TROPICAL FOREST COMPOSITION AND STRUCTURE

ON NEW BRITAIN ISLAND,

PAPUA NEW GUINEA

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A Thesis

Presented

to the Faculty of

California State University, Chico

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Environmental Science

_____

by

© Jeffrey Lauder

Spring 2015

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DEDICATION

I would like to dedicate this thesis to my parents, Gary and Carol Lauder, for instilling in me a love of the natural world through yearly vacations to innumerable beautiful destinations. I can safely say I would not be where I am now without my wonderful childhood experiences in the mountains and forests of the American west, for which I am extremely grateful. I would also like to dedicate this thesis to my fiancé (and likely wife by the time of publication), Alicia. I can never thank you enough for your sacrifice, love, and understanding through this whole process.

ACKNOWLEDGEMENTS

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ABSTRACT

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Tropical forests contain significantly greater species richness and overall diversity than temperate systems. Stand enumeration is often used to describe and map patterns of diversity. In the Lake Hargy Caldera (LHC), West New Britain, Papua New Guinea, all trees >5cm DBH in seven 0.04ha plots established within four distinct habitat types were sampled to begin to assemble a species list and describe variation across the forest.

Plot enumeration found 92 species, 73 genera, and 49 families. Enumeration also showed that the LHC forest does not have the high α-diversity seen in some other tropical forests (H = 2.88).

Ordination of forest plots showed distinct forest types separated by location within the caldera (species-level MRPP $T = -3.02$, $A = 0.099$, $p = 0.007$), with taxanomic clustering within particular forest types. Soil analysis found significant differences between sampled areas in nine of the 21 sampled parameters. All areas had very high sand content (>56% sand). Overlay of soil variables onto a species ordination showed correlation among species distributions and soils, with conductivity and copper concentration being highly associated with species variation, but soils alone did not explain the majority of forest species variation.

This study was the first enumeration and description of the forest within the LHC. Results show that the LHC forest is species-rich and consists of multiple distinct forest types. Soil characteristics were shown to partially contribute to observed variation, but other variables, such as disturbance, may also be driving shifts in composition.

CHAPTER I

INTRODUCTION

Format of this Thesis

This thesis is written following the "publishable article" format, with each chapter written as a standalone research article, with slight modifications to fit within the format and style required by the thesis format. With the exception of Chapter VI, which is a summary/synthesis essay, each chapter will begin with its own abstract and introduction, followed by methods, discussion, and conclusion sections, as well as their own references.

Chapters II and III are written as stand-alone articles to be submitted for publication in peer-reviewed journals. Chapter II outlines results from a stand-level enumeration of the forest within the Lake Hargy Caldera (LHC), Papua New Guinea and provides a comprehensive species list and description of observed variation in forest composition. Chapter III discusses variation in soil chemistry and texture relative to the forest composition outlined in Chapter II. Chapter IV, as described above, is written as a small "synthesis" essay that outlines possible theoretical implications of results from Chapters II and III.

Background

The sheer volume of species known to exist across the globe is astounding in its own right. Multiple theories regarding possible determinants of diversity have been proposed, tested, and validated or discarded. These theories range from very simple models of biotic and abiotic interactions to complex theories on the nature of energetics and biogeography. Much of this work is an attempt to quantify and describe species that may or may not exist within a model's endpoints of interpolation. Many of the models produced and used in an attempt to describe patterns in diversity are either global, with much of the model being driven by climatic variation and known species distributions, or regional, with small-scale factors such as substrate and disturbance being deemed most significant.

Statement of the Problem

Understanding what factors directly and indirectly contribute to diversity in particular systems is a question that continues to be examined by biologists and ecologists alike. Describing which species are found where is the first major step toward understanding what factors contribute to a location's diversity. Basic species inventories are still needed in much of the world's landscapes in order to better understand the complex interactions among abiotic and biotic factors, as well as large-scale determinants of species distributions and small-scale associations. Plot-specific enumeration is still a

useful tool in such analyses, as analysis of local diversity may reveal trends not predicted by larger-scale models.

Purpose of the Study

Here I present the first species list compiled for the Lake Hargy Caldera (LHC), West New Britain, Papua New Guinea. This study describes spatial patterns within the LHC forest, as well as associations between those patterns and soil characteristics. Comparisons between the LHC forest and other tropical forests are also made. This study ends with a discussion of current theories of diversity and proposes a hybrid approach to understanding determinants of diversity.

Limitations of the Study

One of the key concepts in the sciences is using quantitative techniques to make inferences about the population from which the data is sampled. Inferential statistics, however, lose power with smaller sample sizes. This study was limited by time spent in a foreign location, and as such is limited by a small sample size, with only seven measured plots across four major areas with the LHC. All analyses conducted and conclusions drawn from those analyses were performed and formulated with these limitations in mind, and as such, focus primarily on the building of a species list and preliminary description of variation in observed parameters within the Lake Hargy Caldera.

The enumeration and description of forest plots presented here was not completed to address any single hypothesis. This study instead used simple exploration and documentation to augment current species lists, known species ranges, and understanding of global and regional patterns of forest diversity

CHAPTER II

VARIATION IN FOREST COMPOSITION

AND STRUCTURE ON NEW

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Abstract

Tropical forests contain significantly greater species richness and overall diversity than temperate systems. Enumeration (measuring of and counting of every tree within a plot) is often used to quantify variation in forest structure and composition across a landscape. Enumeration methods vary, however, with studies using a range of plot sizes and numbers. In the Lake Hargy Caldera (LHC), West New Britain, Papua New Guinea, all trees >5cm DBH in seven 0.04ha plots within four distinct forest areas were sampled to begin to assemble a species list and describe variation in this previously un-sampled forest. Plot enumeration found 92 species, 73 genera, and 49 families. Ordination of forest plots showed distinct forest types separated by location within the caldera, with a broadly mixed distribution of families and genera but species-level clustering in specific locations. Results show that the LHC forest may not be as diverse as other tropical forest

locations when considering Shannon's diversity index (H = 2.88) alone. When comparing

taxa-level richness and structure, however, the LHC forest has greater than 300% more

species per hectare ($\bar{X}$ = 629, SD = 68) than similar forests in Southeast Asia, and slightly

more (1% greater) families per hectare ($\bar{X}$ = 479, SD = 50) than other tropical forests

worldwide. Significant differences were found in forest composition by location (species-

level MRPP T = -3.02, A = 0.099, p = 0.007). Structural variation was also observed, with

basal areas by plot ranging from 68.68 m² ha^{-1} to 21.37 m² ha^{-1}, and differences in

calculated structural metrics including canopy and sub-canopy stem densities. Results

show differing stand dynamics across the caldera, with some plots dominated by a large

number of small stems of a single species, and others showing more homogeneous

composition. Observed variation reveals possible site-specific interactions between

disturbance and species pool.

Introduction

Many estimates have been made regarding the true magnitude of global

biodiversity, but extensive gaps remain in our knowledge of the global distribution and

drivers of that diversity (Raven and Wilson 1992, Colwell and Coddington 1994, Wilson

2000). Tropical forests contain some of the most diverse species assemblages on the

planet, and collectively represent some of the most highly diverse regions on Earth; while

they are estimated to cover only 7% of global land surface, they contain more than half of

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the world's species (Wilson 1988). Gradients in tropical forest diversity and structure have been directly linked to wildlife community integrity (Gentry 1992, DeWalt et al. 2003), and various ecosystem services such as forest product production and climate refugia for threatened species (Costanza et al. 1997, Chapin et al. 2000). Diversity of tropical forest systems, however, varies greatly across the globe, and locations of higher and/or lower diversity, as well as drivers of those patterns of diversity are still not well understood.

Remote sensing and other techniques have made considerable progress in the realm of mapping tropical forest types globally, however species-level stand enumeration is still necessary and valuable tool for the tropical forest ecologist (Arul Pragasan and Parthasarathy 2010). Landscape-level estimation of beta and gamma diversity, however, is not always possible from stand-specific surveys (Decocq 2002, Arul Pragasan and Parthasarathy 2010), demonstrating significant variation in the spatial distribution of forest diversity, and an increased need for systematic forest inventories.

Forest structural variation, stand-specific forest diversity (i.e. species pools), forest species life history traits, and disturbance history may all interact to influence tropical forest diversity and succession. De Cáceres et al. (2012) found that species richness alone does not always explain beta diversity at a global scale. Instead, other spatially-explicit factors may influence landscape diversity through limits on species evenness and aggregation.

Tropical forests are often under dynamic disturbance pressures ranging from large-scale, infrequent volcanic eruption to small-scale, frequent gap creation via coupled wind and flood effects (Foster et al. 1998, Turner et al. 1998). A wide range of disturbance histories has long been studied and debated in relation to overall biome diversity (Connell 1978, Platt and Connell 2003), but gaps remain in understanding how disturbance and diversity interact at differing scales. Stand-replacement events such as volcanic disturbance can dramatically shift forest composition (Scheffer et al. 2001, Pitman et al. 2005) and, when coupled with high-frequency disturbance during the colonization period, can cause regeneration to follow unpredictable mosaic patterns (Swaine and Hall 1988, Chazdon 2003). Life history traits such as disturbance tolerance and shade intolerance can collectively cause entire stand species shifts following larger disturbances (Goodale et al. 2012), providing further noise in models of succession. Through floristic enumeration of permanent forest plots, it is possible to begin to piece together disturbance histories (Onaindia et al. 2004) as well as examine local and regional distributions of diversity and succession patterns relative to land history.

The island nation of Papua New Guinea (PNG) contains approximately 1.5% of the world's tropical forests (Saulei 1997), which covers over 25 million hectares (Shearman et al. 2009) on the mainland and surrounding islands. Given the variable terrain and multiple island chains, few studies have been conducted which provide in-depth enumeration and description of the forest types within the PNG landscape. Those studies that do quantify forest structure, biomass, or species composition vary widely in

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method and scope. Paijmans (1970), Wright et al. (1997), Keppel et al. (2010), and Fox et al. (2010) all measured trees > 10 cm diameter at breast height (DBH), but used varying sample plot sizes, ranging from 0.04 ha to 1 ha. Read et al. (1990) and Whitfeld et al. (2012) both measured trees >5 cm DBH, but sampled 20 x 100 m and 50 x 50 m plots, respectively. More interestingly, while island biogeography would lead us to expect increased overall diversity and variation across an island nation, the majority of studies with at least one component focusing on forest diversity within PNG have been carried out primarily on the mainland (Paijmans 1970a, Smith 1975, Read et al. 1990, Wright et al. 1997, Shearman 2010, Whitfeld et al. 2012).

Bachman et al. (2004) provide one of the most extensive analyses of the region, but focus strictly on factors associated with palm growth. By examining all known palm voucher records from mainland PNG and surrounding islands, Bachman et al. found that species ranges overlapped in mid-elevations, demonstrating distinct elevation gradients in palm diversity. Focusing strictly on palm species, as well as voucher specimen analysis, limits findings to regions that have had vouchers collected, as well as simply to regions which have been scientifically described. Regions with no extensive collections cannot be included in a voucher-based analysis. Fox et al. (2010) provide the most large scale field monitoring data from permanent sampling plots across the region to date, but focused primarily on total aboveground biomass as opposed to tree enumeration and measures of diversity. While many studies have focused on diversity and forest dynamics within the

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PNG landscape, the lack of extensive stand enumeration in the region represents an important gap in range and distribution maps and models of diversity.

PNG has experienced extremely rapid conversion of forested lands (Saulei 1997, Shearman et al. 2009) across much of the landscape, including the highly diverse forests across the various islands. Further forest enumeration across PNG and description of previously unexplored areas is needed in order to increase accuracy of estimates of diversity in the region. This study presents the first enumeration and description of the forest within the Lake Hargy Caldera, West New Britain Papua New Guinea. The caldera borders the Nakanai Mountains, which were recently nominated for World Heritage Site recognition due their unique geology and flora. The proximity of the relatively undisturbed caldera to proposed conservations lands provides further impetus for botanical exploration of this unique landscape. Variation in forest composition and structure within a volcanic caldera, as well as estimates of landscape diversity within that caldera are provided. Species richness and diversity measures are compared to other plots within PNG, as well as other tropical regions. Variation in understory composition relative to overstory species is also assessed to describe patterns of succession and co-occurrence within the Lake Hargy Caldera.

Methods

<u>Study Site</u>

All sample plots were located within the Lake Hargy Caldera (LHC, 5°19'49.59"S, 151°06'55.17"E), within the highly diverse Coral Triangle region of the south pacific (Figure 1). The Coral Triangle encompasses Oceania and Southeast Asia, and is often cited as containing some of the greatest marine diversity on Earth (Veron 1995). The region is also considered a global biodiversity hotspot (Briggs 2005, Allen 2007).

The LHC itself is one of several major calderas on the island of New Britain. The island breached the ocean surface in the late Miocene (8-10 million years ago) as the result of volcanic uplift, and the Quaternary volcanoes found there define the Bismark volcanic arc that formed in response to northward subduction of the small Solomon plate beneath the Bismark plate (Woodhead et al 1998, Sinton et al 2003).

The latest caldera-forming eruption of Hargy volcano took place about 11,000 years ago. The dacitic Galloseulo lava cone rises above and partially overtops the western rim of the caldera. A double crater occupies a larger 700-m-wide crater. Numerous small eruptions have taken place at Galloseulo over the past 7000 years, the last occurring about 1000 years ago (Lolok and McKee, 1993). Bordering the caldera on the East and Southeast is the Nakanai mountain range, a carbonate-based range formed via uplift as a result of the nearby subduction zone. The LHC is named such because it contains the ~8 km² Lake Hargy, which is drained to the North by the Lobu River. The Lobu River starts

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at Lake Hargy, travels along the base of an elevated plateau (East Ridge), then through a flat floodplain region (North Caldera) before leaving thr caldera through a narrow canyon to the North. The region has an average monthly temperature ranging from ~30°C to ~32°C and mean annual rainfall of ~2000 mm, with a distinct dry season from June through September when average monthly precipitation declines by ~50%. Highly variable topography within the caldera itself, however, leads to daily orographic precipitation in addition to the regional precipitation patterns.
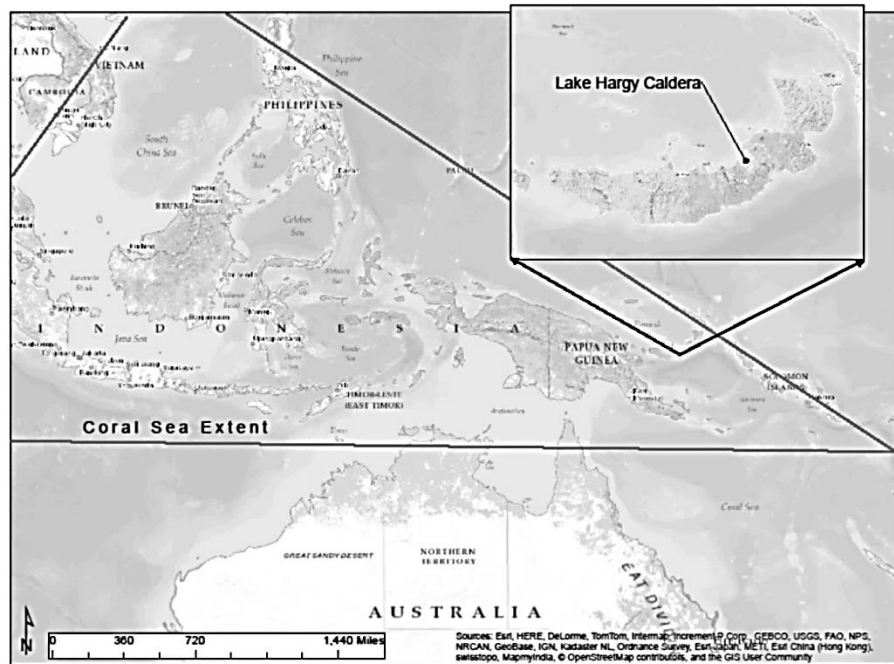
Figure 1. Map of study site location within the South Pacific. The Lake Hargy Caldera (LHC) is on the border of East and West New Britain, on New Britain Island, Papua New Guinea. Map was produced by the author using the spatial datasets listed in the figure.

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<u>Sample Locations</u>

Sites were chosen at naturally assembled but distinct forest stands in various regions of the LHC to quantify a random selection of the most representative sites within these regions (i.e., a stratified random sampling scheme). Four particular forest types were identified via visual reconnaissance and consideration of variation in disturbance type. Plots were then randomly established within each of this distinct forest types.

<u>Data Collection</u>

Forest plots measuring 20m x 20m were established, demarcated into 4 quadrants of 10m x 10m, and labeled. Two plots were established per geographic area and previously identified forest type, with four areas sampled (with one area having only one plot due to temporal and spatial constraints), for a total of seven plots. Plots were abbreviated to represent their locations as follows: North Caldera Plots 1 and 2 (NCP1, NCP2), Crater plots 1 and 2 (CC1, CC2), East Ridge plots 1 and 2 (ER1, ER2), and Lake Hargy plot (LH1) (Figure 2). All stems >5cm DBH (diameter at breast height or above buttresses) within the plots were numbered, measured, and identified to Family, Genus, and Species. Species identification was conducted in the field with assistance of Kipiro Damas, botanist with the Forest Research Institute (FRI) of PNG, and later confirmed via vouchers by Mr. Damas at the FRI in Lae, PNG. Tree height was measured using a laser rangefinder and recorded to the nearest 0.1 m.

Belt transects measuring 20m x 2m were laid bisecting each 20m x 20m plot from South to North, and all vegetation <1.5m tall within the belts was identified to species to quantify understory composition, as well as potentially identify patterns in succession and recruitment. Voucher specimens were also collected for species that were difficult to identify in the field or were thought to be previously unreported or undescribed in the region.
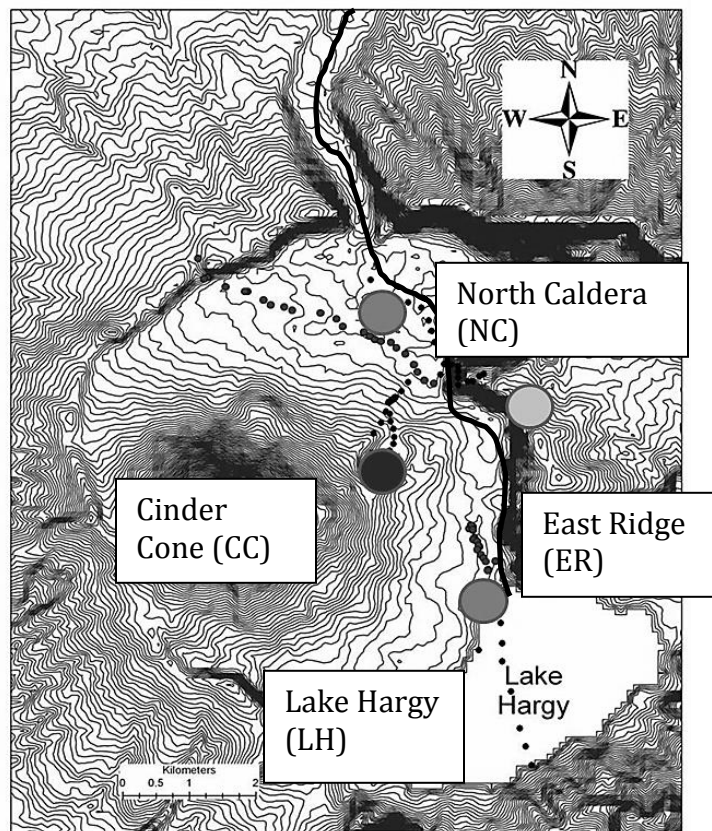
Figure 2. LiDAR-derived topographic map (NASA 2011) of the Lake Hargy Caldera with plot locations labeled. The Lobu River is approximated by the bold line. Small circles represent travel track logs. Large circles represent forest plot pair locations.

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To examine differences in DBH and height by site and by area, Kruskal-Wallis tests were used, based on the non-normal but homoscedastic nature of the data. Outliers in height and DBH were not removed, as the goal of this analysis was to examine plot structure *in situ*, and examine possible effects large or small trees may have on plot composition and structure. DBH and height size distributions were determined by plot, by area, and for the total data set in order to examine distribution curves.

Family Importance Values and Individual Importance Values were calculated to measure structure and ecological influence. Family Importance Value (FIV) was calculated using the method outlined in Mori et al. (1983):

$$FIV_i = R_i + N_i + B_i \qquad \text{(eq. 1)}$$

where i indexes families, R = relative richness (number of species in family / total species richness), N = relative stem density (number of stems in family/ total number of stems), and B = relative dominance (ratio of family basal area to total basal area).

To examine compositional effects of dominant single species, Individual Importance Value (IVI) was calculated as:

$$IVI_j = F_j + N_j + B_j \qquad \text{(eq. 2)}$$

where j indexes individual species, F = relative species frequency, and N and B are the same as in equation (1), but referencing species instead of families. Both measures of family and individual importance are used as proxies for ecological significance in the

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plot, as more dominant and frequent trees are assumed to more directly influence plot structure.

Diversity Analysis

Measures of α-diversity were determined using Simpson's Diversity Index (D), and Shannon's Index (H'). Both indices were used to account for differing sensitivity to evenness and richness in the two metrics (DeJong 1975). Species area curves were used to assess sampling efficiency and estimates of potential α- and γ-diversity. Diversity measures were then compared to other tropical forest enumerations within the PNG and South Tropics regions, as well as studies in both the Amazon and Congo Basin regions.

β-diversity was calculated across the LHC using a "modified" version of Whitaker's β-diversity, sometimes referred to as "dissimilarity β" (McCune et al. 2002), calculated as:

$$B_D = \frac{\log(1-\overline{D})}{\log(0.5)} \qquad \text{(eq. 3)}$$

where $\overline{D}$ = average dissimilarity using statistical distance. Sorenson (Bray-Curtis) distance was used for all dissimilarity measures.

For community analysis, relativizations were used to dampen effects of rare or abundant species without completely removing them. Tree abundance data were relativized based on examination of coefficients of variation (CV) before and after relativization, with a threshold of CV less than 50 being acceptable (McCune et al. 2002). Family-level and species-level tree data were relativized by species maximum, while

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genus-level data were log(x+1) transformed and then relativized by species maximum due to high CVs following simple relativization.

NMS (Non-metric Multidimensional Scaling) ordination (Kruskal 1964, Mather 1976) and hierarchical cluster analysis of community data were performed on all taxonomic data using PC-ORD v6 (Mccune and Mefford 2011) to examine changes in overall community composition across the landscape. NMS is an ordination method that uses selected distance measures (in this case Sorenson Distance) to compare overall sample similarity based on all sample variables (taxa). Unlike Principle Components Analysis (PCA) and similar ordination methods, NMS does not assume linear relationships among ordinated variables, and often outperforms other ordination techniques when analyzing non-normal or depauperate datasets, which is often the case with ecological data (McCune et al. 2002). An "autopilot" NMS run was done using the "slow and thorough" PC-ORD settings.

Structural metrics adapted from Seydack et al. (2011), listed in Table 1, were overlaid via simple linear biplot on final species ordinations to assess relationships between structure and composition. Overlaid variables can be assessed for linear correlation with each indivudal ordination axis and the distribution of species or plots along that axis.

To examine how each taxonomic level varied across the landscape, and identify groups relative to species, genus, and family composition, hierarchical cluster analyses were performed. Dendrograms were constructed using the Flexible Beta linkage method

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where β=-0.25. Flexible Beta is a linkage method that is compatible with Sorenson Distance, and a β of -0.25 was chosen because results from this type of analysis are most comparable to other clustering methods, such as Ward's method (McCune et al. 2002).

All understory belt transect data were screened through Kipiro Damas and the PNGTrees database (Conn and Damas 2006) to identify woody versus non-woody seedlings. Non-woody species were removed from understory analysis. Understory data were then ordinated along with overstory data using NMS to examine successional pathways within each site, and similarity between overstory and understory. All understory data was recorded at the genus level, and was only compared directly to the genus-level overstory data.

Lastly, all ordinations were accompanied by multi-response permutation procedures (MRPP), which is roughly akin to a non-parametric analysis of variance. MRPP assesses overall group differences relative to overall community composition (i.e. abundance of all species), and provides quantitative estimates of both the size and statistical significance of those differences (McCune et al. 2002).

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Table 1. Description of structural metrics calculated for comparison among forest plots in Lake Hargy Caldera (LHC), Papua New Guinea. All metrics were adapted from Seydack et al. (2011).

Abbreviation	Description
CR3	**Canopy-level crowding** (= SD3 x MD3)
MD3	Mean diameter of trees > 30cm DBH on the sample plot
MD3/SD3	Ratio reflecting degree of **canopy-level stem density intolerance**
MD1	Mean diameter of trees > 10cm DBH on the sample plot
SD12	Stems 10–20cm DBH: **sub-canopy stem persistence**
SD13	Stems 10–30cm DBH: **sub-canopy forest matrix stem density**
SD23	Stems 20–30cm DBH: **lower canopy stem density**
SD3	Stems > 30cm DBH: **canopy-level stem density**
MD3/12	(= SD3 / SD12): **canopy to sub-canopy stem density saturation**
SD2	Stems > 20cm DBH: **index of stem density packing**
SMP	Stand maturity phase index: MD3/SWS
SWS	Sum of the species-specific mean diameters of trees > 30cm DBH in sample plots divided by the number of trees > 30cm in the sample plot (species-weighted canopy-level mean diameter of trees in a plot)

Floristics

We measured a total of 343 stems across the seven sample plots ($\bar{X} = 49$, $SD = 12.37$), and identified 92 species within 73 genera from 49 families. Species area curves show a larger number of expected species than the number observed, with first and second-order jackknife estimates of 136 and 158 total expected species, respectively (Figure 3).
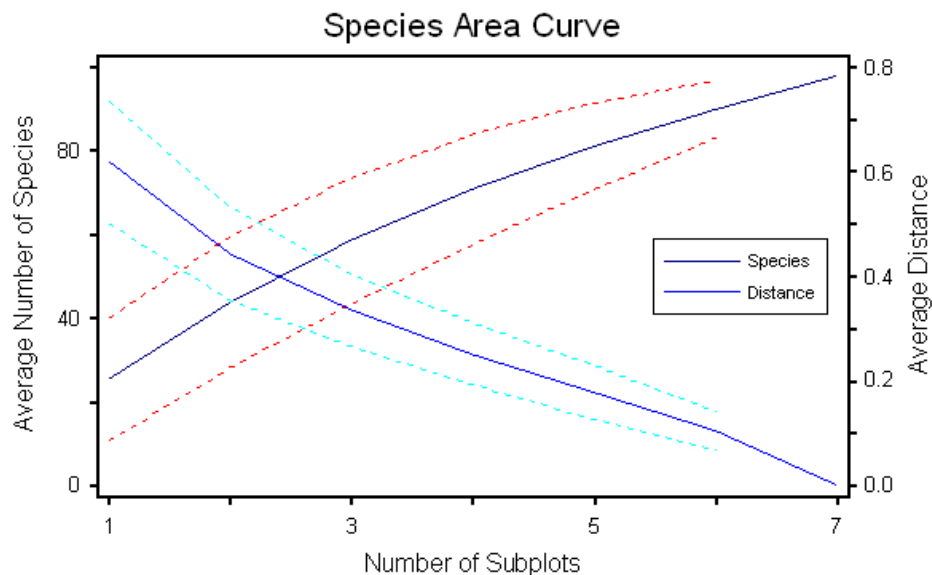
Figure 3. Species-area curve for sample plots within the LHC, Papua New Guinea.

Three of the species identified, *Magnolisa tsiampacca*, *Eriandra fragrans*, and *Turpinia pentandra* are considered rare, with the genus *Eriandra* being endemic to the papuasia region, and *M. tsiampacca* being native from the Malay Archipelago to Papua

New Guinea. With no previous inventories having been conducted in the LHC, all recorded individuals are considered previously unreported and contribute to adjustments of documented ranges.

The East Ridge 1 plot had 68 stems, 16% more than any other plot, and 54% more than the least dense plot (Figure 4). The East Ridge plots also collectively had the highest mean Shannon's and Simpson's diversity index (3.19 and 0.94, respectively), but CC2 had the highest individual plot diversity (Table 2). Overall β-diversity across the LHC was 2.17.
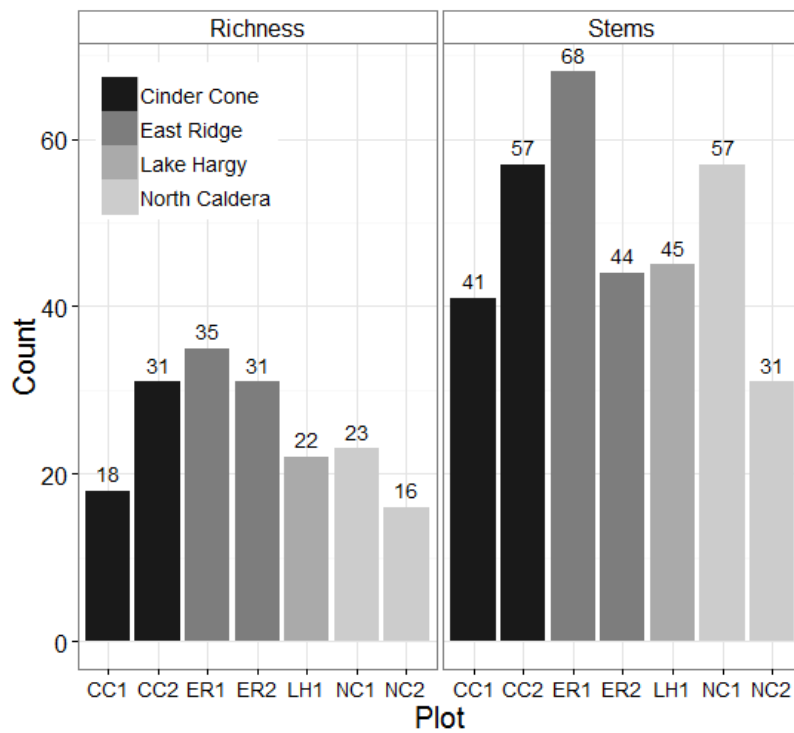
Figure 4. Stem density and species richness of each sampled plot. CC = Cinder Cone. ER = East Ridge. LH = Lake Hargy. NC = North Caldera.

Table 2. Summary statistics of seven 0.04 ha forest plots in the LHC. N = numer of stems in the plot. S = species richness. E = evenness. H = Shannon's diversity index. D' = Simpson's diversity index. B. area = Basal area. Values in bold represent top three values in that column.

Plot	N	S	E	H	D'	H Area	D' Area	B. area (m² ha⁻¹)	Largest species		B. area of lrg sp.	B. area per stem
CC1	41	18	0.88	2.56	0.90	2.902	0.925	28.82	**Weinmannia**	**trichophora**	0.623	0.078
CC2	**57**	**31**	0.95	**3.25**	**0.95**	2.902	0.925	37.52	Garcinia	latifolia	0.576	0.115
ER1	**68**	**35**	0.89	**3.17**	0.93	3.198	0.937	68.68	Magnolia	tsiampacca	**1.131**	**1.131**
ER2	44	**31**	0.94	**3.23**	**0.95**	3.198	0.937	23.08	Pometia	pinnata	0.363	0.363
LH1	45	22	0.94	2.92	**0.94**	2.915	**0.937**	21.37	Garcinia	latifolia	0.385	**0.385**
NC1	**57**	23	0.82	2.56	0.85	2.523	0.869	62.86	**Eucalyptus**	**deglupta**	1.327	1.327
NC2	31	16	0.90	2.49	0.89	2.523	0.869	38.12	**Pometia**	**pinnata**	**0.861**	0.287

Cluster analysis shows grouping of families and genus within each area (i.e., both plots within an area cluster separately from plots in other areas, Figure 5a and 5b). However, clustering by species is not observed in the Cinder Cone plots, with CC1 clustering with the North Caldera plots, and CC2 being compositionally distinct from all other plots (Figure 5c). NMS ordinations show similar results.
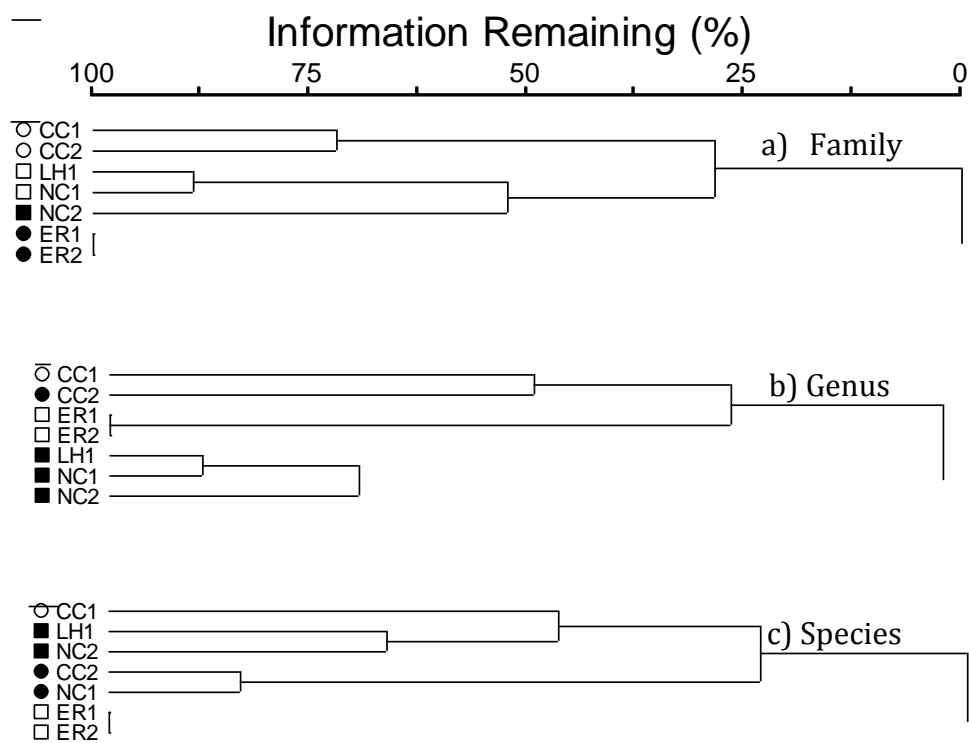
Figure 5. Cluster analyis of plot composition by each taxonomic level. 5a) Family-level cluster analysis, 5b) Genus-level cluster analysis, 5c) Species-level cluster analysis.

The species-level NMS ordination explained 54.6% of the variance in the species distance matrix (final stress = 0.00), with axis one explaining the majority of the variance (Axis 1 R^2 = 0.369, Axis 2 R^2 = 0.178). Along axis one, each of the areas cluster by species, with the Lake Hargy (LH1) plot clustering with the other "Caldera Floor" (NC1 and NC2) plots (Figure 6). The Cinder Cone (CC1 and CC2) plots, however, have the largest Sorenson distance between any pairs of plots observed, and are plotted at opposite ends of axis one. Along axis two, the East Ridge plots (ER1 and ER2) and "Caldera Floor" plots are at opposite ends, while the CC plots cluster toward the center of the axis.

MRPP was conducted on the plots comparing clusters identified in the cluster analysis. Results include a degree of difference between groups (T), a measure of within-group homogeneity (A), and a p value. Highly negative T values represent significant differences in group composition, while positive A values denote more homogeneity within groups (i.e. less within-group variance) than expected due to chance. MRPP of the plots by species using groups identified in the cluster analysis found significant differences in species composition by group (T = -3.02, A = 0.099, p = 0.007). The most significant pairwise difference was between the cluster with the two East Ridge plots and the cluster with CC1, LH1, and NC2 (T = -2.13, A = 0.08, $p < 0.0001$).
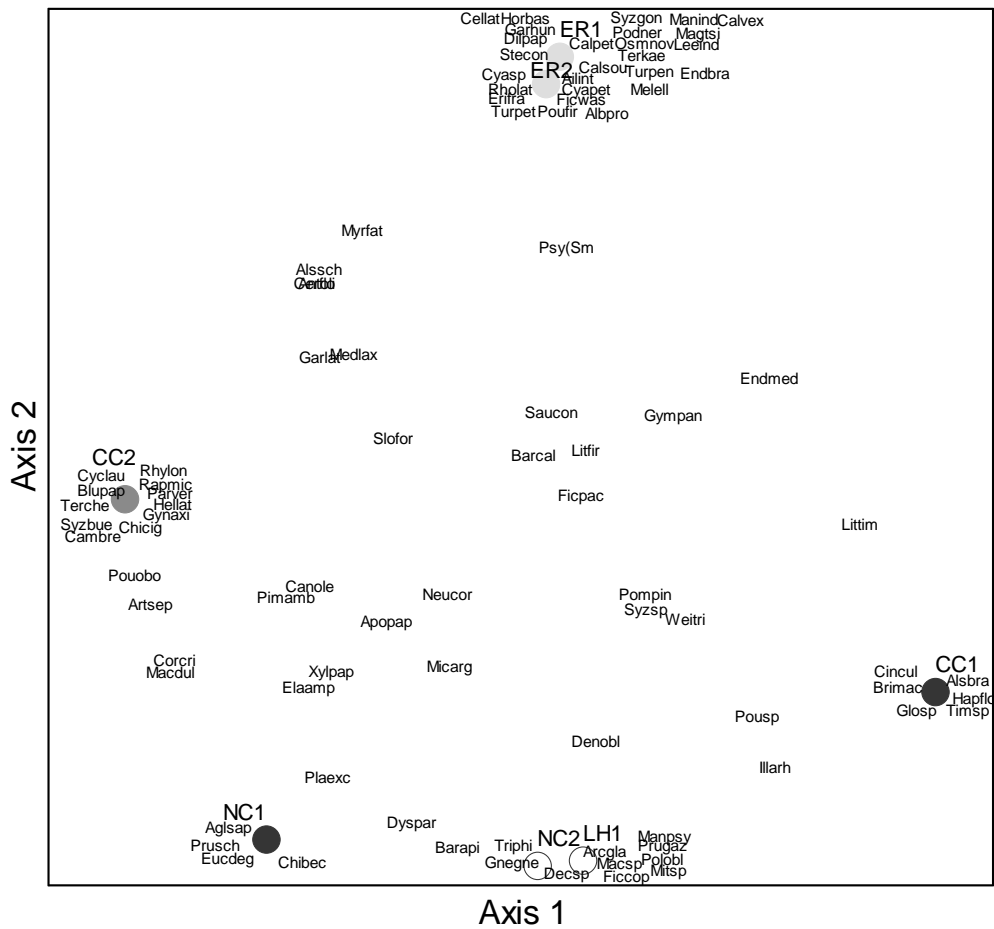
Figure 6. Non-metric Multidimensional Scaling (NMS) ordination of plots in species composition space by Sorenson (Bray-Curtis) distance. Plot colors represent group as identified via species-level cluster analysis (Figure 5c).

Understory versus Overstory

Ordination of belt transect genera versus overstory genera explained 76.8% of the variance (final stress = 8.57) in the aggregated overstory and understory genus matrix, with axis one explaining the slight majority of the variance (Axis 1 R^2 = 0.282, Axis 2 R^2 = 0.260, Axis 3 R^2 = 0.226). Understory of ER and CC plots was most similar to

overstory plots along axis one, while NC understory and overstory plots differed primarily along axis one, showing specific gradients in generic composition (Figure 7) that differed by forest type. East Ridge and Cinder Cone plots both followed uni-directional succession pathways along axis 2, while the North Caldera plots primarily followed succession pathways along axis 1, with some change along axis 2. Results demonstrate genus-level gradients that are distinct between the three areas, with the North Caldera having a succession pathway unlike the other two areas. The variation along axis one seen in NC2 is associated with *Platea*, *Garcinia*, and *Psychotria*, while the variation along axis one in NC1 is associated with *Eucalyptus*.
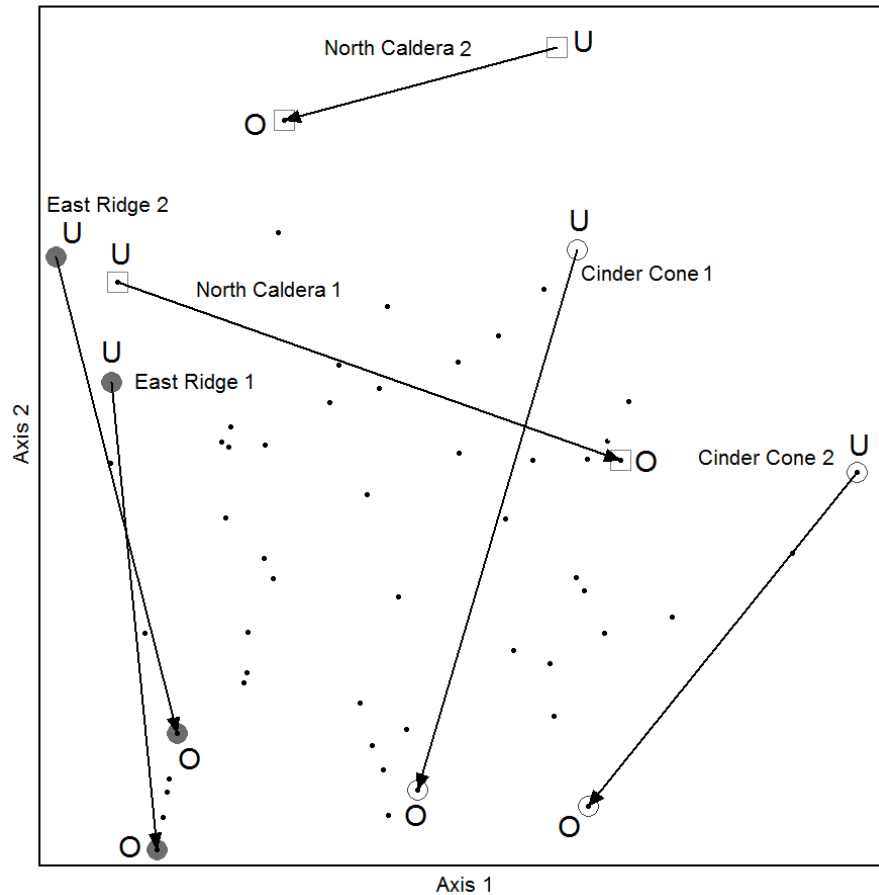
Figure 7. Non-metric Multidimensional Scaling (NMS) ordination of plots in genus space using Sorenson (Bray-Curtis) distance. Plots labeled "O" are overstory 0.04ha plots, while plots labeled "U" are understory belt transects through overstory plots with all individuals <1.5m tall identified to genus. Arrows represent successional vectors between within-plot understory and overstory communities. LH1 was excluded due to no belt transect measurement

<u>Structure</u>

DBH distributions of all four areas show high densities of small stems, with the East Ridge and North Caldera plots having the largest DBH range (Figure 8). The largest

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overall trees were found within the North Caldera plots, with the single largest tree observed being a 130 cm DBH, 45 m tall *Eucalpytus deglupta*. Kruskal-wallis tests showed no significant difference in DBH among all plot areas (χ^2=5.85, p = 0.119), and individual Wilcoxon rank-sign tests between within-area plot pairs found no significant difference in DBH between two paired plots. Height was significantly different among plots (p<0.05), with the only significant pair-wise difference being between cinder cone (CC) plots and the Lake Hargy (LH) plot (χ^2=14.76, p = 0.002).
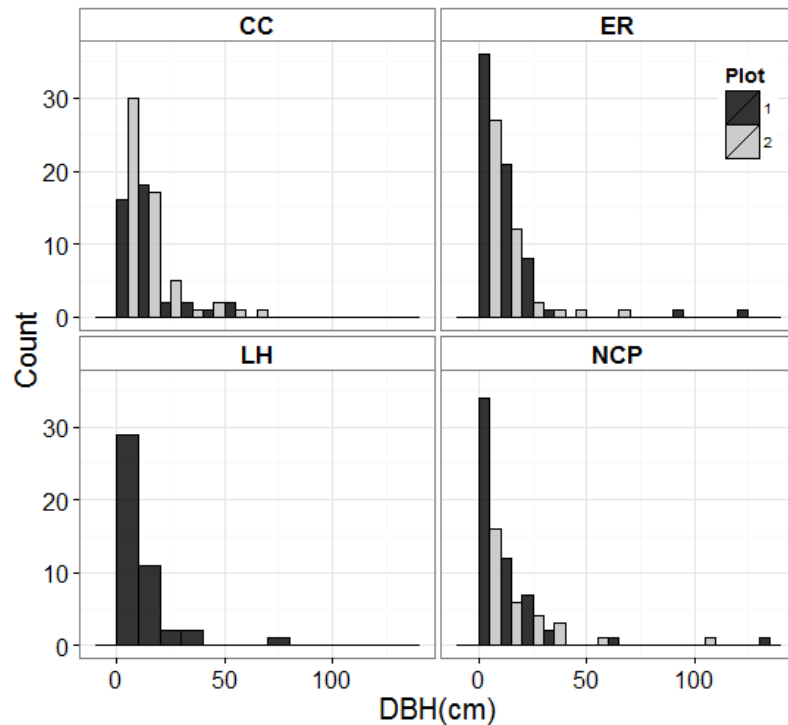
Figure 8. Diameter at Breast Height (DBH) distribution of all trees >5cm with all measured plots within the Lake Hargy Caldera. Kruskal-wallis tests showed no significant difference in mean distribution among sampled plots.

ER1 had the highest total basal area (2.75 m² ha^{-1}, Table 2), but ER2 had the second lowest (0.92 m² ha^{-1}). ER1 and NC1 had the largest single-stem basal areas, demonstrating dominance of single large trees. Structural metrics varied widely by plot (Table 3). Calculated stand maturity (SMP) indices suggest that all plots are in an advanced species-specific forest phase, with CC1 being the most mature. The SMP index, as developed and used by Seydack et al. (2011), is not a direct representation of stand maturity, per se, but is instead an indication of stage based on current composition. In other words, a high SMP simply shows that a plot has reached a temporary climax, and that species have reached a type of competitive equilibrium, and may or may not advance to a more advanced stage should direct competition cause mortality of neighboring trees.

Table 3. Summary of structural metrics calculated for each plot. See Table 1 for a description of all calculated metrics.

Plot	MD3	MD1	SD12	SD23	SD13	SD3	MD/ SD3	SD2	MD/ 12	CR3	SMP
CC1	42.98	20.64	16	2	18	5	8.60	7	0.31	214.9	1.82
CC2	47.72	21.72	16	5	21	5	9.54	10	0.31	238.6	1.66
ER1	82.57	22.56	21	8	29	3	27.52	11	0.14	247.7	1.00
ER2	47.50	20.25	12	2	14	3	15.83	5	0.25	142.5	1.00
LH1	50.75	19.97	10	2	12	2	25.38	4	0.20	101.5	1.00
NC1	66.00	27.20	11	7	18	4	16.50	11	0.36	264	1.00
NC2	53.20	28.91	5	4	9	4	13.30	8	0.80	212.8	1.44

The majority of structural metrics were correlated with the two NMS axes (Figure 9), with differences along axis two (i.e. between caldera floor and East Ridge plots)

primarily being associated with differences in canopy to sub-canopy stem density saturation and sub-canopy and forest matrix stem densities. The high forest matrix and sub-canopy stem densities observed in the East Ridge plots are consistent with lower SMP indices relative to other plots (1.0 compared to a high of 1.82 and 1.66 in the Cinder Cone plots). Cinder Cone plots had the lowest lower canopy and upper canopy stem densities, yet the highest SMP indices, demonstrating an even-aged yet sub-canopy-sized forest.
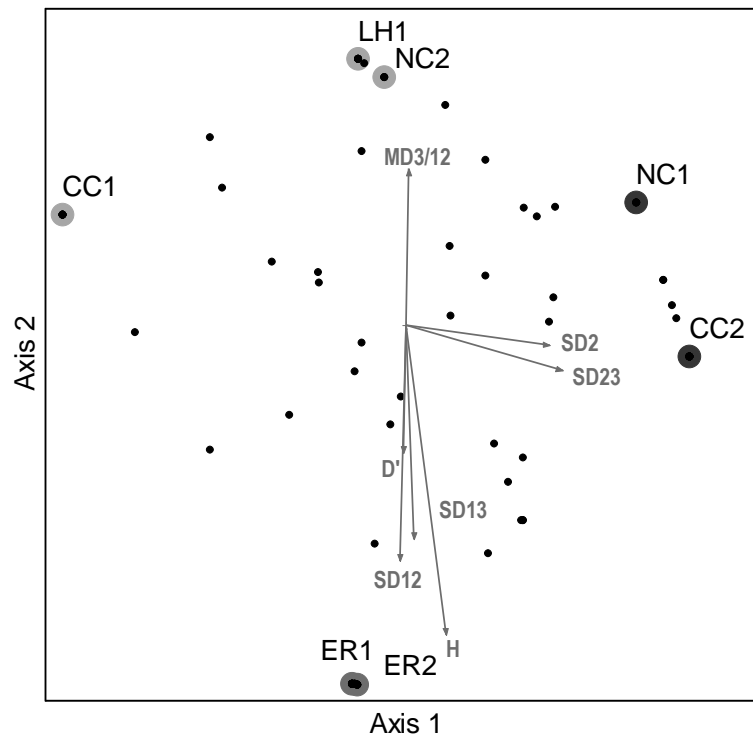
Figure 9. Non-metric Multidimensional Scaling (NMS) ordination of plots within species space (same ordinate as Figure 8), with bi-plot overlay of structural metrics. Bi-plot vector length represents correlation, with longer vectors demonstrating higher values. H = Shannon's diversity index. D' = Simpson's diversity index. Structural metrics are defined in Table 1.

From a specific species standpoint, *Pometia pinnata*, *Platea excelsa*, and *Garcinia latifolia* were the three species with the highest IVI values (24.46, 16.72, and 14.88, respectively). Three of the top ten most important species had only one stem recorded (*Eucalytpus deglupta*, *Magnolia tsiampacca*, and *Dillenia papuana*), demonstrating significance of large individual trees (Table 4). Individual importance was also reflected in relative proportion of basal area in a plot contributed by each species, with the six most important species listed above making up the majority of biomass in each plot (Figure 10). Family importance differed by plot location (Table 5). Clusiaceae was one of the top three most important families in three of four sampling locations. Clusiaceae shared the highest single FIV, at 0.53, with Icacinaceae.

Table 4. Top 10 most important species in the LHC, the total number of stems per species, and the calculated Importance Value Index (IVI), calculated as the sum of the relative frequency, relative density, and relative dominance of each species.

Species	Stems	IVI
Pometia pinnata	21	24.46
Platea excelsa	31	16.72
Garcinia latifolia	10	14.88
Eucalyptus deglupta	1	12.69
Psychotria (small leaf)	29	12.42
Magnolia tsiampacca	1	10.94
Weinmania tricophora	12	10.69
Dillenia papuana	1	7.18
Pouteria obovoidea	8	6.53
Pouteria sp.	10	6.42
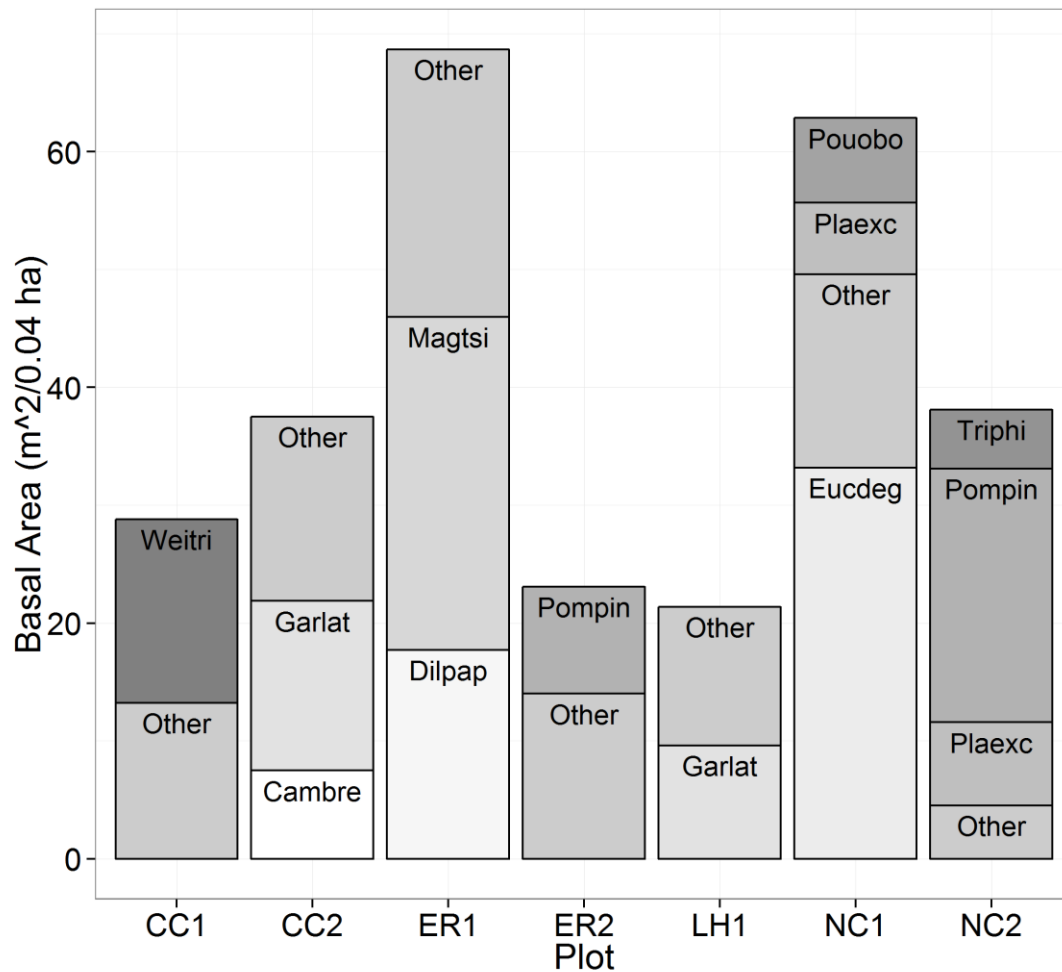
Figure 10. Relative basal area (m² $0.04ha^{-1}$) of all sample plots including relative basal area of dominant species. The majority of sampled plots were dominated by one or two either large-stemmed or dense species. Species codes are defined in the species list (Appendix A)

Table 5. Top three most important families per sampling area, with species per family, in the sampled plots, and the calculated Family Importance Value (FIV), calculated as the sum of the relative diversity, relative density, and relative dominance of each family.

Area	Family	Spp	FIV
ER	Magnoliaceae	1	0.34
ER	Clusiaceae	4	0.26
ER	Rubiaceae	1	0.25
CC	Euphorbiaceae	8	0.47
CC	Cunoniaceae	1	0.41
CC	Clusiaceae	1	0.3
NC	Icacinaceae	2	0.53
NC	Myrtaceae	2	0.44
NC	Sapindaceae	1	0.31
LH	Clusiaceae	1	0.53
LH	Sapindaceae	1	0.33
LH	Anonaceae	2	0.23

Discussion

Comparisons to other New Guinea inventories

The mean basal area and stems ha^{-1} found in the LHC plots was average relative to other Papua New Guinea and South Pacific forests (Table 6). The number of species ha^{-1}, however, was significantly higher in LHC stands than in surrounding forests. This can be simply a sampling artifact due to the number of species ha^{-1} being extrapolated from seven 0.04 ha plots as opposed to the use of unique 1 ha plots. Richness estimates generated via species area curves (Figure 3) infer that species counts in LHC plots are in fact well below the expected diversity. The large discrepancy between predicted and measured richness is likely due to sample size. Wagner et al.

(2010) found that census interval and plot number directly influence estimates of diversity and basal area. For a 0.25 ha plot, a minimum of four plots per sampling location is recommended for estimating aboveground biomass, and two plots per sampling location is recommended for estimating basal area. This number increases exponentially with smaller plot sizes. Plots in this study were 0.04 ha, representing significant influence of small sample plot size on species richness estimates.

Table 6. Comparison of LHC diversity and structure to other plots sampled within Papua New Guinea and surrounding SE Asia and South Pacific Island forests. Bold values represent the highest value in that column.

Country	Forest	Basal Area	Stems ha^{-1}	Reference
Papua New Guinea	LHC	37.4	554	This Study
Papua New Guinea	Crater Mountain	31.5	602	Weiblen (1998)
Papua New Guinea	Crater Mountain 2	37.1	693	Wright et al. (1997)
Papua New Guinea	Halowia	40.1	529	Keppel et al. (2010)
Papua New Guinea	Sewa	**46.3**	612	Keppel et al. (2010)
Solomon Islands	Lauru	34.4	662	Keppel et al. (2010)
Solomon Islands	Kolombangara	43.3	537	Keppel et al. (2010)
Solomon Islands	Tetepare	31.2	409	Keppel et al. (2010)
Vanatu	Erromango	37.7	916	Keppel et al. (2010)
Fiji	Savura	42	905	Keppel et al. (2010)
Fiji	Kubulau	49	754	Keppel et al. (2010)
Fiji	Gau	45.7	840	Keppel et al. (2010)
American Samoa	Tiavea	36.8	712	Keppel et al. (2010)
American Samoa	Vatia	30	580	Webb & Fa'aumu (1999)
Borneo	Mount Kinabalu	37.7	**1047**	Aiba and Kitayama (1999)

In one of the earliest species inventories of mainland Papua New Guinea, Lauraceae, Meliaceae, Moraceae, Myrtaceae, and Euphorbiaceae were found to be the

most represented families, both in terms of number of species and number of individuals in sample plots (Paijmans 1970b), while only Euphorbiaceae and Myrtaceae were also important in the LHC forest. The 1970 inventory also found single-plot clustering of *Garcinia* similar to that observed in the LHC. *Pometia* were primarily in the larger DBH size classes on the mainland, but present only in smaller size classes in the LHC.

<u>Comparisons to other Tropical Forest Regions</u>

The forest within the LHC has fairly high diversity relative to other tropical regions where inventories have been completed, with the largest number of families ha^{-1} (479 ±50) when compared to forests in Borneo and Central and South America (Table 7). The LHC forest also has higher genera ha^{-1} ($\bar{X}$ = 586, *SD* = 57) and species ha^{-1} ($\bar{X}$ = 629, *SD* = 68) than most of the forests compared. Shannon diversity in the LHC is similar to other Southern Pacific, Indian, and Costa Rican forests (Figure 11). LHC diversity is much lower, however, than that of forest plots in Jalisco, Mexico, and much higher than those measured in Northern Puerto Rico. One important caveat in these comparisons is the effect of sample plot size. All estimates of species, genera, and families per hectare were calculated via extrapolation from 0.04 ha plots, possibly yielding much higher estimates of diversity than would realistically be sampled across a simple 1 ha plot.

Table 7. Family, generic, and species richness of LHC plots relative to other tropical forests worldwide. Bold values represent largest values in that column.

Country	Forest	Fam ha^{-1}	Gen ha^{-1}	Spp ha^{-1}	Reference
Papua New Guinea	LHC	**479**	586	629	This Study
Borneo	Mount Kinabalu	127	221	356	Aiba and Kitayama (1999)
Solomon Islands	Kolombangara			86**	Burslem and Whitmore (1999)
Ecuador	Cordillera El Consuelo			**932.5**	Homeier et al. (2010)
Costa Rica	Cordillera de Talamanca	686*	990*	1266*	Oosternhorn and Kappelle (2000)
Nicaragua	Cosquina	270	420	480	Gillespie et al. (2000)
Costa Rica	Santa Rosa	330	**690**	750	Gillespie et al. (2000)
Costa Rica	Palo Verde	290	550	650	Gillespie et al. (2000)
Nicaragua	Chacocente	280	470	540	Gillespie et al. (2000)
Nicaragua	Masaya	280	410	440	Gillespie et al. (2000)
Nicaragua	La Flor	250	520	590	Gillespie et al. (2000)
Nicaragua	Ometepe	310	420	450	Gillespie et al. (2000)
Puerto Rico	Guanica	190		340	Gentry (1995)
Puerto Rico	Mogotes	280		370	Gentry (1995)
Jamaica	Round Hill	320		540	Gentry (1995)
Mexico	Chamela	370		790	Lott et al. (1987)
Mexico	Chamela 2	340		800	Lott et al. (1987)
Colombia	Galerazamba	200		360	Gentry (1995)
Colombia	Tayrona	310		490	Heybrock (1984)
Colombia	Los Colorados	410		810	Gentry (1995)
Colombia	Coloso	460		750	Gentry (1995)

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Table 7 cont.

Venezuela	Boca de Uchire	200	530	Gentry (1995)
Venezuela	Blohm Ranch	310	510	Gentry (1995)
Ecuador	Capeira	270	420	Dodson & Gentry (1992)
Ecuador	Perro Muerte	330	540	Gentry (1995)
Peru	Cerros de Amotape	290	430	Gentry (1995)
Peru	Tarapoto	380	750	Gentry (1995)
Argentina	Riachuelo	270	390	Gentry (1995)
Argentina	Parque El Rey	270	310	Brown et al (1985)
Bolivia	Chaquimayo	290	500	Gentry (1995)
Paraguay	Mbaracayui	300	560	Keel et al (1993)
Paraguay	Taruma	240	370	Keel et al (1993)
Paraguay	Parabel	280	520	Keel et al (1993)

* All stems >1cm DBH, **all stems >10cm DBH
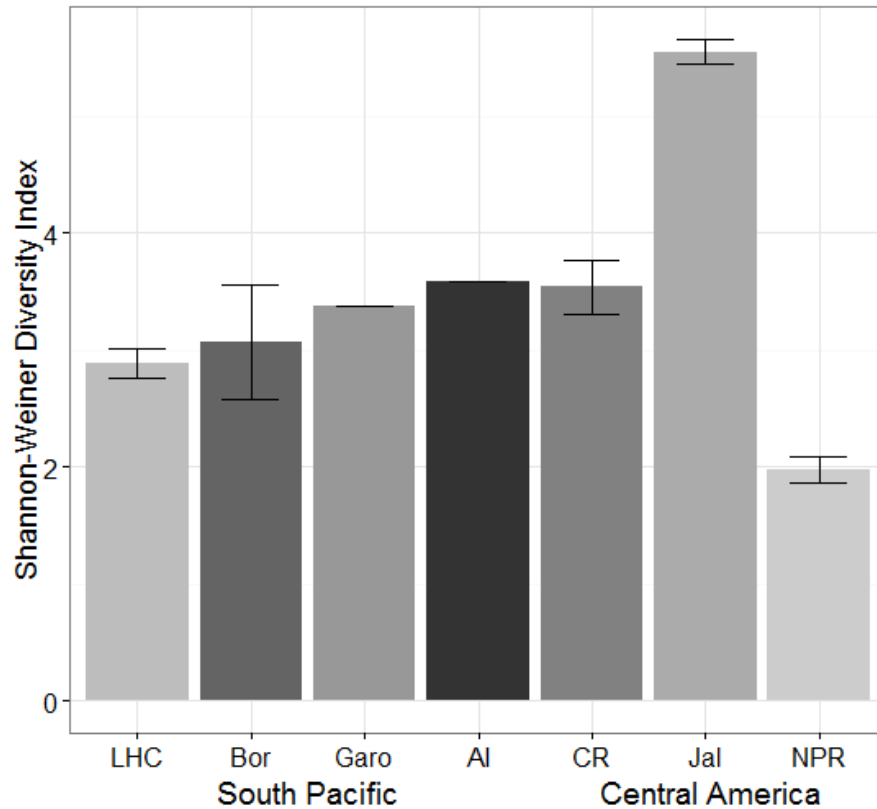
Figure 11. Comparison of mean Shannon's diversity index values as reported from various tropical forests worldwide. Error bars represent standard error. LHC = Lake Hargy Caldera; Bor = Mt. Kinabalu, Borneo; Garo = Garo Hills, India; AI = Andaman Island; CR = Cordillera de Talamanca, Costa Rica; Jal = Jalisco, Mexico; NPR = Northern Puerto Rico

Structurally, the LHC forest plots have an average basal area (m^2ha^{-1}) similar to other forests within Papua New Guinea and the South Pacific region, but contain a similar number of stems ha^{-1} to Central American forests (Table 8). Structurally, Euphorbiaceae and Myrtaceae were dominant in forests in Borneo (Aiba and Kitayama 1999). In the forests of South Yunnan, China, *Pometia tomentosa* was significantly more

dominant than the next most important species in the forests (Zhu 1997). In the LHC,

Pometia pinnata was similarly found to be significantly more important than the next

most important species, *Platea excelsa*.

Table 8. Structural comparison of LHC plots to other tropical forests worldwide. Bold values represent largest value in the column when using similar sampling methods. Values in italic were taken from fully enumerated 1 hectare plots. All other values extrapolated from 0.04ha and 0.2ha plots.

Country	Forest	Basal area ($m^2\ ha^{-1}$)	Stems ha^{-1}	Reference
Papua New Guinea	LHC	40.07	1225	This Study
Papua New Guinea	Mainland	36.98***	575***	Paijmans (1970)
Borneo	Mount Kinabalu	**43.86**	**2680**	Aiba and Kitayama (1999)
China	South Yunan		629.6	Zhu (1997)
Cameroon	Korup National Park	32.14*	512.2**	Chuyong et al. (2011)
Puerto Rico	Karst Forest	19.63*	3234.01*	Brandeis (2006)
Ecuador	Cordillera El Consuelo	39	1650	Homeier et al. (2010)
Costa Rica	Cordillera de Talamanca	42.3		Oosternhorn and Kappelle (2000)
Nicaragua	Cosquina	23.3	1180	Gillespie et al. (2000)
Costa Rica	Santa Rosa	25	1690	Gillespie et al. (2000)
Costa Rica	Palo Verde	22.8	1850	Gillespie et al. (2000)
Nicaragua	Chacocente	21.2	1770	Gillespie et al. (2000)
Nicaragua	Masaya	21.2	2230	Gillespie et al. (2000)
Nicaragua	La Flor	22.8	2020	Gillespie et al. (2000)

Table 8 cont.

Nicaragua	Ometepe	17.7	1070	Gillespie et al. (2000)
New Guinea	Crater Mountain	*31.5*	*602*	Weiblen (1998)
New Guinea	Halowia	*40.1*	*529*	Keppel et al. (2010)
New Guinea	Sewa	*46.3*	*612*	Keppel et al. (2010)
Solomon Islands	Lauru	*34.4*	*662*	Keppel et al. (2010)
Solomon Islands	Kolombangara	*43.3*	*537*	Keppel et al. (2010)
Solomon Islands	Tetepare	*31.2*	*409*	Keppel et al. (2010)
Vanatu	Erromango	*37.7*	*916*	Keppel et al. (2010)
Fiji	Savura	*42*	*905*	Keppel et al. (2010)
Fiji	Kubulau	*49*	*754*	Keppel et al. (2010)
Fiji	Gau	*45.7*	*840*	Keppel et al. (2010)
SA	Tiavea	*36.8*	*712*	Keppel et al. (2010)
SA	Vatia	*30*	*580*	Webb & Fa'aumu (1999)

* only trees >2.5cm DBH, ** only trees >10cm DBH, *** only trees >30cm DBH

Structural Variation and Forest Phase

The Stand Maturity Phase (SMP) indices are ≥ 1.0 across all seven plots, suggesting that all plots are at fairly advanced stages of plot composition-specific maturity, with stands at a climax stage that may or may not transition to the next forest phase. SMP, however, does not correlate with successional stage, but is instead an indicator of the relative age distribution of the stand within its particular successional

stage (Seydack et al. 2011). An interesting example of this pattern can be seen in the Cinder Cone plots (Table 2 and Table 3).

For example, the Cinder Cone plots have the highest SMP of all seven plots (1.82 and 1.66 for CC1 and 2, respectively), but are dominated by multiple small stems of one dominant species (*Weinmania tricophora*), as opposed to smaller numbers of larger stems, which is the case in the remaining plots. The large basal area of a single species split over multiple pole-size stems shows that the stands in the Cinder Cone plots may either be younger than the other sampled forest plots, or somehow "stunted" in that they have reached full maturity with very little canopy emergence and very few large individual stems (Read et al. 1990).

The types of variation in structure and composition observed in the LHC may allow indirect inference of stand dynamics and possible drivers of turnover. In Peninsular Malaysia, for example, stand enumeration was used to categorize forests as being under either dynamic equilibrium (i.e. natural turnover) or non-dynamic recovery from disturbance (Ho et al. 1987). Composition of a species-poor forest plot sampled on the Eno River in Ecuador was similarly explained by recovery from anthropogenic disturbance, unique soil characteristics, or recovery from catastrophic disturbance (Pitman et al. 2005). Recovery from disturbance does seem a viable hypothesis for explaining the observed variation across the LHC landscape, particularly when considering the wide variation of disturbance types potentially present, but further stand enumeration and classification of disturbance intensity across the landscape is needed.

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The LHC stands also do not show the same large density of Pioneer species (such as *Eucalyptus deglupta*) as those observed in the Eno River, Ecuador plot. A similar study in Ghana, however, found that high rainfall and low Pioneer species presence directly correlated with high stem packing, and that disturbance can place a direct limit on the maximum size distribution of a forest stand (Poorter et al. 2008). Both of these patterns are consistent with findings in the CC plots. It is not possible to know the age of the Cinder Cone plots without coring and aging the trees therein, but the significance of disturbance (either large scale volcanism or small-scale volcanic effects on edaphic conditions) in determining plot structure is a hypothesis worthy of examination in future studies.

Increasing SMP has also been found to be negatively correlated with number of stems ha^{-1} when only considering trees >20cm DBH (Seydack et al. 2011), which provides some explanation for the relatively low stems ha^{-1} in the LHC when compared to other forests while still having a large overall basal area and large number of taxa ha^{-1}, as well as the low number of stems in the Cinder Cone plots relative to other plots within the LHC. The East Ridge plots and NC1 all have SMPs of 1.0 and the East Ridge plots have the highest numbers of stems of all sampled plots. A low maturity phase, presence of a single large dominant Pioneer (*Eucalyptus deglupta*), and large number of stems, coupled with suppressed diversity overall, is consistent with both the Pioneer species-stem packing relationship reported by Poorter et al. (2008)and negative correlation between SMP and stem packing (Seydack et al. 2011).

Conclusions

This study represents the first intensive inventory and enumeration of the forest within the LHC. The area represents a unique, dynamic landscape that remains relatively undisturbed by anthropogenic pressures. All species identified were previously unreported from the region. Patterns identified in the LHC relative to structural and composition variation across the landscape demonstrate the value of the forest from both a conservation perspective (due to inherently high biodiversity) but also from a standpoint of future analysis. The rugged nature of the LHC coupled with its location make the forest within a primary candidate for use as a "natural laboratory" for long term ecological surveys. Further enumeration of the forest stands within the LHC can provide further insights into potential catastrophic origin and/or mediation of forest successional patterns within a disturbance and diversity context, and also further calibrate species-richness estimates and other such extrapolations by augmenting the small sample size employed in this study.

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CHAPTER III

VARITION IN SOIL CHARACTERISTICS

OF THE LAKE HARGY CALDERA,

PAPUA NEW GUINEA

Abstract

Forest diversity can be influenced by a number of factors, including biotic interactions and abiotic processes. In the Lake Hargy Caldera (LHC), West New Britain, Papua New Guinea, all trees >5cm DBH in seven 0.04ha plots were sampled and compared to soil samples taken from each plot to evaluate soil-forest interactions. Soil analysis found significant differences between sampled areas in 11 of the 21 sampled parameters. All areas had very high sand content (>56% sand). Overlay of highly variable soil variables onto a species-level NMS ordination showed that only conductivity and Cu concentrations were associated with variation in forest composition. Overall patterns showed widely variable soil types across the LHC. Observed patterns of soil variation, however, did not match trends in variation in forest composition. Plots with very similar forest composition had very dissimilar soil chemistry, and vice versa. Soil characteristics were shown to partially contribute to observed variation, but other variables, such as disturbance, may also be driving shifts in composition. Observed significant relationships also demonstrate the importance of future sampling within the

LHC, as building of a larger dataset will allow more robust modeling of interactions among soils, disturbance, and forest diversity.

Introduction

Ecosystem diversity can stem from a range of factors, ranging from simple environmental gradients such as variation in topography and local climate to substantially more complex interactions among biotic communities and abiotic processes. Forest diversity, for example, has been shown to be directly influenced by not only disturbance (Denslow 1995, Burslem and Whitmore 1999, Poorter et al. 2008, Sahu et al. 2008, Seydack et al. 2011, Carreño-Rocabado et al. 2012, Uriarte et al. 2014) or equilibrium dynamics (Enright 1982, Pollock et al. 1998, Kalacska et al. 2004, Alvarez-Añorve et al. 2012), but also by interactions among climatic variables (Comita and Engelbrecht 2009, Gazol and Ibáñez 2010, Boucher-Lalonde et al. 2012) and soil chemistry (Golley 1986, Lopez-Toledo et al. 2008, Andersen et al. 2012, Peña-Claros et al. 2012). While attempts at condensing complex multivariate interactions into simple, broadly-applicable models have yielded surprisingly significant results (Boucher-Lalonde et al. 2012), simple models for describing the distribution of global diversity are more often the exception than the rule. This disparity between model predictions and observed diversity is primarily due to the inability of simple models to predict within-site variation in soil chemistry and disturbance, as well as the interactions among soils and the biotic community.

Soil characteristics and disturbance regime can directly interact to influence forest dynamics and successional patterns in ways that structure the forest community by allowing Pioneer species to fully develop in light-rich post-disturbance environments, but limit colonization based on the soil chemistry preferences of a particular species (Goodale et al. 2012). Peña-Claros et al. (2012) also found that the influence of soil texture and nutrient content depends directly on soil moisture, with wet soil nutrient content and texture significantly associated with dominance of single species and tree vigor in high-light environments, respectively. Soil nutrient content, however, was more strongly correlated with measures of forest structure such as stem density and basal area. The effect is also bi-directional, with soils influencing forest composition and forest composition, density, and canopy cover directly influencing soil characteristics (Cardelús et al. 2008, Ushio et al. 2010).

The forests of Papua New Guinea, as demonstrated in the previous chapter, harbor very diverse forests relative to nearby South Pacific forests, with greater numbers of species per hectare than forests measured using similar methods. This study describes variation in soil chemistry and texture at seven sites within the Lake Hargy Caldera, Papua New Guinea, and how that variation relates to overstory forest plot composition.

Methods

Study Site

The Lake Hargy Caldera (LHC, 5°19'49.59"S, 151°06'55.17"E) lay within the highly diverse Coral Triangle region of the south pacific (Figure 1). The Coral Triangle

encompasses Oceania and Southeast Asia, and is often cited as containing some of the greatest marine diversity on Earth (Veron 1995). The region is also considered a global biodiversity hotspot (Briggs 2005, Allen 2007).
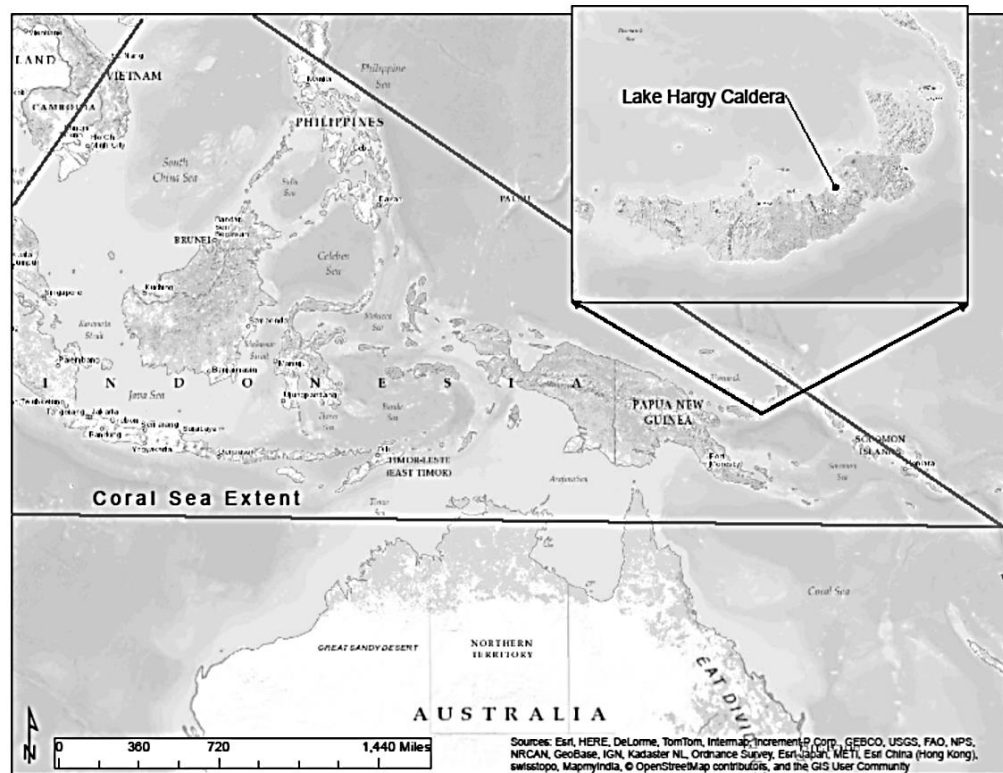
Figure 1. Map of the Lake Hargy Caldera (LHC) on New Britain Island, Papua New Guinea.

The LHC floor is approximately 350m a.s.l., and contains a lowland tropical rainforest. The region has an average monthly temperature ranging from ~30°C to ~32°C and mean annual rainfall of ~2000 mm, with a distinct dry season from June through September when average monthly precipitation declines by ~50%. Highly variable

topography within the caldera itself, however, leads to daily orographic precipitation in addition to the regional precipitation patterns.

Bordering the caldera on the East and Southeast is the Nakanai mountain range, a Carbonate-based range formed via uplift as a result of the nearby subduction zone. The Northern and Western flanks of the caldera are volcanic in nature, with the dacitic Galloseulo lava cone being the dominant peak in the western portion of the caldera. The LHC is named such because it contains the ~8 km² Lake Hargy, which is drained to the North by the Lobu River (Figure 2).

Data Collection

Sites were chosen at naturally assembled but distinct forest stands in various regions of the LHC to quantify a random selection of the most representative sites within these regions (i.e., a stratified random sampling scheme). Four particular forest types were identified via visual reconnaissance and consideration of variation in disturbance type. Plots were then randomly established within each of this distinct forest types (Figure 2).
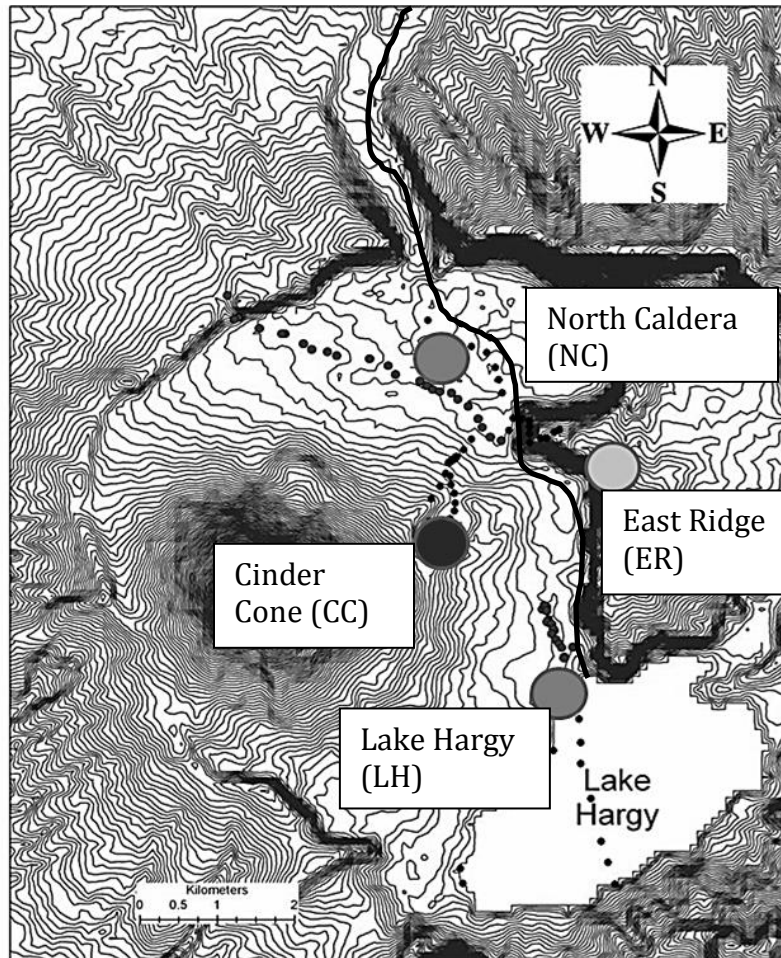
Figure 2. LiDAR-derived topographical map (NASA 2011)
of the Lake Hargy Caldera, West New Britain. Small
circles represent track log. Large circles represent sample
site locations.

Forest plots measuring 20m x 20m were established, demarcated into 4 quadrants

of 10m x 10m, and labeled. Two plots were established per previously identified forest

type, with four areas sampled (with one area having only one plot due to temporal and

spatial constraints), for a total of seven plots. Plots were abbreviated to represent their

locations as follows: North Caldera Plots 1 and 2 (NCP1, NCP2), Crater plots 1 and 2 (CC1, CC2), East Ridge plots 1 and 2 (ER1, ER2), and Lake Hargy plot (LH1). The CC, NCP, and LH plots are all at approximately 350m elevation, while the ER plots are at approximately 640m elevation. Forest plots were enumerated using methods described in the previous chapter.

Soil samples were taken by sampling from approximately 30cm depth at the center point of each of four quadrants in each sampled forest plot and combining all four samples into one aggregate sample per plot. Samples were bagged and labeled, and air dried back at the expedition base camp. Soils were stored in freezers at Hargy Oil Palms, Ltd. until shipment to Chico for further analysis. Soils were split into two sub-samples, with one sample retained for texture analysis and the other sent to the soils lab at Louisiana State University for chemical analysis. Texture analysis was carried out by the author in the CSU Chico soil lab via a combination of both mechanical sieving and hydrometer analysis (Brower and Zar 1984). A list of all sampled soil variables can be found in Appendix B.

<u>Data Analysis</u>

All soil data was screened and appropriate transformations were applied to achieve normality. Analysis of Variance (ANOVA) was used to find variables that varied significantly between sample areas across the landscape. A Pearson correlation matrix of variables that significantly vary across the landscape was then used to identify collinear soil variables for further variable reduction, using Pearson's r $\geq$ 0.80 as a threshold.

Variables that were collinear with multiple other variables were dropped so long as each remaining variable was a significant proxy for all deleted variables. This variable reduction was performed in a step-wise fashion until only three dominant variables remained: conductivity, Cu concentration, and organic matter concentration. Cluster analysis using the Flexible Beta method with $\beta=-0.25$ was used to examine spatial distribution of soil types relative to sample plot locations. Flexible Beta is a linkage method that is compatible with Sorenson Distance, and a β of -0.25 was chosen because results from this type of analysis are most comparable to other clustering methods, such as Ward's method (McCune et al. 2002).

Ordination of plot species composition was performed in the previous chapter using Non-metric Multidimensional Scaling (NMS) on species data that were relativized (i.e. standardized) by species maximum using PC-ORD v. 6 (Mccune and Mefford 2011). Soil chemistry was then compared to this original species ordination by overlaying the three dominant soil variables onto the species NMS ordination. This overlay then allows analysis of linear correlation of soil variables with NMS axes and species axis scores.

Results

Significant differences were found between sampled areas (i.e. pairs of plots) in nine of the twenty one sampled parameters (Table 9). Appendix B lists ANOVA results for all measured soil variables, including those that were not significantly different. The

Table 9. ANOVA results from nine soil variables that significantly varied across the LHC landscape.

Variable	F	p	df
B	16.44	0.0103	3
Cond	9.262	0.0284	3
Cu	26.77	0.00415	3
Fe	8.415	0.0334	3
Mg	8.957	0.0301	3
Mn	8.756	0.0313	3
OM	8.85	0.0307	3
Pb	6.997	0.0454	3
S	12.91	0.0159	3

East Ridge plots had the highest levels of both copper (Cu, Figure 12a) and iron (Fe, Figure 12b), while the Cinder Cone plots had the highest concentrations of lead (Pb) and sodium (Na).
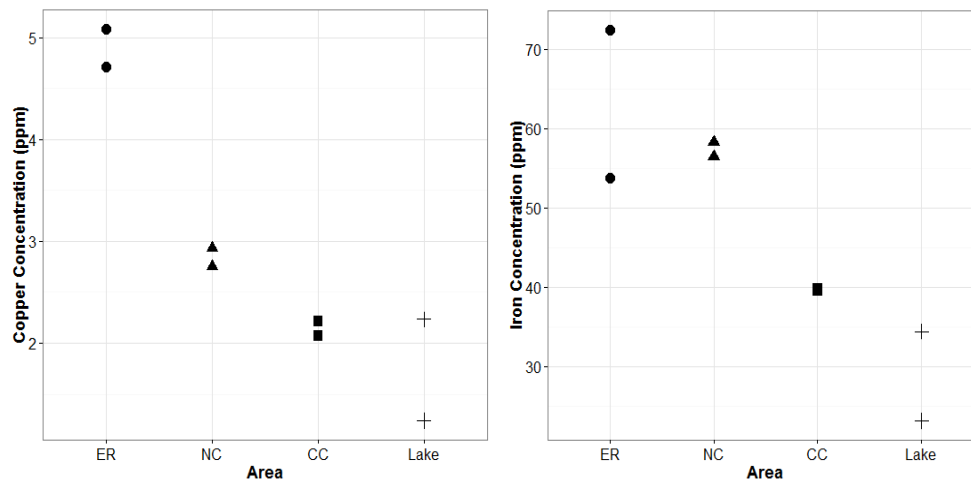
Figure 12. Copper (a) and iron (b) concentrations in each of two soil samples from all four sampled locations.

There was no significant difference between the areas in concentrations of many of the metals sampled, including arsenic (As), cadmium (Cd), and nickel (Ni). The North Caldera plots had the highest conductivity, coupled with the highest concentrations of the major salts, including boron, potassium, magnesium (Figure 13a), and manganese (Figure 13b).
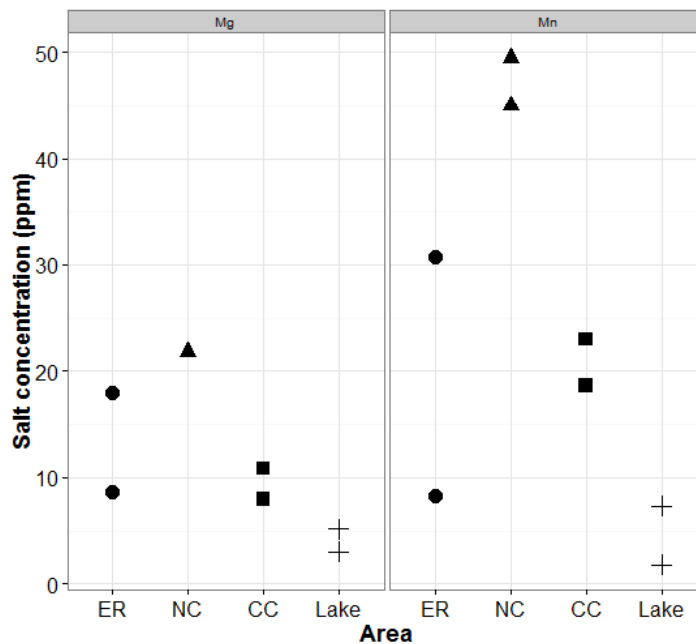
Figure 13. Magnesium (a) and manganese (b) concentrations in each of two soil samples from all four sample locations within the Lake Hargy Caldera.

The Lake Hargy plot had the lowest concentration of all sampled nutrients and the lowest conductivity. While a significant difference was observed in organic matter content, this was primarily due to low levels in the Lake Hargy plot, as the remaining three plots

showed no significant differences. No significant differences were found in pH across the sample plots. The trend, however, was toward slightly lower average pH in the North Caldera plots than the others, except for the Lake Hargy plot, which had higher pH (Figure 14).
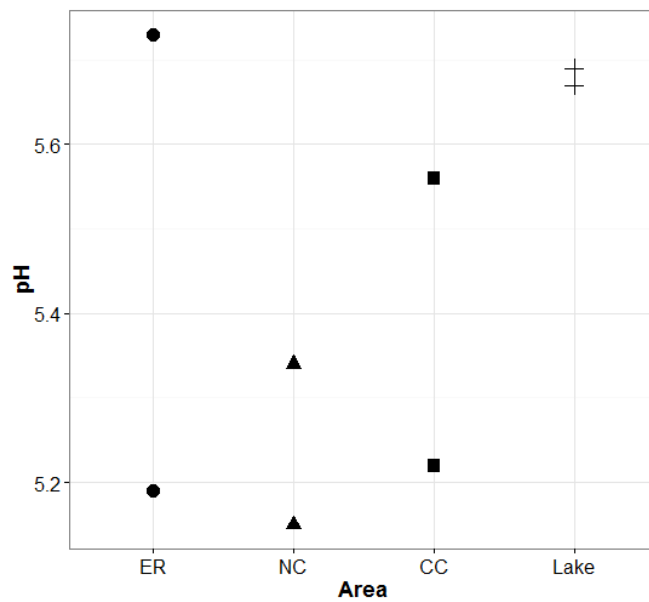
Figure 14. Measured pH of two soil samples from each of four sampling locations within the Lake Hargy Caldera.

Soil Texture

All plots contained large amounts of sand. ER2, NC2, and CC1 and 2 were classified strictly at Sand, while ER1, NC1, and LH1 instead were classified as Loamy

Sand, Loamy Sand, and Sandy Loam, respectively. The Lake Hargy plot had a relatively low sand composition (56.1%), while the remaining plots all have >75% sand.

Cluster analysis of all seven plots based on soil characteristics (chemistry and texture) shows very different clustering than that observed in species composition (Figure 15). For example, the CC plots were in opposite clusters based on species composition, while the ER plots clustered perfectly. In the soil chemistry cluster analysis, the ER plots are in opposite clusters, while the CC plots are very similar.
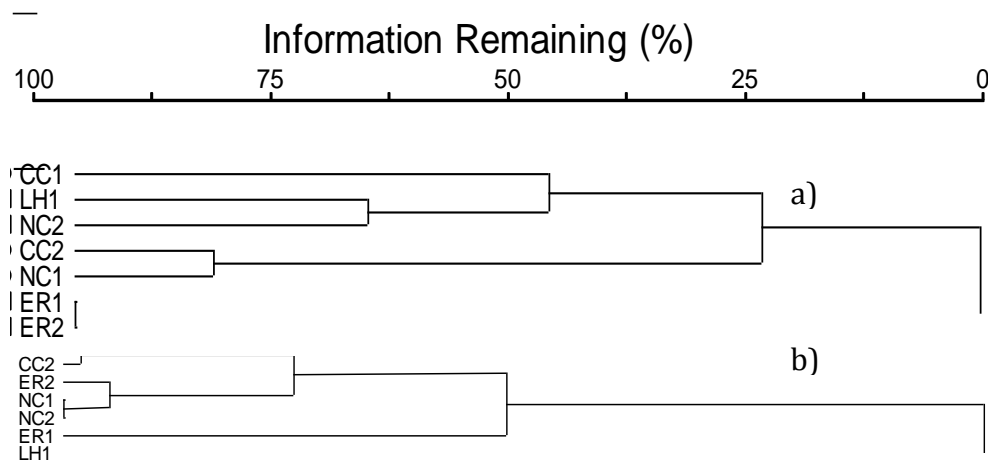
Figure 15. Cluster dendrograms of sampled plot associations based on species composition (a) and measured soil characteristics (b). Information Remaining is roughly akin to R². Plots with a link under a higher "information remaining" are similar.

The original NMS ordination explained 54.6% of the variance (final stress = 0.00) in the original species matrix (axis 1 R^2 = 0.369, axis 2 R^2 = 0.178). The bi-plot overlay of the dominant soil variables (Figure 16) found that conductivity and Cu concentration were most highly associated with species composition. Cu concentrations were high correlated with NMS axis two (r = 0.839), which is associated with the variation in

composition between the East Ridge and the "Caldera Floor" (LH and NC) plots. Axis two is therefore a gradient in both elevation and Cu concentrations, with ER plots having high Cu and elevation, and Caldera Floor plots having low Cu and elevation. Conductivity was correlated with NMS axis one (r = -0.396), which is associated with variation between the two Cinder Cone plots. CC2 is associated with high conductivity, while CC1 is associated with low conductivity.
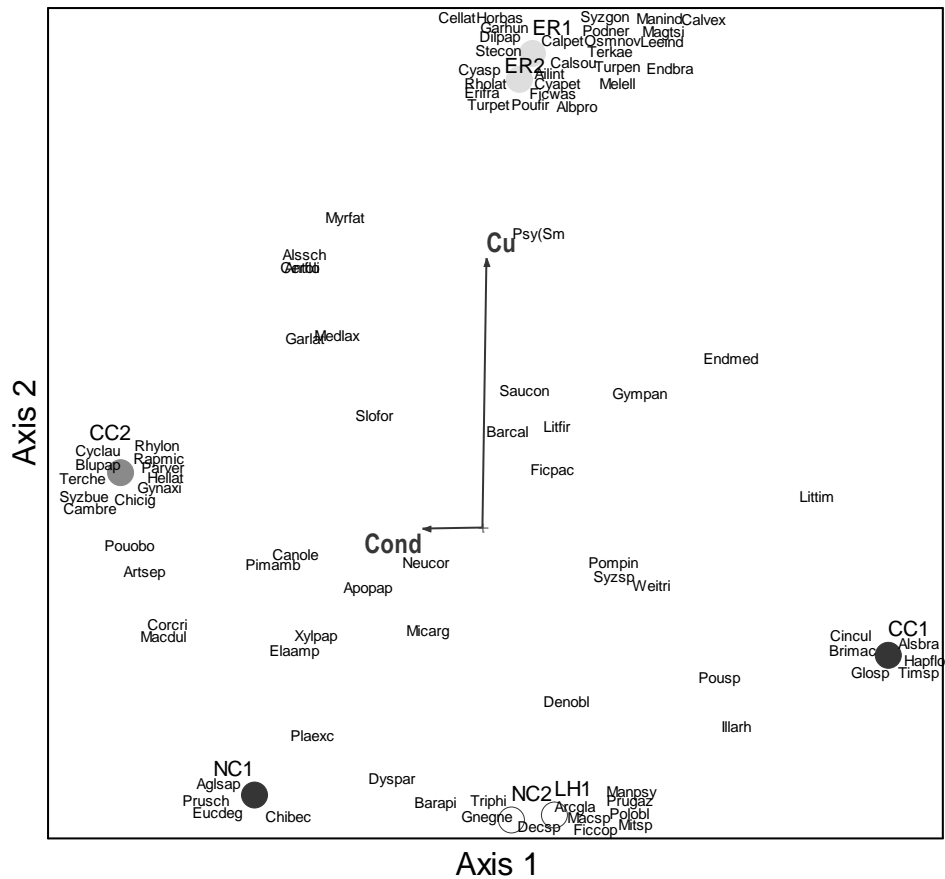
Figure 16. NMS ordination of plots relative to species composition, with overlay of soil variables that were correlated with species distributions. Cu = copper concentration (ppm), Cond = conductivity (dS/cm).

All five of the most important species (by IVI) are highly correlated with one of the two major NMS axes (Table 3). Soil correlations with these axes show that *Platea excelsa* is highly associated with high conductivity and low copper, *Pometia pinnata* is associated with low conductivity and low copper, *Garcinia latifolia* is associated with high conductivity and high copper, *Eucalyptus deglupta* is associated with high conductivity and low copper, and *Pyschotria* (Sm. Leaf) is associated with low conductivity and high copper.

Table 10. Species associations with each NMS ordination axis (axis scores). IVI = previously calculated importance value index, representing species "importance" across all plots.

Species	IVI	Axis 1 (Cond)	Axis 2 (Cu)
Pometia pinnata	24.46	0.829	-0.253
Platea excelsa	16.72	-0.425	-0.447
Garcinia latifolia	14.88	-0.568	0.467
Eucalyptus deglupta	12.69	-0.412	-0.349
Psychotria (small leaf)	12.42	0.107	0.755

Pometia pinnata, the most important species, seems to be more evenly distributed across all plots than the other species, and thus not as significantly associated with either of the main soil variables. Regression of two of the most abundant species, *P. excelsa* and *Psyhotria* (small leaf), found significant associations with soil variables. *P. excelsa* abundance showed a significant linear correlation with conductivity ($R^2 = 0.52$, $p = 0.04$,

Figure 17a), while *Psychotria* showed significant linear correlation with Cu concentration (R² = 0.74, p = 0.008, Figure 17b).
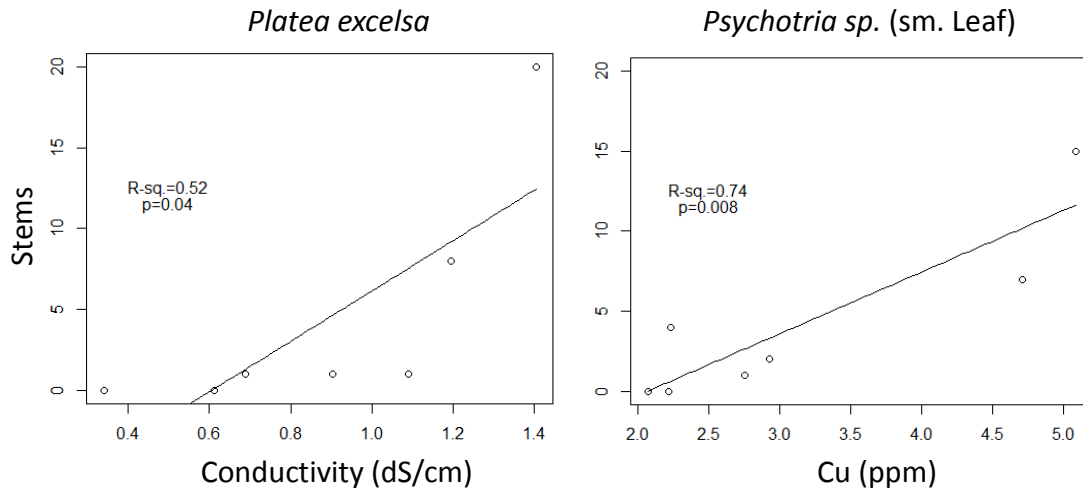
Figure 17. Linear regression of *Platea excelsa* abundance versus conductivity (a) and *Psychotria* sp. (Small leaf) versus copper concentration (b).

Discussion

Correlations between soil chemistry and species abundance

Variation in soil chemistry and texture was not constant across the landscape. Some plots showed high within-area variability while others were very similar to each other. The high within-area heterogeneity of soil variables could be characteristic of interactions among disturbance and parent material, as well as topographic variation and species composition itself (i.e. organic matter composition). Variation in soil characteristics also did not directly mimic variation in forest plot composition. The most

similar plots in terms of species composition, the East Ridge plots, were the most different in terms of soil chemistry and texture, while the opposite pattern was seen in the CC plots.

Comparison of variation in soil characteristics to ordination of species composition did show that two variables, conductivity and Cu concentration, were highly associated with variation along the two dominant NMS axes. This shows that variation in soils does not match variation in forest composition, but that some soil variables may be highly associated with some of the variation in forest composition. Significant differences in soils by plot that differ from the differences observed in forest composition demonstrate that both soil conductivity and Cu concentration are indeed drivers of variation in forest composition, but do not vary in relation to forest composition in the same way as other studies that have shown significant influence of soil nutrients on vegetation dynamics (Jha and Singh 1990, Holste et al. 2011).

Soil variation can also be interacting with disturbance history (Sagar et al. 2003, Carreño-Rocabado et al. 2012), species soil preferences and life history (Goodale et al. 2012), topography(Homeier et al. 2010, Liu et al. 2014), and microclimatic variation. Sagar et al. (2003) used PCA to describe variation in forest composition and structure relative to simulated disturbance gradients and actual soil variation, and found distinct influences, with one PCA axis being associated with soil N concentration and the other being associated with disturbance treatment, demonstrating the significant impact both

factors can have individually as well as interactively. Disturbance history, in this study, was not directly described or sampled, and can only be inferred. Cluster analysis, however, showed that distinct areas within the caldera that were assumed to be under particular disturbance pressures (i.e. volcanic disturbance for CC plots, flooding for NC plots) varied widely in soil type. This disparity could be due to either a lack of significant association between disturbance and soil characteristics, or in fact that variation in local disturbance type and intensity has significantly altered soils, even within sampling areas.

Comparisons to Other Tropical Forests

Soils in the Lake Hargy Caldera were similar in many ways to other reported tropical forest soils (Table 11). Carbon and Nitrogen concentrations were in the middle to high range of reported values, while macronutrients and salts such as calcium and manganese were relatively low. LHC soils were in the middle of the reported pH range of 3.9 to neutral, with an average pH of 5.44. Texturally, soils in the Lake Hargy Caldera were most similar to a plot in Kondi, Congo, which was the only reported forest to have as high of a sand content as Lake Hargy plots.

Table 11. Selected soil chemistry and texture within the Lake Hargy Caldera (LHC), New Britain Island, Papua New Guinea, compared to selected tropical forests across the globe. All nutrient concentrations are ppm, sand is % sand by weight.

Location	C	N	Ca	Mg	Fe	Mn	pH	P	K	Sand	Reference
ER1	36459	3466	20.1	8.7	72.4	8.3	5.7	35.0	71.5	75.8	This study
ER2	75000	6228	49.8	17.9	53.8	30.8	5.2	33.2	79.4	89.5	This study
NC2	83000	7231	51.1	21.8	58.3	45.0	5.3	33.7	118.9	95	This study
NC1	65000	5592	52.8	21.7	56.4	49.4	5.2	30.0	110.0	89	This study
CC1	58000	4069	12.6	7.9	39.8	18.6	5.6	36.6	41.7	89.8	This study
CC2	90000	5856	23.0	10.9	39.5	23.0	5.2	37.1	95.4	87.8	This study
LH1	21796	1997	13.1	5.2	34.4	7.3	5.7	35.8	39.8	56.1	This study
LH floodplain	9000	330	9.3	3.1	23.1	1.8	5.7	16.0	26.3	95.8	This study
San Mateo, Mexico	20.32	2.16					7.1	0.5			Barajas-Guzmán et al. 2006
Kade, Ghana	19500	2050					4.9	5.7	290		Greenland and Kowal 1960
Kumasi, Ghana		3000					6.4	6.5	110		Greenland and Kowal 1960
Vindhyan Plateau, India	18000	1400					6.1	270.0			Raghubanshi 1991
India	4700	500					6.3	210.0			Raghubanshi 1991
Mt. Kinabalu, Borneo*	2813.75	210.88	16.28	11.2				0.2			Aiba and Kitayama 1999
Chorro, Panama			97	18.9	55		3.9	2.7			Andersen et al 2010
Samudio, Panama			249	53.2	176		5.1	3.7			Andersen et al 2010
Palo Seco, Panama			135	40.3	161		5.1	3.9			Andersen et al 2010
Hornito, Panama			1358	254	212		5.8	10.9			Andersen et al 2010
Kondi, Congo	8900	530	20	10	130				10	87.7	Versini et al 2014

Conclusions

Ricklefs (2004), in his thorough review and discussion of patterns of global biodiversity, discusses how many studies describe local variation in soils and elevation and statistically demonstrate their importance as drivers of diversity, but do not account for the dramatic disparity in scale. For example, the influence of soil chemistry on species diversity is much more difficult to reconcile in a tropical plot with 100 individuals that are all a different species than in a temperate forest with 25 individuals each of four species. The issue of scale has led to numerous theories of how species respond to availability of regeneration niches, many of which could be at play in the LHC.

This study described variation in soil nutrient content and texture as it relates to variation in overstory tree species composition. Overall patterns showed widely variable soil types across the LHC. Observed patterns of soil variation, however, do not sufficiently explain measured shifts in forest composition across the landscape. These patterns demonstrate the potential significance of soils in structuring plot diversity, but also show limited contribution, perhaps muted or only significant in the context of disturbance history or species assemblages. Distinct relationships were observed, however, between two dominant species, *P. excelsa* and *Psychotria* (Small leaf) and salt and Cu concentrations, respectively. These species-specific correlations, as well as broader relationships across the landscape, signify relationships among soil characteristics and forest tree species that may not have been adequately sampled. These specific yet significant relationships also demonstrate the importance of future sampling

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within the LHC, as building of a larger dataset will allow more robust modeling of interactions among soils, disturbance, and forest diversity.

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CHAPTER IV

DRIVERS OF TROPICAL FOREST

BIODIVERSITY: A SYNTHESIS

Abstract

Factors contributing to diversity may vary from system to system. Understanding the theoretical implications of long-standing hypotheses regarding characteristics that govern site diversity can allow construction of robust models that either conceptually or quantitatively predict diversity based on a number of factors. Here I discuss the merits of two prominent disturbance-diversity hypotheses, the Intermediate Disturbance Hypothesis (IDH) and the Mass Ratio Hypothesis (MRH) relative to real-world observations. While both hypotheses may appear to predict observed diversity in some cases, the success of the two models is not universal. Multivariate models that consider both categorical and quantitative variation, such as State-and-Transition models, are a useful alternative that take a hybrid approach to predicting overall ecosystem state, including diversity. The Lake Hargy Caldera (LHC), in West New Britain, Papua New Guinea, appears to not follow the predictions of any one model, but instead is more accurately described using conceptual models based on state-and-transition models. Future analyses of diversity should consider multivariate relationships and use a hybrid approach that may use one or many of the prominent diversity hypotheses.

Introduction

Determinants of diversity in a given ecosystem have long been debated. Clements (1936) proposed the climax theory of communities, which argued that species communities are discrete and predictable. He also argued that communities are entities or "super-organisms" that follow whole-community shifts rather than single-species turnover. Gleason (1926), however, posed a much different theory. He argued that single-species niche differentiation is what drives community composition, and that a community is an arbitrary grouping of the species at a particular site. Modern ecology has continued to modify and hybridize these concepts. Much of the current debate still centers on these (albeit heavily modified and updated) arguments.

Ecologists continue to examine some long-standing theories of diversity relative to disturbance, topography, climate, soil nutrients, and species interactions in order to better understand patterns of global diversity. Modern theories of the relationship between diversity and disturbance, for instance, have recently been re-examined, leading to an open debate in the literature (Fox 2013).

Here I summarize some of the major theories regarding the origins of biodiversity specifically in the context of response to disturbance, and discuss findings from a survey of the forest within the Lake Hargy Caldera, Papua New Guinea in the context of biodiversity theory. I also propose the adoption of a hybrid view of drivers of diversity, with multiple theories of diversity and disturbance being applicable, depending on the system and time frame in question.

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Prominent Disturbance-Diversity Theories

Modern analyses of diversity have the benefit or large datasets and enhanced modeling capacity. Many of the recent models and theories of global distribution of diversity, which will be discussed later, are built off of long-standing hypotheses. While many hypotheses have been formulated and tested, the bulk of this review will focus on the Mass Ratio Hypothesis (MRH, Grime 1998) and Intermediate Disturbance Hypothesis (IDH, Connell 1978). This is done due to the substantial crossover of some theories, such those related to productivity, with either IDH or MRH. Relationships of MRH and IDH with species-pool concepts will also be discussed.

Egler (1952) first described the initial floristic composition concept. Potential site climax community composition, Egler argues, is primarily pre-determined by the species pool from which that site draws constituent species (i.e. the present seed bank). While logical, this concept is too simplistic, as this theory does not take into account edge effects and dispersal mechanisms, nor does it include the basic species association concept of Gleason (1926). Following a disturbance, the initial floristic composition does indeed determine which species have the potential to succeed the previous community. The ability of those species to take advantage of the newly available niche, however, is limited by site characteristics that may or may not limit the competitive ability of those species. The importance of seed bank and available species pools, however, is undoubtedly important in determining succession and final site composition and diversity.

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Connell's (1978) IDH has long been touted as one of the most defensible hypotheses relative to maintenance of diversity. The IDH states that diversity follows a Gaussian (i.e. hump-shaped) response to disturbance, with peak diversity expected under conditions of intermediate disturbance. High disturbance (i.e. frequent and intense) would be expected to allow constant competition on the part of all species, as new niches are continuously available and dominant species cannot establish quickly enough to out-compete subordinate species. This high turnover would now allow any stable community to establish, thus limiting diversity. Low disturbance (i.e. infrequent and less intense), on the other hand, would be expected to allow dominant species to establish enough to directly outcompete subordinates to the extent that only dominant species remain, thus suppressing diversity. Intermediate disturbance, however, allows rapid turnover but does not allow dominant species to entirely outcompete subordinates, thus allowing peak diversity (Figure 18).
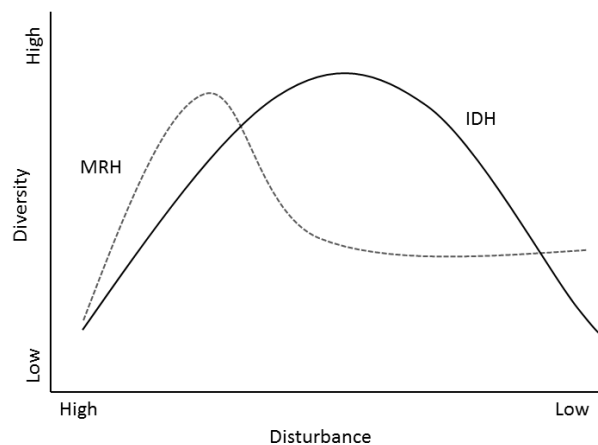

Figure 18. Predicted relationships between disturbance intensity and diversity by the Intermediate Disturbance Hypothesis (IDH) and the Mass Ratio Hypothesis (MRH). See text for description of each hypothesis.

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The MRH (Grime 1998) argues that species functional traits such as productivity are the most significant determinants of final plot species composition. The MRH posits that single-species dominance (here defined relative to biomass) is the most significant determinant of community composition. The MRH also predicts lower overall community biomass in an MRH-mediated community, due to one species out-competing all others and not allowing production of increased biomass (Figure 19). Following a disturbance, MRH would predict peak diversity early in the succession trajectory, followed by a decrease in diversity due to mediation by dominant species. This theory accepts the idea that disturbance can have a confounding effect on species composition, but also states that this observed effect of disturbance on species composition is itself evidence of the significance of dominant species in controlling plot composition. The question then, Grime argues, is not whether disturbance influences diversity, but whether subordinate species in a community can exert the same or similar pressures on dominant species as dominant species do on subordinates. In other words, disturbance is not itself influencing diversity, but is instead slowing productivity of the largest species, allowing less competitive species to compete. Subordinate species that then propagate within the community do not, however, exert the same controls on dominants (e.g. shading, nutrient competition, etc.). This scenario, termed a "filter effect", would point to limited productivity of the dominant species as the primary determinant of subordinate success, and disturbance as a small contributor to that decline in productivity.
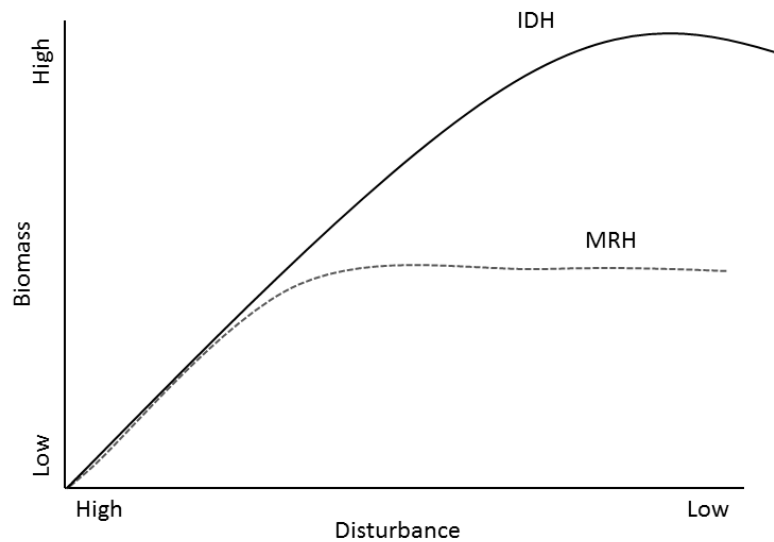
Figure 19. Predicted relationships between disturbance intensity
and productivity (biomass) by the Intermediate Disturbance
Hypothesis (IDH) and the Mass Ratio Hypothesis (MRH).

Kershaw and Mallik (2013) provide a thorough review of both the IDH and the

MRH, including their use and rates of validation in prior studies. They cite multiple meta-

analyses that show only 16% to 18% of studies found evidence of the classic hump-

shaped diversity response curve to disturbance proposed in the IDH. A new meta-analysis

performed by Kershaw and Mallik, however, found a slight increase in conformance,

with up to 40% of studies finding evidence in support of the IDH, and 17% of studies

rejecting the IDH outright. Studies focusing specifically on MRH showed 53%

conformity and 27% rejection. It should be noted here, however, that of all of the papers

reviewed in the above meta-analysis, only five focused on tropical forest ecosystems.

Ecosystem type did, however, play an important role in predicting support for either

MRH or IDH. MRH was found to be most highly associated with low-productivity ecosystems, such as grasslands.

An important distinction noted by Kershaw and Mallik among studies that propose either acceptance or rejection of either MRH or IDH is that very few studies (in their case, only two) performed experiments directly within a MRH or IDH framework, and that instead, the majority of studies discussed their findings relative to MRH or IDH *post hoc*.

The IDH continues to be tested and debated, with some recent research arguing for its abandonment on the grounds that while disturbance does explain diversity, it is not as directly associated as previously thought (Fox 2013). Outright abandonment of a theory such as IDH, however, may not be in the best interest of ecologists struggling to describe large scale variation in diversity, such as that observed in global patterns of forest diversity. Sheil (1999) rightly pointed out that much of the debate regarding diversity-disturbance relationships stems from the desire for model simplicity. Ecological systems, however, are extremely complex, and no single theory may ever describe the variation observed in natural systems without error.

Both theories have seen multiple studies that attempt either direct testing of the theories, or discuss merits and pitfalls of each in particular systems. Interestingly, simple mechanistic studies focusing on particular species or systems seem to have the most direct contributions to understanding of the MRH or IDH. Studies of tree-gap dynamics, for example, contain interesting questions of scale in the context of disturbance. Seedling

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density (Denslow 1995), tree gap size (Feeley et al. 2007), and initial floristic composition (Brokaw and Scheiner 1989), as well as life history traits of that initial composition (Goodale et al. 2012) can all directly influence forest gap dynamics. These interactions among disturbance and competition provide more evidence for a hybrid approach to modeling diversity response curves.

The Lake Hargy Caldera: A Case Study

Neither IDH, nor MRH, or similar such productivity or disturbance-based hypotheses, are entirely sufficient in explaining biodiversity. Combinations of the two theories, however, seem to accurately describe progression of diversity following a disturbance, at least in some ecosystems.

Results from a preliminary forest enumeration of the Lake Hargy Caldera (LHC), Papua New Guinea show possible examples of both MRH and IDH dependent on site location. Four distinct sampling areas were surveyed and labeled from the Northern Caldera (NC1 and NC2), East Ridge (ER1 and ER2), Cinder Cone (CC1 and CC2), and Lake Hargy shore (LH1). Sampling methods and overall results of that study are described in chapters two and three, above.

Plot diversity within the LHC was negatively correlated with single-species dominance ($R^2 = 0.825$, $p<0.05$), with higher single-species dominance being associated with low diversity (Figure 20). This distinct relationship between dominance and diversity provides evidence for the significance of both MRH and IDH within the LHC in a number of ways. The Caldera Floor plots have suppressed diversity and large single-

species dominance, which may be evidence of dominant species-mediated diversity (MRH), where dominant species have already out-competed any understory species that can increase diversity.
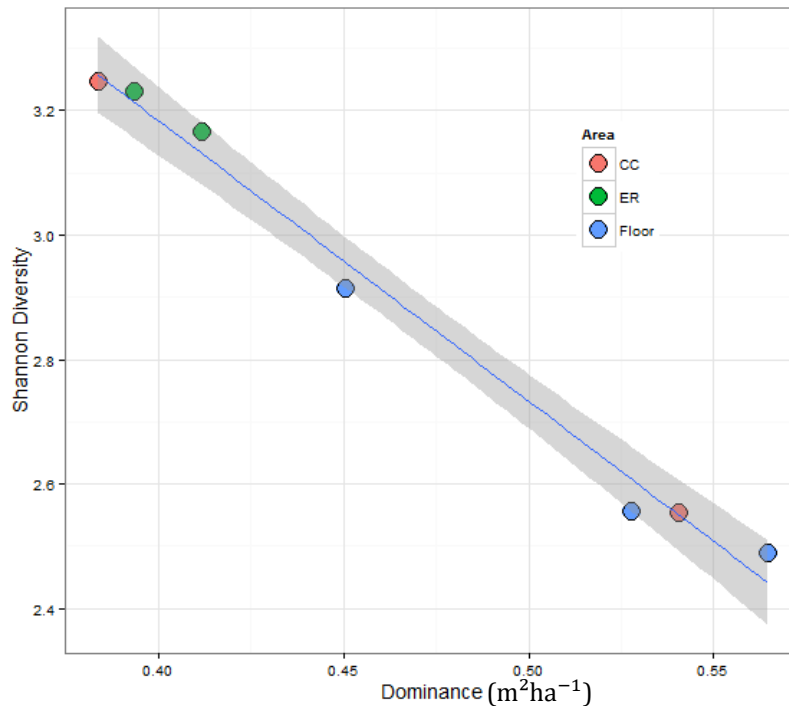
Figure 20. Plot of Shannon Diversity (H) versus dominance (single-species basal area) with linear regression line.

NC1 is dominated by a single large *Eucalyptus deglupta*, a known Pioneer species. This single stem, while large, makes up only 2.1% of the biomass of the NC1 plot. An often under-cited aspect of the MRH versus the IDH is the idea that plots conforming to IDH have larger final biomass, on average, than those conforming to MRH (Figure 19). While MRH-mediated plots have larger single-stem dominance, they may in

fact have lower overall dominance due to competitive suppression. Thus the high biomass of NC1, even with a larger single-stem, provides support for IDH.

CC1 is also dominated by a single species; large number of smaller *Weinmania tricophora* stems, which collectively sum to a large single-species dominance. CC1 has less than half, however, of the total plot basal area of NC1 and other larger plots. The unique distribution of one dominant species in a plot with relatively low biomass may in fact provide evidence of an MRH-mediated forest stand. The unique distribution of dominant species in CC1 could also, however, be evidence of arrested succession. Goldsmith et al. (2011) found significantly fewer seedling densities in forests that were either degraded or contained thicker leaf litter layers, and hypothesizes that disturbance type may directly induce a state of arrested succession in secondary or degraded forests.

In either case, time since disturbance and disturbance type are relatively unknown, and disturbance intensity can only be assumed based on landscape patterns. Large-scale disturbances can often have dramatic community-shifting effects (Foster et al. 1998, Turner et al. 1998, Scheffer et al. 2001) and have been shown to be a possible explanation of species-poor or arrested tropical forest plots (Pitman et al. 2005), sometimes at small, patchy scales (Swaine and Hall 1988, Limberger and Wickham 2012).

While neither the IDH nor MRH were specifically tested within the LHC, the patterns observed do point to an interesting overlap of the two theories. One interpretation of the IDH includes the idea that disturbance "intensity" may also include

time since disturbance, with the "high disturbance" end of the scale representing recent disturbance and the "low disturbance" end representing a long time since disturbance. Succession patterns would predict a climax community at the low end of the disturbance spectrum, as the community has had a chance to equilibrate and stabilize. In certain instances, however, fast-growing pioneer species and the pressures they exert over the surrounding community can actually be more associated with an MRH-type relationship, instead of a climax community in an IDH-driven landscape. Evidence of one type of relationship, therefore, must be reconciled with time since disturbance, disturbance type, and even community type (e.g. presence of Pioneers, succession stage, etc.). MRH and IDH may also be interchangeably descriptive theories for describing the same community in different ecosystems or at different community maturity phases.

<center>Ecosystem State: A Hybrid Approach</center>

Because of the inability to differentiate between MRH and IDH at different scales, I propose use of a modified State-and-Transition model to describe the relationship between disturbance and diversity. State-and-transition models were first developed as a technique to describe community turnover in grassland ecosystems (Stringham et al. 2003). Their hybridization of conceptual models and quantitative descriptions, however, provide an ideal framework for examining maintenance of diversity at differing scales in multiple ecosystems.

Figure 21 represents a rough conceptual state-and-transition model constructed using the plots of the LHC as a case study example. Ordination of community types can

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be used as the basis for constructing state-and-transition models, on which axis overlays can be used to interpret underlying gradients that may contribute to state change. Examining plots relative to each other along axes consisting of productivity and disturbance intensity (which in this case is only assumed) provides a visual representation of various ecosystem states, each of which can either conform to or reject one or neither of MRH or IDH.
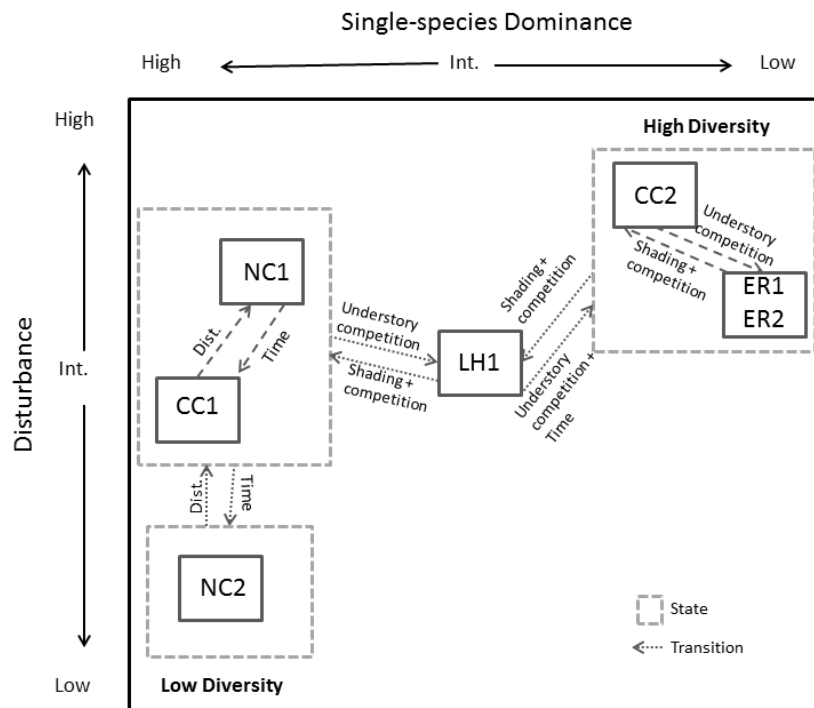

Figure 21. Conceptualization of a state-and-transition model approach to examining applicability of disturbance-diversity relationships within the Lake Hargy Caldera, Papua New Guinea. States are distinct forest community types, and transitions are distinguishable transitions between those states that are correlated with particular ecosystem dynamics via ordination.

In this theoretical example, diversity does not show a Gaussian response to either disturbance intensity or single-species dominance, but instead shows an almost linear correlation to combinations of the two. Conceptualizing plot differences in this way also allows easier interpretation of possible causes ("transitions") of changes in state (in this case, forest "type" and diversity).

This approach is not entirely novel. Cardinale et al. (2009) discuss a multivariate productivity-diversity hypothesis (MPD), which appears to be an amalgamation of multiple diversity theories, augmented with discrete quantification of community differences using multivariate analyses. By examining diversity-productivity relationships in a stream ecosystem, Cardinale et al. found that MPD predictions of producer biomass-mediation of diversity, as well as resource limitation, were upheld. While MPD seems to be a more resource-driven hypothesis, similar multivariate approaches that incorporate responses along multiple axes and incorporate conceptual models are likely to be a useful tool in describing diversity.

Conclusions

Here I discussed the merits of two often debated theories regarding the response of diversity to disturbance. Both MRH and IDH have been upheld or refuted in multiple studies, with causes of rejection ranging from ecosystem-specific variation to direct observation of conformity to one hypothesis. Neither MRH nor IDH, however, take temporal variation into account.

In the LHC of Papua New Guinea, plots appear to conform to either MRH or IDH, or sometimes, both. Results from this case study show that MRH and IDH may in fact be complimentary, and can describe the same community at different maturity phases, age since disturbance, or under different disturbance types.

State-and-transition models provide a robust conceptual framework in which to examine diversity response curves, and should be readily incorporated into future studies specifically formulated to test diversity hypotheses. The ease of interpretation of state-and-transition models, as well as advent of other multivariate approaches to understanding disturbance-diversity relationships, such as the MPD, lend support to hybrid approaches. Multivariate and conceptual approaches also provide support against the argument for abandonment of any one long-standing ecological theory. Instead, incorporation of past theories into the synthesis of new models is needed, as simple univariate models of diversity are still relevant when considered in a multivariate context.

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CHAPTER V

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Plot enumeration found 92 species, 73 genera, and 49 families. Enumeration also showed that the LHC forest does not have the high α-diversity seen in some other tropical forests (H = 2.88). The LHC forest has greater than 300% more species per hectare ($\bar{X}$ = 629, SD = 68), however, than similar forests in Southeast Asia, and slightly more (1% greater) families per hectare ($\bar{X}$ = 479, SD = 50) than other tropical forests worldwide.

Ordination of forest plots showed distinct forest types separated by location within the caldera (species-level MRPP T = -3.02, A = 0.099, p = 0.007), with a broadly mixed distribution of families and genera but species-level clustering in specific locations. Structural variation was also observed, with basal areas by plot ranging from 68.68 m² ha^{-1} to 21.37 m² ha^{-1}. Soil analysis found significant differences between sampled areas (i.e. pairs of plots) in 11 of the 21 sampled parameters (B, Cl, Conductivity, Cu, Fe, K, Mg, Mn, Na, Organic Mater, Pb, and S). All sampled areas had very high sand content (>56% sand). Overlay of soil variables onto a species-level ordination showed that conductivity and copper concentrations were highly associated with variation along the major ordination axes. The low correlation between conductivity and one of the axes, however, and wide variation in soil types across the caldera that did

not mirror the variation in species across the caldera show that soils alone do not explain the majority of the variance observed in tree species. Instead, other factors may be influencing soil composition and thus species composition across the landscape, laying the foundation for future sampling.

This study was the first enumeration and description of the forest within the LHC. Results show that the LHC forest is very species-rich and consists of multiple distinct forest types that are highly variable across the landscape. Soil characteristics were shown to contribute to some of the observed variation, but other variables may also be driving shifts in composition, such as disturbance intensity and frequency.

Recommendations

Patterns identified in the LHC relative to structural and composition variation across the landscape demonstrate the value of the forest from both a conservation perspective (due to inherently high biodiversity) but also from a standpoint of future analysis. The small yet significant relationships seen between soils and species composition also demonstrate the importance of future sampling within the LHC, as building of a larger dataset will allow more robust modeling of interactions among soils, disturbance, and forest diversity.

The rugged nature of the LHC coupled with its location make the forest within a primary candidate for use as a "natural laboratory" for long term ecological surveys. Further enumeration of the forest stands within the LHC can provide further insights into potential catastrophic origin and/or mediation of forest successional patterns within a

disturbance and diversity context. For these reasons, future sampling using the protocols employed in this study is recommended. Establishment of a larger number of permanent plots to augment the current plots can increase overall sample size and analytical power. Longitudinal sampling of all permanent plots through time will also allow future work to detect succession patterns and trends in community composition. Future work should also attempt to quantify disturbance type and history where possible in order to further explore the question of diversity relative to disturbance.

APPENDIX A

APPENDIX A

Appendix A. List and frequency count of all recorded species within the Lake Hargy Caldera, Papua New Guinea. List includes all observed families, genera, and species and their corresponding species code, as well as individual species stem counts.

Family	Genus	Species	SPCode	Freq
Meliaceae	*Aglaia*	*sapindina*	Aglsap	1
Simaraubaceae	*Ailanthus*	*integrifolia*	Ailint	2
Fabaceae	*Albizia*	*procera*	Albpro	1
Apocynaceae	*Alstonia*	*brassii*	Alsbra	1
Apocynaceae	*Alstonia*	*scholaris*	Alssch	2
Euphorbiaceae	*Antidesma*	*olivaceum*	Antoli	2
Euphorbiaceae	*Aporusa*	*papuana*	Apopap	5
Fabaceae	*Archidendron*	*glabra*	Arcgla	1
Moraceae	*Artocarpus*	*sepicanus*	Artsep	3
Barringtoniaceae	*Barringtonia*	*apiculata*	Barapi	7
Barringtoniaceae	*Barringtonia*	*calyptrocalyx*	Barcal	8
Euphorbiaceae	*Blumeodendrum*	*papuanum*	Blupap	2
Euphorbiaceae	*Bridellia*	*macrocarpa*	Brimac	3
Clusiaceae	*Calophyllum*	*soulatrii*	Calpet	2
Clusiaceae	*Calophyllum*	*vexans*	Calsou	2
Arecaceae	*Calyptrocalyx*	*petiolaris*	Calvex	2
Anacardiaceae	*Campnosperma*	*brevipetiolata*	Cambre	2
Burseraceae	*Canarium*	*oleosum*	Canole	8
Ulmaceae	*Celtis*	*latifolia*	Cellat	1
Apocynaceae	*Cerbera*	*floribunda*	Cerflo	2
Oleaceae	*Chionathus*	*cigas*	Chibec	1
Meliaceae	*Chisocheton*	*beccarii*	Chicig	1
Lauraceae	*Cinamonum*	*cullilawan*	Cincul	1
Corynocarpaceae	*Corynocarpus*	*cribbianus*	Corcri	6
Cyatheaceae	*Cyathea*	*sp*	Cyapet	2
Anonaceae	*Cyathocalyx*	*petiolaris*	Cyasp	1
Rosaceae	*Cyclandrophora*	*laurina*	Cyclau	1
Myrtaceae	*Decaspermum*	*sp*	Decsp	1
Urticaceae	*Dendrochnide*	*oblonga*	Denobl	7
Dilleniaceae	*Dilleina*	*papuana*	Dilpap	1
Meliaceae	*Dysoxyllum*	*parasiticum*	Dyspar	9
Elaeocarpaceae	*Elaelocarpus*	*amplifolia*	Elaamp	2

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Appendix A cont.

Lauraceae	*Endiandra*	*brassii*	Endbra	2
Euphorbiaceae	*Endospermum*	*medullosum*	Endmed	2
Polygalaceae	*Eriandra*	*fragrans*	Erifra	1
Myrtaceae	*Eucalyptus*	*deglupta*	Eucdeg	1
Moraceae	*Ficus*	*copiosa*	Ficcop	1
Moraceae	*Ficus*	*pachystemon*	Ficpac	6
Moraceae	*Ficus*	*wasa*	Ficwas	1
Clusiaceae	*Garcinia*	*hunsteinii*	Garhun	3
Clusiaceae	*Garcinia*	*latifolia*	Garlat	10
Euphorbiaceae	*Glochideon*	*sp*	Glosp	1
Gnetaceae	*Gnetum*	*gnemon*	Gnegne	1
Myristicaceae	*Gymnacranthera*	*paniculata*	Gympan	4
Rhizophoraceae	*Gynotroches*	*axillaris*	Gynaxi	1
Burseraceae	*Hapololobus*	*floribunda*	Hapflo	1
Proteaceae	*Helicia*	*latifolia*	Hellat	2
Myristicaceae	*Horsfieldia*	*bassifisa*	Horbas	1
Aquifoliaceae	*Illex*	*arhemensis*	Illarh	2
Leeaceae	*Leea*	*indica*	Leeind	5
Lauraceae	*Litsea*	*firma*	Litfir	2
Lauraceae	*Litsea*	*timoriana*	Littim	4
Euphorbiaceae	*Macaranga*	*dulcis*	Macdul	2
Euphorbiaceae	*Macaranga*	*sp*	Macsp	1
Magnoliaceae	*Magnolia*	*tsiampacca*	Magtsi	1
Anacardiaceae	*Mangifera*	*indica*	Manind	1
Fabaceae	*Maniltoa*	*psylogyne*	Manpsy	1
Icacinaceae	*Medusanthera*	*laxiflora*	Medlax	4
Rutaceae	*Melicope*	*elleryana*	Melell	2
Tiliaceae	*Microcos*	*argentea*	Micarg	9
Loganiaceae	*Mitrasacne*	*sp*	Mitsp	1
Myristicaceae	*Myristica*	*fatua*	Myrfat	5
Loganiaceae	*Neuburgia*	*corynocarpa*	Neucor	3
Araliaceae	*Osmoxylon*	*novoguinensis*	Osmnov	1
Rosaceae	*Parastemon*	*versteegii*	Parver	1
Euphorbiaceae	*Pimeleodendron*	*amboinicum*	Pimamb	5
Icacinaceae	*Platea*	*excelsa*	Plaexc	31
Podocarpaceae	*Podocarpus*	*neriifolius*	Podner	1
Annonaceae	*Polyalthia*	*oblongifolia*	Polobl	4

Appendix A cont.

Sapindaceae	*Pometia*	*pinnata*	Pompin	21
Sapotaceae	*Pouteria*	*firma*	Poufir	1
Sapotaceae	*Pouteria*	*obovoidea*	Pouobo	8
Sapotaceae	*Pouteria*	*sp*	Pousp	10
Rosaceae	*Prunus*	*gazelpeninsulae*	Prugaz	2
Rosaceae	*Prunus*	*schlecterii*	Prusch	2
Rubiaceae	*Psychotria*	*(Sm Lf)*	Psy(Sm	29
Myrsinaceae	*Rapanea*	*micrantha*	Rapmic	2
Myrtaceae	*Rhodamnia*	*latifolia*	Rholat	1
Icacinaceae	*Rhyticaryum*	*longifolium*	Rhylon	1
Actinidaceae	*Saurauia*	*conferta*	Saucon	9
Elaeocarpaceae	*Sloanea*	*forbesii*	Slofor	2
Sterculiaceae	*Sterculia*	*conwentzii*	Stecon	2
Myrtaceae	*Syzygium*	*buettnerianum*	Syzbue	1
Myrtaceae	*Syzygium*	*gonatanthum*	Syzgon	1
Myrtaceae	*Syzygium*	*sp*	Syzsp	8
Combretaceae	*Terminalia*	*kaernbachii*	Terche	2
Theaceae	*Ternstromia*	*cheryii*	Terkae	5
Rubiaceae	*Timonius*	*sp*	Timsp	2
Flacourtiaceae	*Trichadenia*	*philipinensis*	Triphi	1
Staphyleaceae	*Turpinia*	*pentandra*	Turpen	2
Stayphyleaceae	*Turpinia*	*petandra*	Turpet	1
Cunoniaceae	*Weinmannia*	*trichophora*	Weitri	12
Anonaceae	*Xylopia*	*papuana*	Xylpap	4

APPENDIX B

APPENDIX B.

Appendix B. Results from analysis of variance (ANOVA) of all measured soil variables. NS = No significant difference. Tukey's p is p value from Tukey's pairwise comparisons. Plots compared are listed under "Pairs".

Variable	ANOVA p	Pairs		95% CI	Tukey p
Al	NS				
As	NS				
B	0.0103				
		CC	NC	-0.87, -0.02	0.045
		LH	ER	-0.92, -0.06	0.032
		LH	NC	-1.13, -0.27	0.009
C	NS				
Cd	NS				
Cl	0.0719				
		LH	ER	-188.98, 5.64	0.060
Conductivity (Cond)	0.0284				
		LH	NC	-1.86, -0.23	0.022
Cu	0.0042				
		CC	ER	-4.31, -1.19	0.007
		LH	ER	-4.72, -1.6	0.004
		NC	ER	-3.62, -0.49	0.020
Fe	0.0334				
		LH	ER	-65.78, -2.9	0.037
		LH	NC	-60.04, 2.84	0.067
K	0.0655				
		LH	NC	-162.85, 0.08	0.050
Mg	0.0301				
		CC	NC	-26.68, 1.93	0.078
		LH	NC	-31.95, -3.34	0.025
Mn	0.0313				
		LH	NC	-77.16, -8.16	0.025
		NC	ER	-6.83, 62.17	0.098
Na	0.0947				
		LH	ER	-10.37, 1.21	0.102

Appendix B cont.

Ni	NS				
Organic Matter (OM)	0.0307				
		LH	ER	-9.88, 0.18	0.056
		LH	NC	-10.21, -0.15	0.045
		LH	CC	-10.52, -0.46	0.038
P	NS				
Pb	0.0454				
		LH	NC	-21.05, 1.34	0.071
		LH	CC	-25.65, -0.3	0.046
pH	NS				
S	0.0159				
		LH	ER	-23.98, -1.59	0.032
		LH	NC	-27.38, -4.99	0.014
		LH	CC	-21.89, 0.5	0.058
Sodium Absorption Ratio (SAR)	NS				
Zn	NS				