degraded and could require active intervention to permit full recovery of forest structure, composition and carbon stocks. The results in Chapter 5 indicated that that tree composition in logged forests on Kolombangara did not recover to pre-cut levels even after 50 years of natural regeneration. Logging roads and the distance of propagule sources from unlogged forests were the most important factors influencing the recovery of tree diversity and composition in logged forests. These forests were dominated by light-demanding tree species, some of which were long-lived. The recovery of primary-forest species have been hampered by the dominance of these long-lived pioneers, particularly *Campnosperma brevipetiolata*. We proposed, finally, that human intervention will likely be required to ensure full recovery of tree diversity and composition in logged forest of Kolombangara.

The findings in Chapter 6 reveal that the influence of light on plant functional types across logged forests of varying ages can be effectively examined at the plant-trait level. The immediate challenge for this application is to determine which plant functional types are the most sensitive to elevated light levels during the recovery process. Identifying the most sensitive plant functional types and corresponding sets of plant-trait elements would significantly improve the accuracy of future predictions of logging impacts and forest recovery dynamics. The results in Chapter 6 also revealed that the functional diversity of understory plant communities are highly resilient and can quickly rebound to pre-cut levels despite intensive logging. Because species composition of understory plant communities are highly similar among forest classes (Katovai et al. 2012), the identification of plant functional types can help researchers to unravel ecological patterns central to the advancement of ecological theories that can describe plant community responses to disturbances (Sheil 2016).

Chapter 7 revealed that harvest intensity and post-logging liana proliferation hampered the recovery of wood functional traits. Consequently, tree community biomass and wood density had not recovered to pre-cut levels even after 50 years of post-logging regeneration. These results indicate that the impacts of logging on wood functional traits are long-term in nature. In contrast, understory tree-specific leaf area (SLA) was influenced by topography and soil fertility, thereby suggesting that other factors, such as local edaphic influences, are playing a relatively strong role for SLA (Westoby 1998).

Chapter 8 revealed that forest structure had not returned to its pre-cut condition within 50 years of logging. Factors influencing or reflecting the regeneration and recovery of these forests were harvest intensity, liana abundance, height of major tree branching and litter depth. These factors were all linked to local logging practices on the island, and their influences on forest structure gradually declined over time after logging but at a relatively slow rate. This suggests that it may take well over 50 years for the impacts of logging on forests to largely subside; the recovery of large old trees, for example could require many centuries. Further, a climax state can only be realized if no further logging or land-use activities are carried out in these forests, and may require appropriate restoration practices to assist the structural recovery process (Harrison and Swinfield 2015; Sist et al. 2015).

Traditionally, restoration in the tropics has mostly focused on rehabilitating deforested landscapes (Lamb 2012; Schwartz et al. 2013). However, in Chapter 9, it was argued that results from this research (Chapters 5–8) suggest that active restoration will be required to improve the biological, functional and structural aspects of intensively logged forests. A similar initiative has recently commenced in the Harapan rainforest in Indonesia upon realization that natural regeneration alone cannot facilitate full recovery of highly degraded forests (Harisson and Swinfield 2015). An array of restoration approaches presented in Chapter 9 has been developed and trialed in tropical landscapes. The success of such approaches will be strongly hinged on the availability of funding and community engagement in forest recovery.

10.4 FUTURE RESEARCH

Research findings included in this thesis highlight a general need for active intervention to rehabilitate heavily logged forests in the Solomon Islands. Future research should be undertaken to, firstly, examine the effectiveness and limitations of currently available restoration approaches across intensively logged forests. Information from this research can then be used to develop restoration and management protocols specifically designed for the Solomon Islands. With logging being a major contributor to export revenue in the Solomons, it is crucial to sustain the economic viability of forest harvesting while preserving the biological and environmental values of logged forests in the region.

10.5 GENERAL CONCLUSIONS AND RECOMMENDATIONS

Forests in the Solomon Islands have experienced some of the heaviest logging practices in the tropics, resulting in the near depletion of timber stocks across the country. Due to high-intensity logging on Kolombangara, natural regeneration alone is inadequate to facilitate full floristic, functional and structural recovery within 50 years after logging. These results indicate that the legacy of logging on Kolombangara and possibly across the Solomon Islands may remain for many more decades or even centuries to come. It is also possible that logged forests will never recover to pre-cut levels due to unregulated re-entry logging which is currently increasing across the Solomons, combined with the long time-periods needed for many slow-growing tree species to attain the large size-classes typical of unlogged forests.

The immediate future of logged forests in the Solomon Islands appears bleak. Persistent logging in this country can potentially lead to a new forest estate bearing low economic and ecological values and reduced biodiversity (Sheil et al.1999; Cazzolla Gatti et al. 2015; Jakovac et al. 2016). To ensure the long-term protection of logged forest in the Solomon Islands from further degradation, it is highly recommended that a policy framework be developed that will address the urgent importance of retaining and recovering the timber stocks, biodiversity, and ecosystem values of these forests. This framework should also legally bind both local and government stakeholders to include forest-regeneration initiatives in future management and conservation strategies. This move is absolutely critical, particularly for a region that is on the verge of losing its remnant tracts of accessible primary forest. Ignoring these imperatives could have long-term repercussions for both human endeavours and nature conservation.

This thesis has provided a sizable body of information that can be used in both precautionary and remedial approaches to managing logged forests in the Solomon Islands. Nevertheless, much more knowledge is required in terms of research and policy development to ensure that logged forests are appropriately managed to achieve both economical and conservation outcomes. This remains a critical challenge for the near- and longer-term management of forests in the Solomon Islands.

The legacy of past logging activities remain intense on Kolombangara (in the background).

Photograph by Bill Laurance 2012

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APPENDICES

Appendix 1

Identified plant taxa collected in the Naoro-brown catchment area.

No.	Genera	Species	Family
1	*Saurauia*	*conferta*	*Actinidiaceae*
2	*Saurauia*	*sp.*	*Actinidiaceae*
3	*Crimun*	*asiatica*	*Amaryllidaceae*
4	*Semecarpus*	*sp.*	*Anacardiaceae*
5	*Cyathocalyx*	*petiolatus*	*Annonaceae*
6	*Cyathocalyx*	*sp.*	*Annonaceae*
7	*Polyalthia*	*glanca*	*Annonaceae*
8	*Xylopia*	*papuana*	*Annonaceae*
9	*Allamanda*	*sp.*	*Apocynaceae*
10	*Papuechites*	*sp.*	*Apocynaceae*
11	*Homalomena*	*cordata*	*Araceae*
12	*Pothos*	*hellwigii*	*Araceae*
13	*Rhaphidophora*	*peekelii*	*Araceae*
14	*Rhaphidophora*	*sp.*	*Araceae*
15	*Polyscias*	*sp.*	*Araliaceae*
16	*Schefflera*	*sp.*	*Araliaceae*
17	*Calamus*	*hollrungii*	*Arecaceae*
18	*Caryota*	*rumphiana*	*Arecaceae*
19	*Heterospath*	*sp.*	*Arecaceae*
20	*Hydriastele*	*costata*	*Arecaceae*
21	*Hydriastele*	*sp.1*	*Arecaceae*
22	*Hydriastele*	*sp.2*	*Arecaceae*
23	*Hoya*	*sp.1*	*Asclepiadaceae*
24	*Hoya*	*sp.2*	*Asclepiadaceae*
25	*Asplenium*	*nidus*	*Aspleniaceae*
26	*Vittaria*	*sp.*	*Aspleniaceae*
27	*Elaphantopus*	*scaber*	*Asteraceae*
28	*Bombax*	*ceiba*	*Bombacaceae*
29	*Canarium*	*acutifolium*	*Burseraceae*
30	*Garcinia*	*sp.1*	*Clusiaceae*
31	*Garcinia*	*sp.2*	*Clusiaceae*
32	*Terminalia*	*sp.*	*Combretaceae*
33	*Cyperus*	*rotundus*	*Cyperaceae*
34	*Fimbristylis*	*dichotoma*	*Cyperaceae*

35	*Drynaria*	*sp.*	*Davalliaceae*
36	*Lindsaea*	*sp.*	*Davalliaceae*
37	*Nephrolepis*	*hirsutula*	*Davalliaceae*
38	*Dioscorea*	*alata*	*Dioscoreaceae*
39	*Dracaena*	*angustifolia*	*Dracaenaceae*
40	*Diospyros*	*sp.*	*Ebenaceae*
41	*Diospyros*	*sogerensis*	*Ebenaceae*
42	*Dimorphanthera*	*dekokii*	*Ericaceae*
43	*Acalypha*	*sogerensis*	*Euphorbiaceae*
44	*Antidesma*	*sp.*	*Euphorbiaceae*
45	*Codiaeum*	*variegatum*	*Euphorbiaceae*
46	*Drapetes*	*bordenii*	*Euphorbiaceae*
47	*Glochidion*	*cf. ferdinandi*	*Euphorbiaceae*
48	*Glochidion*	*phillipicum*	*Euphorbiaceae*
49	*Macaranga*	*punchata*	*Euphorbiaceae*
50	*Phyllanthus*	*sp.*	*Euphorbiaceae*
51	*Pimelodendron*	*amboinicum*	*Euphorbiaceae*
52	*Archidendron*	*glabrum*	*Fabaceae*
53	*Desmodium*	*sp.*	*Fabaceae*
54	*Gigasiphon*	*schlecterii*	*Fabaceae*
55	*Maniltoa*	*psylogyne*	*Fabaceae*
56	*Maniltoa*	*sp.*	*Fabaceae*
57	*Milletia*	*pinnata*	*Fabaceae*
58	*Lithocarpus*	*celebicus*	*Fagaceae*
59	*Casearia*	*sp.*	*Flacourtiaceae*
60	*Flagellaria*	*indica*	*Flagellariaceae*
61	*Cyrtandra*	*erectiloba*	*Gesneriaceae*
62	*Dicranopteris*	*linearis*	*Gleicheniaceae*
63	*Curculigo*	*recurvata*	*Hypoxidaceae*
64	*Cryptocarya*	*sp.*	*Lauraceae*
65	*Endiardra*	*sp.1*	*Lauraceae*
66	*Endiardra*	*sp.2*	*Lauraceae*
67	*Litsea*	*timoriana*	*Lauraceae*
68	*Litsea*	*sp.1*	*Lauraceae*
69	*Litsea*	*sp.2*	*Lauraceae*
70	*Dianella*	*sp.*	*Liliaceae*
71	*Dianella*	*ensifolia*	*Liliaceae*
72	*Strychnos*	*minor*	*Loganiaceae*
73	*Lycopodium*	*cernuum*	*Lycopodiaceae*
74	*Medinilla*	*crassinervia*	*Melastomataceae*
75	*Aglaia*	*sp.*	*Meliaceae*
76	*Chisocheton*	*sp.*	*Meliaceae*
77	*Dysoxylum*	*sp.1*	*Meliaceae*
78	*Dysoxylum*	*sp.2*	*Meliaceae*

79	*Tinospora*	*sp.*	*Menispermaceae*
80	*Kibara*	*fugax*	*Monimiaceae*
81	*Palmeria*	*sp.*	*Monimiaceae*
82	*Palmeria*	*brassii*	*Monimiaceae*
83	*Artocarpus*	*communis*	*Moraceae*
84	*Ficus*	*sp.1*	*Moraceae*
85	*Ficus*	*sp.2*	*Moraceae*
86	*Ficus*	*sp.3*	*Moraceae*
87	*Ficus*	*sp.4*	*Moraceae*
88	*Ficus*	*molior*	*Moraceae*
89	*Gymnacranthera*	*paniculata var. zippelliana*	*Myristicaceae*
90	*Maesa*	*haplobotrys*	*Myearsinaceae*
91	*Rapanea*	*leucantha*	*Myearsinaceae*
92	*Syzygium*	*plumeum*	*Myrtaceae*
93	*Syzygium*	*acuminatissima*	*Myrtaceae*
94	*Syzygium*	*malaccense*	*Myrtaceae*
95	*Syzygium*	*longipes*	*Myrtaceae*
96	*Syzygium*	*claviflorum*	*Myrtaceae*
97	*Chionanthus*	*brassii*	*Oleaceae*
98	*Chionanthus*	*sessiliflorum*	*Oleaceae*
99	*Bulbophylum*	*sp.*	*Orchidaceae*
100	*Dendrobium*	*sp.*	*Orchidaceae*
101	*Glossoryncha*	*sp.*	*Orchidaceae*
102	*Tropidia*	*disticha*	*Orchidaceae*
103	*Freycinetia*	*linearis*	*Pandanaceae*
104	*Freycinetia*	*sp.1*	*Pandanaceae*
105	*Freycinetia*	*sp.2*	*Pandanaceae*
106	*Piper*	*macropiper*	*Piperaceae*
107	*Piper*	*sp.*	*Piperaceae*
108	*Pittosporum*	*sp.*	*Pittosporaceae*
109	*Arundo*	*sp.*	*Poaceae*
110	*Bambusa*	*sp.*	*Poaceae*
111	*Coix*	*lachyma-jobi*	*Poaceae*
112	*Eriachne*	*sp.*	*Poaceae*
113	*Imperata*	*cylindrica*	*Poaceae*
114	*Paspalum*	*conjugatum*	*Poaceae*
115	*Setaria*	*sp.*	*Poaceae*
116	*Christella*	*arida (Don)*	*Polypodiaceae*
117	*Diplazium*	*sp.*	*Polypodiaceae*
118	*Drynaria*	*sp.*	*Polypodiaceae*
119	*Humata*	*pectinata (J.J.Sm)*	*Polypodiaceae*
120	*Lindsaea*	*repens (Bory)*	*Polypodiaceae*
121	*Microsorium*	*sp.3*	*Polypodiaceae*
122	*Microsorium*	*sp.1*	*Polypodiaceae*

123	*Microsorium*	*sp.2*	*Polypodiaceae*
124	*Nephrolepis*	*sp.*	*Polypodiaceae*
125	*Polypodium*	*sp.*	*Polypodiaceae*
126	*Pteris*	*cretica*	*Polypodiaceae*
127	*Pteris*	*sp.*	*Polypodiaceae*
128	*Sphaerostephanos*	*sp.1*	*Polypodiaceae*
129	*Sphaerostephanos*	*sp.2*	*Polypodiaceae*
130	*Sphaerostephanos*	*unitus*	*Polypodiaceae*
131	*Tectaria*	*siifolia (Wild)*	*Polypodiaceae*
132	*Tectaria*	*semibipinnata (Wall)*	*Polypodiaceae*
133	*Tectaria*	*sp.*	*Polypodiaceae*
134	*Helicia*	*sp.*	*Proteaceae*
135	*Ziziphus*	*angustifolius*	*Rhamnaceae*
136	*Gynotroches*	*axillaris*	*Rhizophoraceae*
137	*Prunus*	*gazel-peninsulae*	*Rosaceae*
138	*Guettadella*	*sp.*	*Rubiaceae*
139	*Guettadella*	*sp.1*	*Rubiaceae*
140	*Lasianthus*	*sp.*	*Rubiaceae*
141	*Mussaenda*	*sp.*	*Rubiaceae*
142	*Psychotria*	*sp.1*	*Rubiaceae*
143	*Psychotria*	*sp.2*	*Rubiaceae*
144	*Cupaniopsis*	*sp.*	*Sapindaceae*
145	*Guioa*	*sp.*	*Sapindaceae*
146	*Guioa*	*crassinervia*	*Sapindaceae*
147	*Harpullia*	*sp.*	*Sapindaceae*
148	*Harpullia*	*longipetala*	*Sapindaceae*
149	*Palaquium*	*warburgianum*	*Sapotacaea*
150	*Manilkara*	*sp.*	*Sapotaceae*
151	*Schizaea*	*dichotoma*	*Schizaeaceae*
152	*Selaginella*	*aspericaulis*	*Selaginellaceae*
153	*Smilax*	*australis*	*Smilacaceae*
154	*Sterculia*	*schumanniana*	*Sterculiaceae*
155	*Sterculia*	*papuana*	*Sterculiaceae*
156	*Gordonia*	*papuana*	*Theaceae*
157	*Gordonia*	*sp.*	*Theaceae*
158	*Elatostema*	*novoguiniense*	*Urticaceae*
159	*Leea*	*indica*	*Vitaceae*
160	*Alpinia*	*sp.*	*Zingiberaceae*
161	*Amomum*	*aculeatum*	*Zingiberaceae*
162	*Curcuma*	*longa*	*Zingiberaceae*
163	*Hornstedtia*	*scottiana*	*Zingiberaceae*

Appendix 2

Complete tree species list (in alphabetical order) enumerated for the study area on Kolombangara Island.

No.	Species	Family
1	*Actinodaphne solomonensis*	*Lauraceae*
2	*Aglaia sp*	*Meliaceae*
3	*Alphitonia incana*	*Rhamnaceae*
4	*Alphitonia sp*	*Rhamnaceae*
5	*Alstonia brassii*	*Apocynaceae*
6	*Alstonia scholaris*	*Apocynaceae*
7	*Alstonia sp*	*Apocynaceae*
8	*Amoora cucullata*	*Meliaceae*
9	*Astronidium novae-georgiae*	*Melastomataceae*
10	*Astronidium solomonensis*	*Melastomataceae*
11	*Astronidium sp*	*Melastomataceae*
12	*Barringtonia sp*	*Lecythidaceae*
13	*Boerlagiodendron novo-guineensis*	*Araliaceae*
14	*Burckella obovata*	*Sapotaceae*
15	*Calophyllum cerasiferum*	*Clusiaceae*
16	*Calophyllum paludosum*	*Clusiaceae*
17	*Calophyllum peekelli*	*Clusiaceae*
18	*Calophyllum sp*	*Clusiaceae*
19	*Calophyllum vitiense*	*Clusiaceae*
20	*Campnosperma brevipetiolata*	*Anarcadiaceae*
21	*Cananga odorata*	*Annonaceae*
22	*Canarium salomonense*	*Burseraceae*
23	*Canarium sp*	*Burseraceae*
24	*Canarium sp 1*	*Burseraceae*
25	*Canarium sp 2*	*Burseraceae*
26	*Celtis philippinensis*	*Ulmaceae*
27	*Cerbera sp*	*Apocynaceae*
28	*Commersonia bartramia*	*Sterculiaceae*
29	*Cryptocarya medicinalis*	*Lauraceae*
30	*Cryptocarya globosa*	*Lauraceae*
31	*Cryptocarya kajewskii*	*Lauraceae*
32	*Cryptocarya medicinalis*	*Lauraceae*
33	*Cryptocarya sp*	*Lauraceae*
34	*Cryptocarya sp 1*	*Lauraceae*
35	*Cryptocarya sp 2*	*Lauraceae*
36	*Cyathocalyx petiolaris*	*Annonaceae*
37	*Cyathocalyx sp*	*Annonaceae*
38	*Decaspermum sp*	*Myrtaceae*

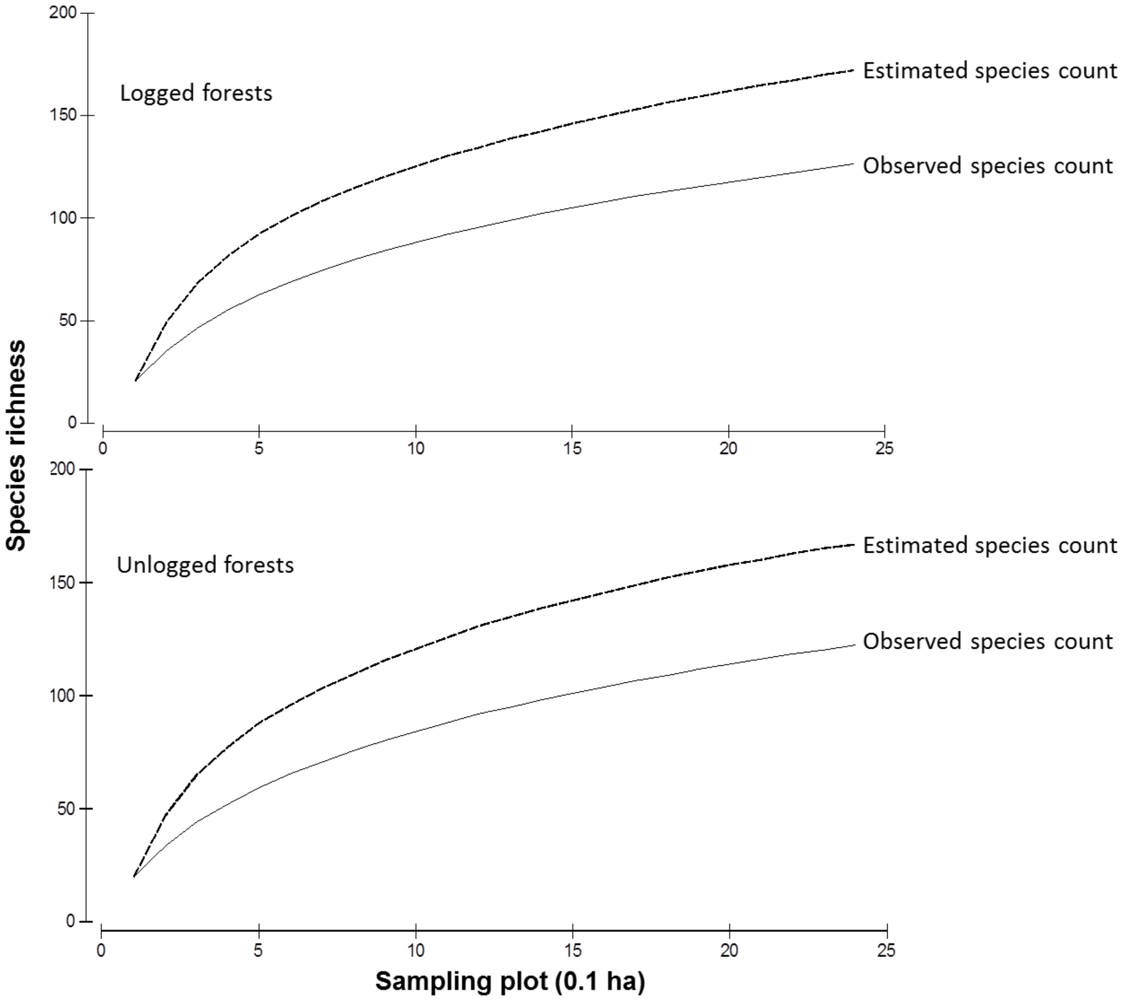
39	*Dendrocnide nervosa*	*Urticaceae*
40	*Dendrocnide salomonense*	*Urticaceae*
41	*Dillenia ingens*	*Dilleniaceae*
42	*Dillenia solomonensis*	*Dilleniaceae*
43	*Diospyros sp*	*Ebenaceae*
44	*Diospyros sp 1*	*Ebenaceae*
45	*Dysoxylum arborescense*	*Meliaceae*
46	*Dysoxylum cauliflorum*	*Meliaceae*
47	*Dysoxylum caulostachyum*	*Meliaceae*
48	*Dysoxylum excelsum*	*Meliaceae*
49	*Dysoxylum gaudichaudianum*	*Meliaceae*
50	*Dysoxylum micranthum*	*Meliaceae*
51	*Dysoxylum sp*	*Meliaceae*
52	*Dysoxylum sp 1*	*Meliaceae*
53	*Dysoxylum sp 2*	*Meliaceae*
54	*Dysoxylum sp 3*	*Meliaceae*
55	*Elaeocarpus floridanus*	*Elaeocarpaceae*
56	*Elaeocarpus polyandrus*	*Elaeocarpaceae*
57	*Elaeocarpus sp*	*Elaeocarpaceae*
58	*Elaeocarpus sp 1*	*Elaeocarpaceae*
59	*Elaeocarpus sphaericus*	*Elaeocarpaceae*
60	*Endospermum formicarum*	*Euphorbiaceae*
61	*Endospermum medullosum*	*Euphorbiaceae*
62	*Euodia solomonensis*	*Rutaceae*
63	*Euodia sp*	*Rutaceae*
64	*Euodia sp 1*	*Rutaceae*
65	*Euodia sp 2*	*Rutaceae*
66	*Euodia triphylla*	*Rutaceae*
67	*Fagraea brassii*	*Loganiaceae*
68	*Fagraea racemosa*	*Gentianaceae*
69	*Fagraea salomonensis*	*Loganiaceae*
70	*Fagraea sp*	*Gentianaceae*
71	*Ficus copiosa*	*Moraceae*
72	*Ficus longifolia*	*Moraceae*
73	*Ficus variegata*	*Moraceae*
74	*Ficus wassa*	*Moraceae*
75	*Finschia waterhousiana*	*Proteaceae*
76	*Flueggia flexuosa*	*Euphorbiaceae*
77	*Garcinia sessilis*	*Clusiaceae*
78	*Garcinia solomonensis*	*Clusiaceae*
79	*Garcinia sp*	*Clusiaceae*
80	*Garuga floribunda*	*Burseraceae*
81	*Geniostoma sp*	*Loganiaceae*
82	*Glochidion glabrum*	*Euphorbiaceae*
83	*Gmelina moluccana*	*Verbenaceae*
84	*Gomphandra montana*	*Icacinaceae*
85	*Gomphandra sp*	*Icacinaceae*

86	*Gonystylus macrophyllus*	*Thymelaeaceae*
87	*Haplolobus salomonensis*	*Burseraceae*
88	*Horsfieldia spicata*	*Myristicaceae*
89	*Litsea perglabra*	*Lauraceae*
90	*Litsea solomonensis*	*Lauraceae*
91	*Macaranga choiseuliana*	*Euphorbiaceae*
92	*Macaranga dioica*	*Euphorbiaceae*
93	*Macaranga similis*	*Euphorbiaceae*
94	*Macaranga sp.*	*Euphorbiaceae*
95	*Macaranga sp 1*	*Euphorbiaceae*
96	*Macaranga sp 2*	*Euphorbiaceae*
97	*Macaranga tanarius*	*Euphorbiaceae*
98	*Maranthes corymbosa*	*Chrysobalanaceae*
99	*Melicope solomonensis*	*Rutaceae*
100	*Melicope sp*	*Rutaceae*
101	*Melochia umbellata*	*Sterculiaceae*
102	*Micromelum minutum*	*Rutaceae*
103	*Myristica hollrungii*	*Myristicaceae*
104	*Myristica fatua*	*Myristicaceae*
105	*Myristica kajewskii*	*Myristicaceae*
106	*Myristica petiolata*	*Myristicaceae*
107	*Myristica salomonensis*	*Myristicaceae*
108	*Myristica sp*	*Myristicaceae*
109	*Myristica sp 1*	*Myristicaceae*
110	*Myristica sp 2*	*Myristicaceae*
111	*Myristica sp 2*	*Myristicaceae*
112	*Nauclea orientalis*	*Rubiaceae*
113	*Neonauclea forsteri*	*Naucleaceae*
114	*Neonauclea orientalis*	*Naucleaceae*
115	*Neonauclea sp*	*Naucleaceae*
116	*Neoscortechinia forbesii*	*Euphorbiaceae*
117	*Palaquium firmum*	*Sapotaceae*
118	*Palaquium sp*	*Sapotaceae*
119	*Paraserianthis (Albizia) falcata*	*Mimosaceae*
120	*Parinari glaberrima*	*Chrysobalanaceae*
121	*Parinari nonda*	*Chrysobalanaceae*
122	*Parinari solomonense*	*Chrysobalanaceae*
123	*Parinari sp*	*Chrysobalanaceae*
124	*Planchonella erythrospermum*	*Sapotaceae*
125	*Planchonella firma*	*Sapotaceae*
126	*Planchonella keyensis*	*Sapotaceae*
127	*Planchonella obovata*	*Sapotaceae*
128	*Planchonella sp*	*Sapotaceae*
129	*Plerandra solomonensis*	*Araliaceae*
130	*Plerandra sp*	*Araliaceae*
131	*Podocarpus salomoniensis*	*Podocarpaceae*
132	*Polyscias sp*	*Araliaceae*

133	*Pometia pinnata*	*Sapindaceae*
134	*Psychotria beccarii*	*Rubiaceae*
135	*Psychotria solomonensis*	*Rubiaceae*
136	*Pterocarpus indicus*	*Fabaceae*
137	*Pullea sp*	*Cunoniaceae*
138	*Schefflera sp*	*Araliaceae*
139	*Schizomeria brassii*	*Cunoniaceae*
140	*Schizomeria serrata*	*Cunoniaceae*
141	*Semecarpus forstenii*	*Anarcadiaceae*
142	*Sterculia conwentzii*	*Sterculiaceae*
143	*Sterculia sp*	*Sterculiaceae*
144	*Syzygium buettneriana*	*Myrtaceae*
145	*Syzygium cinctum*	*Myrtaceae*
146	*Syzygium effusa*	*Myrtaceae*
147	*Syzygium myriadena*	*Myrtaceae*
148	*Syzygium myriadenum*	*Myrtaceae*
149	*Syzygium nemorale*	*Myrtaceae*
150	*Syzygium onesima*	*Myrtaceae*
151	*Syzygium sp*	*Myrtaceae*
152	*Syzygium sp 1*	*Myrtaceae*
153	*Syzygium sp 2*	*Myrtaceae*
154	*Syzygium sp 3*	*Myrtaceae*
155	*Syzygium sp 4*	*Myrtaceae*
156	*Syzygium sp 5*	*Myrtaceae*
157	*Syzygium tierneyana*	*Myrtaceae*
158	*Teijsmanniodendron ahernianum*	*Verbenaceae*
159	*Teijsmanniodendron hollrungii*	*Verbenaceae*
160	*Terminalia brassii*	*Combretaceae*
161	*Terminalia calamansanai*	*Combretaceae*
162	*Terminalia sepicana*	*Combretaceae*
163	*Terminalia sp*	*Combretaceae*
164	*Terminalia sp 1*	*Combretaceae*
165	*Timonius longitubes*	*Rubiaceae*
166	*Timonius pulposus*	*Rubiaceae*
167	*Timonius solomonensis*	*Rubiaceae*
168	*Trema orientalis*	*Ulmaceae*
169	*Trichospermum psilocladum*	*Tiliaceae*
170	*Unidentified sp 1*	*Unknown*
171	*Unidentified sp 2*	*Unknown*
172	*Unidentified sp 3*	*Unknown*
173	*Vitex cofassus*	*Verbenaceae*
174	*Weinmannia blumei*	*Cunoniaceae*
175	*Weinmannia sp*	*Cunoniaceae*
176	*Weinmannia urdanetensis*	*Cunoniaceae*

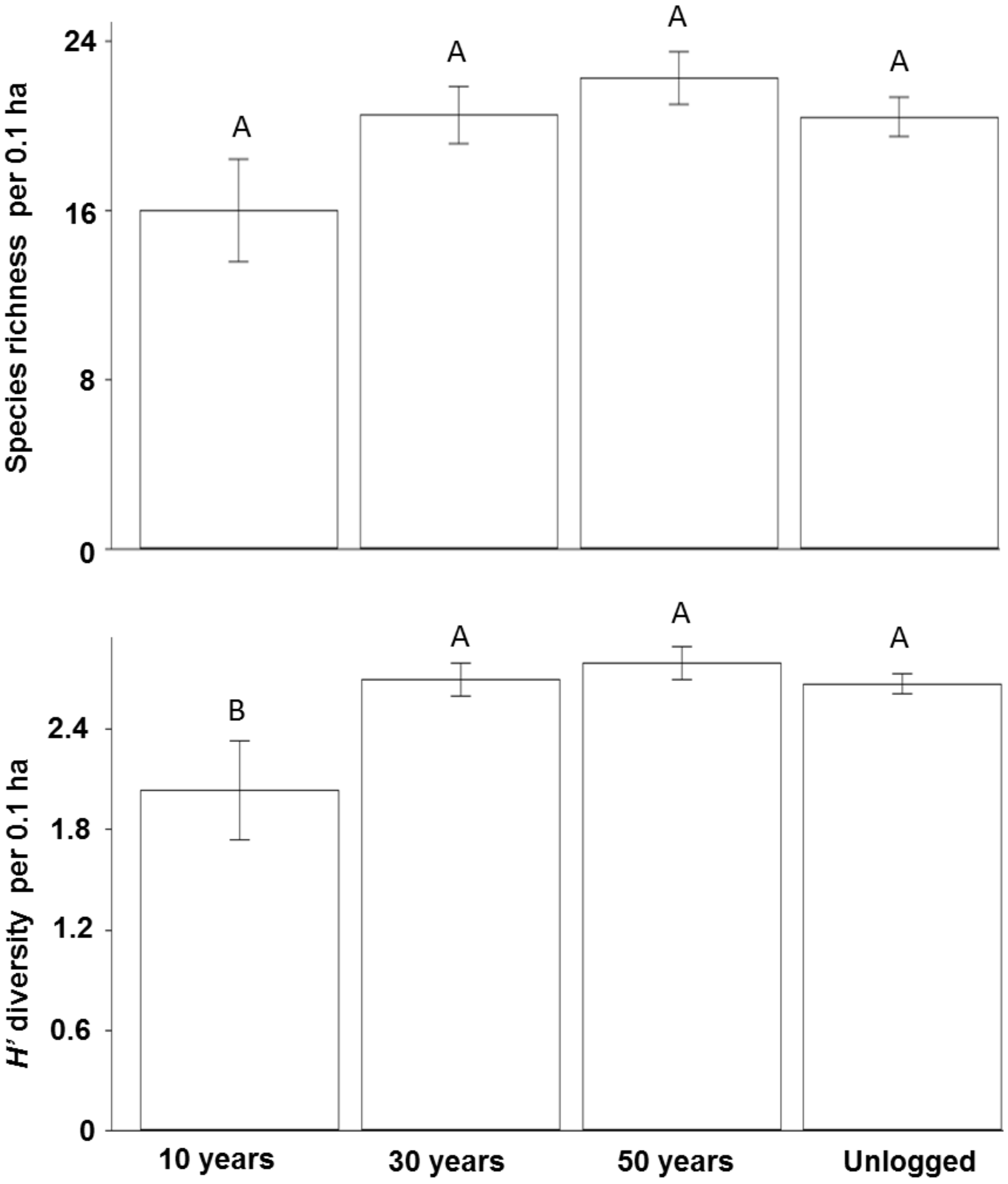
Appendix 3

Species accumulation curves showing the observed and estimated species count across both (a) logged and (b) unlogged forests. Estimated species counts were determined by Jackknife 1 estimator which accounts for sampling bias.



Appendix 4

Comparison of mean tree species richness and *H'* diversity across logged forests at 10, 30 and 50 years of regeneration, and unlogged forests. Error bars represent ±1 standard error and letters above denote significant pairwise differences across land use types and elevation bands using Tukey's HSD post-hoc tests. Bars with the same letter above them do not differ significantly.



Appendix 5

Plot-level dataset summary for this study.

Forest time class (Years of post-logging regeneration)	Coupe	Topographical elevation	Topographical slope	Soil pH	Soil temperature (Degree Celsius)	Soil litter depth (cm)	Root mesh thickness (cm)	Soil nitrogen (%)	Distance to nearest unlogged forest (km)	Distance to nearest logging road	Species richness (0.1ha)	Liana abundance per hactare	Basal area harvest (m^2)	Relative light intensity (%)	Treelet stem abundance (DBH<10cm to 1cm)	Cut stump per hactare	Growth form diversity (proportion)	Chlorotype diversity (proportion)	Leaf area class diversity (proportion)	Functional diversity index	Tree biomass (Tonnes per hactare)	Understory specific leaf area ($cm^2.g^{-1}$)	Tree wood density ($g.cm^{-3}$)	Tree (DBH>30cm) abundance per hactare	Tree (DBH>10cm to 30cm) abundance per hactare	Tree (DBH<10cm to 5cm) abundance per hactare	Tree (DBH<5cm to 1cm) abundance per hactare	Height of major branching (m)	Tree height (m)	canopy cover (proportion)	Ground cover (proportion)
50	1	111	22	4.8	27.1	2.3	0.6	0.2	2.3	0.2	16	550	11.24	5.1	3675	14	0.53	0.30	0.35	0.39	389.1	174.8	0.514	170	340	575	3100	20.1	29.6	0.95	0.21
50	1	140	5	5	27	2.3	1	0.5	2.9	0.5	22	800	10.55	5.4	4050	11	0.51	0.29	0.30	0.37	316.7	161.0	0.476	170	440	650	3400	19.1	28.5	0.95	0.44
50	1	145	33	4.8	27.9	2	1	0.3	3.3	0.8	24	775	12.59	5.4	4300	18	0.44	0.33	0.30	0.35	313.1	146.0	0.580	140	300	600	3700	19.4	28.9	0.95	0.28
50	1	148	2	4.7	29	2.3	0.6	0.4	3.6	0.7	20	900	12.34	4.3	4925	18	0.48	0.30	0.35	0.38	317.8	165.2	0.657	110	500	1025	3900	19.9	28.5	0.98	0.35
50	1	214	11	4.8	26.4	3.3	3.2	0.3	2.6	1.1	19	950	11.44	17.1	4575	14	0.52	0.30	0.31	0.38	360.4	209.7	0.565	210	500	575	4000	17.9	26.1	0.94	0.24
50	1	236	30	4.7	27.1	3.1	4	0.2	2.1	1.2	17	600	10.81	16.8	2900	14	0.53	0.33	0.36	0.41	372.1	236.5	0.582	240	380	500	2400	18.8	25.8	0.96	0.2

50	1	245	19	4.6	27	3	1.5	0.2	3.5	1.7	22	875	12.46	2.5	4650	18	0.58	0.33	0.48	0.46	305.8	275.2	0.494	210	460	550	4100	17.3	25.1	0.94	0.24
50	1	248	35	4.6	26.8	3.1	1.8	0.2	2.9	0.8	13	525	12.33	4.6	4200	14	0.58	0.25	0.39	0.41	355.3	219.0	0.496	210	490	700	3500	18.2	24.9	0.91	0.38
50	1	315	35	4.7	25	3.9	5.6	0.3	3.8	0.6	22	604	12.88	12.1	2525	14	0.60	0.41	0.33	0.45	189.4	272.0	0.462	110	320	625	1900	18.2	26.8	0.81	0.23
50	1	318	26	4.6	25.5	4.3	5.5	0.3	2.5	1.2	23	406	10.68	7.1	3775	11	0.56	0.34	0.29	0.40	324.0	190.9	0.567	170	280	675	3100	18.4	26.3	0.96	0.25
50	1	330	27	4.6	25.5	4.3	5.5	0.3	3.4	0.9	26	398	14.28	11.4	5400	21	0.56	0.34	0.29	0.40	243.8	282.2	0.482	190	470	1300	4100	18.4	26.3	0.96	0.25
50	1	400	20	4.1	25.5	4.6	5.5	0.3	4.3	0.5	18	700	13.29	10.6	2950	21	0.46	0.30	0.28	0.34	235.2	196.0	0.618	90	660	650	2300	18.4	28.1	0.95	0.27
50	2	159	5	3.8	27.9	1	1.3	0.5	3.8	0.3	19	800	10.81	1.3	5725	11	0.49	0.33	0.31	0.37	307.9	376.5	0.427	170	420	525	5200	18.8	27.7	0.96	0.55
50	2	163	15	4.3	28.2	1.3	0.4	0.5	2.2	0.5	23	850	10.29	1.3	6900	14	0.63	0.36	0.29	0.43	325.5	279.6	0.429	150	350	600	6300	19.4	28.1	0.90	0.66
50	2	159	7	4.6	29	1.3	1.5	0.5	2.8	0.7	25	900	7.31	1.6	2150	7	0.60	0.39	0.31	0.43	638.8	324.8	0.475	380	530	450	1700	17	28.2	0.95	0.33
50	2	182	17	4.7	28.2	1.6	0	0.5	3.1	1.1	26	900	10.34	0.9	5825	11	0.53	0.33	0.30	0.39	390.5	324.2	0.450	190	510	525	5300	18.7	28.3	0.98	0.37
50	2	222	14	5.5	27.3	2.2	0	0.4	4.7	1.2	15	1007	9.55	0.6	5375	11	0.49	0.27	0.25	0.34	224.6	295.0	0.508	100	300	975	4400	18.8	28.7	0.97	0.49
50	2	240	1	4.7	27.3	2.6	1.2	0.4	1.1	1.5	23	575	4.75	0.6	3125	4	0.42	0.29	0.27	0.33	524.9	301.1	0.520	180	350	425	2700	19.6	29.7	1.00	0.29
50	2	176	5	5.7	26.5	1.9	0	0.6	1.3	1.8	21	875	6.22	1	2925	4	0.41	0.26	0.27	0.31	394.5	297.3	0.488	170	270	625	2300	18.6	29.5	1.00	0.22
50	2	184	6	5.6	27.5	2	0	0.9	3.4	0.5	19	1000	9.86	1.8	3600	14	0.39	0.28	0.36	0.34	289.0	284.9	0.492	180	280	600	3000	19	28.3	0.98	0.36
50	2	289	18	4.4	26.6	4	5	0.4	1.5	0.8	25	1972	9.07	8.4	2925	11	0.50	0.39	0.36	0.41	266.9	124.3	0.740	80	320	525	2400	19	25.4	0.95	0.26
50	2	285	10	4.3	27.3	4.1	5.3	0.4	1.2	1.2	26	1122	11.08	13.9	6100	21	0.58	0.39	0.25	0.40	160.8	111.2	0.487	70	520	700	5400	18.3	22.6	0.76	0.24
50	2	298	5	4.2	26.5	4.3	7.3	0.4	3.8	1.5	18	461	8.08	7.6	6800	7	0.44	0.36	0.26	0.36	384.4	155.3	0.461	210	330	600	6200	16.8	27.7	0.96	0.24
50	2	304	10	4.1	26.3	4	4.8	0.5	3.4	1.4	19	709	12.26	10.2	4500	18	0.49	0.36	0.38	0.41	183.2	186.3	0.517	110	300	600	3900	15.9	26	0.88	0.23
30	3	78	15	4.2	28.2	2.2	1.3	0.3	2.9	0.3	17	1400	11.39	1.4	4650	21	0.60	0.29	0.32	0.40	141.2	225.3	0.587	50	550	850	3800	15.9	25.6	0.95	0.55
30	3	70	3	4.8	28.4	1.8	1.2	0.2	2.5	1.2	21	1650	10.31	1.5	5275	14	0.51	0.34	0.33	0.39	248.0	234.2	0.523	140	200	775	4500	16.2	24.9	0.94	0.39
30	3	73	5	4.4	27.9	1.7	1.1	0.4	3.1	0.8	24	1400	6.74	1	6375	14	0.39	0.30	0.24	0.31	261.1	228.0	0.633	180	510	775	5600	17	25.3	0.95	0.45
30	3	92	3	4.7	27.9	1.5	1	0.4	2.7	1	19	1550	10.34	0.9	6950	14	0.39	0.31	0.19	0.30	275.9	231.4	0.616	140	470	1150	5800	18.5	25.6	0.96	0.44
30	3	268	14	4.3	26.6	2.3	3.5	0.4	3	0.5	18	825	9.55	1.4	2800	7	0.44	0.30	0.39	0.38	266.9	188.5	0.506	160	430	700	2100	16.2	24.9	0.98	0.25
30	3	242	5	4.4	26	2.4	3.3	0.2	1.6	0.7	22	875	9.68	1.9	3475	18	0.39	0.31	0.34	0.35	296.6	198.9	0.521	170	370	775	2700	16	24.9	0.96	0.21
30	3	221	9	4.6	26.5	2.4	3.5	0.3	1.7	0.2	21	800	11.57	2	3000	21	0.42	0.33	0.36	0.37	273.7	209.6	0.492	170	430	700	2300	16.2	25.1	0.96	0.23
30	3	191	20	4.5	26.4	2.3	3.5	0.3	2.1	0.8	17	825	6.08	1.5	3175	7	0.35	0.31	0.32	0.33	342.4	179.9	0.489	180	400	575	2600	15.9	24.7	0.98	0.21
30	3	325	20	4.1	25.7	4.3	4.3	0.3	1.5	1.1	25	1100	13.09	3.5	3475	18	0.58	0.34	0.52	0.48	311.2	210.1	0.474	190	350	575	2900	17.8	26.4	0.90	0.38
30	3	319	20	4.5	25.7	1.9	2.1	0.3	1.9	0.5	25	1300	8.14	3.1	3875	11	0.53	0.35	0.68	0.52	233.6	207.5	0.516	130	430	675	3200	15.2	24.6	0.93	0.37
30	3	318	25	4.4	25.2	2.7	13.1	0.3	1.7	1.4	21	1050	9.51	3.7	4200	11	0.59	0.36	0.47	0.47	319.4	202.1	0.542	110	340	500	3700	18.8	28.3	0.90	0.32

30	3	346	27	4	25.7	3.4	6.1	0.3	1.8	0.8	24	1300	12.03	4.2	4475	18	0.52	0.33	0.47	0.44	262.9	236.1	0.427	180	390	675	3800	15	23.3	0.88	0.26
30	4	59	1	5.3	27.4	1.4	0.4	0.3	5.2	0.4	15	1850	10.22	9	5000	21	0.50	0.31	0.39	0.40	188.3	213.8	0.556	120	300	700	4300	17.2	25.8	0.96	0.36
30	4	78	1	5.4	27.4	1.4	0.1	0.3	5	1.1	17	1825	12.25	5.6	4825	18	0.56	0.28	0.36	0.40	420.1	248.5	0.542	230	520	725	4100	16.7	25.6	0.98	0.44
30	4	72	1	5.1	27.7	1.4	0.1	0.3	4.5	0.8	19	775	12.79	7.9	3900	18	0.51	0.33	0.31	0.38	296.9	247.8	0.458	140	600	600	3300	17.1	25.4	1.00	0.34
30	4	47	3	4.5	26.6	1.5	0.3	0.3	4.8	1.3	21	900	12.16	9.3	3475	21	0.54	0.31	0.34	0.40	327.8	189.6	0.496	230	370	475	3000	16.9	25.3	0.96	0.29
30	4	220	24	4.5	25.6	2.6	3.8	0.3	4.8	0.7	15	645	7.58	2.1	3675	11	0.43	0.30	0.46	0.40	365.7	180.1	0.579	210	210	975	2700	16	26	0.94	0.25
30	4	222	22	4.3	25.7	3	5.1	0.3	5.3	0.4	14	1290	12.03	2.1	2725	21	0.42	0.36	0.43	0.40	236.8	207.5	0.585	110	340	425	2300	13.9	24.7	0.93	0.27
30	4	257	2	4.4	26.2	2.9	4.9	0.3	5.1	0.5	17	366	9.45	2.4	2725	11	0.50	0.35	0.53	0.46	374.7	204.6	0.542	180	470	525	2200	18.1	25.5	0.86	0.45
30	4	240	15	4.8	26.3	3.1	2.3	0.2	4.4	0.8	20	900	8.61	2.4	3950	11	0.43	0.31	0.44	0.39	260.4	185.1	0.531	110	320	950	3000	14.9	23.9	0.88	0.29
30	4	306	3	4.9	25.6	4	5.6	0.4	2.5	0.8	15	725	12.08	19.2	5100	18	0.63	0.35	0.62	0.53	224.9	180.1	0.506	140	470	700	4400	18.4	24.9	0.91	0.39
30	4	337	38	3.9	25.3	4	8.1	0.3	1.5	1.1	17	1275	12.47	12.8	6550	18	0.70	0.33	0.62	0.55	243.4	198.9	0.472	180	480	850	5700	18	24.4	0.89	0.34
30	4	322	4	4.4	24.2	4.4	4	0.2	1.8	1.2	14	625	11.24	3.4	3125	14	0.54	0.31	0.40	0.42	196.4	204.6	0.485	140	440	825	2300	16.5	24	0.98	0.26
30	4	321	5	4.3	24.2	4.2	5	0.3	1.4	0.4	18	875	12.35	4.4	6225	18	0.49	0.25	0.36	0.36	156.6	199.2	0.536	120	410	725	5500	16.1	37.1	0.90	0.38
10	5	136	5	5.6	26.3	1.2	0.4	0.5	1.2	0.6	13	1225	16.24	13.8	6900	18	0.71	0.28	0.31	0.43	102.5	236.1	0.398	40	480	1000	5900	7.7	12.3	0.75	0.52
10	5	170	7	5.5	25.6	1.4	0.1	0.4	1.3	0.4	11	1100	14.86	17	4875	25	0.69	0.26	0.22	0.39	64.0	270.9	0.366	0	620	575	4300	7.2	12.5	0.76	0.66
10	5	171	3	5.7	26.1	1.4	0.1	0.4	1.5	1.1	15	1200	14.64	10.6	8150	25	0.69	0.33	0.33	0.45	161.5	259.3	0.415	80	740	1050	7100	7.8	11.9	0.89	0.54
10	5	173	15	5.8	26	1.4	0	0.3	1.8	0.7	13	1275	15.15	11.6	6875	25	0.72	0.28	0.34	0.45	103.3	276.3	0.372	30	520	975	5900	8.2	12.8	0.63	0.54
10	5	255	10	4.8	27.2	1	1.6	0.3	2.3	1.1	22	462	15.78	23.8	7525	14	0.56	0.26	0.34	0.39	191.8	304.3	0.358	80	410	1325	6200	7.7	13.3	0.78	0.53
10	5	263	22	4.4	26.8	1	1.4	0.4	2.4	0.9	17	430	14.10	23.4	6500	14	0.55	0.28	0.38	0.40	232.8	268.2	0.339	130	210	1600	4900	7.9	13.6	0.80	0.53
10	5	290	13	4.5	26.7	1.2	1.3	0.4	2.5	0.5	17	215	17.56	23.4	7775	36	0.55	0.26	0.29	0.37	121.0	271.9	0.364	80	470	1475	6300	7.6	12.8	0.70	0.67
10	5	295	1	4.3	26	1.2	1.4	0.3	2.4	0.7	23	613	15.74	22.8	7350	25	0.58	0.25	0.26	0.36	155.1	260.0	0.362	100	450	1350	6000	5.8	10.8	0.64	0.62
10	5	422	4	5.5	24.6	1.5	0.1	0.3	1.4	0.6	18	1400	15.09	17.4	5250	32	0.64	0.24	0.31	0.39	207.2	222.7	0.437	110	410	550	4700	6.4	11.6	0.49	0.57
10	5	419	2	5.2	24.8	1.6	0	0.4	1.5	0.6	19	1200	16.12	16.6	5900	21	0.70	0.24	0.28	0.41	184.0	213.9	0.388	90	480	800	5100	6.5	14.2	0.55	0.59
10	5	369	10	5.4	23.6	1.7	0	0.2	1.8	0.4	10	850	14.96	18.3	4925	21	0.69	0.23	0.31	0.41	143.0	215.4	0.415	80	330	625	4300	10	13.1	0.55	0.63
10	5	352	5	5.2	24.6	1.5	0.1	0.4	1.2	0.3	17	1000	12.11	20.8	4050	18	0.63	0.25	0.28	0.39	159.2	187.8	0.348	90	490	750	3300	6.8	15.3	0.73	0.47
10	6	90	3	5.3	26.1	1.4	0	0.3	1.5	0.8	10	1100	14.14	23.3	3425	18	0.76	0.26	0.31	0.45	172.2	209.9	0.469	170	270	525	2900	7.3	13.1	0.59	0.58
10	6	92	5	5.3	26.5	1.4	0	0.7	1.2	0.7	9	1025	14.75	21.5	4625	18	0.65	0.28	0.41	0.44	119.3	214.4	0.467	60	360	925	3700	7.6	12.5	0.59	0.63
10	6	81	8	5.4	27.4	1.4	0	0.5	1.6	1.3	7	925	11.55	20	3125	14	0.67	0.29	0.32	0.43	251.2	192.6	0.471	150	440	625	2500	7.4	12.6	0.61	0.57
10	6	102	15	5.4	27.4	1.3	0.1	0.3	1.2	0.8	6	1350	12.86	20.9	6125	21	0.62	0.29	0.32	0.41	146.5	200.2	0.339	80	380	1025	5100	6.8	12.6	0.58	0.61

10	6	158	1	5	26.1	1.3	1.3	0.4	1.5	0.5	5	1700	15.41	20.8	10075	25	0.61	0.31	0.43	0.45	76.0	197.9	0.379	20	750	1575	8500	6.5	11.7	0.54	0.62
10	6	156	4	5.2	26	1.3	1.3	0.3	1.8	0.7	7	1350	17.26	17.5	6200	32	0.58	0.28	0.40	0.42	35.7	197.7	0.294	0	340	1300	4900	5.9	12.5	0.59	0.58
10	6	178	1	5.5	25.4	1.4	1.4	0.3	1.8	1.8	20	1250	11.45	20.4	7725	21	0.58	0.29	0.48	0.45	227.2	195.3	0.422	70	540	1525	6200	6.1	12.3	0.55	0.6
10	6	208	4	5.3	25.4	1.5	1.7	0.5	1.9	0.9	16	2075	15.95	18.4	8600	32	0.56	0.31	0.48	0.45	75.1	191.0	0.349	40	500	1600	7000	6.3	12.3	0.51	0.66
10	6	265	5	4.9	24.1	2.1	4.8	0.4	2.1	0.8	8	573	8.69	16.4	5900	14	0.69	0.25	0.44	0.46	268.4	260.4	0.454	190	310	1200	4700	6.1	12.5	0.60	0.58
10	6	254	6	5.1	24.9	2.2	4.6	0.2	2.6	1.1	9	327	10.07	15.6	6325	14	0.68	0.26	0.46	0.47	270.7	143.6	0.392	190	340	1125	5200	7.9	15.8	0.59	0.49
10	6	252	3	5	25	2.1	4.6	0.4	2.5	0.5	5	200	10.42	14	4375	18	0.67	0.25	0.48	0.46	162.1	305.4	0.422	90	260	875	3500	8	15.2	0.63	0.53
10	6	256	9	5	24.9	2	4.7	0.4	2.7	0.3	6	351	11.96	18.5	6525	18	0.63	0.29	0.46	0.46	211.2	222.2	0.521	120	450	1025	5500	8.3	15.4	0.61	0.54
UL	7	135	40	5.4	27.1	1.6	0.2	0.2	-	-	23	850	-	1.8	4575	-	0.47	0.38	0.42	0.42	699.9	236.4	0.617	160	480	675	3900	20.4	30.3	0.95	0.32
UL	7	147	5	5.6	27.4	1.7	0	0.3	-	-	26	725	-	1.2	2350	-	0.47	0.38	0.37	0.40	439.6	190.2	0.594	150	190	450	1900	19.7	30.5	0.90	0.2
UL	7	144	10	5.6	25.6	1.5	0	0.2	-	-	28	525	-	2.4	2075	-	0.40	0.40	0.33	0.38	647.7	276.4	0.735	150	270	375	1700	23.7	33	0.98	0.22
UL	7	163	8	5.6	25.6	1.5	0	0.3	-	-	23	550	-	3.1	2150	-	0.40	0.40	0.33	0.38	702.4	210.4	0.610	190	180	450	1700	23.7	33	0.98	0.22
UL	7	276	10	5.6	27.2	1.5	0	0.4	-	-	29	575	-	1.4	3875	-	0.40	0.33	0.34	0.35	584.1	247.4	0.574	100	410	575	3300	23.4	31.3	0.99	0.2
UL	7	294	12	4.8	26.1	1.9	3.6	0.4	-	-	19	850	-	1.2	4425	-	0.40	0.35	0.39	0.38	381.9	218.2	0.569	140	290	825	3600	21.2	30.2	0.94	0.22
UL	7	292	5	4.5	26.1	1.9	3.3	0.4	-	-	22	775	-	1.4	3650	-	0.44	0.30	0.39	0.38	423.1	200.4	0.514	180	390	550	3100	20.2	30.6	0.98	0.19
UL	7	269	12	5	25.9	1.7	3.5	0.4	-	-	22	875	-	2.2	3325	-	0.45	0.25	0.38	0.36	380.9	212.8	0.561	150	570	725	2600	19.9	30.1	0.95	0.23
UL	7	380	10	4.9	26	1.9	3.5	0.4	-	-	16	470	-	1.2	2250	-	0.38	0.25	0.34	0.32	402.5	294.1	0.525	170	290	450	1800	21.2	30.4	1.00	0.16
UL	7	347	38	4.5	25.4	1.8	1.8	0.4	-	-	17	128	-	1.9	2425	-	0.37	0.38	0.34	0.36	620.6	255.1	0.642	170	390	525	1900	19.8	27.7	0.94	0.16
UL	7	350	20	4.5	25	2.2	10.3	0.4	-	-	18	534	-	2.1	3450	-	0.38	0.35	0.42	0.38	522.8	227.0	0.565	150	300	550	2900	20.8	27.9	0.90	0.26
UL	7	420	5	4.5	25.1	1.8	11.2	0.4	-	-	11	378	-	1.5	3400	-	0.41	0.29	0.41	0.37	533.6	237.8	0.643	260	160	600	2800	18.2	28.1	0.89	0.35
UL	8	104	1	5.7	26.4	1.4	1.4	0.4	-	-	22	725	-	0.7	2250	-	0.51	0.28	0.33	0.37	603.5	233.2	0.619	270	320	450	1800	21.2	29.9	1.00	0.13
UL	8	116	1	5.4	27	1.3	1.1	0.2	-	-	21	900	-	1.1	2425	-	0.42	0.31	0.32	0.35	544.5	228.1	0.650	170	370	425	2000	20.6	28.8	0.99	0.15
UL	8	143	1	6	27.1	1.4	0.9	0.5	-	-	18	850	-	1.5	2775	-	0.47	0.29	0.41	0.39	455.1	260.5	0.589	210	370	475	2300	20.7	28.9	0.96	0.2
UL	8	129	5	5.7	27	1.4	0.7	0.4	-	-	25	1150	-	6.6	2750	-	0.40	0.29	0.34	0.34	458.6	287.8	0.625	230	300	450	2300	20.2	27.9	0.99	0.16
UL	8	205	15	4.3	25.2	2.4	3.4	0.2	-	-	29	650	-	2.1	2875	-	0.42	0.32	0.23	0.32	640.3	221.4	0.544	160	260	475	2400	21.4	31.9	0.99	0.18
UL	8	257	25	4.5	25.7	2	3.8	0.2	-	-	19	675	-	0.5	2125	-	0.46	0.28	0.24	0.33	521.1	250.6	0.627	150	280	525	1600	23.7	31.1	0.95	0.23
UL	8	235	28	4.5	25.4	2.4	2.2	0.2	-	-	17	600	-	0.7	3050	-	0.45	0.29	0.39	0.38	807.3	240.2	0.622	240	200	550	2500	24.1	34.4	0.94	0.25
UL	8	210	22	4.4	25.4	2.2	3.5	0.3	-	-	22	550	-	0.8	2675	-	0.41	0.28	0.34	0.34	647.2	287.1	0.608	210	260	375	2300	19.5	30.6	1.00	0.17
UL	8	385	14	3.9	24.5	4.6	5.6	0.2	-	-	17	176	-	1.2	3025	-	0.43	0.26	0.27	0.32	516.0	185.5	0.665	130	520	625	2400	22.3	29.4	0.98	0.16

UL	8	301	16	3.9	25.5	5.8	7	0.2	-	-	21	160	-	1.1	2600	-	0.40	0.34	0.30	0.35	740.3	167.7	0.676	200	550	500	2100	20.3	28.6	0.95	0.22
UL	8	324	15	4.2	25.5	6	6.4	0.2	-	-	23	168	-	1.1	4225	-	0.44	0.31	0.29	0.35	516.6	121.3	0.687	200	430	625	3600	20.4	28.7	0.95	0.26
UL	8	331	22	4.4	24.4	6.2	7.3	0.3	-	-	22	239	-	1.2	3575	-	0.40	0.31	0.37	0.36	576.6	164.6	0.623	160	620	575	3000	18.3	26.5	0.94	0.25
UL	9	104	40	6.3	26.3	1.5	0	0.4	-	-	24	475	-	3.3	2850	-	0.47	0.40	0.43	0.43	635.8	200.2	0.567	210	200	450	2400	23.6	31.5	1.00	0.19
UL	9	116	42	5	26.9	1.6	3.2	0.5	-	-	26	625	-	4.9	4325	-	0.52	0.39	0.56	0.49	722.5	201.3	0.719	190	260	525	3800	26.4	32.9	0.97	0.19
UL	9	143	40	5.4	26.5	1.5	0.9	0.4	-	-	23	550	-	3.3	3075	-	0.40	0.38	0.60	0.46	683.1	299.4	0.635	210	300	375	2700	25.7	32.1	0.97	0.18
UL	9	129	10	5.7	26.6	1.5	0.1	0.3	-	-	24	750	-	2.7	3350	-	0.47	0.40	0.55	0.47	737.9	230.5	0.550	200	320	550	2800	25.5	32.6	0.98	0.18
UL	9	205	34	5.3	25.7	1.5	0.2	0.3	-	-	20	575	-	1.1	3775	-	0.33	0.39	0.40	0.37	543.2	231.7	0.637	160	140	575	3200	22.6	31.1	0.93	0.22
UL	9	251	19	4.9	25.6	2.5	0.5	0.5	-	-	28	525	-	1.3	3325	-	0.48	0.36	0.49	0.44	545.2	209.5	0.662	130	460	525	2800	25.3	32.3	0.89	0.21
UL	9	235	9	5	25.9	1.6	0.5	0.3	-	-	12	600	-	1.5	2700	-	0.34	0.36	0.42	0.37	670.8	192.8	0.655	160	130	400	2300	24.5	34	0.92	0.26
UL	9	210	14	4.1	25.7	1.5	2.5	0.3	-	-	16	700	-	1.1	4400	-	0.41	0.35	0.45	0.40	716.1	213.6	0.627	140	220	700	3700	23.3	32	0.96	0.21
UL	9	310	12	3.7	24.5	3.7	6.9	0.3	-	-	15	525	-	3.2	2375	-	0.35	0.29	0.33	0.32	481.7	229.1	0.623	220	210	375	2000	18.8	26.2	0.98	0.21
UL	9	301	8	3.7	25.2	3.5	5.7	0.3	-	-	13	625	-	2.9	2800	-	0.40	0.44	0.28	0.37	458.5	206.3	0.636	140	260	400	2400	18.7	26.7	0.98	0.17
UL	9	324	8	4.6	25.2	3.4	3.3	0.3	-	-	10	850	-	2	3075	-	0.38	0.35	0.29	0.34	499.8	242.4	0.603	190	200	375	2700	18.9	26.7	0.94	0.19
UL	9	331	20	4.4	25.3	3.4	4.2	0.3	-	-	12	725	-	2.3	3075	-	0.37	0.36	0.26	0.33	516.0	213.9	0.613	150	340	475	2600	25.3	31.9	0.98	0.19
UL	10	45	8	5.2	27.4	1.5	2.6	0.6	-	-	19	500	-	0.9	2100	-	0.41	0.40	0.33	0.38	680.5	215.0	0.593	170	230	300	1800	21	31.8	0.98	0.2
UL	10	54	13	5.1	28	1.4	2.6	0.7	-	-	26	450	-	0.8	2550	-	0.40	0.33	0.31	0.34	534.9	214.5	0.505	160	410	450	2100	21	31.1	0.98	0.18
UL	10	55	12	5.3	27.5	2.6	0	0.3	-	-	25	650	-	1	2500	-	0.41	0.29	0.31	0.34	555.8	242.2	0.577	170	340	400	2100	20.8	30.4	0.96	0.19
UL	10	20	1	6.4	27.3	1.9	0	0.3	-	-	27	650	-	1.1	1300	-	0.38	0.26	0.29	0.31	607.6	261.1	0.508	160	170	200	1100	20	29.8	0.96	0.12
UL	10	215	38	3.7	26.4	3.2	7.2	0.3	-	-	20	600	-	0.8	3125	-	0.34	0.32	0.29	0.32	535.9	253.0	0.577	180	280	425	2700	20.9	31.4	0.94	0.24
UL	10	226	9	4.6	26.4	2.8	3.4	0.3	-	-	17	425	-	1.3	2675	-	0.46	0.35	0.27	0.36	552.5	235.3	0.589	200	270	475	2200	20.5	30.4	0.94	0.14
UL	10	210	34	4.7	25.3	3.4	3.9	0.3	-	-	24	525	-	0.7	2475	-	0.42	0.35	0.17	0.31	547.7	234.6	0.560	160	310	375	2100	20.7	30.2	0.96	0.2
UL	10	202	5	6	26.5	3.1	3.7	0.2	-	-	17	350	-	0.6	1400	-	0.36	0.23	0.13	0.24	630.3	268.8	0.620	150	180	200	1200	21.6	31.5	1.00	0.11
UL	10	380	22	3.5	23.5	4	9.2	0.3	-	-	12	600	-	4.8	2500	-	0.44	0.30	0.49	0.41	414.0	250.1	0.617	150	430	300	2200	19	26.4	0.96	0.13
UL	10	397	19	3.5	23.7	4.4	9.9	0.2	-	-	14	475	-	5	1750	-	0.39	0.31	0.34	0.35	445.0	161.5	0.658	150	390	350	1400	18.6	27.6	0.96	0.17
UL	10	365	10	3.5	23.5	4.1	9.5	0.2	-	-	14	625	-	5	2575	-	0.44	0.33	0.43	0.40	402.3	179.2	0.736	110	420	475	2100	19.1	26.5	0.96	0.13
UL	10	370	12	3.5	23.4	4.6	10.2	0.2	-	-	16	500	-	4.2	2625	-	0.45	0.30	0.33	0.36	399.7	176.7	0.681	110	330	325	2300	19.1	27.6	1.00	0.13
UL	11	90	9	5.4	26.2	1.7	1.1	0.6	-	-	25	650	-	1.3	2675	-	0.34	0.33	0.24	0.30	695.1	230.6	0.575	210	470	375	2300	20.8	29.5	0.98	0.15
UL	11	73	8	5.5	26.7	1.4	0.4	0.6	-	-	26	575	-	0.7	2675	-	0.40	0.34	0.25	0.33	593.2	195.1	0.582	150	290	475	2200	22.9	30.2	0.98	0.12

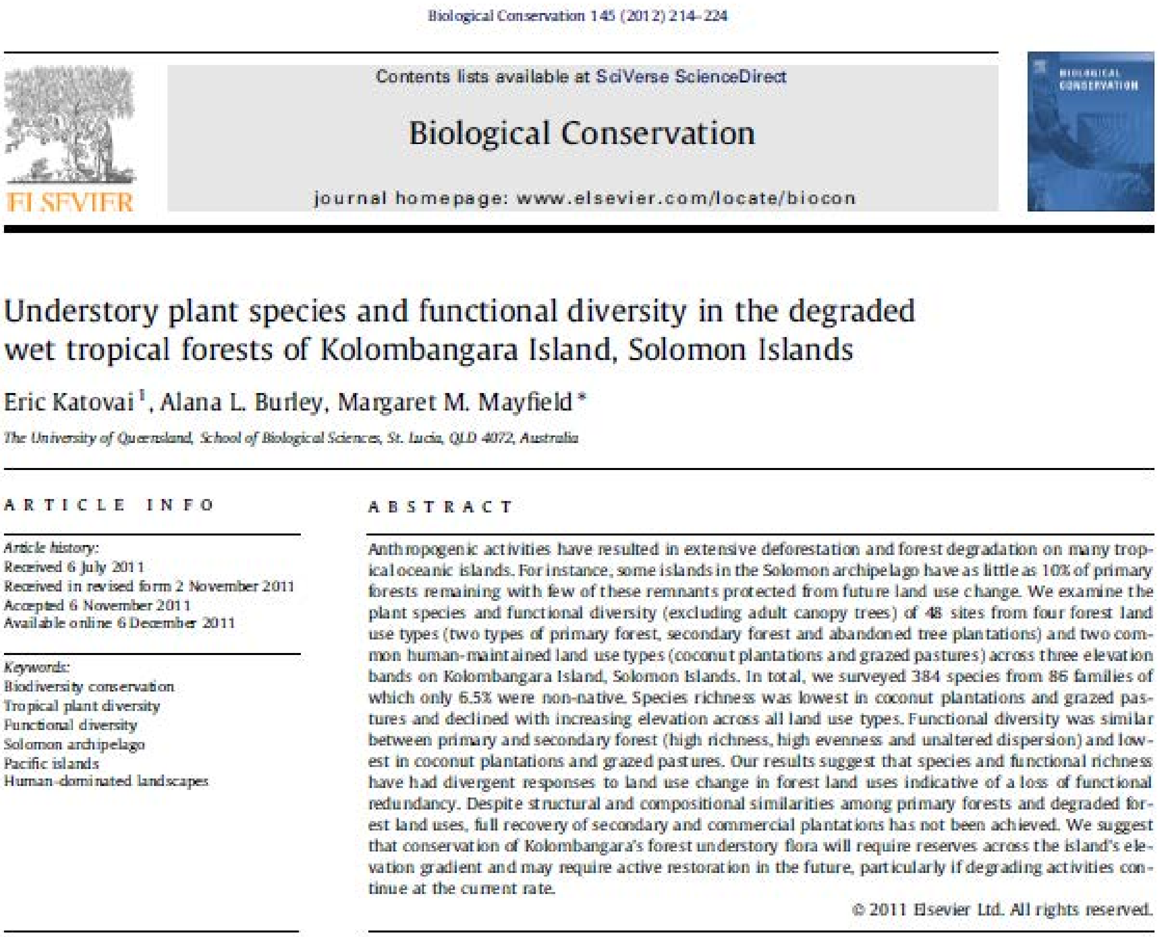
UL	11	61	5	5.6	27.2	1.3	0	0.7	-	-	28	825	-	1.3	3400	-	0.51	0.36	0.30	0.39	612.2	273.2	0.497	170	370	700	2700	23	32.5	0.93	0.19
UL	11	40	5	5.7	27.6	1.6	0.1	0.4	-	-	28	650	-	1.4	2275	-	0.35	0.28	0.23	0.29	696.1	241.0	0.553	230	160	375	1900	23.4	30.6	0.95	0.15
UL	11	287	8	3.8	24.3	2.4	6	0.3	-	-	24	475	-	5.8	1875	-	0.38	0.33	0.29	0.33	504.3	183.0	0.537	180	380	275	1600	20.5	30.4	0.98	0.17
UL	11	284	5	4.1	24.6	2.2	6.2	0.3	-	-	18	400	-	8.3	2300	-	0.41	0.30	0.31	0.34	553.7	185.7	0.634	170	300	400	1900	20.6	30.6	0.98	0.17
UL	11	288	11	3.9	25.6	2.5	6.4	0.4	-	-	21	450	-	2.8	2175	-	0.42	0.36	0.31	0.36	614.9	234.1	0.569	200	340	375	1800	33.2	31.3	0.96	0.15
UL	11	264	23	4	25	2.3	5.6	0.2	-	-	20	600	-	1.2	1950	-	0.44	0.35	0.26	0.35	622.2	272.7	0.691	180	280	250	1700	20.6	29.7	1.00	0.14
UL	11	350	12	3.6	23.3	4.7	7.6	0.2	-	-	12	550	-	3.7	2650	-	0.42	0.26	0.33	0.34	337.9	175.7	0.509	150	540	450	2200	19.4	27.4	1.00	0.18
UL	11	321	10	3.6	23.4	4.4	7.5	0.2	-	-	15	475	-	4.5	2925	-	0.46	0.29	0.28	0.34	477.9	157.5	0.670	190	350	325	2600	19.5	28.5	1.00	0.15
UL	11	349	4	5.9	23.3	4.1	7.7	0.3	-	-	16	500	-	5.3	2400	-	0.50	0.26	0.21	0.33	408.5	153.7	0.687	180	560	500	1900	20.1	28.9	0.98	0.17
UL	11	315	15	3.4	23.6	4.2	6.9	0.2	-	-	16	450	-	2.2	2175	-	0.38	0.31	0.29	0.32	421.0	199.0	0.530	150	330	375	1800	20.2	30.2	1.00	0.19
UL	12	58	5	4.6	25.6	1.4	2.6	0.5	-	-	25	625	-	0.7	2650	-	0.43	0.29	0.34	0.35	807.3	237.1	0.613	220	240	550	2100	20.2	29.4	0.98	0.19
UL	12	45	3	4.8	25.5	1.5	2.1	0.4	-	-	26	625	-	0.7	2450	-	0.40	0.29	0.21	0.30	874.9	219.3	0.620	160	320	550	1900	21.4	30.5	0.98	0.2
UL	12	38	3	4.7	26	1.4	2.5	0.4	-	-	25	675	-	0.8	2550	-	0.35	0.28	0.22	0.28	867.0	235.1	0.609	160	310	550	2000	20.8	29.8	1.00	0.17
UL	12	35	1	4.7	25.9	2.4	2.2	0.5	-	-	28	675	-	0.8	2800	-	0.36	0.28	0.18	0.27	884.2	231.9	0.595	160	280	600	2200	20.8	31.4	1.00	0.17
UL	12	134	8	5	24.7	2.6	1	0.6	-	-	14	400	-	0.8	1725	-	0.42	0.28	0.33	0.34	565.1	171.7	0.623	150	310	225	1500	19.3	30.3	1.00	0.19
UL	12	121	36	5.1	25.2	2.6	0.9	0.4	-	-	15	550	-	1.1	2800	-	0.42	0.32	0.23	0.32	454.8	178.0	0.583	130	230	400	2400	21.4	31.9	0.98	0.24
UL	12	79	4	5.1	25.2	2.6	0.7	0.4	-	-	14	425	-	1.2	1650	-	0.43	0.31	0.27	0.34	758.7	137.5	0.731	230	160	250	1400	20.4	31.3	0.05	0.2
UL	12	102	1	5.3	26.1	2.6	0.2	0.5	-	-	26	750	-	1.2	3200	-	0.44	0.32	0.26	0.34	563.8	210.5	0.598	110	340	700	2500	20.6	31.9	0.99	0.18
UL	12	400	11	3.6	23.7	4.5	9.5	0.4	-	-	15	525	-	4.8	2650	-	0.48	0.28	0.26	0.34	370.8	188.1	0.611	120	230	450	2200	18.9	28	1.00	0.18
UL	12	372	4	3.7	23.5	5.1	6	0.3	-	-	14	500	-	5.9	2600	-	0.40	0.25	0.19	0.28	428.3	168.0	0.589	170	340	500	2100	18.7	29.1	0.98	0.18
UL	12	358	32	3.7	23.7	3.9	5.9	0.3	-	-	11	525	-	6.7	3450	-	0.46	0.28	0.26	0.33	327.2	225.2	0.666	180	300	950	2500	19.2	28.5	0.98	0.22
UL	12	302	6	4	24	6.4	5	0.2	-	-	12	600	-	5.6	4500	-	0.47	0.29	0.28	0.34	455.9	213.7	0.620	180	340	500	4000	18.8	28.9	1.00	0.13

UL = Unlogged forest

Appendix 6

A prior study published by Katovai and colleagues that examined understory plant species and functional diversity in degraded landscapes of Kolombangara Island. This is one of the few publications that address land use change and its impact on plant communities in Solomon Islands.

Katovai, E., Burley, A.L., Mayfield, M.M., 2012. Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation* 145, 214–224.



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Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands

Eric Katovai[1], Alana L. Burley, Margaret M. Mayfield*

The University of Queensland, School of Biological Sciences, St. Lucia, QLD 4072, Australia

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ABSTRACT

Anthropogenic activities have resulted in extensive deforestation and forest degradation on many tropical oceanic islands. For instance, some islands in the Solomon archipelago have as little as 10% of primary forests remaining with few of these remnants protected from future land use change. We examine the plant species and functional diversity (excluding adult canopy trees) of 48 sites from four forest land use types (two types of primary forest, secondary forest and abandoned tree plantations) and two common human-maintained land use types (coconut plantations and grazed pastures) across three elevation bands on Kolombangara Island, Solomon Islands. In total, we surveyed 384 species from 86 families of which only 6.5% were non-native. Species richness was lowest in coconut plantations and grazed pastures and declined with increasing elevation across all land use types. Functional diversity was similar between primary and secondary forest (high richness, high evenness and unaltered dispersion) and lowest in coconut plantations and grazed pastures. Our results suggest that species and functional richness have had divergent responses to land use change in forest land uses indicative of a loss of functional redundancy. Despite structural and compositional similarities among primary forests and degraded forest land uses, full recovery of secondary and commercial plantations has not been achieved. We suggest that conservation of Kolombangara's forest understory flora will require reserves across the island's elevation gradient and may require active restoration in the future, particularly if degrading activities continue at the current rate.