Dynamics and diversity patterns of multiple life stages of tropical trees following selective logging

by

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

The University of Sheffield
School of Biosciences
Ecology & Evolutionary Biology

23rd September 2021

CONTENTS

ABSTRACT....................13

ACKNOWLEDGEMENTS....................14

AUTHOR'S DECLARATION....................15

GENERAL INTRODUCTION....................17

1.1 Hyper-diversity of the tropics....................17
1.2 The sixth mass extinction....................18
1.3 Tropical forest degradation & conversion....................20
1.4 Tropical selective logging....................21
1.5 Recovery of logged forests and their communities....................22
1.6 Maintenance of tropical diversity....................24
1.7 Thesis aims and rationale....................25

LIMITED CONTRIBUTIONS OF FUNGAL PATHOGENS TO DENSITY-DEPENDENT SEEDLING MORTALITY OF MAST FRUITING BORNEAN TREES....................28

2.1 Abstract....................28
2.2 Introduction....................29
2.3 Methods and Materials....................33
2.4 Results....................37
2.5 Discussion....................42
2.6 Author Contributions....................47
2.7 Funding....................48
2.8 Acknowledgements....................48
2.9 Data Accessibility....................48

ASKING THE WRONG QUESTION IN EXPLAINING TROPICAL DIVERSITY....................49

3.1 Abstract....................49
3.2 Modelling coexistence: asking the wrong question?....................49
3.3 Variation affects coexistence....................51
3.4 Under what circumstances is variation in C-NDD and species' sensitivity to C-NDD likely to erode diversity?....................53
3.5 Future study: Asking the right question....................55
3.6 Glossary....................56
3.7 Acknowledgements....................57

LOCAL DRIVERS OF ß-DIVERSITY IN MULTIPLE LIFE STAGES OF TROPICAL TREES FOLLOWING SELECTIVE LOGGING....................58

4.1 Abstract 58
4.2 Introduction 59
4.3 Methods and Materials 62
4.4 Results 67
4.5 Discussion 74
4.6 Conclusion 79
4.7 Acknowledgements 79

PATTERNS OF TRAIT SIMILARITY ALONG LIANA INFESTATION GRADIENTS IN A SELECTIVELY LOGGED TROPICAL FOREST 80

5.1 Abstract 80
5.2 Introduction 81
5.3 Methods and Materials 84
5.4 Results 90
5.5 Discussion 99
5.6 Conclusion 104
5.7 Acknowledgements 104

GENERAL DISCUSSION 105

6.1 Summary 105
6.2 Drivers of altered logged forest composition 106
6.3 Maintenance of tropical diversity 107
6.4 Conservation implications 109
6.5 Conclusion 112

SUPPORTING INFORMATION FOR CHAPTER 2 113

SUPPORTING INFORMATION FOR CHAPTER 4 130

SUPPORTING INFORMATION FOR CHAPTER 5 134

REFERENCES 139

LIST OF TABLES

Table 4. 1. The relative importance of each environmental disturbance variable and geographic distance in explaining changes in tree community ß-diversity between sample points. Mean expected ß-diversity from 999 null communities produced by randomising species identities and abundances, included as a predictor. Values represent the sum of coefficients across three I-splines from GDMs with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with community dissimilarity represented by a dash and significant relationships indicated in bold...........70

Table 5. 1. Description of the six functional plant traits (discrete = D, and continuous = C) and their related functions...87

Table 5. 2. Summary statistics of linear mixed-models (LMM) of the relationship between SES_{RaoQ} values and liana infested canopy cover (liana load) for sapling, juvenile, and adult communities at both the plot- and block-level. SES_{RaoQ} values generated using null models of trait convergence (EF) or trait divergence (LS). Significant terms in bold. Marginal R^2 denotes variance explained by just liana infestation and conditional R^2 the variance explained by both liana infestation and the spatial arrangement of sample points as random effects...94

Table 5. 3. Summary statistics of linear mixed-models (LMM) of the relationship between SES_{RaoQ} values and the proportion of liana infested individuals (liana prevalence) for sapling, juvenile, and adult communities at both the plot- and block-level. SES_{RaoQ} values generated using null models of trait convergence (EF) or trait divergence (LS). Significant terms in bold. Marginal R^2 denotes variance explained by just liana infestation and conditional R^2 the variance explained by both liana infestation and the spatial arrangement of sample points as random effects...95

Table 5. 4. Pearson's correlation coefficients and associated *p*-values of the relationship between community weighted trait means (CWM) and liana infested canopy cover (liana load) for sapling, juvenile, and adult communities at both the plot- and block-level. Significant terms in bold. 99

Table A. 1. Description of the eight lowland tree species used in the experiment. Relative abundance and stem densities calculated using data from the 50-Hectare Plot Project Danum Valley, part of the CTFS-ForestGEO network (Anderson-Teixeira et al., 2015). 113

Table A. 2. Tropical studies manipulating seed or seedling densities of trees. 114

Table A. 3. Overall and species-level effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on seedling mortality. Coefficients estimated using generalized linear mixed models with binomial distribution and log-link function within a hierarchical Bayesian framework allowing for estimation of coefficients despite no mortality recorded within some pots. Random uncorrelated slopes for fungus and density were estimated per species..118

Table A. 4. Summary of analysis of variance tables of fitted models for seedling height, stem diameter and leaf damage score. Significant terms in bold. 120

Table A. 5. Analysis of variance table of individual species linear regressions for seedling height. Significant terms in bold. 121

Table A. 6. Analysis of variance table of individual species linear regressions for seedling stem diameter. Significant terms in bold. 124

Table A. 7. Individual species analysis of variance table for seedling leaf damage score. Significant terms in bold. 127

Table B. 1. Relationships of observed dissimilarity in tree community ß-diversity between pairs of life stages. Values represent the sum of coefficients across three I-splines from GDMs with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with community dissimilarity represented by a dash and significant relationships indicated in bold. All models contained geographic distance as a significant predictor. 133

Table B. 2. The relative importance of each environmental variable and geographic distance in explaining nestedness and turnover components of logged forest tree ß-diversity (Bray-Curtis index). Values represent the sum of coefficients across three I-splines from GDMs, with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with components of ß-diversity represented by a dash and significant relationships indicated in bold. Coefficients of all predictors of GDMs of sapling and adult nestedness equalled zero. 133

Table C. 1. Summary statistics of fixed effects from linear mixed models (LMM) of the relationships between within-forest disturbance measures and liana infestation (load and prevalence) at the plot-level. Both models include sample block and site as a nested random effects structure. Significant terms in bold ($p < 0.05$). 136

Table C. 2. Statistics of phylogenetic signal for the six functional traits. 137

Table C. 3. Description of plant functional trait matrix with species- and genus-level coverage from which missing species' values were phylogenetically imputed. Trait data was recorded for a total of 5605 species from all 199 genera found in our study data, including 392 of the 503 (77.9%) focal species. 138

LIST OF FIGURES

Figure 2. 1. Daily seedling death rate between pots planted at high and low density and treated with (+) or without (-) fungicide aggregated across all 8 species. Data points represent means of 90 replicates (*n* = 900 individuals for each high-density treatment, and *n* = 90 for low-density treatment) and error bars denote standard error. 37

Figure 2. 2. Daily seedling death rate between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means of 8-13 replicates (*n* = 80-130 individuals for each high-density treatment, and *n* = 8-13 for low-density treatment) and error bars denote standard error..38

Figure 2. 3. Overall and species-level effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on seedling mortality for eight lowland tree species. Points represent the difference between the means of treatments and controls (i.e., the difference between high and low density, and fungicide and controls). Bars represent 95% Bayesian credible intervals of parameter estimates. Random uncorrelated slopes for fungus and density were estimated per species. 39

Figure 2. 4. Relationships of variation in the strength of (a) planting density effects and (b) fungicide application effects on seedling survival with local adult tree abundance (> 10 cm d.b.h). The strength of treatment effects represent regression coefficients estimated using generalized linear mixed models with binomial distribution and log-link function within a hierarchical Bayesian framework. Pearson correlation coefficients (*r*) and *p*-values (*p*) given in text. 40

Figure 2. 5. Model coefficients of the effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on; (a) mean seedling height, (b) stem diameter, and (c) leaf damage score for eight lowland tree species. Model coefficients estimated using linear and

analysis of variance models. Filled points represent significant terms ($p < 0.05$) and error bars represent ± 1 SE..41

Figure 3. 1. Variation in relationships between species' per capita growth rates and abundance and changes in community diversity over time under different scenarios of species' susceptibility to C-NDD. (a) Variation in species' 'fitness' (average population growth rate) varies the y-intercept of the relationship between species' per capita growth rates and abundances, with each line representing a species and the slope equal for all species. (b) Variation in species' susceptibility to C-NDD represents variation in the slope, with more negative relationships for species with high susceptibility to C-NDD. (c) Variation in species' 'fitness' and susceptibility to C-NDD create less even abundances between species when at equilibrium (black lines). (d) The turquoise region represents communities varying in the strength of C-NDD and where species susceptibility to C-NDD is equal (i.e., approaches consistent with applying the Janzen-Connell mechanism to otherwise neutral models.). The pink region represents communities with different strengths of variation in species' susceptibility to C-NDD or variation in species' per capita growth rates (i.e., models of competitive exclusion). Grey regions represent the effect of limited dispersal on each scenario. This figure was adapted from Chisholm and Fung (2020). 54

Figure 4. 1. Study area and sampling design. View of the surrounding twice-logged forests of the Malua Forest Reserve (MFR), taken from an old secondary logging road, still partly visible 12 years after logging extractions (a). The location of the MFR in the northeastern tip of Sabah, Malaysian Borneo (b; inset). Map of the three twice-logged forest sites in relation to the Malua Research Station (c). Arrangement of 100 m^2 core sampling area within each 200 x 200 m sample blocks within sites (d). Arrangement of the five randomly positioned 20 x 20 m tree community sample plots and nested sub-plots in which turnover in tree composition was measured (e). Reproduced, with permission, from Catherine Finlayson (a)...63

Figure 4. 2. ß-diversity (Bray-Curtis index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test. 68

Figure 4. 3. Relationships between observed ß-diversity of tree communities and predicted environmental distance (within-forest disturbance measures, expected ß-diversity, and spatial distance) between pairs of logged forest sample blocks. ß-diversity was estimated using Bray-Curtis index (a, d, and g), Chao-Jaccard index (b, e, and h), and Jaccard index (c, f, and i). Mean expected ß-diversity from 999 null communities produced by randomising species identities and abundances, included as a predictor. 71

Figure 4. 4. Rates of change in tree community ß-diversity of each life stage along gradients of: (a) spatial distance, and (b) expected ß-diversity. Mean expected ß-diversity generated from 999 null communities produced by randomising species identities and abundances at each sample point. The height of each curve depicts the compositional dissimilarity explained by each predictor when all other variables are held constant. 72

Figure 4. 5. Turnover (species replacement) and nestedness (species loss) components of ß-diversity (Bray-Curtis index) between life stages. Boxplots present median components of dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages denoted by different letters, comparisons estimated separately for each component using ANOVA and accompanying Tukey's post-hoc test. 74

Figure 5. 1. Differences in trait-based community assembly mechanisms between sapling, juvenile, and adult trees at both the plot- and block-level. Trait-based assembly mechanisms inferred via standardised effect size of Rao's quadratic entropy (SES_{RaoQ}) of observed and null communities. Positive values denote trait divergence and negative values trait convergence. Null expected values derived from two complementary null models: limiting similarity (LS) models specifically detect trait divergences via limiting similarity (a), whilst environmental filtering (EF) models detect trait converge via environmental filtering (b). Expected values from LS and EF null models generated from 999 iterations of 'richness' and 'frequency' algorithms, respectively. Boxplots present median SES_{RaoQ}, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Filled box plots denote values significantly different to zero (patterns of non-random assembly), tested using Student's t-test ($p < 0.01$). 91

Figure 5. 2. Changes in the degree of community trait convergence and divergence across gradients of liana infestation for sapling, juvenile, and adult trees. Convergence or divergence of communities' functional composition inferred from the standardised effect size of Rao's quadratic entropy (SES_{RaoQ}) of observed and null communities at the plot-level (white filled plots) and block-level (grey shaded plots). Positive values denote trait divergence and negative values trait convergence. Null expected values derived from two complementary null models: limiting similarity (LS) models specifically detect trait divergences via limiting similarity (a, b, c, and d), whilst environmental filtering (EF) models detect trait converge via environmental filtering (e, f, g, and h). Expected values from LS and EF null models generated from 999 iterations of 'richness' and 'frequency' algorithms, respectively. 93

Figure 5. 3. Changes in the community weighted means (CWM) and ranges of individual morphological plant traits at each sample block across gradients of increasing liana infestation. CWM given for saplings (red; a, d, g, and j), juveniles (blue; b, e, h and k), and adults (yellow; c, f, i, and l) separately. Vertical bars indicate the maximum and minimum trait value of each community. Solid horizontal lines indicate significant correlation coefficients (Pearson's: $p < 0.05$). WD = wood density, SLA = specific leaf area, LNC = leaf nitrogen content per leaf dry mass, and MMH = mean mature height. 97

Figure 5. 4. Changes in the community weighted means (CWM) and ranges of individual morphological plant traits at each sample plot across gradients of increasing liana infestation. CWM given for saplings (red; a, d, g, and j), juveniles (blue; b, e, h, and k), and adults (yellow; c, f, i, and l) separately. Vertical bars indicate the maximum and minimum trait value of each community. Solid horizontal lines indicate statistically significant relationships from linear regressions ($p < 0.05$). WD = wood density, SLA = specific leaf area, LNC = leaf nitrogen content per leaf dry mass, and MMH = mean mature height..98

Figure A. 1. Mean seedling height (cm) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error...............123

Figure A. 2. Mean stem diameter (mm) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error...............126

Figure A. 3. Mean leaf damage score (1 to 4 ordinal scale) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error..129

Figure B. 1. Proportions of total explained deviance in observed ß-diversity (Bray-Curtis index) attributed to environmental, spatial, and both environmental and spatial predictors, for each tree life stage. Null community ß-diversity included as a predictor in all GDMs. 130

Figure B. 2. ß-diversity (Chao-Jaccard index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test (Life stages ANOVA: $F_{(2,206)} = 87.75$, $p < 0.001$, Null-expected ANOVA: $F_{(1,206)} = 1237.69$, $p < 0.001$). 131

Figure B. 3. ß-diversity (Jaccard index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test (Life stages ANOVA: $F_{(2,206)} = 30.97$, $p < 0.001$, Null-expected ANOVA: $F_{(1,206)} = 781.17$, $p < 0.001$)...132

Figure C. 1. Model coefficients of the effects of adult basal area, adult abundance, canopy openness and tree species diversity on plot-level liana infestation (a). Model coefficients estimated using linear mixed models, with nested study design included as random effects. Significant terms denoted by *** ($p < 0.001$), and error bars represent ± 1 SE and marginal R^2 given in text. Relationships between significant variables in linear mixed models and liana load (b & c) and liana prevalence (d & e). Dotted lines represent 95% CIs and marginal R^2 given in text..135

ABSTRACT

Global biodiversity loss is accelerated by the pervasive loss and degradation of tropical forests. What maintains the immense but imperilled diversity of tropical forests remains a principal question in ecology. Efforts to conserve tropical species could be strengthened by a more detailed understanding of how anthropogenic disturbances impact forest diversity and dynamics, including the mechanisms that maintain and structure diverse plant communities. In this thesis, I first examine the contributions of fungal pathogens, as specialist natural enemies, in driving diversity enhancement in Borneo's mast fruiting forests. Using a manipulative shadehouse experiment, I demonstrate that fungal pathogens are responsible for weak conspecific density-dependent mortality, that is unlikely to promote overall diversity in this mast fruiting system. I then review recent modelling approaches explaining tropical plant diversity and highlight that the effectiveness of coexistence mechanisms is sensitive to species' demographic variations and dispersal ability. Next, I explore how tropical selective logging affects the composition of multiple life stages of Borneo's diverse tree assemblages. I find persistent patterns of high spatial turnover in tree communities of all life stages 12 years after two successive logging rotations. Turnover is the result of greater dispersal limitations from increasingly isolated and aggregated adult trees as opposed to increased environmental heterogeneity after logging. Finally, I consider the impacts of liana (woody-vine) proliferation on patterns of tree functional trait similarity following logging. Combining freely available plant functional trait data with local tree community and liana infestation data, I find that local-scale patterns of liana infestation do not strongly relate to the simplification of host tree functional composition after harvests. Collectively, my results suggest that selective logging causes long-term modifications to tree communities with the potential to severely disrupt the still largely unknown mechanisms and drivers of tropical diversity enhancement. To reduce the impacts of future degradation on the diversity and dynamics of logged tropical forests there is a need to foster sustainable forestry and forest restoration practices, and consider more widely how diversity is maintained, to infer how it can be conserved.

ACKNOWLEDGEMENTS

Firstly, a massive and sincere thanks to my supervisors; Prof Robert Freckleton and Prof David Edwards. Your opinions and guidance have been invaluable throughout.

I thank the Leverhulme Trust's Centre for Advanced Biological Modelling (CABM) for their three years of funding.

Thanks to my local collaborator, Dr Kalsum Yusah, for your logistical support, encouragement, and luxury food items during fieldwork. For permission to work in Sabah and the Malua Forest Reserve (MFR), I thank the South East Asia Rainforest Research Partnership (SEARRP), Sabah Biodiversity Council, Danum Valley Wildlife Management Committee, and Yayasan Sabah. I thank my collaborators at the Sabah Forestry Department; Mr Indra Purwandita Sunjoto and Mr. Julsun Joseph Sikui. Thanks to Datuk Dr Glen Reynold, Dr Michael O'Brien, Adrian Karolous, and all the staff at the Malua research camp for facilitating my field work. In particular, I thank Remmy Murinus for the incredible logistical effort in aiding the running of the project. For assistance with field work, I thank; Udin Jaga, Jude, Ridly, Eglie, Japin Rasiun, Viddi Saidi, Vendi Vens Aishiteru, Mohammad Fauzi Osman, Yvonne Koid Qian Qun, Emma Watson, Lucy Watson, Rob Davies, Daniel Simonsen, Gillian Gabriel Gallus Gawis, Grace Juman, Rui Wong Yu, and Frolyin Felix.

A huge thanks to all members of the Conservation Bites, Mynas and Freckleton lab groups, past and present, for your helpful ideas, discussion, feedback, and support. In particular, a massive thanks to Catherine Finlayson and Gianluca Cerullo for all the fieldwork adventures/misadventures, and who's advice, support, friendship and patience, was so integral to this thesis getting finished.

Finally, to my family and friends. Thanks for being ever encouraging, patient, and supportive. It cannot have been easy.

AUTHOR'S DECLARATION

The research presented here is my own (P.G.C) and has not been submitted for any other qualification at this or any other institution. This thesis is a collaborative piece of research from myself (P.G.C) and several other researchers: Robert P Freckleton (R.P.F), David P Edwards (D.P.F.), Michael J O'Brien (M.J.B), Felicity A Edwards (F.A.E), and Kalsum M Yusah (K.M.Y).

Chapter 2 has been published as:

Cannon, P. G., O'Brien, M. J., Yusah, K. M., Edwards, D. P., & Freckleton, R. P. (2020). Limited contributions of plant pathogens to density-dependent seedling mortality of mast fruiting Bornean trees. *Ecology and Evolution*, 10(23), 13154–13316. doi: 10.1002/ece3.6906

The manuscript is reproduced in full, with only minor formatting alterations. Author contributions, as follows: P.G.C, R.P.F, and M.J.O conceptualized the study; P.G.C coordinated the study and collected seedling data; M.J.O collected the seeds and the light and temperature data; P.G.C led data analysis, with contributions from R.P.F and M.J.O; and P.G.C wrote the initial draft of the manuscript with all authors contributing significantly to revisions. All authors gave final permission for publication.

Chapter 3 has been published as:

Cannon, P. G., Edwards, D. P., & Freckleton, R. P. (2021). Asking the Wrong Question in Explaining Tropical Diversity. *Trends in Ecology and Evolution*, 36(6), 482–484. doi: 10.1016/j.tree.2021.02.011

The manuscript is reproduced in full, with only minor formatting alterations. Author contributions, as follows: P.G.C and R.P.F. conceptualized the piece; P.G.C wrote the initial draft of the manuscript, with R.P.F. and D.P.E contributing substantially to the final manuscript.

Chapter 4 is currently in preparation for submission to *Journal of Ecology* as:

Cannon, P. G., Edwards, D. P., Yusah, K. M., & Freckleton, R. P. (2021). Local drivers of ß-diversity in multiple life stages of tropical trees following selective logging.

The manuscript is reproduced in full, with only minor formatting alterations. Author contributions, as follows: P.G.C conceptualized the study; Field work and data collection was carried out by P.G.C, with logistical support from K.M.Y; P.G.C performed all statistical analyses, with support from R.P.F; P.G.C wrote the initial manuscript with R.P.F, D.P.E, and K.M.Y all contributing substantially to the final manuscript.

Chapter 5 is currently in preparation for submission to *Journal of Ecology* as:

Cannon, P. G., Edwards F.A., Edwards, D. P., Yusah, K. M., & Freckleton, R. P. (2021). Patterns of trait similarity along liana infestation gradients in a selectively logged tropical forest.

The manuscript is reproduced in full, with only minor formatting alterations. Author contributions, as follows: P.G.C and F.A.E conceptualized the study; Field work and data collection was carried out by P.G.C, with logistical support from K.M.Y; P.G.C performed all statistical analyses, with support from F.A.E and R.P.F; P.G.C wrote the initial manuscript with R.P.F, F.A.E, D.P.E, and K.M.Y all contributing substantially to the final manuscript.

CHAPTER ❶

GENERAL INTRODUCTION

1.1 Hyper-diversity of the tropics

The vast majority of global terrestrial biodiversity is held within tropical biomes, including over three quarters of terrestrial flowering plants, mammals and amphibians, and 91% of birds (Barlow et al., 2018). Beyond those species already described, the tropics still account for the majority of annual species discoveries for many taxa and most undiscovered terrestrial species are also predicted to be found in tropical regions (Barlow et al., 2018; Gueńard, Weiser, & Dunn, 2012; Jenkins, Pimm, & Joppa, 2013).

Forests are the powerhouses of much tropical diversity. Covering just 12 % of the Earth's land surface (Bonan, 2008), tropical forests are home to half of the world's species (Scheffers, Joppa, Pimm, & Laurance, 2012). The extraordinary diversity of tropical forests is exemplified by their trees. Consisting of an estimated forty to fifty-three thousand species (Slik et al., 2015), a single hectare of tropical forest can hold as many as 650 tree species - more than all of North America (Coley & Kursar, 2014). Moreover, estimates of tropical diversity are almost certainly conservative. Tropical latitudes are under-sampled relative to temperate regions, with tropical data collection biased to more accessible areas and aggregated around established research sites (Barlow et al., 2018; Collen, Böhm, Kemp, & Baillie, 2012; Gardner et al., 2009).

Although remarkable, why should we care about the hyper-diversity of the tropics? Biological diversity is critical for the functioning of natural environments, and thus the delivery of a multitude of natural products and services used by people (Balmford et al., 2002; Schmid & Hector, 2004). Such provisioning and regulating services, including climate regulation, carbon sequestration, watershed protection, soil formation, pest control, timber production, crop pollination, supply of fresh water, and disease control, are all dependent on the functioning of diverse natural environments. The value of such goods and services provided by nature stand at an estimated US$124 trillion per year (Costanza et al., 2014). Beyond monetary worth, natural environments and their biodiversity warrant protection through their intrinsic value, with international conservation agendas increasingly recognising such inherent living value (Millennium Ecosystem Assessment, 2005).

Tropical forests represent one of the most valuable of Earth's biomes (Lewis, Edwards, & Galbraith, 2015), underpinning fundamental processes of evapotranspiration, primary productivity, cloud formation, and atmospheric circulation (Devaraju, Bala, & Modak, 2015; Malhi, 2012; Spracklen, Arnold, & Taylor, 2012). Intact tropical forests contribute significantly to the global carbon cycle, sequestering between a quarter and a third of global anthropogenic emissions, totalling 2.4 – 2.7 billion tons of CO_2 annually (Grace, Mitchard, & Gloor, 2014; Pan et al., 2011; Schimel, Stephens, & Fisher, 2015). At local scales, tropical forests provide a variety of human benefits, supporting the livelihoods of one billion disadvantaged people whose subsistence is reliant upon natural resources and services (Barlow et al., 2018; D. P. Edwards, Fisher, & Boyd, 2010). Despite the value of natural environments and their biodiversity to people, species and ecosystems are continuing to be lost and degraded at an alarming rate.

1.2 The sixth mass extinction

We are living in the sixth mass extinction event. Conservative estimates of current rates of species loss are 100 times greater than at any point in the last 65 million years, with 800-10,000 years of species extinctions occurring in the last century (Ceballos et al., 2015). Recent analyses have revealed that as many as half the world's trees (Botanic Gardens Conservation International, 2021) and amphibians (González-del-Pliego et al., 2019), and 42 % of terrestrial invertebrates (Collen et al., 2012) are at risk of extinction. Moreover, many species characterized as at 'least concern' are declining dramatically in their population sizes and ranges (Ceballos, Ehrlich, & Dirzo, 2017). Despite successful conservation actions thwarting the extinction of many species, rates of biodiversity loss have continued apace (Butchart et al., 2010).

It is no coincidence that the arrival of the global extinction crisis coincides with the Anthropocene – a period in the last ~10,000 years where human activities have increasingly driven fundamental shifts in the Earth's systems (Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014). Currently, no biome on the Earth's surface or in the majority of its oceans is free of human interference (Jones et al., 2018; Malhi et al., 2014). Environmental perturbations and species loss are therefore unmistakably human driven, with human population size accurately predicting the last 126,000 years of species extinctions (Andermann, Faurby, Turvey, Antonelli, & Silvestro, 2020). Currently, land-use change, pollution, climate change, over-exploitation, and invasive species represent the key drivers of global species loss, with the most significant biodiversity declines caused by land-use change (Newbold et al., 2015).

Loss of biological diversity depletes overall ecosystem resilience and stability, reducing the redundancy of species contributing to the same ecological functions, and the adaptive capacity of ecosystems to respond to further environmental change (Cardinale et al., 2012; Elmqvist et al., 2003). Consequently, human-driven loss and degradation of natural environments and their biodiversity are severely diminishing the provision of ecosystem services integral to sustaining humanity (Butchart et al., 2010; Lewis et al., 2015). Interactions between global biodiversity loss and other planetary boundaries are predicted to cause cascading impacts to the Earth's systems that may exceed the hypothesised 'safe operating space' for people (Rockström et al., 2009).

The effects of species loss and environmental degradation have been, and will continue to be, hardest felt in the tropics (Barlow et al., 2018; D. P. Edwards et al., 2019; Lewis et al., 2015). For example, degradation and deforestation in conjunction with climate change are predicted to transform tropical forests into a net carbon source, relinquishing their benefits in offsetting billions of tons of anthropogenic CO_2 (Mitchard, 2018). Simultaneously, the same forces will impede species range shifts as they attempt to track favourable climates across increasingly fragmented landscapes (Senior, Hill, & Edwards, 2019). The loss of tropical species and associated impacts to ecosystem stability and services will disproportionately affect some of the world's most vulnerable people and nations. Here, weak governance and limited capacity for mitigation predispose tropical nations to further degrade their natural resources and environments (Barlow et al., 2018).

1.3 Tropical forest degradation & conversion

The greatest threat to tropical forests and diversity comes from their conversion to agricultural lands and plantations (Giam, 2017), with large scale land acquisition for oil palm, wood fibres and timber plantations consistently linked to forest loss (Davis, Koo, Angelo, & Odorico, 2020). As a result, in the 12 years preceding the millennium, 2.3 million square kilometres of forest were lost, with tropical forests the primary source of new agricultural lands (Gibbs et al., 2010; M C Hansen et al., 2013).

Global agriculture currently covers over 38 % of the Earth’s land surface (Ramankutty, Evan, Monfreda, & Foley, 2008). Future food and timber demands are projected to continue to rise as a result of a growing and increasingly affluent human population (Kastner, Rivas, Koch, & Nonhebel, 2012), with a further 10-25 % land required for global agriculture by 2050 (Schmitz et al., 2014). Advancements in tropical crop yields are likely to shift the increased production of many crops from temperate to tropical regions. Strong governance and policy is therefore required to minimise the effects of further expansion on natural environments (D. R. Williams et al., 2021), and prevent greater profitability of tropical crops from inadvertently incentivising agricultural expansion into wild habitats (Carrasco, Larrosa, Milner-Gulland, & Edwards, 2014; Hertel, Ramankutty, Lantz, & Baldos, 2014).

Beyond their direct conversion, tropical forests are increasingly subjected to a diverse array of interacting stressors, the results of which will see future forests represent smaller, steeper, simpler, and emptier environments (D. P. Edwards et al., 2019). Deforestation of lowland forests will increasingly shift forest cover to higher elevations. Commercial logging, forest fires, and secondary effects of deforestation, including fragmentation and defaunation for bush meat and the emerging global wildlife trade, will also continue to degrade standing forest. Despite not contributing to overall forest loss, the effects of forest degradation are predicted to double biodiversity losses from deforestation (Barlow et al., 2016).

1.4 Tropical selective logging

The prevalence of tropical deforestation is dwarfed by forest degradation. Between 2000 and 2005, nearly four million square kilometres of tropical forest underwent commercial selective logging – 14 times more than was deforested (Asner, Rudel, Aide, Defries, & Emerson, 2009; Matthew C. Hansen et al., 2008). Despite recent advances in identifying logging activity via remote sensing (Hethcoat et al., 2019), the extent of tropical logging is almost certainly far greater than this, with illegal logging likely contributing significantly to overall logging extent and timber volumes (Brancalion et al., 2018). Today, only parts of the north-western Amazon and eastern Congo remain relatively free from human disturbances including logging (Asner et al., 2009).

Removing only adult trees of marketable timber species, selective logging maintains much of the existing forest canopy but simplifies forest size and age structures and reduces overall canopy height (D. P. Edwards et al., 2019; Milodowski et al., 2021). Fragmentation of the persisting canopy opens up the forest understory to increased light, temporarily altering microclimates (Jucker et al., 2020; Mollinari, Peres, & Edwards, 2019), and benefiting the establishment of low wood density pioneer tree species, bamboos, rattans and lianas (Schnitzer & Bongers, 2011), degrading standing forest carbon (Huang & Asner, 2010). In addition, extraction by heavy logging machinery and the creation of skid trails, log dumps, and extensive logging roads, compacts soils (Putz, Sist, Fredericksen, & Dykstra, 2008), and increases edge and fragmentation effects facilitating access for hunting (Brodie et al., 2015).

Despite significant disturbances, logged forests represent important refugia for tropical biodiversity, retaining the vast majority of primary forest species (D. P. Edwards, Tobias, Sheil, Meijaard, & Laurance, 2014), and many times more than when converted to croplands and plantations (Gibson et al., 2011). For example, 85-100% of primary forest plants, birds, mammals, and invertebrates can persist following a single logging operation (Putz et al., 2012) and nearly as many birds and dung beetles following a second rotation, including many bird species of conservation concern (D. P. Edwards et al., 2011). Logged forests also rapidly regain their thermal buffering potential following harvests, enabling temperature-sensitive species to persist under increasing influence from climate change (Senior, Hill, Benedick, & Edwards, 2018).

The severity of logging disturbances and their impacts on biodiversity, as well as timber and carbon, depend heavily on the intensity and frequency of harvests and the specific logging practices applied (Burivalova, Şekercioğlu, & Koh, 2014; Roopsind, Caughlin, van der Hout, Arets, & Putz, 2018). For example, a meta-analysis by Burivalova, Şekercioğlu, & Koh, (2014), found the diversity of many animal taxa declined with increasing overall logging intensity, with increased diversity of other taxa resulting from the encroachment of habitat generalists.

The development of reduced impact logging practices (RIL) that harness high-lead extraction techniques, pre-harvest logging inventories, and directional felling, can reduce collateral damage of smaller trees and minimise disturbances (Putz et al., 2008, 2012). Despite such practices, the majority of past logging has been carried out unsustainably (D. P. Edwards et al., 2019). Prescribed minimum cutting diameters and lengths of logging rotations are often lowered to maximise timber revenues, resulting in greater reductions to residual timber, carbon, and biodiversity (Putz et al., 2012). For example, forests of Southeast Asia, especially in Indonesia, Malaysia, and the Philippines, have been exposed to some of the most frequent and intensive timber harvests globally, whilst also being some of the most diverse and carbon dense (D. P. Edwards, Tobias, et al., 2014; Sullivan et al., 2017). Once depleted, logged forests are often at greater risk of conversion to other, now more profitable land-uses (Murdiyarso, Dewi, Lawrence, & Seymour, 2011). Preventing such scenarios is partly dependent on the ability of these heavily disturbed forests to recover lost economic and conservation value (D. P. Edwards, Tobias, et al., 2014).

1.5 Recovery of logged forests and their communities

The extent to which forests can recover from logging operations is partly dependent on whether previously logged forests remain in the permanent timber estate, or whether the emergence of large-scale tropical timber plantations result in the retirement of many concessions (D. P. Edwards, Tobias, et al., 2014) Recovery rates of timber volumes and carbon stocks post-logging can vary massively between regions, and with initial harvest intensity and logging practices (Putz et al., 2012). In the Amazon, pre-harvest biomass can take between 10-100 years to recover (Huang & Asner, 2010; Rutishauser et al., 2015), whilst in Indonesia, timber yields may not reach primary forest levels before a successive harvest , even when cutting cycles are doubled to 60 years (Ruslandi, Cropper, & Putz, 2017). Forest restoration activities, including climber cutting and underplanting of commercial species (reviewed in Cerullo & Edwards, 2019), can significantly accelerate recovery, recuperating initial carbon and timber stocks within 35-40 years (Ruslandi et al., 2017).

For those forests that avoid future harvests, a greater consideration is whether they will ever recover primary forest tree composition, or whether logged forests will remain in a permanent state of stalled succession. This question is inherently difficult to answer given forest succession operates at timescales of decades to centuries whilst the majority of selective logging has occurred in the last 20 years. To date, evidence from field experiments comparing old-growth forest to previously logged stands, suggests 40-45 years is insufficient to recover initial tree species composition following logging (Osazuwa-Peters, Chapman, & Zanne, 2015; Shima, Yamada, Okuda, Fletcher, & Kassim, 2018). High spatial turnover of tree composition can persist for decades, as late successional species decline in abundance and disturbance-insensitive generalists establish (Berry, Phillips, Ong, & Hamer, 2008; Osazuwa-Peters, Jiménez, Oberle, Chapman, & Zanne, 2015). Despite such subtractive homogenisation of tree communities, the drivers of persistent spatial turnover (beta-diversity) following logging are yet to be quantified. I address this in Chapter 4, using tree community data from a twice-logged Bornean forest to assess the contributions of different environmental variables in governing the spatial arrangement of logged forest tree diversity.

Over the past twenty years, it has emerged that lianas (woody-vines) likely play a crucial role in delaying the recovery of disturbed forests, including following selective logging (Marshall et al., 2020; Schnitzer, 2018). Although prevalent across tropical forests globally (Schnitzer & Bongers, 2011), prolific liana growth is one of the most conspicuous features of disturbed tropical forests (Chandler, van der Heijden, Boyd, & Foody, 2021; Magrach et al., 2016). Negatively affecting host tree growth, survival and reproduction, lianas have the propensity to significantly alter forest composition, recovery, and dynamics (Marshall et al., 2020). I address this idea in Chapter 5. Combining tree community data with freely available tree functional trait data and local measures of liana infestation, I tested the hypothesis that increased liana infestation following logging in Borneo alters the functional composition of tree communities, with implications for forest recovery.

1.6 Maintenance of tropical diversity

Critical to the recovery and conservation of tropical forests is understanding the mechanisms that structure and maintain their imperilled diversity (Caughlin et al., 2014; Krishnadas, Bagchi, Sridhara, & Comita, 2018; Pillay, Hua, Loiselle, Bernard, & Fletcher, 2018). For example, understanding how diversity enhancing mechanisms can be impeded by forest fragmentation (Viswanathan, Ghazoul, Lewis, Honwad, & Bagchi, 2020) and edge effects (Krishnadas et al., 2018), is vital in gauging whether remaining forests can act as long-term reservoirs of biodiversity.

In order to maintain hyper-diversity, ecological theory dictates that coexisting species must be able to share resources in order to avoid the exclusion of less competitive species. However, in tropical forests, ecologists have previously struggled to explain how the limited number of resources required by plants (light, water, nutrients, and space) can be sufficiently partitioned to support the extraordinary number of recorded species (Coley & Kursar, 2014). The search for an alternative explanation as to why so many species occur in tropical forests has highlighted the importance of species specific natural enemies in facilitating compensatory mechanisms (Coley & Kursar, 2014; Terborgh, 2012). Referring to a diverse array of insects, fungi, and vertebrate herbivores (Bell, Freckleton, & Lewis, 2006; Jia et al., 2020; Mangan et al., 2010), natural enemies can account for significant proportions of seed and young seedling mortality (Granados, Brodie, Bernard, & O'Brien, 2017; P. J. Williams, Ong, Brodie, & Luskin, 2021). Such mortality is greatest at high conspecific densities beneath parent trees, promoting the recruitment of locally rare species and preventing competitive dominance of a single species (Connell, 1971; Janzen, 1970).

Diversity enhancing mechanisms have been reported in many tropical forests globally and are now widely considered the most plausible explanation for maintaining tropical diversity. However, recent modelling approaches have questioned whether established mechanisms can realistically maintain diversity (reviewed in Chapter 3; Cannon et al. 2021), with important implications for how future studies approach questions of how tropical diversity is maintained. Moreover, many previous studies do not attribute observed density-dependent mortality to a particular natural enemy, preventing inferences of how forest degradation may impact the maintenance of diversity. Fungal and plant pathogens are largely considered the most important of natural enemies facilitating diversity enhancement (Mangan et al., 2010). However, this knowledge is assumed for many tropical forests and regions, with evidence of the role of fungal pathogens in maintaining tropical plant diversity derived from a limited number of Neotropical studies (Chapter 2; Cannon et al. 2020). In Chapter 2, I test, for the first time, the role of fungal pathogens in mediating tree species density-dependent mortality in a mast fruiting forest in Borneo.

1.7 Thesis aims and rationale

The main aim of this thesis is to improve our understanding of the dynamics and resulting diversity patterns of the diverse tree communities of Borneo's selectively logged forests. I begin by conducting a manipulative shadehouse experiment to quantify the contributions of a specific natural enemy – fungal pathogens – in driving diversity enhancement of tropical trees on Borneo. I then review previous approaches to explaining tropical diversity and the advances made by recent modelling to suggest a new direction for studies testing the effectiveness of coexistence mechanisms. Finally, using field data, I examine how selective logging influences Bornean tree communities, assessing the impacts of logging operations on the spatial arrangement of tree diversity, and the interactions between tree community composition and the altered liana loads characteristic of logged forests across the tropics.

Chapter 2 – Limited contributions of plant pathogens to density-dependent seedling mortality of mast fruiting Bornean trees

Plant pathogens are suggested to be influential drivers of diversity maintenance in tropical forests by facilitating strong density-dependent mortality of seeds and young trees at high conspecific densities. However, such knowledge is derived from only a handful of manipulative experiments, predominantly in Neotropical forests. Thus, our understanding of the role of plant pathogens in maintaining diversity in other tropical regions and forest types is distinctly lacking, including the species rich mast fruiting forests of Southeast Asia. Using a manipulative shadehouse experiment in Malaysian Borneo, the main objectives of this chapter were: 1) to test whether fungal pathogens mediate density-dependent seedling mortality in a range of dominant tree species, and 2) determine the role of fungal pathogens in maintaining the diversity of this globally important and relatively understudied forest type.

Chapter 3 – Asking the wrong question in explaining tropical diversity (short review)

In search of an explanation for the extraordinary diversity of tropical forests, many studies have demonstrated the potential for diversity enhancement via the presence of specific mechanisms. However, whether such mechanisms are capable of maintaining the number of species observed in tropical forests is partly dependent on how we ask the question of what maintains diversity. Within this chapter I aim to: 1) review recent modelling advances that suggest established mechanisms posited to maintain the diversity of tropical forests globally are ineffective when incorporating variation between species, and 2) describe the narrow conditions under which mechanisms do maintain diversity and suggest a shift in how future research should approach testing the effectiveness of diversity enhancing mechanisms.

Chapter 4 – Local drivers of ß-diversity in multiple life stages of tropical trees following selective logging

Selective logging is the most prevalent form of forest degradation effecting imperilled tropical diversity. High spatial turnover of tree communities has been detected decades after selective logging operations. The intensity of selective logging and the severity of its associated disturbances varies substantially over small spatial scales. The resulting small-scale mosaic of logging disturbances is posited to explain the altered spatial arrangement of tropical tree communities. However, no study has assessed the contributions of different environmental drivers and spatial distance in driving patterns of species turnover following logging, nor how these patterns differ between the different life stages of trees. The main objectives of this chapter were to: 1) assess patterns of community turnover (beta-diversity) across tree life stages over a decade after selective logging operations, and 2) assess the importance of specific environmental variables in governing the spatial arrangement of logged forest tree diversity.

Chapter 5 – Patterns of tree species trait similarity along liana infestation gradients in a selectively logged tropical forest

A key characteristic of selectively logged and other degraded tropical forests is the proliferation of lianas (woody-vines). Lianas can alter forest tree composition by exerting severe and unequal effects on host tree species and their functional traits. However, we do not know whether increased liana infestation following logging operations relate to the functional simplification of tree communities. This chapter utilises freely available trait data in combination with variation in tree community composition and liana infestation from a selectively logged forest in Borneo, to determine: 1) whether tree communities across life stages exhibit trait convergence or divergence following selective logging, and 2) whether such variation in tree community trait similarity relates to variation along intensified gradients of logged-forest liana infestation.

CHAPTER 2

LIMITED CONTRIBUTIONS OF FUNGAL PATHOGENS TO DENSITY-DEPENDENT SEEDLING MORTALITY OF MAST FRUITING BORNEAN TREES

This chapter has been published as:

Cannon, P. G., O’Brien, M. J., Yusah, K. M., Edwards, D. P., & Freckleton, R.P. (2020). Limited contributions of plant pathogens to density-dependent seedling mortality of mast fruiting Bornean trees. *Ecology and Evolution*, 10(23), 13154–13316.

2.1 Abstract

Fungal pathogens are implicated in driving tropical plant diversity by facilitating strong, negative density-dependent mortality of conspecific seedlings (C-NDD). Assessment of the role of fungal pathogens in mediating coexistence derives from relatively few tree species and predominantly the Neotropics, limiting our understanding of their role in maintaining hyper-diversity in many tropical forests. A key question is whether fungal pathogen-mediated C-NDD seedling mortality is ubiquitous across diverse plant communities. Using a manipulative shadehouse experiment, we tested the role of fungal pathogens in mediating C-NDD seedling mortality of eight mast fruiting Bornean trees, typical of the species rich forests of Southeast Asia. We demonstrate species-specific responses of seedlings to fungicide and density treatments, generating weak negative density-dependent mortality. Overall seedling mortality was low and likely insufficient to promote overall community diversity. Although conducted in the same way as previous studies, we find little evidence that fungal pathogens play a substantial role in determining patterns of seedling mortality in a Southeast Asian mast fruiting forest,

questioning our understanding of how Janzen-Connell mechanisms structure the plant communities of this globally important forest type.

2.2 Introduction

Tropical regions contain ~53,000 tree species (Slik et al., 2015), with as many as 1,200 species coexisting in just 52 hectares of moist tropical forest (Lee et al., 2002). Understanding the mechanisms that maintain such extraordinary plant diversity remains a central question in ecology. After nearly 50 years of study, the Janzen-Connell (JC) hypothesis (Connell, 1971; Janzen, 1970) remains the most widely posited explanation for preventing competitive exclusion. Central to JC-theory are the effects of conspecific negative density-dependence (C-NDD), whereby high densities of conspecific recruits are more likely to succumb to specialist natural enemies, such as insect herbivores (Jia et al., 2020), and soil and fungal pathogens (Bagchi et al., 2010; Mangan et al., 2010). Evidence of C-NDD has been reported globally (Carson, Anderson, Leigh, & Schnitzer, 2008; Comita et al., 2014), with a variety of observational, experimental, and modelling approaches linking pathogen-induced C-NDD to the enhancement of plant community diversity (Bagchi et al., 2011; Harms, Wright, Calderón, Hernández, & Herre, 2000; Krishnadas et al., 2018). Density dependence, therefore, represents an important regulator in the maintenance and structuring of hyper-diverse plant communities.

Although seed predators and herbivores alter seedling recruitment and plant community composition in both the New- and Old-World (Granados et al., 2017; Villar et al., 2020), whether their effects are sufficient to drive C-NDD remains unclear (Hautier et al., 2010; Kurten & Carson, 2015). In contrast, host-specific impacts of fungal pathogens responsible for driving C-NDD are well-documented (Augspurger & Kelly, 1984; Freckleton & Lewis, 2006), with fungal pathogens the most important seedling enemies (Sarmiento et al., 2017). However studies demonstrating fungal contributions to the Janzen-Connell mechanism are limited to a small number of tree species and systems, with pervasive Neotropical bias (Bagchi et al., 2011; Comita et al., 2014). Examination of the C-NDD literature identified 17 studies manipulating seed or seedling densities of tropical trees, of which only five experimentally tested the impacts of fungal pathogens on just 12 species, with the majority of studies focusing on the Neotropics (65% -Table A.2). Most notably, representation of fungal-induced C-NDD is dominated by a single common Neotropical species–*Pleradenophora longicuspis* (Standl.) Esser.– demonstrating intense overcompensating density-dependence and causing up to 100% seedling mortality (Bagchi et al., 2010; Bell et al., 2006; Swinfield, Lewis, Bagchi, & Freckleton, 2012).

The strength and presence of reported C-NDD varies considerably between studies (Bagchi et al., 2011; Harms et al., 2000). Recent work has highlighted the pervasive use and mismanagement of error-prone predictors when quantifying C-NDD (Detto, Visser, Wright, & Pacala, 2019), resulting in the erroneous detection and overestimation of the strength of density dependence in many studies. Observational studies are particularly prone to such errors in comparison to manipulative experiments, highlighting the importance of considering methodological approach in addition to ecological context when examining evidence of C-NDD. Bagchi et al. (2014) for example used a design that explicitly accounts for census error, a known bias in measurement of NDD (Freckleton & Lewis, 2006), when estimating forest-wide impacts.

Notwithstanding methodological issues, variation in the strength of C-NDD likely reflects differences amongst species (Carson et al., 2008; Comita et al., 2014), with negative effects of conspecific density posited to more strongly influence rare rather than locally common species (D. J. Johnson, Beaulieu, Bever, & Clay, 2012; Mangan et al., 2010). Species life-history strategies also affect the strength of C-NDD (Jia et al., 2020), with trade-offs between axes of growth and defence, at least partly, governing variation in species susceptibility of pathogens (Milici, Dalui, Mickley, & Bagchi, 2020; Spear, Coley, & Kursar, 2015), potentially influencing seedling recruitment patterns. Shade-tolerant species are more susceptible to fungal pathogens (Kobe & Vriesendorp, 2011; McCarthy-Neumann & Kobe, 2008), particularly in fragmented forests (Krishnadas et al., 2018). Interactions between abiotic gradients and species life-histories may also work to maintain and enhance plant diversity via C-NDD and other mechanisms, including by heightening niche partitioning along light gradients (McCarthy-Neumann & Kobe, 2008) and increasing conspecific seedling mortality under higher precipitation (Milici et al., 2020). It is, therefore, important that future studies investigate a wider suite of species (Bagchi et al., 2010; Bell et al., 2006; Carson et al., 2008; Comita et al., 2014; McCarthy-Neumann & Kobe, 2008; Pillay et al., 2018; Segnitz, Russo, Davies, & Peay, 2020) encompassing variation in species life-history strategies and local abundance, particularly in tropical forests where the majority of species are locally rare.

Forests of the Indo-pacific region, in particular Southeast Asia, are amongst the most species rich on Earth (Sullivan et al., 2017). Dominated by trees of the *Dipterocarpaceae* (Saner, Loh, Ong, & Hector, 2012), reproduction occurs in supra-annual community-wide mast fruiting events, with hundreds of tree species fruiting synchronously (Curran & Leighton, 2000; Janzen, 2004). Such events are preceded by years of limited or no fruit fall, and are suggested to have evolved to satiate a reduced number of seed predators (Curran & Leighton, 2000; Visser et al., 2011). Masting-induced predator satiation decreases mortality in areas of high density, directly undermining C-NDD. In addition, although common seed predators such as bearded pig (*Sus barbatus*) are a significant source of seed and seedling mortality within mast-fruiting forests (Granados et al., 2017), such predation pressure is not host-specific and consequently is incapable of driving C-NDD (Freckleton & Lewis, 2006). It is, therefore, hypothesised that determinants of the Janzen-Connell mechanism, including density-dependence, may be substantially weaker or entirely absent amongst mast-fruiting species (Bagchi et al., 2011; Comita et al., 2014; Janzen, 1970). In contrast, the reservoir of host-specific fungal pathogens will be greatest in soils under adult trees and greater still in areas of high adult density (Liang et al., 2016). During mast events these areas will also experience the greatest densities of seeds and young seedlings with the potential to exert strong NDD mortality of conspecific seedlings.

Despite comprising ~48% of tropical tree species (Slik et al., 2015), there are just three studies manipulating seed or seedling densities from the Asian tropics (Table A.2). Only one of these studies investigated the impacts of fungal pathogens (Krishnadas & Comita, 2018), finding significant pathogen-induced mortality of three of the four focal species but that these effects were independent of density. The two remaining studies from tropical Asia did not experimentally test the contributions of different natural enemies for one (Lott, Harrington, Irvine, & McIntyre, 1995) or two (Takeuchi & Nakashizuka, 2007) species, respectively. Fungal pathogens are often posited to represent a hugely influential demographic force despite limited evidence from many tropical forests and with fungal pathogen driven seedling mortality varying widely between species (Bell et al., 2006; Gripenberg et al., 2014). Determining whether C-NDD is present across species, communities, and other forest systems remains a key unanswered question.

Although more numerous than experimental approaches, observational studies examining C-NDD in Asian tropical forests demonstrate contrasting evidence for C-NDD. Some provide support for C-NDD (Bagchi et al., 2011; Pillay et al., 2018), while others have found limited evidence of density-dependent effects (Itoh, Yamakura, Ogino, & Lee, 1995; Maycock, Thewlis, Ghazoul, Nilus, & Burslem, 2005), or only at specific life-stages (Blundell & Peart, 2004). Additionally, in masting systems, many studies utilise partial fruiting episodes (Harms et al., 2000; Maycock et al., 2005) when near-complete seed and seedling mortality is likely unrepresentative of intense masting events when the vast majority of recruitment occurs (Curran & Leighton, 2000). To date, only a single study has experimentally tested for mechanisms underlying C-NDD during an intense masting event (Pillay et al., 2018). Focusing on a single locally common species, Pillay *et al.*, 2018 attributed a proportion of density-dependent mortality to vertebrate seed predators and seedlings herbivores. Importantly, contributions of fungal pathogens to C-NDD within mast fruiting forests and across multiple species have yet to be quantified.

We describe a manipulative shadehouse experiment using seedlings of eight species, from a lowland tropical forest in Sabah, Malaysian Borneo. During the 2019 mast fruiting event, we artificially manipulated seedling planting density and exclude fungal pathogens via the application of broad-spectrum fungicides to assess fungal pathogen-induced density-dependent mortality across the seed-to-seedling transition. We test the predictions that: 1) despite the hypothesised influence of masting on the Janzen-Connell mechanism, seedlings will express C-NDD mortality across species (Comita et al., 2014), finding greater mortality of individuals planted at higher density; 2) C-NDD is driven by fungal pathogens, with limited mortality of individuals planted at either density when receiving fungicide treatments; and 3) the strength of fungal-induced density-dependence varies widely between species (Freckleton & Lewis, 2006), with rare species, comprising fewer stems in the surrounding forest, experiencing stronger C-NDD mortality (McCarthy-Neumann & Kobe, 2008). Our aim is to determine the role of fungal pathogens in mediating C-NDD across our focal species, giving insight to their role in maintaining and structuring the hyper-diverse plant communities of a globally important forest type (D. P. Edwards & Laurance, 2013; Sullivan et al., 2017).

2.3 Methods and Materials

2.31 Study area

The experiment was conducted from the 31st August to 8th November 2019 in a single shadehouse at the Malua Field Station (MFS), Sabah, Malaysian Borneo (N05°05′20″ E117°38′32″; 102 m a.s.l.). Mean (SD) monthly precipitation at the site (averaged between August 2008 and December 2019) was 266.8 (105.7) mm. Across the duration of the study, mean (SD) monthly precipitation was 219.4 (71.3) mm (141.2 mm September, 280.9 mm October and 236.1 mm November), with mean ambient air temperature ranging from 21.8 °C – 35.7 °C. Climatic data was recorded at the MFS weather station (available at; http://www.searrp.org/scientists/available-data/). Shadehouse construction consisted of two sheets of rain permeable 70% shadecloth, creating a light environment with a mean (SD) of 9.34% (1.01) of full daylight photosynthetically active radiation (PAR), with means from five measurement locations across the shadehouse varying between 3.40% and 20.13%. Variability in the light environment was recorded using a quantum sensor (QS5 sensors; Delta-T Devices, Burwell, Cambridge, UK), comparing simultaneous shadehouse readings to those from an unobstructed forest clearing. Ambient air temperature within the nursery averaged 24.8 °C (0.07), with mean relative humidity 99.43% (0.11).

We collected seeds from mature individuals of eight lowland tree species during the 2019 community-wide mast fruiting event, including six species of *Dipterocarpaceae*, one *Malvaceae* and one *Leguminosae* (Table A.1, nomenclature standardised to that of *The Plant List*, V 1.1). Together, the selected species represent 2.32% of adult stems within neighbouring primary forest (data from the 50-Hectare Plot Project Danum Valley, part of the CTFS-ForestGEO network (Anderson-Teixeira et al., 2015). Seeds of six species were collected from the surrounding logged forests of the 1 million ha Yayasan Sabah Forest Management Area (YSFMA), including the Ulu Segama, Taliwas and Malua Forest Reserves. Additionally, seeds of two species (*Scaphium macropodum*, Miq. and *Shorea pauciflora*, King) were collected from the nearby Danum Valley Conservation Area (DVCA). The DVCA is an 43,800 ha area of old-growth forest, predominantly of *Dipterocarpaceae* (Saner et al., 2012). Forests of the YSFMA were selectively logged during the 1970's and 1980's, with much re-logged 1999-2007. The majority of marketable hardwood stems over 40 cm d.b.h were removed, with extractions of ~113 m^3 ha^{-1} and ~144 m^3 ha^{-1} in once- and twice-logged forest, respectively (Fisher, Edwards, Giam, & Wilcove, 2011).

2.32 Fungal exclusion and density-dependence experiment

During the peak of the 2019 mast fruiting event (23rd – 27th August 2019), we collected the topmost *c.* 15 cm of soil and humic matter from 12 once logged sites surrounding the Malua Field Station. All sites were located at least 50 m from the forest edge, with obvious signs of prior seed fall preceding soil collection in the majority of sites. Soil was sieved by hand, removing larger debris, roots and seeds. Once processed, 364 circular pots (20 cm D x 20 cm H; 6.1 l V; 0.342 m^2) were filled with *c*. 15 cm depth of unmixed soil, with each soil site replicated across treatments and species.

Seeds were germinated in optimal conditions using wet burlap sacks. Once germinated, viable seeds were randomly selected and planted in a uniform pattern at either a high or low density. Ten seeds were planted in High-density pots and a single seed in Low-density pots, corresponding to densities of 318 seeds m^{-2} and 31.8 seeds m^{-2}, respectively. High-density treatments were, by design, significantly higher than recorded in local seedling banks, with seed densities under Dipterocarp trees during the 2019 fruiting ranging from 1 to 183 m^{-2} (O'Brien, Unpublished data). This was done to ensure that any effects of density (particularly over-compensating density dependence) would be clearly evident or, conversely, that weak or undetectable effects of density would clearly indicate that such effects are ecologically unimportant.

Pots were arranged in blocks of four, at least 15 cm apart, with each pot receiving one of four treatment combinations: (1) High-density/non-fungicide, (2) High-density/fungicide, (3) Low-density/non-fungicide and (4) Low-density/fungicide. Treatments were randomly assigned to pots with each treatment represented in each block (following Bell, Freckleton and Lewis, 2006).

Within fungicide-treated pots, seedlings were sprayed with a combination of Amotan 22.8SC®, a selective methalaxyl-based systemic fungicide (Advansia Ltd, Malaysia, active ingredient: azoxystrobin), and Kencozeb M45®, a broad-spectrum di-thiocarbamate non-systemic fungicide (Kenso corporation, Selangor, Malaysia, active ingredient: mancozeb). Active ingredients of both fungicides are frequently used to test fungal contributions to seedling mortality (Krishnadas et al., 2018; Szefer, Molem, Sau, & Novotny, 2020; Xu, Wang, & Yu, 2015), providing protection against plant pathogenic fungi and oomycetes, with low toxicity to other soil biota and with minimal inhibitory effects on arbuscular mycorrhizal associations with tropical seedlings (Gripenberg et al., 2014). Fungicides were applied to seedling leaves, or to the surface of germinated seeds prior to leaf development, once every 10 days for 60 days (6 treatments) at the recommended concentration (Amotan22.8SC®; 0.05 mL m^{-2}, Kencozeb M45®; 0.11 g m^{-2}) using a hand mister, with 50 mL of solution per pot. The same volume of water was applied to non-treated pots as a control. To prevent accidental treatment of control pots, a spray guard was used when applying fungicide. The number of seedling deaths in each pot was recorded every two days for the first month of the experiment, every four days for the second month, and once every 30 days thereafter. Any additional, newly germinated seedings were removed during the first two months of censusing.

After 60 days, we measured the height and diameter at soil of all remaining seedlings. Fungal pathogens are responsible for many damping-off diseases, causing foliar damage and mortality in young seedlings (Cohen & Coffey, 1986). To quantify fungal damage to leaves, we also recorded a measure of leaf damage, using an established four-point ordinal scale (0 = no damage, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%).

2.33 Statistical analysis

We analysed the proportion of planted seedlings surviving after 60 days using hierarchical linear models, assuming a binomial error distribution and logit-link function. The model included seedling density, fungicide treatment, and the interaction between density and fungicide as fixed factors, owing to the fully balanced factorial experimental design. We included pot identity as a random intercept to account for spatial variation between replicates, and random uncorrelated slopes for fungus and density per species to account for interspecific variation in seedling responses to treatments. Model parameters were estimated within a hierarchical Bayesian framework using R package *brms* (Bürkner, 2017), sampling the model posterior using the NUTS algorithm within Stan software (version 2.17.050). The framework uses statistical shrinkage to produce robust estimates of species coefficients. Models converged without divergent transitions.

We extracted species-level regression coefficients of density and fungicide effects from seedling survival models to determine the strength of C-NDD effects on species survival. We use a simple ordinary least squares model to analyse the relationship between the strength of C-NDD effects and species' relative abundances from sample plots in the unlogged 50-Hectare Plot Project, Danum Valley (Anderson-Teixeira et al., 2015). We chose to use community data from an undisturbed site, rather than surrounding sites that provided seeds and soils, as this more accurately reflects true species' abundances prior to logging activity. Note that these density data are independent of the experimental results.

We used ordinary least squares models (LM) to test the effects of density and fungicide treatments on seedling diameter, height, and leaf damage score. Data were modelled both collectively for all seedlings and for each species separately, including species, seedling density, fungicide treatment, and the interaction between density and fungicide as fixed factors. The level of independent replication was the pot. Analyses were carried out using R v. 3.5.2. statistical software (R Core Team, 2020).

2.4 Results

2.41 Seedling survival

Overall, mortality during the course of the experiment was low (Fig 2.1.). Of the original 990 seedlings not exposed to fungicide, 920 survived (92.9%), whereas of the 990 fungicide treated seedlings, 943 survived (95.3%). Planting density and fungicide treatment all affected seedling mortality at both the species and overall community-level, with greater survival of seedlings planted at low density and receiving fungicide treatments (Fig 2.2.). The effects of fungicide application and planting density were present for all species. However, effects were relatively weak across species, with Bayesian CI for parameter estimates of fungicide application and planting density intersecting 0 for all species (Fig 2.3 and Table A3). Variation in the strength of treatment effects amongst species correspond to variation in species daily death rate (Fig 2.2.), with *S. pauciflora* exhibiting the greatest difference between high density fungicide treatments and having the greatest parameter estimate of fungicide application (Fig 2.3.).

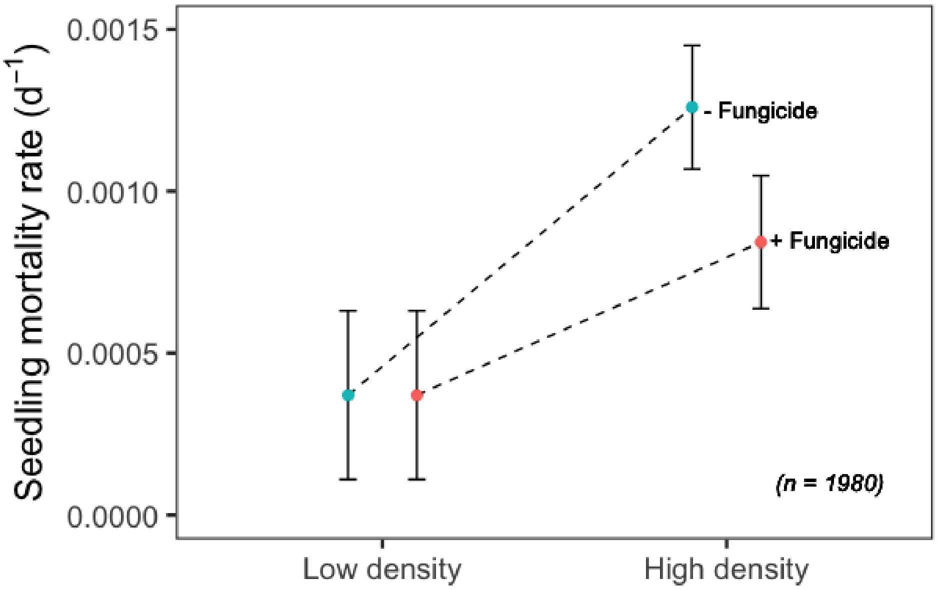

Figure 2. 1. Daily seedling death rate between pots planted at high and low density and treated with (+) or without (-) fungicide aggregated across all 8 species. Data points represent means of 90 replicates (*n* = 900 individuals for each high-density treatment, and *n* = 90 for low-density treatment) and error bars denote standard error.

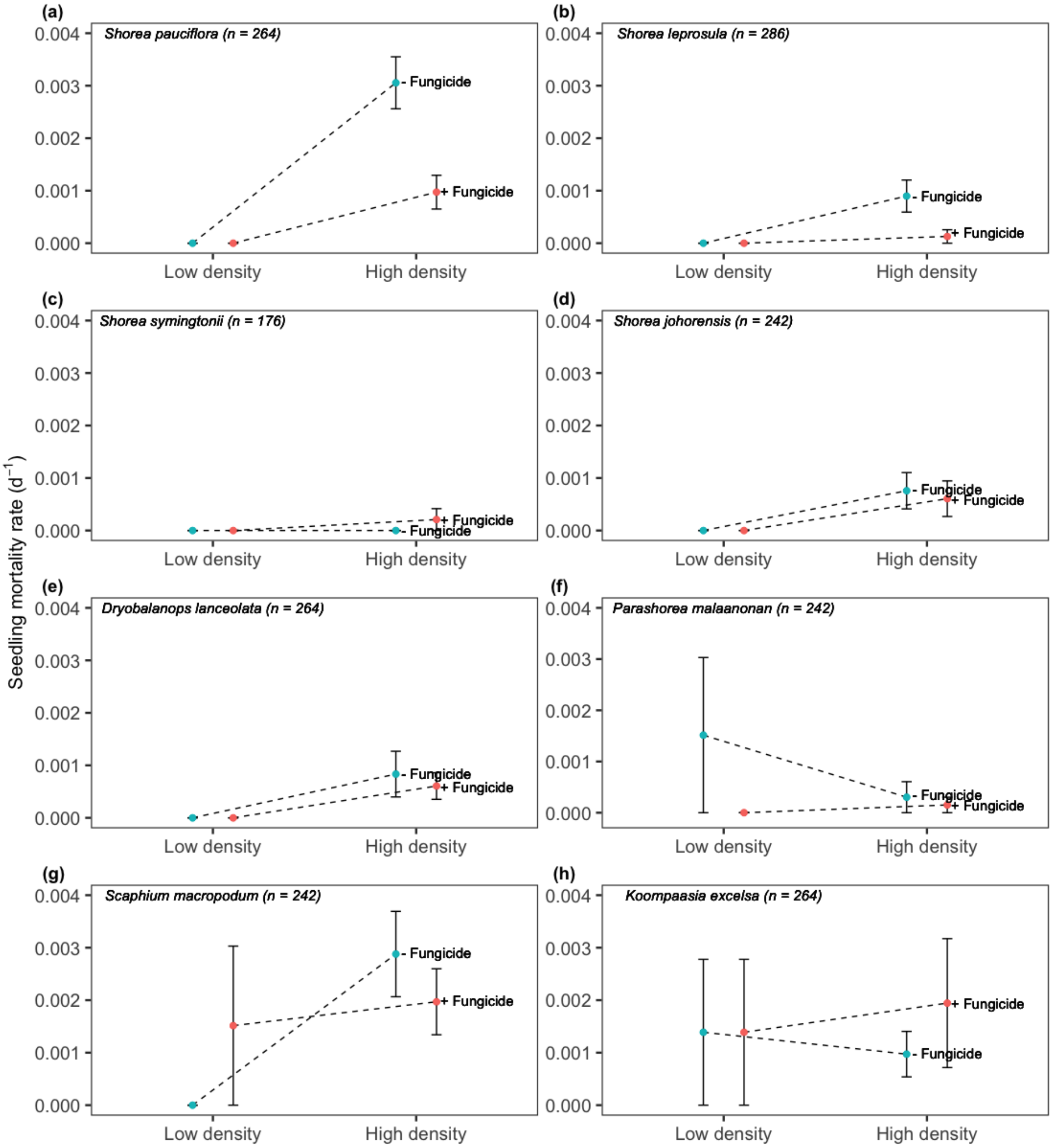

Figure 2. 2. Daily seedling death rate between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means of 8-13 replicates (*n* = 80-130 individuals for each high-density treatment, and *n* = 8-13 for low-density treatment) and error bars denote standard error.

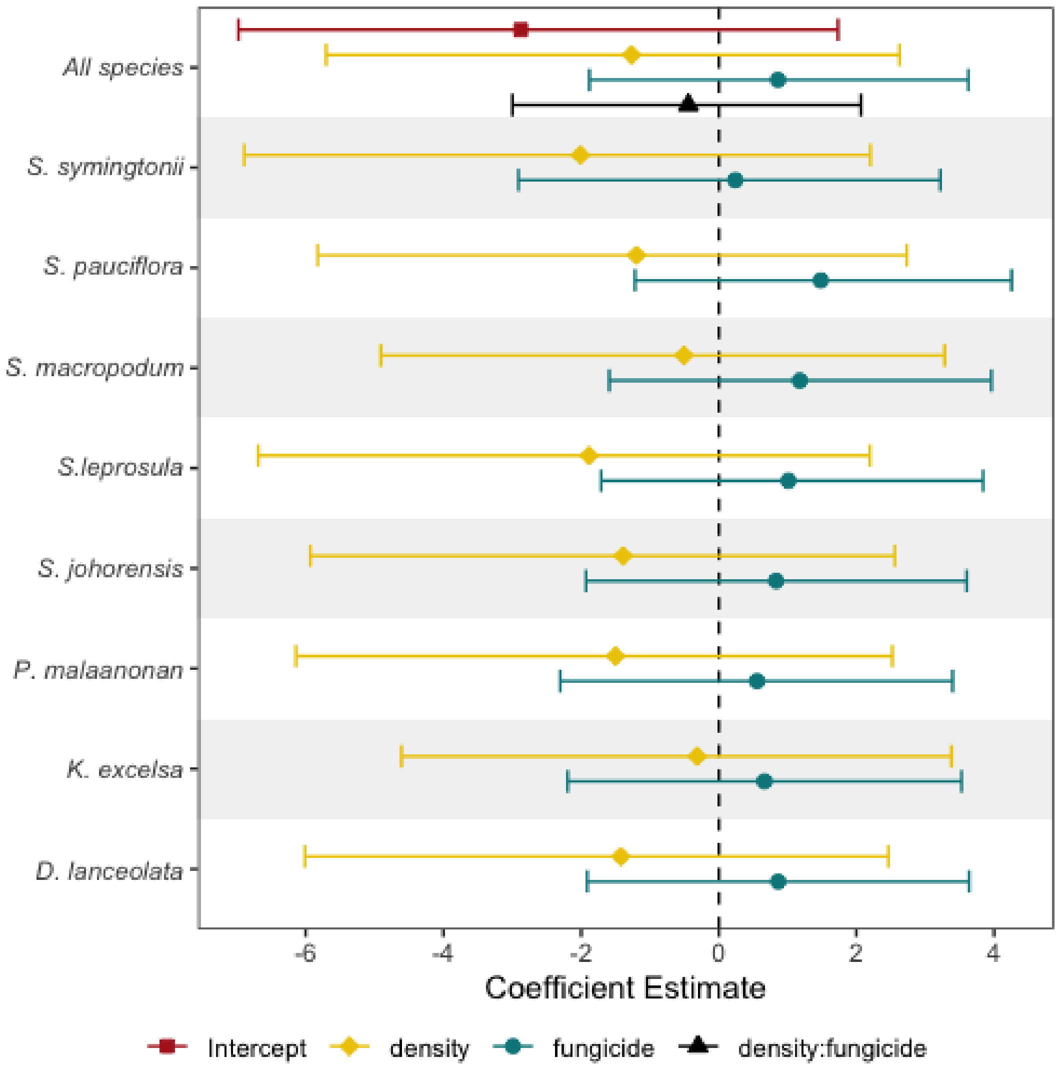

Figure 2. 3. Overall and species-level effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on seedling mortality for eight lowland tree species. Points represent the difference between the means of treatments and controls (i.e., the difference between high and low density, and fungicide and controls). Bars represent 95% Bayesian credible intervals of parameter estimates. Random uncorrelated slopes for fungus and density were estimated per species.

2.42 Relationships between local tree abundance and the strength of C-NDD effects

The strength of species-level planting density effects on seedling survival was positively correlated with local adult abundances (*F* value = 8.01, *p* = 0.029, d.f. = 1,7), with species exhibiting stronger density effects being more abundant in the surrounding forests of Danum Valley (Fig 2.4a). In comparison, the strength of fungicide application effects on seedling survival were uncorrelated with local adult abundances (Fig. 3b; *F* value = 0.41, *p* = 0.546, d.f. = 1,7).

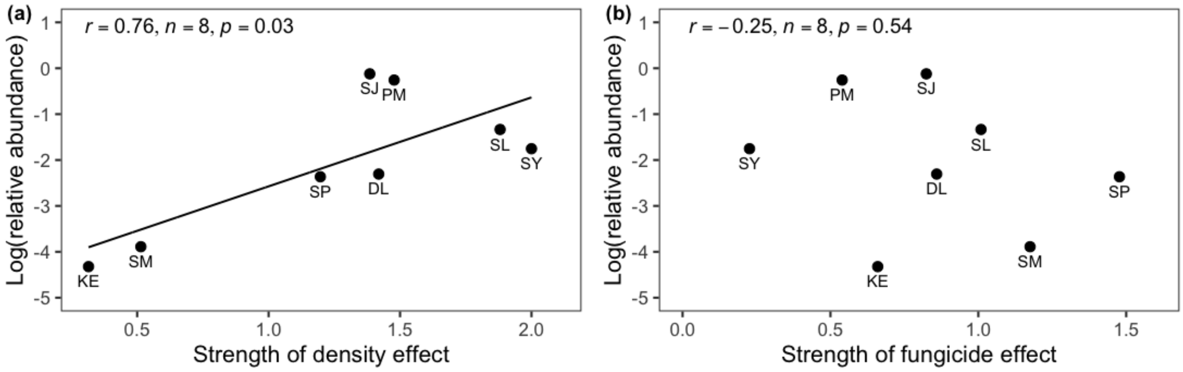

Figure 2. 4. Relationships of variation in the strength of (a) planting density effects and (b) fungicide application effects on seedling survival with local adult tree abundance (> 10 cm d.b.h). The strength of treatment effects represent regression coefficients estimated using generalized linear mixed models with binomial distribution and log-link function within a hierarchical Bayesian framework. Pearson correlation coefficients (*r*) and *p*-values (*p*) given in text.

2.43 Seedling height, stem diameter, and leaf damage score

Mean seedling height, stem diameter, and leaf damage score, across all seedlings, were affected by species identity but not density and fungicide treatment (Table A4). When modelling species separately, only four of the eight species were affected by either density or fungicide treatments (*S. symingtonii, S. leprosula, D. lanceolata* and *K. excelsa*).

Planting density, fungicide application and the interaction between the two, each affected seedling height of a single species, with significantly taller individuals grown in low density pots or those treated with fungicide (Fig A.1, Table A5). Seedling stem diameter was also affected by fungicide treatment and density in three of the eight species (Fig A2). *S. symintonii* was the only species to be affected by both fungicide and density treatments, with greater mean stem diameter of seedlings planted at low density and sprayed with fungicide (Table A6). Leaf damage score of seedlings was affected by fungicide application but not density, with two species exhibiting significantly greater leaf damage scores when treated with fungicide (Fig A3, Table A7). Additionally, only a single species exhibited interactive effects between treatments, with the effects of fungicide application on *S. leprosula* seedling height (*F* value = 22.4, $p < 0.001$, d.f. = 1) and leaf damage score (*F* value = 12.59, $p < 0.001$, d.f. = 1) varying with planting density.

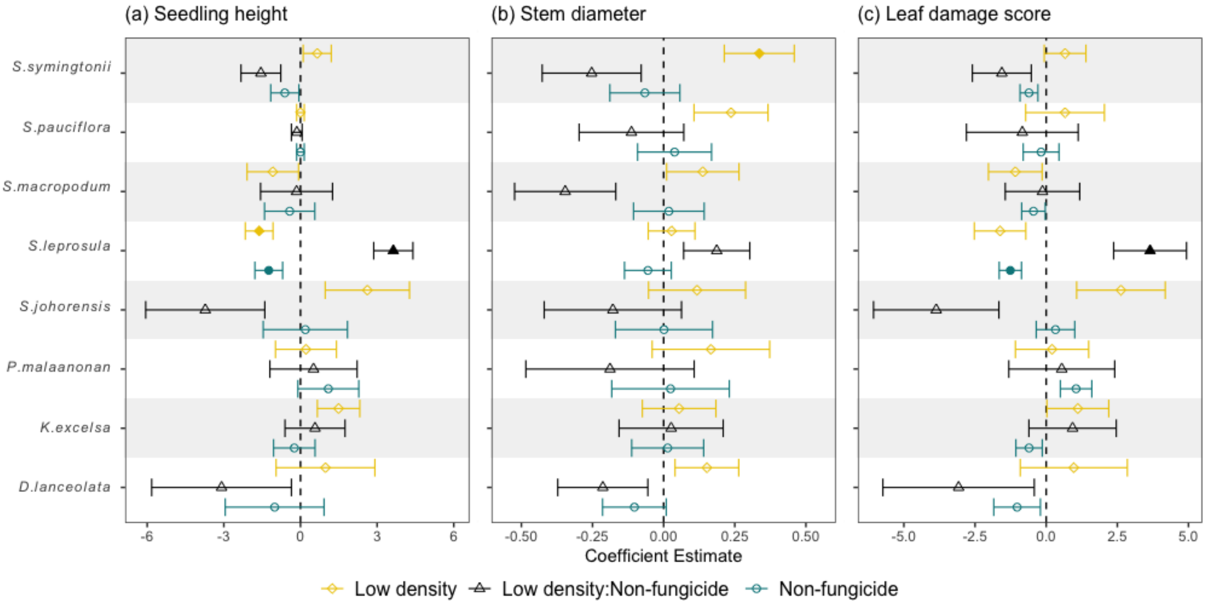

Figure 2. 5. Model coefficients of the effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on; (a) mean seedling height, (b) stem diameter, and (c) leaf damage score for eight lowland tree species. Model coefficients estimated using linear and analysis of variance models. Filled points represent significant terms ($p < 0.05$) and error bars represent ± 1 SE.

2.5 Discussion

Assessing the contributions of plant pathogens to C-NDD across species and systems represents a key step in understanding their role in maintaining and structuring plant communities (Bagchi et al., 2010; Bell et al., 2006; Comita et al., 2014; Swinfield et al., 2012). Our results demonstrate weak overall C-NDD (Fig 2.1.), with varied but limited effects of fungal exclusion and planting density on seedling mortality across species. Manipulating both seedling density and pathogen infection, our experiment represents one of only a handful of studies assessing Janzen-Connell mechanisms within Southeast Asia's mast-fruiting forests (Blundell & Peart, 2004; Comita et al., 2014; Kurten & Carson, 2015) and the first of such studies to provide direct evidence of the role of fungal pathogens in mediating C-NDD. Our findings indicate that, alone, fungal pathogens are likely insufficient to elicit significant diversifying effects on the mortality of seedlings. Despite strong evidence of plant pathogens as a powerful demographic force governing seedling mortality in Neotropical forests (Bell et al., 2006; Sarmiento et al., 2017), this pattern is not ubiquitous, at least for our focal species, and appears comparatively less important in this mast-fruiting system.

Previous studies of C-NDD seedling mortality are rare in the Asian tropics, leading to the reporting of limited differences in the strength of density-dependence between tropical regions (Carson et al., 2008; Comita et al., 2014). Our results are consistent with predictions that density-dependent effects are substantially weaker amongst mast-fruiting systems (Bagchi et al., 2011; Comita et al., 2014; Janzen, 1970), and starkly contrast with the consistent, strong pathogen-induced C-NDD seedling mortality observed in Neotropical studies (Bagchi et al., 2010; Bell et al., 2006; Swinfield et al., 2012). Although strong pathogen induced CNDD is not reported ubiquitously across Neotropical species (Gripenberg et al., 2014), it seems likely that ecological differences between masting and annually fruiting systems result in variation in the strength of C-NDD between regions, at least in terms of the contributions of fungal pathogens.

Recent studies have attributed variation in the strength of C-NDD to differences between species and their associated traits (Jia et al., 2020; Kobe & Vriesendorp, 2011). Different mycorrhizal associations vary in their ability to protect hosts from soil pathogens, with ectomycorrhizal (ECM) associations potentially reducing susceptibility of seedlings to fungal pathogens via positive plant-soil feedbacks (PSFs), including the facilitation of nutrients and providing direct protection from antagonistic pathogens (Laliberté, Lambers, Burgess, & Wright, 2015). Temperate studies from the New- and Old-World have found contrasting effects of mycorrhizal associations on the strength of C-NDD (Bennett et al., 2017; Jia et al., 2020), with ECM-associated species experiencing greater negative effects of C-NDD in comparison to AM species in a temperate Asian forest but the reverse across North American forests.

In the tropics, ECM species experience positive plant-soil feedback on seedling growth in Malaysian Borneo (Segnitz et al., 2020). We would expect to find strong C-NDD under high-density treatments, thus, our findings of limited density-dependent seedling mortality across all six of our focal ECM species at first appear consistent with potential positive PSFs from ECM associations. However, the strength of C-NDD was similarly weak across species, irrespective of mycorrhizal association suggesting that, at least for our focal species, mycorrhizal association did not dramatically effect seedling mortality. This dichotomy is likely due to mycorrhizal associations commonly being established later than the seedling stage and, thus ECM fungi are unable to convey recruitment advantages until much later in development (Jia et al., 2020). As tropical recruitment is highly constrained by seedling mortality during the seed-to-seedling transition (Bell et al., 2006; Harms et al., 2000), later establishment of fungal associations would greatly limit their role in mediating the strength C-NDD, in comparison to other systems.

Ectomycorrhizal-associated species are far more prevalent in Borneo and other SE Asian forests, compared to the Neotropics, including all ~270 Bornean Dipterocarp species (M. E. Smith et al., 2013). Variation in the prevalence of different mycorrhizal associations between forest systems may partly be responsible for driving patterns of fungal-induced C-NDD. However, such mechanisms directly oppose J-C with positive PSFs reducing the capacity for species coexistence by removing 'rare species advantage'(Stump & Comita, 2018).

Contrasting most previous studies examining C-NDD via in situ field experiments (Table A2.), we manipulated seedling density in pots filled with forest soil. This method enabled us to maintain experimental densities throughout the experiment and effectively isolate the effects fungal pathogens from those of insect and vertebrate herbivores. However, pathogen densities are likely to be greatest closest to the parent trees, resulting in high mortality close to parent trees as well as at high densities. Our experimental design is incapable of differentiating between such interacting distance- and density-dependent mortality, potentially underestimating the contributions of fungal pathogens to distance-dependent seed and seedling mortality.

Natural enemies are unlikely to enhance plant community diversity unless the functional form of density-dependence is overcompensating (Freckleton & Lewis, 2006). C-NDD can be regarded as overcompensating when the number of recruits decline at higher initial densities, maximising the likelihood of replacement by heterospecifics. Although uncommon among plant communities (Freckleton & Watkinson, 2002), Bagchi *et al.* (2010) demonstrate strong overcompensating C-NDD of *P. longicuspis* seedlings, resulting in complete mortality at the highest seedling densities. In contrast, we observed weak overall mortality at very high densities, suggesting that density-dependence is unlikely to represent an overcompensating form. Our high-density treatment was much higher than typically observed in natural seedling banks. Thus, we would have expected to see extremely high mortality if density-dependence was overcompensating. Although other functional forms of C-NDD can contribute to coexistence by limiting species population sizes (Muller-Landau & Adler, 2007), the likelihood of significant diversifying effects is severely reduced and such mechanisms differ to that originally proposed by Janzen 1970 (Janzen, 1970) and Connell 1971 (Connell, 1971).

Previous studies have demonstrated that locally abundant species are less susceptible to pathogen infection, experiencing weaker C-NDD relative to locally rare species (D. J. Johnson et al., 2012; Mangan et al., 2010). The observed strength of C-NDD may thus be underestimated due to selection of locally common species with sufficient availability of seeds for experimental manipulation

(Comita et al., 2014). Instead, we find the strength of density effects on seedling survival was positively correlated with species' relative abundances, with more common species experiencing greater density effects (Fig 2.4a). Our approach avoids many of the pitfalls of previous C-NDD studies that often cause underestimation of the strength of C-NDD, particularly for more abundant species (Detto et al., 2019). Moreover, seedling mortality during the experiment was low across species, irrespective of local abundance and fungicide treatment, suggesting that the strength of C-NDD in this system potentially weak.

Although limited to species with sufficient seed availability, our focal species represent 40% of all species included in studies experimentally testing the effects of fungal pathogens on C-NDD across the tropics and is the largest set of species assessed from a single site (Table A2). Although we are reticent in suggesting our results depict community-level contributions of plant pathogens to C-NDD, we find little evidence to suggest fungal pathogens play a considerable role in determining seedling recruitment patterns across a range of masting species. Further studies are required to test the generality of our results for a greater number of species, encompassing a broader range of plant traits, and decipher the complex drivers regulating fungal-pathogen contributions to C-NDD (Jia et al., 2020).

The limited contribution of plant-pathogens to early seedling mortality measured across our species suggests that other natural enemies are, at least partly, responsible for generating mortality and structuring the community. Previous studies have repeatedly emphasised large mammalian vertebrates as important drivers of both seed and seedling mortality in the tropics (Rosin, Poulsen, Swamy, & Granados, 2017), mediating abundances and densities of young stems (Harrison et al., 2013; Kurten & Carson, 2015; Villar et al., 2020) and causing the majority of mortality (Bagchi et al., 2011; Itoh et al., 1995). For example, four studies in Malaysian Borneo attribute up to 70-86% of seed and young-seedling mortality to herbivore browsing and seed predation (Bagchi et al., 2011; Granados et al., 2017; Hautier et al., 2010; Pillay et al., 2018). Although small, host-specific herbivores can contribute to C-NDD in isolation (Hautier et al., 2010), it remains unclear whether complete herbivore communities, including generalists, are capable of promoting plant diversity, either by mediating C-NDD or by controlling populations of competitively dominant species (Kurten & Carson, 2015). Limited but host-specific fungal-induced C-NDD mortality, in addition to generalist vertebrate seedling mortality, could lead to overcompensating forms of density-dependence sufficient to enhance plant community diversity. However, comparative field studies are needed to test this prediction, manipulating pathogen abundance, planting density and vertebrate seed predation and herbivory. Such work could reveal the roles of different groups of natural enemies in collectively mediating density-dependent mortality in mast fruiting systems.

Seedlings experienced below average rainfall during the first month of the experiment. Drier conditions may have contributed to weaker recorded C-NDD, as increased moisture availability can enhance transmission of both above- and below-ground soil pathogens (Dorrance, Kleinhenz, McClure, & Tuttle, 2003; Rossi & Caffi, 2012), with reduced precipitation limiting their ability to cause early mortality (Milici et al., 2020). Swinfield et al., (2012) found increased frequency of watering resulted in significantly greater pathogen induced seedling mortality, although even the most infrequently watered seedlings experienced substantially greater mortality than observed in our study. Moreover, previous studies from our field site demonstrate similarly low mortality of young seedlings despite frequent watering, including many of our chosen species (O’Brien, Burslem, Caduff, Tay, & Hector, 2015; O’Brien, Reynolds, Ong, & Hector, 2017), suggesting that limited mortality likely reflects lower overall susceptibility of our seedling species to pathogens.

We observed an array of complex seedling growth responses to density and fungicide treatments (Fig 2.5, A1, A2 and A3), with the effects of density and fungal pathogens on seedling growth being diverse and highly species specific. However, for the majority of species, seedling mortality rates were unaffected by density-dependence in the absence of fungal pathogens, irrespective of effects on growth. This trend mirrors that of similar studies (Bagchi et al., 2010; Bell et al., 2006), suggesting that competition between conspecific seedlings is not a major contributor to early mortality in this tropical forests (Wright, 2002). However, growth advantages secured early in seedling development, potentially in response to plant pathogens, could also benefit long-term survival by enabling larger individuals to outcompete their peers for limited resources such as light and space.

By focusing on the fate of seedlings immediately following germination, our results may not represent other life stages. For example, conditions beneficial to seed germination might coincide with substantial pathogen-induced seed mortality by facilitating spread of infection. However, our treatments represent high but naturally occurring seedling densities, suggesting seed mortality attributed to fungal pathogens does not tightly limit seedling density. Furthermore, the proportion of seed mortality caused by pathogens is likely to be inconsequential given the majority of seeds are consumed by vertebrate seed predators during masting episodes (Bagchi et al., 2011; Granados et al., 2017). As with many short-term manipulative studies, we do not track seedling survival past the seed-to-seedling transition. Longer-term studies are required to test whether patterns of seedling dynamics structure adult community composition. This is particularly relevant in human-modified forests where disturbances impact individuals long after their recruitment (Caughlin et al., 2014; Kurten & Carson, 2015).

In summary, we find evidence of fungal-driven C-NDD, with variation in the susceptibility of tree species to pathogen attack consistent with host-specificity of pathogens. However, overall contributions of fungal pathogens to seedling mortality are low and resulting C-NDD is unlikely to represent overcompensating forms. Thus, in the absence of other natural enemies, fungal pathogens appear insufficient in promoting the diversity of mast-fruiting plant communities. Our study highlights the need to assess multiple species and regions, serving as an example of how the bias in tropical understanding from the Neotropics can lead to commonly held beliefs that are not supported in other tropical systems. Further study is required to quantify the combined and separate roles of different natural enemies in driving patterns of seedling mortality and decipher how tree species traits, including fungal association, impact such patterns, and reveal how plant communities are maintained and structured within this globally important forest type.

2.6 Author Contributions

P.G.C, M.O.B and R.P.F conceived and designed the study; P.G.C coordinated the study and collected seedling data; M.O.B collected the seeds and the light and temperature data; P.G.C led data analysis, with contributions from R.P.F and M.O.B; and P.G.C wrote the initial draft of the manuscript with all authors contributing significantly to revisions. All authors gave final permission for publication.

2.7 Funding

P.G.C was supported by a PhD studentship from the Leverhulme Trust – Centre for Advanced Biological Modelling (CABM). M.O.B was supported by the Atracción de Talento Investigador Modalidad I Fellowship from the Comunidad de Madrid (2018-T1/AMB-11095). This publication is number 23 from the Malua Research Team associated with the Sabah Biodiversity Experiment.

2.8 Acknowledgements

We thank the Sabah Biodiversity Council, Danum Valley Management Committee, Sabah Forestry Department, the State Secretary, Sabah Chief Minister's Department and the Malaysian Economic Planning Unit for site access and research permissions. We also thank the Royal Society's South East Asia Rainforest Research Program (SEARRP), especially Director Dr Glen Reynolds and Site Manager Remmy Murinus, for research and logistical support, in addition to research assistants Eglie, Visdi Saidi, Vendi Vens Aishiteru, and Emma Watson.

2.9 Data Accessibility

Seedling leaf damage score, diameter growth, height, and mortality data: Dryad doi: https://doi.org/10.5061/dryad.xksn02vdh.

ASKING THE WRONG QUESTION IN EXPLAINING TROPICAL DIVERSITY

This chapter has been published as:

Cannon, P. G., Edwards, D. P., & Freckleton, R. P. (2021). Asking the Wrong Question in Explaining Tropical Diversity. *Trends in Ecology and Evolution*, 36(6),482–484. doi: 10.1016/j.tree.2021.02.011.

3.1 Abstract

Enhancement of plant diversity via the Janzen-Connell mechanism is often measured relative to neutral models that ignore species' competitive differences. Recent modelling indicates this mechanism is ineffective when included in models incorporating species' demographic variations. This suggests we have been asking the wrong question when measuring the effectiveness of diversity-enhancing mechanisms.

3.2 Modelling coexistence: asking the wrong question?

What drives the incredible diversity of tropical forests and other hyper-diverse systems is one of the oldest unresolved problems in ecology. The **Janzen-Connell hypothesis (JC)** (see Glossary) posits that specialist natural enemies maintain diversity by disproportionately reducing the survival of conspecific seeds and seedlings at high densities and close to parent trees (Connell, 1971; Janzen, 1970). Such **conspecific negative density-dependence** (C-NDD) provides a 'rare species' advantage that prevents any one species from becoming competitively dominant, thus preserving and enhancing diversity.

A second influential theory over the last 20 years has been **neutral theory** (Hubbell, 2001). In its simplest form, no single species is competitively dominant and, consequently, large numbers of species are able to persist without invoking additional **stabilizing mechanisms**. However, in the long-term, without replenishment by immigration or speciation, this is a **non-equilibrium model** that supports only a single species. Although it is unlikely that any communities strictly fit the assumptions of this model, it is arguably a useful null or alternative model against which others can be tested (Gotelli & McGill, 2006).

A simple test of the effectiveness of the Janzen-Connell mechanism is to ask how much more diversity is generated relative to expectations under a neutral model. Comparisons of this sort have suggested evidence of considerable diversity enhancement (Levi et al., 2019). Consequently, evidence of the presence of C-NDD in real systems is taken as evidence for the role of the JC mechanism in maintaining local diversity, although whether it is capable of governing large-scale diversity patterns remains contentious (Hülsmann, Chisholm, & Hartig, 2020).

Recent work has questioned this logic. Conventional ecological theory states that competitive differences between species lead to **competitive exclusion**. Consequently, another way of asking what drives diversity is to ask whether the JC mechanism can slow or prevent this exclusion. Recent modelling suggests the answer to this question may be ‘no’, questioning the strength of evidence for C-NDD in maintaining diversity (Chisholm & Fung, 2020; Stump & Comita, 2018). Thus, our answer to whether the JC mechanism increases diversity may depend on how the question is asked.

3.3 Variation affects coexistence

3.31 Differential susceptibility to C-NDD

In nature, variation in species' performance is ubiquitous and plant species can vary by orders of magnitude in their abundances and population growth rates (Kraft, Godoy, & Levine, 2015). In temperate and tropical forest seedlings, for example, mycorrhizal association, shade tolerance and growth rate substantially affect species' susceptibility to C-NDD (Jia et al., 2020), directly affecting their population growth rates. Addressing such high and pervasive variation in natural systems is important in developing realistic assessments of the JC theory.

Parameterized with estimates of demographic variation from tropical seedlings from Barro Colorado Island, Panama, recent approaches by Stump and Comita (2018), and Chisholm and Fung (2020) demonstrate that two aspects of species' variation can create competitive differences between species that undermine coexistence: (i) variation in **intrinsic fitness**, also referred to as variation in species' density-independent per capita growth rate (PGR; Fig 3.1a), and (ii) variation in species' susceptibility to C-NDD (Fig 3.1b). Although these two related mechanisms result in similar quantitative effects for coexistence (i.e., fewer species being maintained by the JC mechanism), they affect the relationships between species' population growth rates and their abundances differently (Figure 3.1a-c).

When species vary in their susceptibility to C-NDD, the most sensitive species are the weakest competitors, whereas those least sensitive to C-NDD are the strongest. Sensitive species are thus quickly competitively excluded and insensitive species rapidly become dominant. Additionally, when species within theoretical communities differ more strongly in their responses to C-NDD, competitive differences are more pronounced leading to steeper losses of species (as seen in the pink region of Figure 3.1d). Even with relatively modest increases in variation, community stability and species richness can be significantly eroded (Stump & Comita, 2018).

Chisholm and Fung (2020) also found that spatially restricted dispersal kernels can severely hinder the maintenance of diversity via the JC mechanism through disproportionately increasing C-

NDD effects for rare relative to common species. When dispersal is low, and seeds fall close to parent trees, rare species are unable to take advantage of low-density sites or sites absent of conspecifics. Including variation in species' susceptibilities to C-NDD accentuates this dispersal dilemma, with non-dispersed seeds still able to recruit when relatively insensitive to C-NDD, whilst highly susceptible species only ever recruit when dispersed far from conspecifics (Stump & Comita, 2018). Consequently, recruitment advantages are greatest for the least susceptible species, and these advantages are greater still under limited dispersal (Figure 3.1. grey regions).

3.32 Effects of demographic variation on species abundance

Whether demographic variation affects coexistence is dependent on how it influences species' abundances. Previous modelling demonstrates that variation influences local abundance (Miranda, Carvalho, & Dionisio, 2015), with less competitive species and those more susceptible to C-NDD having lower abundances. Smaller population sizes then render less abundant species more vulnerable to stochastic events and local extinction. Empirical studies of tropical plant communities often support these predictions, with rare species frequently more sensitive to C-NDD.

Variation in C-NDD is most likely to result in species loss when common species are insensitive to C-NDD relative to rare species (Stump & Comita, 2018). In such instances, the recruitment of common species is no longer tightly constrained by density, eroding the 'rare species' advantage and resulting in rapid competitive exclusion. Furthermore, species made rare by high susceptibility to C-NDD are more vulnerable to stochastic processes and local extinction than those governed by other competitive traits affecting per capita growth rates (i.e., lower overall fecundity or survival) (Stump & Comita, 2018). This is a consequence of variation in relationships between species' per capita growth rates and abundance, resulting in less equal abundances of species when at equilibrium in communities varying in C-NDD than those varying in other competitive traits (Stump & Comita, 2018) (Figure 3.1a-c). Thus, variation in traits that directly affect a species' susceptibility to C-NDD is most influential in mediating coexistence, maintaining larger, more stable communities (Stump & Comita, 2018).

3.4 Under what circumstances is variation in C-NDD and species' sensitivity to C-NDD likely to erode diversity?

Tests of the JC mechanism relative to expectations under a neutral model assert that the long-term maintenance of diversity does not rely on replenishment by migration, greater partitioning of recourses or speciation, but simply on a small area under parent trees within which seedlings cannot recruit (Levi et al., 2019). While recent modelling does not entirely dispute this assertion, this requirement may rarely be met given variation in species demographic rates and competitive abilities. In essence, only when dispersal is unimpeded, and all species are equally and strongly affected by C-NDD, is community diversity maintained by the JC mechanism (topmost turquoise line, Figure 3.1d).

As illustrated in Figure 3.1d, multiple alternative scenarios exist in which species can either be lost or maintained by C-NDD over time. When C-NDD is equal across species, diversifying effects are dependent on the strength of C-NDD, with stronger C-NDD maintaining a greater number of species while diversity is quickly eroded under weak C-NDD (turquoise region). When species differ more strongly in their susceptibility to C-NDD, community diversity is quickly eroded as insensitive species rapidly become competitively dominant and sensitive species are quickly lost from the community (pink region). Under all scenarios of equal or varying susceptibility to C-NDD, limited dispersal erodes the number of species maintained by the JC mechanism (grey regions).

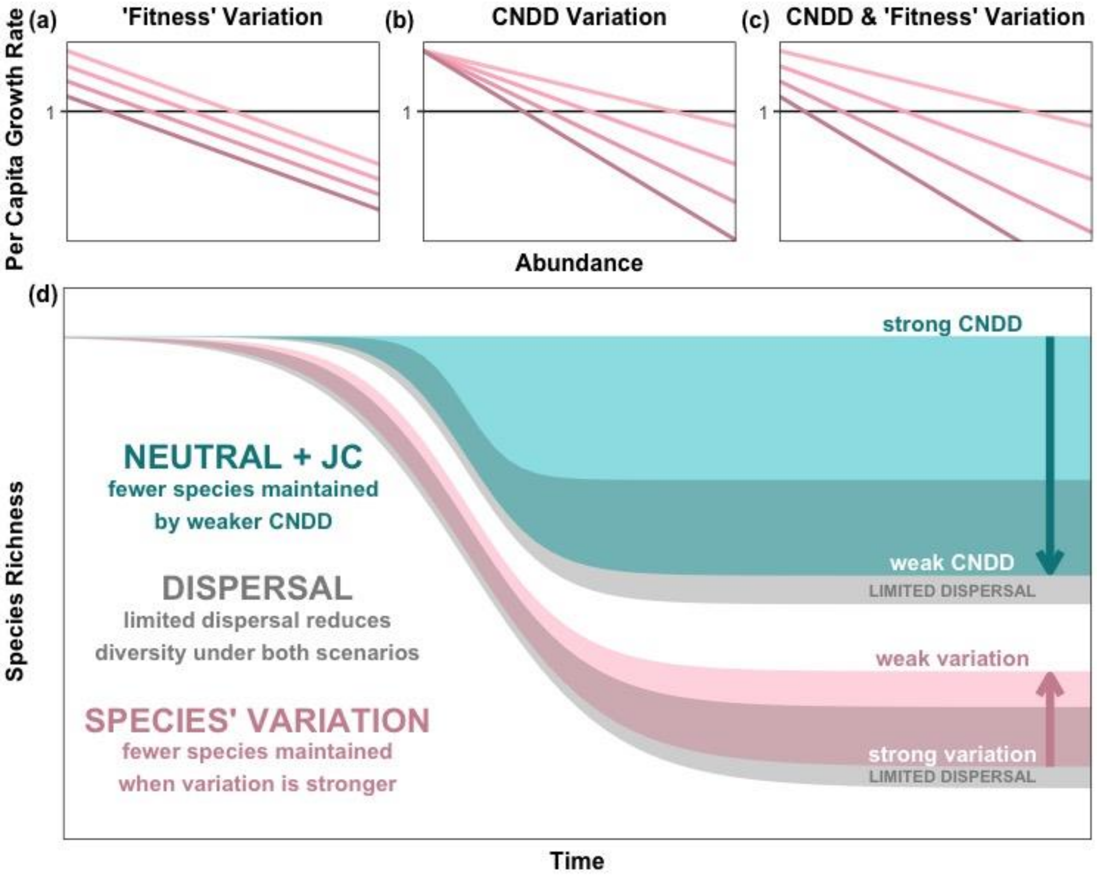

Figure 3. 1. Variation in relationships between species' per capita growth rates and abundance and changes in community diversity over time under different scenarios of species' susceptibility to C-NDD. (a) Variation in species' 'fitness' (average population growth rate) varies the y-intercept of the relationship between species' per capita growth rates and abundances, with each line representing a species and the slope equal for all species. (b) Variation in species' susceptibility to C-NDD represents variation in the slope, with more negative relationships for species with high susceptibility to C-NDD. (c) Variation in species' 'fitness' and susceptibility to C-NDD create less even abundances between species when at equilibrium (black lines). (d) The turquoise region represents communities varying in the strength of C-NDD and where species susceptibility to C-NDD is equal (i.e., approaches consistent with applying the Janzen-Connell mechanism to otherwise neutral models.). The pink region represents communities with different strengths of variation in species' susceptibility to C-NDD or variation in species' per capita growth rates (i.e., models of competitive exclusion). Grey regions represent the effect of limited dispersal on each scenario. This figure was adapted from Chisholm and Fung (2020).

3.5 Future study: Asking the right question

The problem of explaining diversity has classically been expressed in terms of niche theory. Assuming that each species requires a different niche and given the restricted range of resources that plants compete for in tropical forests (e.g., light, nutrients, and space), together with the limited suite of life-history strategies (e.g., pioneer versus emergent), it is intuitively difficult to imagine how there are sufficient niches to accommodate the vast number of species. Neutral theory offered a fresh perspective, which, in combination with the JC mechanism, offered an alluringly straightforward explanation to an apparently **wicked problem**: in an otherwise neutral world, demonstrating the existence of the JC mechanism is enough to explain considerable additional diversity.

Looking forward, it is clear that the problem is far more complicated and suggests that future studies need to integrate several key elements together with C-NDD. Recently highlighted future directions include: generating more robust and less error-prone estimates of C-NDD; assessing multispecies coexistence across regions and life stages; and integrating C-NDD modelling into both community ecology and macroecology frameworks (Hülsmann et al., 2020). We agree, and our perspective is that significant challenges remain in doing this. The problem boils down to finding approaches that can accurately quantify whether differences between species contribute positively or negatively to coexistence. This is difficult and requires linking species' traits to both short- and long-term ecological outcomes. In a non-neutral world, the impacts of variation between species' susceptibility, competitive ability, and dispersal negate the effects of C-NDD (Figure 3.1d). The challenge is to develop experimental designs and analyses that permit such effects to be measured and their role tested, requiring the re-emergence of considerable interest in the field. In the meantime, we return to our initial and evidently now more-complex question, what drives the incredible diversity of tropical forests and other hyper-diverse systems?

3.6 Glossary

Janzen-Connell hypothesis: An ecological theory proposed by Janzen (1970) and Connell (1971) positing that diverse plant communities are maintained by the actions of specialist natural enemies causing increasingly high mortality of conspecific seeds and seedlings at high densities and close to parent trees.

Conspecific negative density-dependence: A key component of various stabilizing mechanisms, describing increased mortality of seeds and seedlings at high conspecific densities. In regard to the Janzen-Connell mechanism, density-dependent mortality is a consequence of high densities of host-specific natural enemies.

Neutral theory: An ecological theory of biodiversity that assumes all species have equivalent probabilities of death and reproduction (Levi et al., 2019), and suggesting that community diversity is maintained by speciation and immigration that counteract stochastic forces that would otherwise lead to extinction.

Stabilizing mechanisms: Processes that impede the transient loss of species from a community over time.

Non-equilibrium model: Models describing change in species diversity over time that, without the stabilizing effects of external mechanisms or environmental perturbations, will eventually result in a single species community. Without speciation, immigration, or stabilizing mechanisms, such as the Janzen-Connell mechanism, neutral theory is an example of a non-equilibrium model.

Competitive exclusion: the gradual decrease in abundance and eventual loss of a less competitive species as a result of competition with others.

Intrinsic fitness: a species' competitive ability, relative to another, describing its fecundity, survival and dispersal ability (Adler, Hillerislambers, & Levine, 2007), and often referred to in equivalence to a species' average population growth rate.

Wicked problem: A seemingly impossible to solve problem given multiple interacting reasons.

3.7 Acknowledgements

Thanks to the two anonymous referees and Editor, Dr Andrea Stephens, for their comments which greatly improved the manuscript. P.G.C was funded by the Grantham Institute's Centre for Advanced Biological Modelling (CABM).

CHAPTER 4

LOCAL DRIVERS OF ß-DIVERSITY IN MULTIPLE LIFE STAGES OF TROPICAL TREES FOLLOWING SELECTIVE LOGGING

4.1 Abstract

Local-scale variation in logging intensity and associated patterns of within-forest disturbance are hypothesised to alter the spatial arrangement of tropical tree communities. Previous studies of tree ß-diversity in logged forest have primarily focused on adult trees, with the contributions of specific environmental factors in driving substantial turnover still relatively unknown. Earlier life stages can provide greater insight into the altered successional pathways of disturbed forests, with multi-stage approaches revealing temporal dynamics of community assembly processes. A key question is disentangling whether patterns of ß-diversity in logged forest are driven by within-forest disturbance or processes related to spatial distance, and whether such drivers differ between life stages. Here, we examine patterns and drivers of tree community ß-diversity for sapling, juvenile, and adult life stages in a twice-logged Bornean forest, which has experienced some of the highest logging intensities globally. We demonstrate that across life stages, ß-diversity was greater than expected given local α-diversity and stem densities 12 years after a second successive logging event, with dissimilarity driven by species turnover and largely explained by processes of community assembly relating to spatial distance between sample points, as opposed to measures of within-forest disturbance. Dissimilarity in juvenile, but not sapling, communities was significantly related to adult dissimilarity. This finding suggests greater isolation and aggregation of adult trees following logging previously shaped ß-diversity patterns of early life stages via increased dispersal limitations, and now influence overall recruitment rates resulting in high spatial variation in recruitment success between sites. Our findings

demonstrate the importance of assessing multiple life stages when examining community change and indicate that alterations to the spatial arrangement of tree diversity following selective logging persist for decades, potentially disrupting mechanisms for maintaining forest diversity.

4.2 Introduction

Selective logging impacts forests pan-tropically, driving the ecological simplification of millions of hectares of forest (D. P. Edwards et al., 2019). Logging substantially modifies forest structure and microclimate (Jucker et al., 2020). It temporarily increases understory light levels and temperatures, altering nutrient availability, and reducing humidity and soil moisture (Mollinari et al., 2019; Riutta et al., 2021; Senior et al., 2018), with understorey microclimates rapidly returning to pre-logging conditions as vegetation recovers (Mollinari et al., 2019; Senior et al., 2018). In turn, the selective removal of large, commercial tree species directly modifies plant communities, allowing lianas and pioneer species to proliferate in abundance and biomass (Magrach et al., 2016; Schnitzer & Bongers, 2011).

Logging activity can vary considerably as a consequence of topography, clumped distributions of many tree species, and overall harvest intensity (Condit et al., 2002; D. P. Edwards, Tobias, et al., 2014). Consequently, within-forest disturbances vary significantly across small spatial scales and often coincide with high liana infestation, with dense liana tangles aggregated within tree fall and logging gaps (Schnitzer & Carson, 2010), and at forest edges (Campbell et al., 2018). As with other ecological disturbances, variation in logging disturbance can alter community assembly processes to either homogenize communities in areas of high disturbance by favouring disturbance-sensitive species (decrease ß-diversity) or diversify communities via increased environmental filtering (increase ß-diversity; Socolar et al. 2016). Differences between communities can also arise through species turnover or nestedness, corresponding to alternative mechanisms of compositional change (Krishnadas, Kumar, & Comita, 2019). Whilst high turnover depicts change in ß-diversity via the replacement of species, nestedness is driven by the loss of species in some sites, resulting in sites containing only a subset of more diverse communities (Baselga, 2013).

In Borneo, selective logging increases tree ß-diversity with spatial distance and vegetation structure, compared to unlogged forest, probably because increased environmental heterogeneity results in the increased recruitment of young pioneer species (Berry et al., 2008). Although tree phylogenetic composition can be relatively resilient to single logging events (Mahayani, Slik, Savini, Webb, & Gale, 2020), high rates of community turnover can persist for decades (Osazuwa-Peters, Jiménez, et al., 2015), halting the recovery of pre-disturbance tree composition. However, it is unknown what drives such persistent compositional changes within logged forests, prompting the need for a broader understanding of how logging disturbances alter future forest communities.

Whilst adult communities are immediately altered by the selective nature of commercial logging, harsh abiotic conditions following extractions and reduced seed production from fewer, more isolated adults (Bagchi et al., 2011; Ghazoul, Liston, & Boyle, 1998) can dramatically reduce recruitment of smaller life stages (Pillay et al., 2018). In Borneo, the effects of altered microclimates are hypothesised to disproportionately affect late successional and commercially valuable dipterocarp species (Jucker et al., 2020) already depleted by logging. In addition, biotic interactions between trees and other taxa can shape forest composition (Mangan et al., 2010). For example, lianas modify disturbed forest communities by unequally affecting different host species (Muller-Landau & Visser, 2019). As structural parasites, lianas reduce tree growth, fecundity, survival and recruitment (García León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2018; Ingwell, Joseph Wright, Becklund, Hubbell, & Schnitzer, 2010; Martínez-Izquierdo, García, Powers, & Schnitzer, 2016; Tymen et al., 2016), via intense competition for above- and below-ground resources (Schnitzer, Kuzee, & Bongers, 2005). Such effects vary substantially between tree species, with liana infestation often reflecting survivorship biases resulting from host species' abilities to either avoid or tolerate lianas (Visser, Muller-Landau, et al., 2018; Visser, Schnitzer, et al., 2018). Increased abundances and altered liana-tree interaction networks in selectively logged forests (Magrach et al., 2016) may therefore contribute to the spatial arrangement of tree diversity post-logging.

The effects of local variation in logging disturbance and liana infestation are likely to result in contrasting changes to tree communities at different life stages. However, much previous research has focused on the responses of adult trees to logging disturbances (Mahayani et al., 2020; Osazuwa-Peters, Jiménez, et al., 2015) and liana infestation (Magrach et al., 2016; Reis et al., 2020), or does not distinguish between responses of trees at different life stages (Berry et al., 2008). Younger life stages may respond differently to disturbance compared with adults. Changes in adult composition can be buffered for decades by the persistence of non-reproductive relics (Rigueira, da Rocha, & Mariano-Neto, 2013), masking the long-term effects of logging on forest composition. In contrast, younger life stages in the community will rapidly reflect the effects of logging disturbances on remnant tree reproduction and seed production, and seedling survival and recruitment. Thus, inclusion of smaller life stages can provide greater insight into the altered successional pathways of disturbed forests, including underlying shifts in their functional composition (Berenguer et al., 2018; Hogan et al., 2018). A key question is disentangling the contributions of spatial and environmental gradients in driving patterns of logged forest ß-diversity, and whether such factors differ between life stages. Understanding how disturbance gradients alter ß-diversity is important in understanding the sensitivity of human-modified systems to further disturbance (Fitzpatrick et al., 2013) and inform how to best to preserve or restore them (Myers, Chase, Crandall, & Jiménez, 2015).

Here, we examine the patterns and drivers of logged forest ß-diversity for sapling, juvenile, and adult trees to assess how spatial variation in within-forest disturbance may impact the recovery of logged forest communities. Specifically, we test the hypotheses that: (i) tree ß-diversity will increase with greater differences in environmental disturbance, liana infestation and geographic distance, and will be predominantly caused by species turnover; (ii) ß-diversity will be greatest for smaller life stages; and (iii) drivers of ß-diversity will differ between life stages, reflecting different responses to altered community assembly processes.

4.3 Methods and Materials

4.31 Study area

The study was carried out in the Malua Forest Reserve, Sabah, Malaysian Borneo (N05°05′20″ E117°38′32″; 102 m a.s.l.), a ~35,000 ha production forest which has experienced some of the highest logging intensities globally (Putz et al., 2012; Edwards et al., 2014). Comprising part of the larger, 1 million ha Yayasan Sabah logging concession (YSFMA), the reserve was intensively selectively logged during the 1970s and 1980s, and again between 1999 and 2007, with harvest volumes exceeding 144 m^3 ha^{-1} (Fisher et al., 2011). The majority of commercial stems over 40 cm d.b.h. were extracted, comprised predominantly of species from the *Dipterocarpaceae* family. Although subject to the same forest-wide logging intensity, forests in the reserve are highly heterogeneous, composed predominantly of pioneer and early successional species (i.e., *Macaranga* spp.), but with some large remnant dipterocarps and dense tangles of lianas, rattans and thickets of climbing bamboos (see Figure 4.1a).

4.32 Sampling tree composition

We selected three logged forest sites located within three neighbouring logging compartments, positioned at least 1 km apart and 100 m from the forest road edge (Figure 4.1c). To capture small-scale variation in forest structure and tree composition, sites were divided into 36 four-hectare blocks (200 x 200 m), each containing five 20 x 20 m sample plots randomly distributed within a core 100 m^2 sampling area within each block (Figure 4.1e). We sampled tree composition at three life stages using a series of nested sub-plots. Saplings were sampled in a central 2 x 3 m plot (> 50 cm tall and < 1 cm d.b.h; diameter at 1.3 m height), juveniles in a central 5 x 20 m plot running the length of the overall plot (≥ 1 cm d.b.h), and adults across the entire 20 x 20 m area (≥ 10 cm d.b.h).

Identification of trees was first carried out by local experts in the field and later confirmed by botanists at Danum Valley Field Centre using voucher specimens and photographs taken in the field. In total, we sampled and identified 8720 individuals from all life stages, totalling 540 sample plots (36 blocks containing 5 plots per life stage) (For detailed sampling design, see Figure 4.1.). A single block containing five adult subplots had <75% of trees identified to species level and was removed from analyses. In the remaining 535 subplots, a total 8664 individuals were recorded (1663 saplings, 5258 juveniles, and 1743 adults), of which 77.3 % were formally identified to species level.

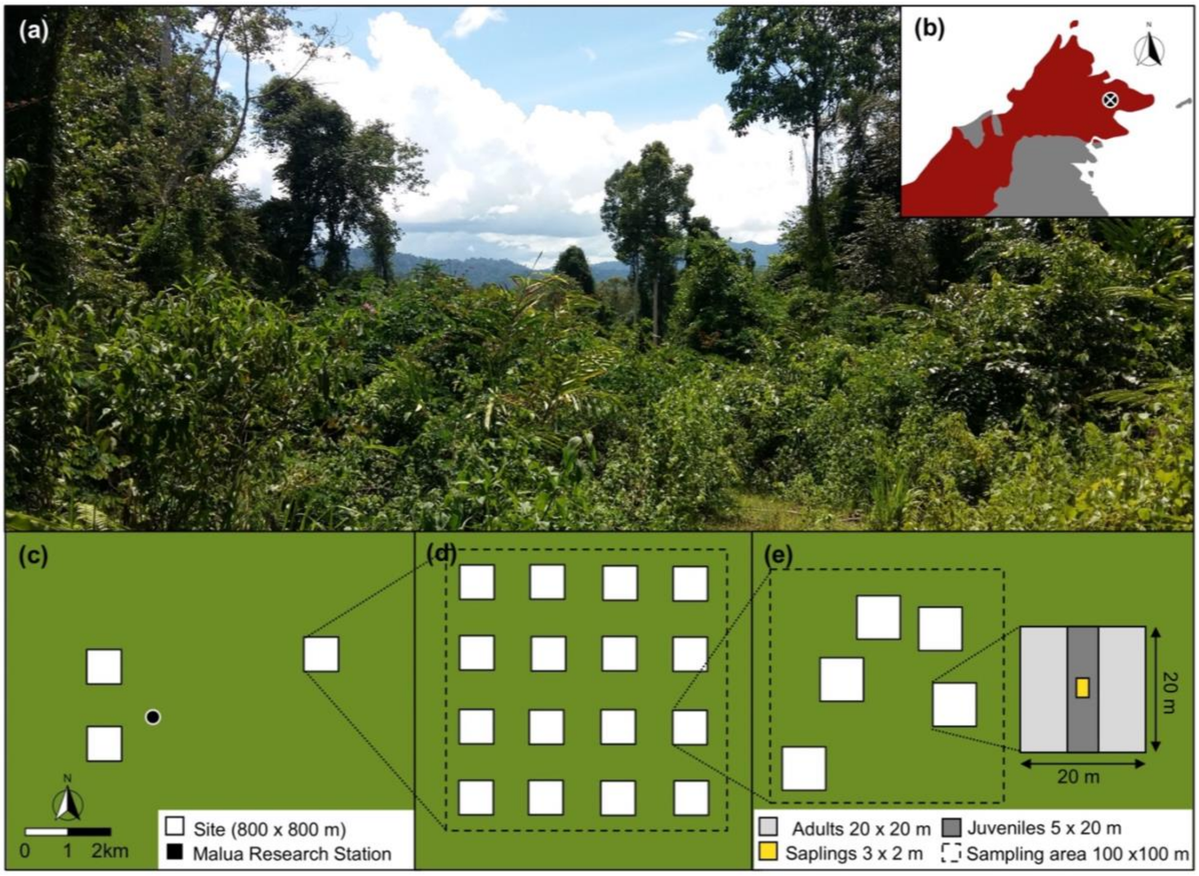

Figure 4. 1. Study area and sampling design. View of the surrounding twice-logged forests of the Malua Forest Reserve (MFR), taken from an old secondary logging road, still partly visible 12 years after logging extractions (a). The location of the MFR in the northeastern tip of Sabah, Malaysian Borneo (b; inset). Map of the three twice-logged forest sites in relation to the Malua Research Station (c). Arrangement of 100 m^2 core sampling area within each 200 x 200 m sample blocks within sites (d). Arrangement of the five randomly positioned 20 x 20 m tree community sample plots and nested sub-plots in which turnover in tree composition was measured (e). Reproduced, with permission, from Catherine Finlayson (a).

4.33 Environmental and spatial gradients

To determine the environmental drivers of turnover in logged forest tree composition, we examined changes in five measures of forest and vegetation structure between sample points, forming five gradients of within-forest disturbance affected by logging activity. These included measures of: adult tree abundance; total basal area (m^2 ha^{-1}); the proportion of liana infested trees (liana prevalence); liana canopy infestation cover (liana load); and canopy openness. Additionally, sample plots ranged up to 6.35 km apart, forming an additional gradient of small-scale spatial distance.

We recorded plot-level adult tree abundance and total basal area (m^2 ha^{-1}) using tree censuses and measurements of stem diameter at breast height for all adult trees. For all adult individuals, we recorded tree liana infestation status (liana prevalence: 1 – infested, 0 – non-infested) and tree canopy infestation rates (liana load), using an established five-point ordinal scale (Muller-Landau & Visser, 2019; Visser, Muller-Landau, et al., 2018). Trees were classed as: 0 when a trees' crown is free of lianas; 1 when lianas are present but covering <25 % of the crown; 2 when covering 26-50 %; 3 when covering 51-75 %; and 4 when covering >75 %. Measures of plot-level canopy openness were recorded using a hemispherical densiometer (1.3 m above the ground), recording canopy closure in all cardinal directions at five locations per sample plot.

4.34 Quantifying ß-diversity and components of nestedness and turnover

To quantify changes in tree community structure at each sample point, we calculated a number of multivariate measures of ß-diversity for each life stage separately, computing pairwise comparisons of each sample point against all others using: (1) the widely used presence/absence-based Jaccard dissimilarity; (2) abundance-based Bray-Curtis dissimilarity; and (3) abundance-based Chao-Jaccard dissimilarity, which reduces sampling bias when working with assemblages comprised of many rare species by accounting for unseen shared species (Chao, Chazdon, & Shen, 2005).

To assess whether dissimilarity between sites of increasing environmental distance was driven by replacement of species (turnover) or by local gains or losses of species (nestedness), we calculated components of nestedness and turnover of ß-diversity (Bray-Curtis index) using the beta.pair.abund function in the *betapart* package (Baselga & Orme, 2012). This, and all other subsequent analyses, were performed using packages in R v. 3.6.3. (R Core Team, 2020).

Random sampling effects can result in greater heterogeneity and high ß-diversity among sample points (Socolar et al., 2016). To separate contributions of local community assembly processes from sampling effects in driving patterns of ß-diversity, we used a null model approach (Chase, Kraft, Smith, Vellend, & Inouye, 2011; Kraft et al., 2011). Null models were produced using existing R code (Tello et al., 2015), randomising species identities and abundances whilst keeping community size constant between blocks. In this way, resultant null communities are constructed free of local processes that cause non-random distributions of species and their abundances (i.e., dispersal limitations and habitat filtering). To test whether observed communities deviated from communities derived from the null expectation, we calculated mean expected ß-diversity from 999 null communities and included this as a predictor in models of community change at each life stage. We repeated this process for each component of ß-diversity, calculating expected turnover and nestedness of Bray-Curtis dissimilarity and including these as predictors in respective models.

Classical measures of ß-diversity are susceptible to variation in both local (α-diversity) and regional (γ-diversity) species pools (Chase & Myers, 2011). Moreover, ß-diversity indices can lose resolution when using sparse datasets in which many sample points share no species, as is common in studies of environmental disturbance gradients (Anderson et al., 2011). As a result, ß-diversity metrics were calculated from communities composed of data pooled across all five sample plots per block, following a similar study examining turnover in tree ß-diversity in a disturbed Indian tropical forest (Krishnadas et al., 2019).

4.35 Generalized Dissimilarity Models

We used Generalized Dissimilarity Models (GDM) to compare non-linear relationships between compositional dissimilarity (Bray-Curtis, Chao-Jaccard, and Jaccard dissimilarity) and environmental and spatial distance between pairs of sample points. Environmental and spatial distance represent pairwise differences in within-forest disturbance measures and spatial coordinates between sample points. Unlike other forms of dissimilarity analyses, GDMs account for spatial variation in compositional turnover and two types of non-linearity: (i) the non-stationary rate of turnover in communities along environmental gradients; and (ii) the curvilinear relationships between community dissimilarity (ß-diversity) and differences in environmental and spatial distance between sample points (Ferrier, Manion, Elith, & Richardson, 2007). Thus, GDMs provide more accurate estimates of the contributions of environmental variables in driving ecological turnover (Fitzpatrick et al., 2013), particularly in systems exhibiting high turnover and where the majority of points share few species (Ferrier et al., 2007), as is common in highly diverse systems with a high proportion of rare species.

We constructed GDMs for each life stage using all three dissimilarity indices (employing functions within the *gdm* package: Fitzpatrick et al., 2021). Initial models included all five environmental disturbance gradients and spatial coordinates as predictors, as well as mean expected ß-diversity derived from 999 null communities. The significance of each predictor was then tested using Monte Carlo matrix permutations (within the gdm.varImp function; 50 permutations), quantifying the importance of each variable as the change in deviance explained between models fit with and without each variable.

To assess whether change in compositional dissimilarity in one life stage was related to change in another, we also constructed simplified GDMs for each combination of life stages. Observed dissimilarity of each comparable life stages were included alongside spatial distance. Variable significance was then derived in the same way as previous models.

4.4 Results

4.41 Local and regional tree diversity and stem abundances

Across the study, we recorded 263 sapling species, 432 juvenile species, and 227 adult species. Local α-diversity in sample blocks was greatest for saplings, with mean (SD) α-diversity of 0.804±0.0268 m^2, compared to 0.069±0.020 m^2 for juvenile trees and 0.0017±0.005 m^2 for adult trees. Similarly, block-level stem densities were greatest for saplings 1.912±0.816 , compared to 0.339±0.174 for juveniles and 0.039±0.012 for adults.

4.42 Expected vs observed ß-diversity

Mean ß-diversity (Bray-Curtis index) differed across life stages (ANOVA: $F_{(2,206)} = 36.08$, $p < 0.001$) and between observed and null-expected communities ($F_{(1,206)} = 826.93$, $p < 0.001$). Across all life stages, ß-diversity was greater in observed communities than null expected communities, constructed free of processes such as dispersal limitations and habitat filtering (Figure 4.2.). In observed communities, saplings had significantly greater ß-diversity than juveniles and adults, with mean observed sapling community dissimilarity between sample points 5.8% higher than juveniles and 8.0% higher than adults. Change in ß-diversity did not differ significantly between adult and juvenile communities. In expected communities, ß-diversity was significantly lower in juveniles than saplings and adults. Quantitatively similar results were observed across all three indices of ß-diversity (Figures B.2. and B.3.).

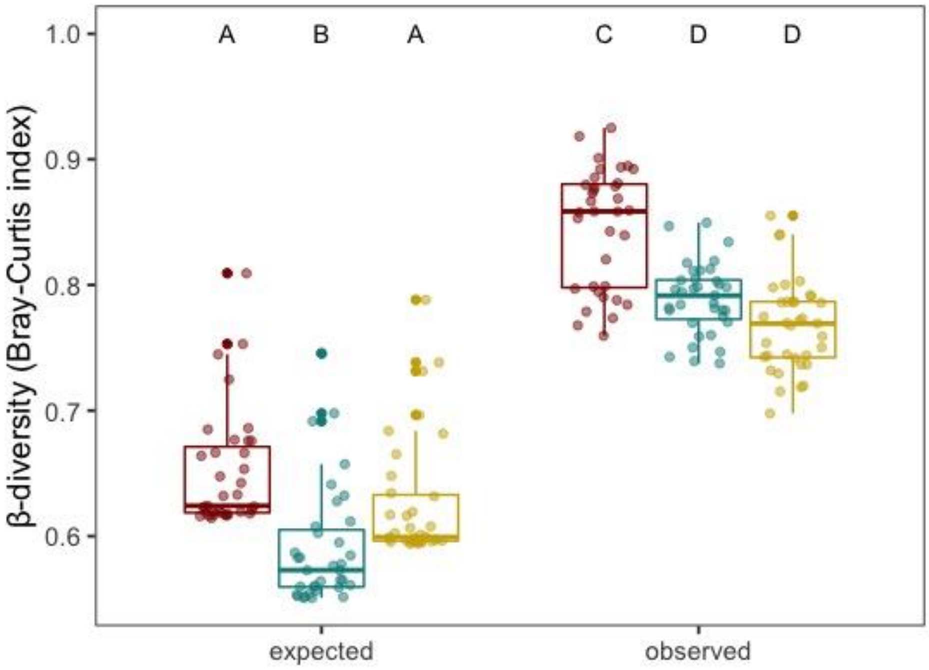

Figure 4. 2. ß-diversity (Bray-Curtis index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test.

4.43 Environmental and spatial influences on ß-diversity

Observed community ß-diversity increased with environmental and spatial distance, across all life stages (Figure 4.3.). GDMs containing both spatial and environmental variables explained only marginally more deviance in observed dissimilarity (Bray-Curtis) than purely spatial models (0.82-1.74 %), but considerably more than models containing only environmental variables in isolation (9.41-20.9 %). The proportions of unique and shared deviance explained by spatial and environmental variables differed minimally between tree life stages (Figure B1). In full models, spatial distance between blocks was a significant predictor of community change for all life stages and across all indices of community dissimilarity, with greater changes in composition between sample blocks occurring further apart (Table 4.1.). The rate of change in community dissimilarity explained by geographic distance increased between points located over 4.6 km apart (Figure 4.4a.). Expected ß-diversity was the most important predictor of observed ß-diversity across all dissimilarity indices and life stages (Table 4.1.). Expected dissimilarity between null communities (i.e., constructed with random distributions of species and their abundances) significantly predicted changes in observed dissimilarity. In comparison, environmental variables related to forest disturbance did not significantly predict changes in community dissimilarity.

Table 4. 1. The relative importance of each environmental disturbance variable and geographic distance in explaining changes in tree community ß-diversity between sample points. Mean expected ß-diversity from 999 null communities produced by randomising species identities and abundances, included as a predictor. Values represent the sum of coefficients across three I-splines from GDMs with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with community dissimilarity represented by a dash and significant relationships indicated in bold.

	Jaccard			Bray-Curtis			Chao-Jaccard		
Gradient	**Sapling**	**Juvenile**	**Adult**	**Sapling**	**Juvenile**	**Adult**	**Sapling**	**Juvenile**	**Adult**
Deviance explained %	20.112	54.846	30.982	53.308	51.359	29.818	32.360	38.284	14.519
Distance (km)	**1.130**	**0.576**	**0.725**	**1.792**	**0.999**	**0.685**	**1.921**	**1.363**	**0.813**
Adult abundance	0.086	-	-	0.373	-	-	0.085	-	-
Basal area (m^2 ha^{-1})	-	-	-	0.063	-	0.093	0.372	0.074	0.009
Canopy openness (%)	-	-	0.063	-	0.175	-	0.037	-	-
Liana Prevalence (%)	0.084	0.102	0.053	0.186	-	0.042	0.099	0.050	-
Liana Load (%)	0.334	0.068	0.252	0.327	0.187	0.142	0.185	0.255	0.321
Expected ß-diversity	**1.171**	**2.272**	**1.923**	**3.390**	**1.796**	**1.092**	**2.547**	**1.055**	**1.135**

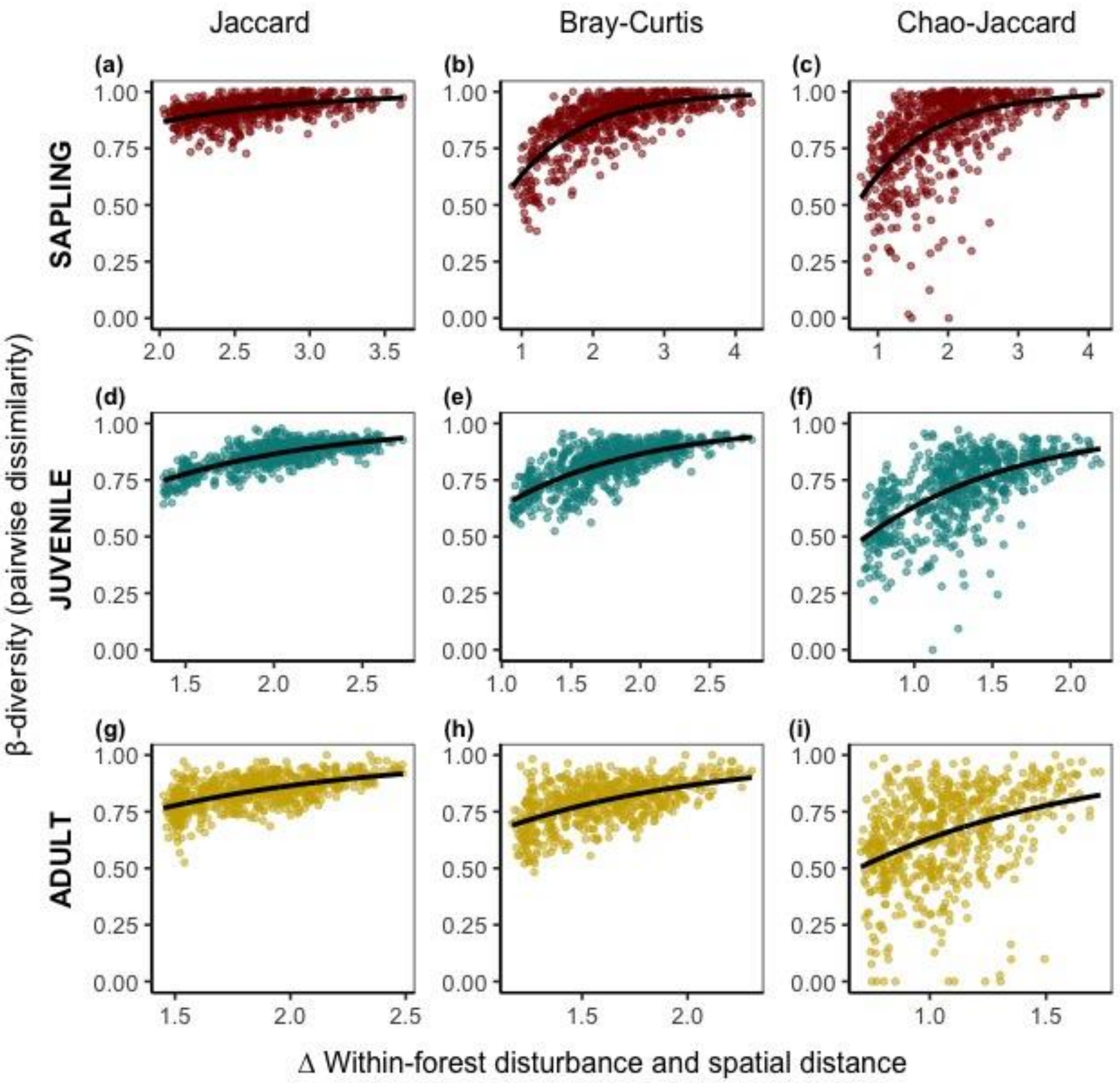

Figure 4. 3. Relationships between observed ß-diversity of tree communities and predicted environmental distance (within-forest disturbance measures, expected ß-diversity, and spatial distance) between pairs of logged forest sample blocks. ß-diversity was estimated using Bray-Curtis index (a, d, and g), Chao-Jaccard index (b, e, and h), and Jaccard index (c, f, and i). Mean expected ß-diversity from 999 null communities produced by randomising species identities and abundances, included as a predictor.

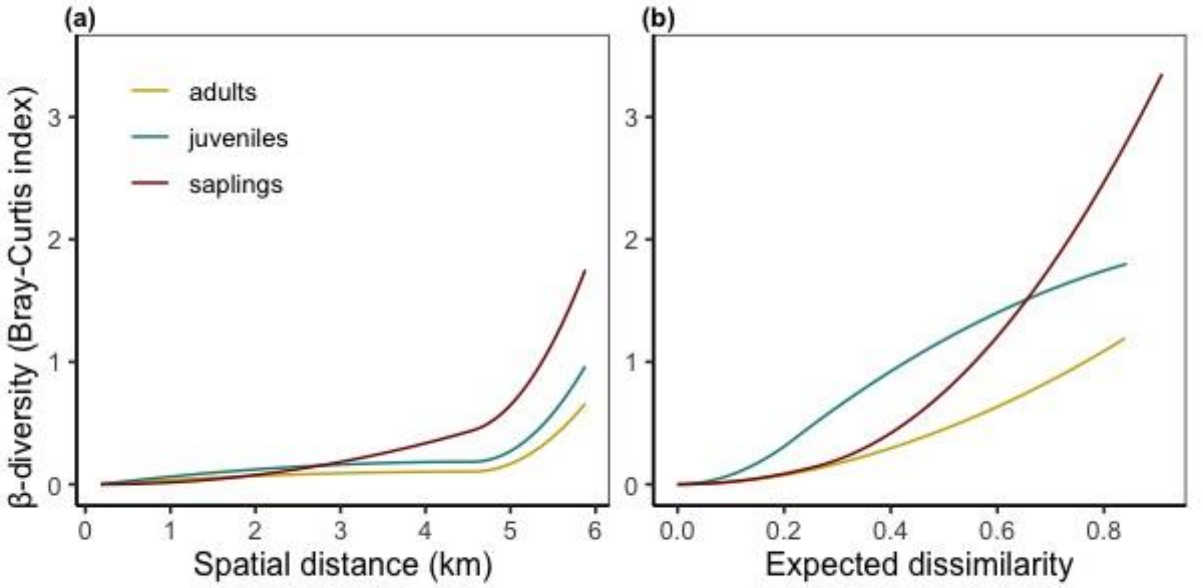

Figure 4. 4. Rates of change in tree community ß-diversity of each life stage along gradients of: (a) spatial distance, and (b) expected ß-diversity. Mean expected ß-diversity generated from 999 null communities produced by randomising species identities and abundances at each sample point. The height of each curve depicts the compositional dissimilarity explained by each predictor when all other variables are held constant.

4.44 Relationships of observed dissimilarity between life stages

Change in sapling ß-diversity was significantly predicted by change in juvenile, but not adult communities (Table B1). In addition, change in adult composition also significantly predicted change in juvenile ß-diversity. In both models, spatial distance between sample points was marginally more important in predicting ß-diversity than dissimilarity in other life stages.

4.45 Environmental and spatial influences on nestedness and turnover components of ß-diversity

Observed dissimilarity between sample points was almost entirely driven by replacement of species (turnover), rather than the loss or gain of species (nestedness). On average, turnover contributed to

94.1% of dissimilarity (Bray-Curtis index) in sapling communities, 90.1% in juveniles, and 91.8% in adults. Mean turnover and nestedness differed significantly between life stages (Turnover: $F_{(2,49)} = 24.57$, $p < 0.001$, Nestedness: $F_{(2,49)} = 4.27$, $p < 0.05$, Figure 4.5.), with sapling communities having greater turnover and lower nestedness than all other life stages (Tukey: all $p < 0.01$).

Turnover of observed community ß-diversity increased with environmental distance across all life stages, with predictors explaining between 10.3 – 29.0% of deviance in GDMs (Table B2). Geographic distance between blocks was the only significant predictor of turnover for all life stages, with greater turnover between sample blocks occurring further apart. In comparison, environmental variables related to forest disturbance did not significantly predict changes in turnover. Nestedness of observed community ß-diversity increased with environmental distance for only juvenile communities, with predictors explaining 41.43% of deviance in GDMs (Table B2.). Generalized dissimilarity models did not reveal any relationship between sapling or adult nestedness and environmental predictors or geographic distance. Canopy openness was the only significant environmental variable influencing juvenile nestedness.

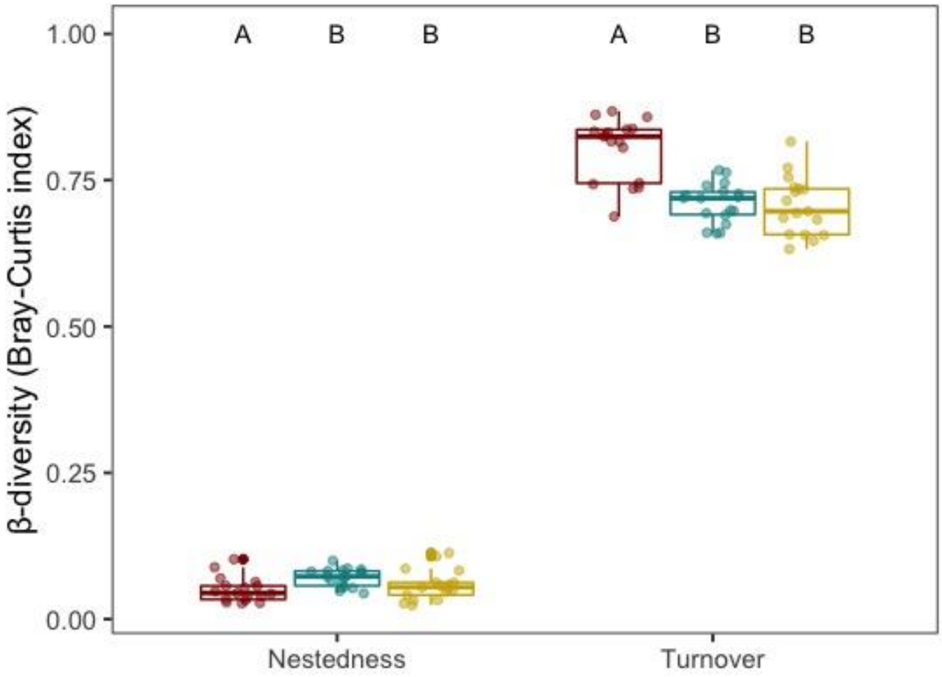

Figure 4. 5. Turnover (species replacement) and nestedness (species loss) components of ß-diversity (Bray-Curtis index) between life stages. Boxplots present median components of dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages denoted by different letters, comparisons estimated separately for each component using ANOVA and accompanying Tukey’s post-hoc test.

4.5 Discussion

Whilst forest loss causes well-documented declines in diversity (Betts et al., 2017), forest disturbances, including selective logging, can cause less distinguishable but equally damaging effects (Barlow et al., 2016), requiring more nuanced approaches to detect alterations to forest composition. We find greater than expected ß-diversity in sapling, juvenile, and adult tree communities 12 years after a second successive logging event. Observed dissimilarity, across life stages, was driven by species replacement and largely explained by spatial distance between sample points, as opposed to measures of within-forest disturbance. Our study is the first to evaluate the different drivers of community change following selective logging across multiple life stages of tropical trees. We find that, despite considerable alterations to forest structure and microclimate following logging events (Jucker et al., 2020; Magrach et al., 2016), local-scale patterns of tree composition more closely reflect community assembly processes related to isolation and dispersal limitation, than environmental heterogeneity.

4.51 Environmental and spatial influences on ß-diversity across life stages

Consistent with the hypothesis that greater environmental heterogeneity following logging facilitates the recruitment of disturbance-tolerant species (Berry et al., 2008), we expected logged forest ß-diversity to increase along gradients of within-forest environmental heterogeneity. However, spatial and environmental predictors only explained marginally more deviance in ß-diversity than purely spatial models, with no single environmental measure significantly predicting community change in any life stage. This finding may be partly explained by the partial recovery of forest structure following initial logging disturbance. For example, fast growing species (i.e., *Macaranga* spp.) have likely recruited into adult size classes in the years following logging (Berry et al., 2008), decoupling potential signals of variation in basal area and tree abundance from community change. However, greater heterogeneity in other disturbance measures (i.e., canopy openness) should still influence turnover of saplings, even when they are not directly related to initial logging disturbances.

Alternatively, our findings suggest that patterns of ß-diversity are explained by assembly mechanisms related to the aggregation and isolation of adult trees, as opposed to increased environmental heterogeneity. Spatial patterns of logging activity, dependent on topography and prior distributions of commercial species (Condit et al., 2002; D. P. Edwards, Tobias, et al., 2014), can cause spatial aggregation in adult communities. Greater isolation of commercial species following logging could reduce total seed fall (Ghazoul et al., 1998) and concentrate seed predators around fewer individuals (Bagchi et al., 2011), potentially affecting multiple stages of seedling recruitment (Pillay et al., 2018). High ß-diversity of younger life stages is consistent with variation in recruitment success between sites (Krishnadas et al., 2019). Additionally, high sapling ß-diversity unrelated to adult turnover suggests only a subset of adult trees retained after logging are reproducing, possibly reflecting the effects of increased isolation on overall recruitment of commercial species.

Juvenile, but not sapling, ß-diversity was related to that of adults, suggesting altered adult distributions may have previously explained turnover in earlier life stages, with such effects fading over time since logging. This likely occurs when dispersal distances are limited, as they are for many commercial timber species in Borneo (J. R. Smith et al., 2015). Thus, younger life stages may have become increasingly spatially varied post-logging due to greater isolation of reproductive adults limiting dispersal. Increased dispersal limitations following logging could, therefore, contribute to the weakening of stabilizing mechanisms that maintain forest diversity (Chisholm & Fung, 2020; Stump & Comita, 2018).

4.52 High turnover and low nestedness drive changes in ß-diversity

Consistent with the replacement of commercial species with early successional species in logged forests (Berry et al., 2008), community dissimilarity between sites was almost entirely driven by the replacement of species. Steeper decay of similarity across environmental and spatial distance when using abundance-based ß-diversity indices also suggests a proportion of turnover was driven by changes in the abundances of species. This pattern was strongest for saplings and diminished in larger life stages, likely reflecting greater aggregation of younger life stages.

4.53 Drivers of local-scale ß-diversity & use of null models

The spatial scale at which ß-diversity is assessed is a key factor governing patterns and mechanisms of compositional change (Arita & Rodríguez, 2002; Chase & Knight, 2013; Chase & Myers, 2011), with ß-diversity at varying spatial scales reflecting the relative importance of different community assembly processes (Chase et al., 2011). Small spatial scales can limit environmental heterogeneity between sites and isolation and dispersal limitations of individuals (Jérôme Chave & Leigh, 2002; Tello et al., 2015).

Thus, small-scale studies of ecological change can underestimate the relative importance of local processes in governing turnover (Orrock & Watling, 2010). Although sample points in our study were spatially clustered, environmental heterogeneity was high, with disturbance measures varying substantially between points.

Many tree species in Borneo have extremely localised seed dispersal. For example, many dipterocarps rarely disperse seeds further than ~30 m (J. R. Smith et al., 2015). Thus, the small spatial scale of our study is likely both relevant to the local-scale mosaic patterns of logging disturbances (Berry et al., 2008), and depict somewhat complete gradients of within-forest disturbance and dispersal. Given the fine scale nature of logging disturbances, our findings suggest that the effects of within-forest disturbance on ß-diversity may be ecologically insignificant at larger scales. For example, when communities are compared across entire logging concessions, each sample unit may encompass near-complete gradients of small-scale disturbance. Further work is required to test this hypothesis but could yield important insights into large-scale diversity patterns of heavily logged regions.

The various classes of ß-diversity indices (classical and multivariate, additive and multiplicative) are dependent on variation in local (α-diversity) and regional (γ-diversity) diversity (Chase et al., 2011; Whittaker, 1972). For example, processes causing variation in local diversity or community size between sample points can alter community dissimilarity, confounding comparison of ß-diversity (Anderson et al., 2011; Kraft et al., 2011). Such neutral sampling effects can be accounted for using null models and calculation of ß-deviation (Chase & Myers, 2011; Kraft et al., 2011), whereby stochastic effects are removed to give estimates of ß-diversity based solely on local assembly mechanisms. We were unable to use ß-deviations within a GDM framework as all values must be 0-1 bounded, instead neutral sampling effects were accounted for by including null model ß-diversity as predictors of observed dissimilarity. Although, null-model dissimilarity was significantly related to ß-diversity for all life stages and indices, observed ß-diversity was consistently greater than that predicted by null models excluding non-random assembly mechanisms. While a proportion of observed ß-diversity within our study results from local variation in α-diversity and community size between sample points, variation in local assembly processes are responsible for the majority of turnover.

Other environmental gradients could contribute to patterns of logged forest tree ß-diversity. For example, edaphic and topographic factors drive significant components of tree community turnover (John et al., 2007; Poulsen, Tuomisto, & Balslev, 2006). However, logging teams often avoid steep slopes, which influence soil properties, potentially confounding patterns of adult extraction. Without tracking temporal changes in pre- and post-logging diversity and within-forest disturbance, it is difficult to select ideal measures of environmental heterogeneity. However, our measures encompass aspects of within-forest disturbance influenced by logging, including altered biotic interactions, microclimates, and recruitment limitations, which can influence deterministic community assembly mechanisms that filter species identity and abundance (Tello et al., 2015).

4.54 Persistent compositional turnover in selectively logged forests

Our study sites were more intensively logged than those of comparable Bornean studies (Berry et al., 2008; Mahayani et al., 2020). Consistently high ß-diversity suggests successive logging does not homogenize tree communities (Socolar et al., 2016), mirroring responses of other taxa (D. P. Edwards et al., 2011). Conversely, persistent turnover 12 years after successive logging indicates forests are not recovering pre-harvest composition. Marginally higher turnover in earlier life stages suggests turnover will persist for decades (Osazuma-Peters et al 2015) or that altered forest communities represent a new baseline.

Although numerous studies demonstrate the considerable value of logged forests for biodiversity (D. P. Edwards et al., 2011; F. A. Edwards et al., 2014; Gibson et al., 2011), our findings of substantial spatial impacts on diversity patterns echo suggestions that selective logging is a driver of degradation (Osazuwa-Peters, Jiménez, et al., 2015). Logged forests' ability to regain timber and carbon value to support subsequent harvests is pivotal in reducing the risk of conversion to plantations (Fisher et al., 2011). Given the narrow functional characteristics of commercial species, restoring the commercial value of logged forests is partly dependent on restoring old-growth forest composition. Without concurrent compositional recovery, future forests could have decoupled diversity and carbon values

(Sullivan et al., 2017), further underlining the need to moderate logging intensities (Burivalova et al., 2014), use reduced-impact harvesting techniques (Bicknell, Struebig, & Davies, 2015), and implement forest restoration practices (Cerullo & Edwards, 2019) to maintain and recover forest diversity.

4.6 Conclusion

Overall, we find the spatial arrangement of logged forest sapling, juvenile, and adult tree communities is more diversified than expected. Local-scale patterns of ß-diversity, across life stages, likely reflect changes to local community assembly processes related to the aggregation and isolation of adult trees, as opposed to greater environmental heterogeneity following logging. Such patterns may influence the ability of diversity enhancing mechanisms to maintain logged forest tree diversity and highlights the need to assess drivers of community change at different stages of tree development. Further study is necessary to assess whether such patterns can be extrapolated to larger spatial scales and should include temporal variation in a greater breadth of within-forest disturbance measures.

4.7 Acknowledgements

We thank all staff at the Malua Research Station and involved members at the South East Asia Rainforest Research Program (SEARRP) for logistical support; and Remmy Murinus, Udin Jaga, Jude, Ridly, Eglie, Japin Rasiun, Vendi Vens Aishiteru, Viddi Saidi, Mohammad Fauzi Osman, Yvonne Koid Qian Qun, Emma Watson, Daniel Simonsen, Lucy Watson, Rob Davies, Gillian Gabriel Gallus Gawis, Grace Juman, Rui Wong Yu, and Frolyin Felix for field assistance. P.G.C was funded by a PhD studentship from the Leverhulme Trust’s Centre for Advanced Biological Modelling (CABM). We also extend our thanks to the Sabah Biodiversity Council, Yayasan Sabah and Sabah Forestry Department, Danum Valley Management Committee, the State Secretary, Sabah Chief Minister's Department, and the Malaysian Economic Planning Unit, for site access and research permissions.

CHAPTER 5

PATTERNS OF TRAIT SIMILARITY ALONG LIANA INFESTATION GRADIENTS IN A SELECTIVELY LOGGED TROPICAL FOREST

5.1 Abstract

Lianas are generalist parasites of trees that alter forest composition by unequally effecting tree species' growth, survival, and reproduction. The strength of these effects and overall rates of infestation are heavily mediated by host functional traits, with lower mortality and greater infestation of tree species that are more prone to, but more tolerant of, liana infestation. A key question is whether the proliferation of lianas after selective logging operations corresponds to patterns of functional simplification in tree community composition. Here, we combine local liana infestation rates and tree community data at different life stages with species' functional trait data, to examine patterns of tree community trait similarity (trait convergence vs divergence) along strong gradients of liana infestation in an intensively logged tropical forest. We find that sapling, juvenile, and adult tree communities exhibited functional trait divergence following logging. Encompassing trees at all stages of liana infestation, patterns of trait similarity across life stages were only modestly associated with gradients of liana infestation and were better explained by variation in the spatial arrangement of sample plots. Liana infestation was also associated with only minimal changes to community-weighted trait values. Our findings demonstrate the variable and dynamic nature of liana infestation in perturbed forest systems and highlight that, despite the substantial effects of lianas on host composition, local patterns of infestation do not translate to equivalent patterns in tree functional composition.

5.2 Introduction

Lianas (woody-vines) are a characteristic and ubiquitous component of tropical forests. As structural parasites, lianas outcompete trees for above- and below-ground resources via decoupled growth-survival trade-offs, relative to trees (van der Sande, Poorter, Schnitzer, Engelbrecht, & Markesteijn, 2019). As a result, lianas negatively affect host tree reproduction, growth, and survival (García León et al., 2018; Ingwell et al., 2010; Martínez-Izquierdo et al., 2016), significantly impeding forest-level biomass and carbon accumulation at high liana densities (di Porcia e Brugnera et al., 2019; Van Der Heijden, Powers, & Schnitzer, 2015).

Lianas often proliferate dramatically following forest disturbance (Chandler et al., 2021; Magrach et al., 2016; Schnitzer & Bongers, 2011), in particular following selective logging, the most pervasive tropical forest disturbance (D. P. Edwards, Tobias, et al., 2014). For example, liana abundances in logged forests can more than double following intensive harvest operations, with modified liana composition substantially altering liana-tree interaction networks (Magrach et al., 2016). Such increases are posited to amplify the detrimental effects of lianas on persisting tree communities that have already undergone significant alterations as a result of selective timber harvests, including reduced representation of dominant late-successional species (Berry et al., 2008; Slik, Verburg, & Kessler, 2002). However, the interactions between disturbance-amplified liana loads and the altered functional characteristics of logged forest tree communities remain poorly understood.

Plant functional traits can mediate species' demographic responses to disturbance (Hogan et al., 2018; Lai, Chong, Yee, Tan, & van Breugel, 2020) and are often used to infer altered community reassembly mechanisms and forest recovery trajectories (Berenguer et al., 2018; Döbert, Webber, Sugau, Dickinson, & Didham, 2017). Following disturbances, novel environmental conditions may filter competitively weak species possessing 'non-adapted' functional traits, driving patterns of increased trait similarity (trait convergence). Alternatively, disturbances that increase local-scale environmental heterogeneity may result in patterns of trait divergence, as functionally dissimilar species are able to occupy the greater breadth of ecological conditions. The simplification of community's functional attributes following disturbances can negatively affect overall ecosystem stability, resilience to further disturbance, and provision of ecological functions (Cardinale et al., 2012; Elmqvist et al., 2003).

Increasing logging intensity often simplifies plant community functional composition, decreasing functional dispersion of understory of plant communities in Borneo (Döbert et al., 2017) and increasing functional evenness of juvenile trees in French Guiana (Baraloto et al., 2012). Logged tree communities also exhibit increased clustering of trait values, with greater representation of species with low wood density, lighter seeds, and higher specific leaf area (Hogan et al., 2018). However, few studies have sought to examine patterns of trait similarity along key gradients of within-forest disturbance associated with logging intensity. A key unanswered question is whether steep gradients of liana infestation following logging relate to variation in the functional composition of tree communities, corresponding to patterns of trait convergence in areas of high liana abundance.

Within logged forests, local-scale liana infestation and the functional composition of host tree communities is likely to be interdependent, with both contributing to the functional and physical characteristics of logged forests. Lianas differentially affect host tree species (Magrach et al., 2016; Muller-Landau & Visser, 2019), with the level of infestation reflecting host species' ability to avoid or tolerate lianas, and strongly mediated by host functional traits (Visser, Muller-Landau, et al., 2018; Visser, Schnitzer, et al., 2018). For example, tree species with fast growth rates, flexible stems, smooth bark, and large compound leaves are more likely to outgrow or avoid liana infestation, but also more likely to die if infested (Putz, 1980; Sfair, Weiser, Martins, Vidal, & Guimarães, 2018; Visser, Muller-Landau, et al., 2018). In contrast, dense wooded and slow-growing species are better adapted to tolerate the increased liana loads they fail to avoid (Visser, Muller-Landau, et al., 2018). Thus, increasing liana densities that filter tree communities along the liana avoidance-tolerance axes may result in patterns of trait convergence and altered community trait distributions. For example, lianas have already been demonstrated to severely impede the recovery of community-level wood density following selective logging in eastern Amazonia (Berenguer et al., 2018).

The functional composition of existing local tree communities is also likely to shape the distribution of liana abundances following logging. Dense liana tangles and high canopy infestation rates may be more likely to accrue where existing functional trait composition is more favourable to liana infestation. Indeed, local-scale liana prevalence is driven by structural variables relating to species traits, as opposed to local environmental conditions (Reis et al., 2020). As a result, lianas are likely symptomatic of disturbance and architects of perturbed plant communities, reflecting both altered functional composition of trees following logging and the resulting survivorship bias of liana infested trees. Understanding how liana infestation and tree community composition interact is of core importance for predicting the successional trajectories of disturbed forests (Marshall et al., 2020).

The effects of logging activity and associated liana loads are likely to result in different patterns of trait convergence versus divergence between life stages. Contrasting selection pressures and disturbance histories early in recruitment will shape communities at different life stages, including their functional trait composition (Hogan et al., 2018). For example, adult tree communities are the result of undisturbed forest assembly mechanisms early in recruitment, but also the filtering of commercial timber and liana-sensitive species following logging operations and the subsequent liana proliferation, once matured (Muller-Landau & Visser, 2019; Slik et al., 2002). In contrast, earlier life stages are the product of reduced seed crops, seed germination, and greater vertebrate seed predation following logging (Bagchi et al., 2011; Pillay et al., 2018). Impeded reproduction of liana-infested adults (García León et al., 2018) and increased competition with higher abundances of more competitive liana seedlings (Luskin, Ickes, Yao, & Davies, 2019; Tymen et al., 2016) then further shape communities of early life stages. Although rare, studies examining the responses of multiple life stages of trees to disturbance are key to understanding future assembly, with important implications for the restoration of logged forests.

Here, we examine patterns of trait similarity for sapling, juvenile, and adult tree communities along gradients of liana infestation within a twice-logged tropical forest in Borneo. We compare the degree of functional trait convergence and divergence, accounting for differences in species richness and abundance. Specifically, we address three key objectives: i) determine whether patterns of trait similarity differ between life stages, reflecting different selection pressures and disturbance histories early in recruitment; ii) test whether trait similarity patterns differ across gradients of increasing liana infestation, with high liana densities relating to increased trait convergence; and iii) evaluate whether the impact of liana infestation on trait similarity and individual trait distributions differ between life stages.

5.3 Methods and Materials

5.31 Study area

Sampling was conducted in the Yayasan Sabah Forest Management Area (YSFMA), a 10,000 km^2 contiguous lowland dipterocarp production forest in Sabah, Malaysian Borneo. Sample sites were located within three neighbouring compartments of the subsidiary Ulu Segama-Malua Forest Reserve (N05°05′20″ E117°38′32″; 102 m a.s.l.). The reserve was commercially selectively logged between 1970 and 1990, extracting 113 m^3 of timber per hectare using a minimum harvest diameter of 60 cm d.b.h and conventional high-lead and tractor extraction techniques (Fisher et al., 2011). The reserve was re-logged between 1999 and 2007, removing a further 31 m^3 ha^{-1}, and reducing the minimum cutting diameter to 40 cm d.b.h. Prior to the study, the forest had been left to naturally regenerate for ~12 years, with low average adult densities and greater representation of early successional pioneer species. The undulating topography of the region has contributed to small-scale mosaic patterns of logging intensity and disturbance (Berry et al., 2008), with some areas experiencing over double the average liana abundance and higher liana richness in logged relative to unlogged forests (Magrach et al., 2016).

5.32 Study design

We sampled three twice-logged forest sites each located more than 1 km apart and 100 m from existing logging road edges (Figure 4.1c). Two of the sites consisted of 16 sample blocks (200 x 200 m) and another site with an additional 4 blocks (totalling 36 blocks). Within each block, we established 5 sample plots (20 x 20 m) distributed randomly within the core 100 square meters of each block (Figure 4.1d and e; 36 blocks x 5 plots = 180 plots in total). Tree communities were sampled at three life stages:

saplings (> 50 cm tall and < 1 cm d.b.h; diameter at 1.3 m height), juveniles (≥ 1 cm d.b.h), and adults (≥ 10 cm d.b.h). Each life stage was sampled within a series of nested sub-plots (36 blocks x 5 plots x 3 life stages = 540 sub-plots in total), with juveniles censused within 2 x 3 m plots, juveniles in 5 x 20 m plots, and adults across the entire sample plot (Figure 4.1e).

5.33 Gradients of liana infestation

To assess relationships between tree communities and liana infestation, we recorded two measures of liana infestation at both the plot- and block-level. Liana infestation status (prevalence) was recorded for all adult trees, denoted as either a presence for infested individuals or absence for non-infested trees. Additionally, liana canopy infestation cover (load) was characterized on a 0-4 ordinal scale (Muller-Landau & Visser, 2019; Visser, Schnitzer, et al., 2018), with 0 indicating adult trees with liana free crowns, 1 indicating < 25 % crown coverage, 2 indicating 26-50 % crown coverage, 3 indicating 51-75 % crown coverage, and 4 when over 75 % of a trees crown is covered in lianas. Mean liana prevalence and load were then calculated at the plot- and block-level. Canopy load was calculated as the average midpoint of liana cover within each percentage class (1 to 4), weighted by abundance. Liana prevalence and load are influenced by both the rate of colonisation and loss of lianas, plus the survival rate of infested trees, whilst load also reflects liana canopy growth rates within host crowns (Muller-Landau & Visser, 2019).

5.34 Functional traits and phylogenetic imputation

To assess the effects of liana infestation on patterns of trait similarity, we compiled measurements for six key plant life-history traits for all focal tree species (*n* = 503). To capture trait variation across species and in relation to liana infestation, we included both general life-history traits (dispersal syndrome and leaf phenology type) and continuous morphological traits (specific leaf area, wood density, leaf nitrogen content, and mean mature height), including those specifically related to liana infestation (Table 5.1.). For example, specific leaf area and wood density represent key traits of both the leaf and wood economics spectra (Baraloto et al., 2010), and strongly relate to growth rate, reflecting species' ability to either avoid or tolerate liana infestation.

Trait values were obtained from various sources, including the TRY plant trait database (Kattge et al., 2011) and Global Wood Density Database (Jerome Chave et al., 2009; Zanne et al., 2009), as well as various additional studies (species trait coverage and additional sources listed in Table C3). Given the extremely high floristic diversity of lowland Bornean tropical forests, and the known sparsity of available trait data for predominantly rare tropical tree species (Döbert et al., 2017), we use phylogenetic imputation techniques to estimate missing trait values (Bruggeman, Heringa, & Brandt, 2009). To improve the statistical power of imputation analyses, we collated all available trait data for species within the 199 genera recorded from our study sites, totalling data for 5605 species. This extended trait matrix was then used to impute missing values for our 503 focal species, with initial species-level trait data obtained for between 24-59 % of species (Table C3). All incorporated traits, exhibited a strong phylogenetic signal (Table C2; Blomberg's *K* and Pagel's $\lambda = 0.59$-1.00), indicating more closely related species had more similar trait values. This means phylogenetic similarity may be reliably used to impute unknown values.

Missing values of continuous traits were imputed using the *Rphylopars* package (v 0.3.2, Goolsby, Bruggeman, & Ané, 2017), which accounts for species relatedness via branch lengths and outperforms other comparative imputation approaches (T. F. Johnson, Isaac, Paviolo, & González-Suárez, 2021). The package uses phylogenetic generalized linear models to impute missing values via phylogenetic covariances within a phylogenetic tree. For imputation, we generated a phylogenetic tree for all species with collated trait data (n = 5605) using the updated mega-phylogeny of plants - "Phytophylo" - as a backbone (available at https://github.com/jinyizju/, Qian & Jin, 2016). Botanical nomenclature for the study was standardised with that of *The Plant List* (v 1.1; http://www.theplantlist.org) using the *TPL* function in the *Taxonstand* package (Cayuela, Granzow-de la Cerda, Albuquerque, & Golicher, 2012). The resulting phylogenetic tree is completely resolved at both the family and genus level. For species absent from *Phytophylo,* we used Scenario 3 within the R function *S.PhyloMaker* to add species to the phylogeny based on their genus.

For discrete traits (dispersal syndrome and leaf phenology), non-conflicting genus-level values were assigned to species with missing trait values, following similar approaches by Berenguer *et al.*, 2018. We then used the imputed functional trait matrix for our focal species to create a dissimilarity matrix using Gower's distance via the *dist.ktab* function within the *ade4* package (Dray & Dufour, 2007), corresponding to pairwise differences between species in regard to all traits.

Table 5. 1. Description of the six functional plant traits (discrete = D, and continuous = C) and their related functions.

Trait	Type	Description	Function
Dispersal syndrome	D	Biotic and abiotic strategies and vectors of seed dispersal	Key life history strategy, influencing population dynamics, succession, competition and species' distributions.
Leaf phenology type	D	Leaf production strategy, timing of emergence, and longevity and rate of production.	Key plant life history strategy reflecting trade-offs of leaf production between rapid leaf turnover and costly physical structures.
Wood density (WD)	C	Ratio of oven dry mass to green volume (g cm^{-3})	Growth and mortality, resistance to splitting, bending, and provision of timber production and carbon accumulation.
Specific leaf area (SLA)	C	Fresh leaf per oven-dry mass (m^2 kg^{-1})	Influences canopy expansion, growth, light interception and capture.
Leaf nitrogen content (LNC)	C	Leaf nitrogen content per leaf dry mass mg/g	Light capture, photosynthetic rate.
Mean mature height	C	Average height of mature individuals (m)	Successional position, carbon accumulation, timber production.

5.35 Trait similarity patterns and null models

To assess whether trait similarity differed between tree life stages, we combined community and functional trait data within the null model approach outlined by F. A. Edwards, Edwards, Hamer, & Fayle, (2021). This approach compares observed patterns in the functional composition of communities to those of numerous null communities generated by chance to discern patterns of non-random trait assembly. First, we quantified differences in the functional composition of observed communities, at each sample point, using our generated dissimilarity matrix and species' abundances to calculate observed values of Rao's quadratic entropy (RaoQ) for each life stage separately. RaoQ represents the summed pairwise distances between species measured across all functional traits and weighted by their abundances (Botta-Dukát, 2005; Mouchet, Villéger, Mason, & Mouillot, 2010), reflecting the functional richness (trait breadth) and divergence (trait uniqueness) of each community.

To account for differences in richness, abundances, and trait composition between life stages, we then compare observed RaoQ values to those derived from simulated null models, by calculating the standardised effect size of RaoQ ($\mathrm{SES}_{\mathrm{RaoQ}}$), following Gotelli and McGill, (2006):

$$SES_{RaoQ} = (RaoQ_{obs} - \ RaoQ_{null}) / \ \sigma_{null}$$

Where $\mathrm{RoaQ}_{\mathrm{obs}}$, is the value of the observed community, and $\mathrm{RaoQ}_{\mathrm{null}}$ and σ_{null} are the mean and standard deviation of the null model indices. Thus, null values of RaoQ represent the functional composition of communities absent of non-random assembly mechanisms (i.e., when species in a community are no more or less functionally similar than expected by chance). In this way, community assembly mechanisms resulting in trait convergence are inferred by negative $\mathrm{SES}_{\mathrm{RaoQ}}$ (i.e., when communities are more functionally similar than expected by chance), whilst mechanisms resulting in trait divergence are inferred by positive $\mathrm{SES}_{\mathrm{RaoQ}}$ values (i.e., when communities are less functionally similar then expected by chance). Alternatively, when $\mathrm{SES}_{\mathrm{RaoQ}}$ is similar to zero, plant communities exhibit random trait assembly. We tested whether $\mathrm{SES}_{\mathrm{RaoQ}}$ values differed significantly from zero using Student's t-tests.

The randomisation algorithm within different null models can substantially alter their ability to detect different community assembly mechanisms, and thus patterns of either convergence or divergence (Götzenberger et al., 2016). In particular, to differentiate between mechanisms of limiting similarity (trait divergence) and environmental filtering (trait convergence), alternative randomisation algorithms can be selected to either remove or retain the relationship between species' abundances and trait values (F. A. Edwards et al., 2021). As a result, we generate null expected values of RaoQ using two complementary null models that use two contrasting randomisation algorithms to specifically detect different non-random trait assembly:

1. Limiting similarity (LS) model: this detects trait divergence by randomising the abundances of co-occurring species within each sample community. In this way, relationships between species' abundances and functional trait values are removed whilst maintaining the overall species richness and total abundance of individuals within the sample community.
2. Environmental filtering (EF) model: this detects trait convergence by randomising the abundances of species across all sample points, whilst fixing species total abundances and frequencies. Here, relationships between species abundances and functional traits are preserved, giving greater ability to detect co-occurrence via environmental filtering.

Null models of limiting similarity (LS) and environmental filtering (EF) were generated using the *randomizematrix* function of the *picante* package (Kembel et al., 2010), corresponding to the 'richness' and 'frequency' arguments, respectively. Overall, RaoQ values were generated from 1000 iterations of each model, for each life stage separately, and at both the plot- and block-level.

5.36 Liana influences on trait convergence and divergence

To assess relationships between SES_{RaoQ} and liana infestation, we used linear mixed-effects models (LMM) within the LME4 package (Bates et al., 2015). We only included either liana prevalence or liana load as fixed predictors. Prior to model fitting, we log-transformed liana prevalence and scaled all variables. As sample plots were nested within blocks and blocks within sites, we included the spatial arrangement of plots as a nested random effect in all models. Although basal area was influential in driving plot-level liana infestation at our site (Analysis C1.1, Appendix C), random slopes of basal area were not included in models due to high singularity in resulting models. We then calculated marginal and conditional R^2-values to apportion the variance explained by just liana infestation, and by both liana infestation and the spatial arrangement of sample points, respectively.

5.37 Liana influences on community trait means

We calculated community-weighted trait means (CWM) for each of the four continuous traits to examine whether lianas influence trait distributions within communities. CWMs were generated for communities at each sample plot and block, and for each life stage independently, following Garnier et al. (2004). We used Pearson's correlation coefficients to discern significant associations between community trait means and liana canopy infestation.

5.4 Results

5.41 Patterns of trait similarity between life stages

We sampled 8720 individuals across all life stages, representing 263 sapling species, 432 juvenile species, and 229 adult species. When assessing community assembly patterns using null models that remove the relationships between species' abundances and traits (Figure 5.1a; models of limiting similarity), trait compositions of all life stages exhibited trait divergence at both the plot- (sapling; *t*-value = 5.52, d.f. = 158, $p < 0.001$, juvenile; *t*-value = 4.53, d.f. = 172, $p < 0.001$, adult; *t*-value = 4.51, d.f. = , $p < 0.001$) and block-level (juvenile; *t*-value = 5.09, d.f. = 35, $p < 0.01$; adult *t*-value = 3.91, d.f. = 35, $p < 0.01$). In contrast, when assessing community assembly patterns using null models that preserve the relationships between species' abundances and traits (Figure 5.1b; models of environmental filtering), juvenile community trait composition at the plot-level indicated trait convergence (*t*-value = -3.81, d.f. = 175, $p < 0.01$). In addition, sapling and adult communities at the plot-level, and communities of all life stages at the block-level exhibited patterns indistinguishable from random assembly.

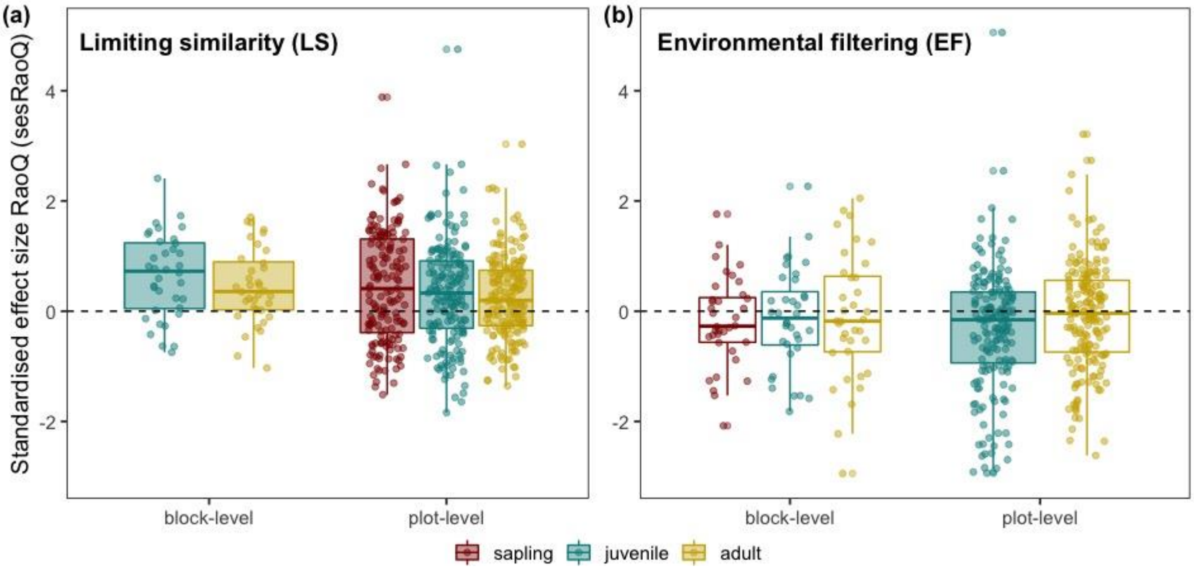

Figure 5. 1. Differences in trait-based community assembly mechanisms between sapling, juvenile, and adult trees at both the plot- and block-level. Trait-based assembly mechanisms inferred via standardised effect size of Rao's quadratic entropy (SES_{RaoQ}) of observed and null communities. Positive values denote trait divergence and negative values trait convergence. Null expected values derived from two complementary null models: limiting similarity (LS) models specifically detect trait divergences via limiting similarity (a), whilst environmental filtering (EF) models detect trait converge via environmental filtering (b). Expected values from LS and EF null models generated from 999 iterations of 'richness' and 'frequency' algorithms, respectively. Boxplots present median SES_{RaoQ}, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Filled box plots denote values significantly different to zero (patterns of non-random assembly), tested using Student's t-test ($p < 0.01$).

5.41 Liana influences on patterns of trait similarity

Gradients of liana infestation (prevalence and load) were related to other within-forest variables (Analysis C1.1, Appendix C), with adult basal area being the most important predictor of local-scale liana infestation (Figure C1). Liana infestation explained minimal variation in trait similarity (SES_{RaoQ}) across life stages, at either the plot- or block-level, or when using null models that specifically detect either trait convergence or divergence (Tables 5.1 & 5.2, Figure 5.2).

In the majority of models, fixed predictors of liana load and prevalence explained less variance in trait similarity than random effects describing the nested structure of sample plots (Table 5.1 & 5.2: Marginal R^2 = 0.0001-0.069, Conditional R^2 = 0.006-0.243). Only plot-level adult trait similarity was significantly related to mean liana canopy infestation (liana load), with adult communities demonstrating a slight shift to trait convergence with increasing canopy load (Figure 5.2a and e). Trait similarity for all life stages was unrelated to liana load at the block level, and to liana prevalence at either the plot- or block -level. However, although non-significant, the majority of LMM models (18 of 20 models) predicted a negative relationship between values of SES_{RaoQ} and liana load and prevalence, with either patterns of decreasing trait divergence or increasing trait convergence (Tables 5.1 & 5.2, Figure 5.2).

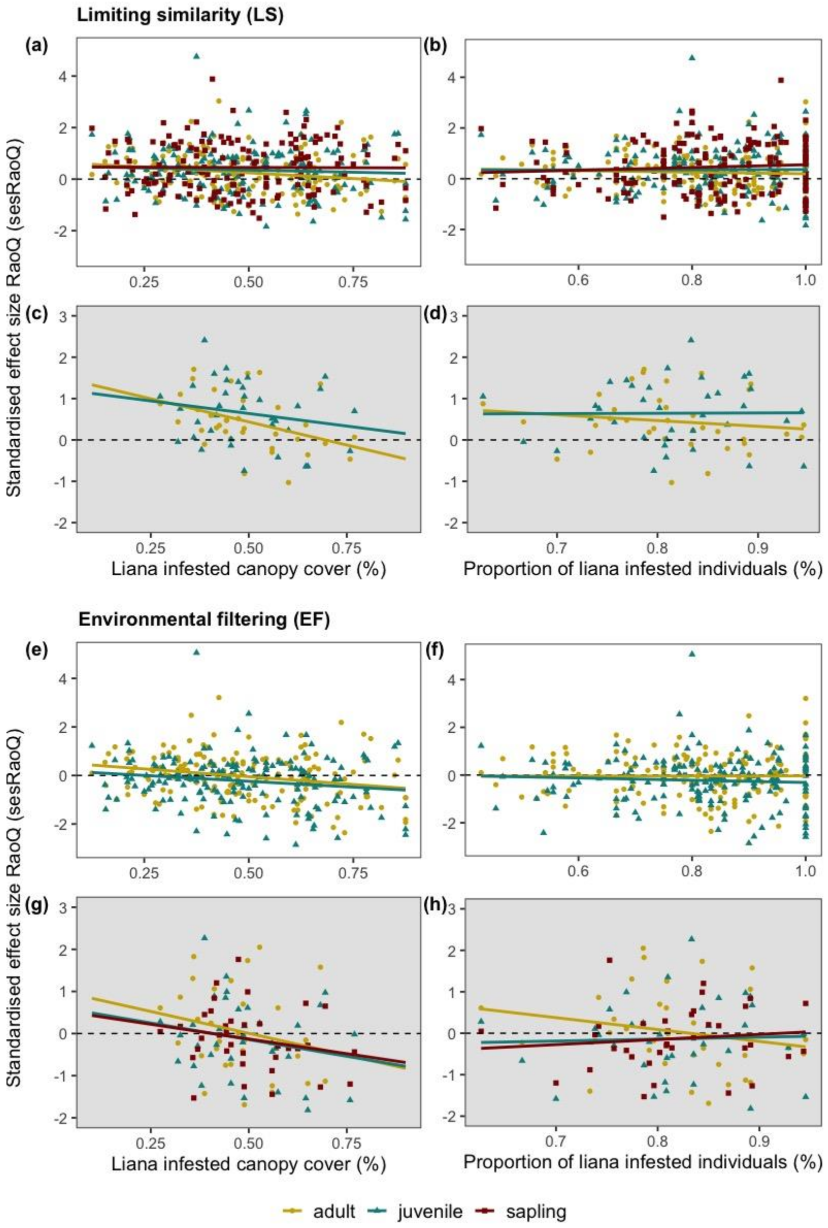

Figure 5. 2. Changes in the degree of community trait convergence and divergence across gradients of liana infestation for sapling, juvenile, and adult trees. Convergence or divergence of communities' functional composition inferred from the standardised effect size of Rao's quadratic entropy (SES_{RaoQ}) of observed and null communities at the plot-level (white filled plots) and block-level (grey shaded plots). Positive values denote trait divergence and negative values trait convergence. Null expected values derived from two complementary null models: limiting similarity (LS) models specifically detect trait divergences via limiting similarity (a, b, c, and d), whilst environmental filtering (EF) models detect trait converge via environmental filtering (e, f, g, and h). Expected values from LS and EF null models generated from 999 iterations of 'richness' and 'frequency' algorithms, respectively.

Table 5. 2. Summary statistics of linear mixed-models (LMM) of the relationship between SES_{RaoQ} values and liana infested canopy cover (liana load) for sapling, juvenile, and adult communities at both the plot- and block-level. SES_{RaoQ} values generated using null models of trait convergence (EF) or trait divergence (LS). Significant terms in bold. Marginal R^2 denotes variance explained by just liana infestation and conditional R^2 the variance explained by both liana infestation and the spatial arrangement of sample points as random effects.

Null model	Scale	Life stage	*Estimate*	*SE*	*P-value*	*Marginal R^2*	*Conditional R^2*
LS	Block	Adult	-0.185	0.119	0.131	0.073	0.199
LS	Block	Juvenile	-0.151	0.127	0.244	0.038	0.038
LS	Block	Sapling	-	-	-	-	-
EF	Block	Adult	-0.302	0.201	0.146	0.069	0.161
EF	Block	Juvenile	-0.1961	0.152	0.206	0.045	0.045
EF	Block	Sapling	-0.084	0.138	0.55	0.011	0.011
Null model	Scale	Life stage	*Estimate*	*SE*	*P-value*	*Marginal R^2*	*Conditional R^2*
LS	**Plot**	**Adult**	**-0.122**	**0.057**	**0.036**	**0.027**	**0.098**
LS	Plot	Juvenile	-0.024	0.077	0.737	0.0006	0.128
LS	Plot	Sapling	-0.027	0.082	0.773	0.0007	0.019
EF	**Plot**	**Adult**	**-0.158**	**0.075**	**0.037**	**0.026**	**0.171**
EF	Plot	Juvenile	-0.094	0.087	0.282	0.006	0.167
EF	Plot	Sapling	-	-	-	-	-

Table 5. 3. Summary statistics of linear mixed-models (LMM) of the relationship between SES_{RaoQ} values and the proportion of liana infested individuals (liana prevalence) for sapling, juvenile, and adult communities at both the plot- and block-level. SES_{RaoQ} values generated using null models of trait convergence (EF) or trait divergence (LS). Significant terms in bold. Marginal R^2 denotes variance explained by just liana infestation and conditional R^2 the variance explained by both liana infestation and the spatial arrangement of sample points as random effects.

Null model	Scale	Life stage	*Estimate*	*SE*	*P-value*	*Marginal R^2*	*Conditional R^2*
LS	Block	Adult	0.043	0.662	0.948	0.000	0.243
LS	Block	Juvenile	-0.015	0.784	0.984	0.000	0.065
LS	Block	Sapling	-	-	-	-	-
EF	Block	Adult	-0.375	1.129	0.741	0.002	0.223
EF	Block	Juvenile	-0.002	0.923	0.998	0.000	0.006
EF	Block	Sapling	-0.945	0.804	0.248	0.037	0.037
Null model	Scale	Life stage	*Estimate*	*SE*	*P-value*	*Marginal R^2*	*Conditional R^2*
LS	Plot	Adult	0.039	0.297	0.894	0.000	0.104
LS	Plot	Juvenile	-0.857	0.386	0.825	0.000	0.133
LS	Plot	Sapling	-0.248	0.433	0.568	0.002	0.009
EF	Plot	Adult	-0.281	0.379	0.460	0.000	0.104
EF	Plot	Juvenile	-0.033	0.432	0.938	0.000	0.182
EF	Plot	Sapling	-	-	-	-	-

5.42 Liana influences on community trait values

Relationships between community weighted trait means (CWM) and liana canopy infestation were inconsistent between scales and varied with life stage (Table 5.3, Figure 5.3 & 5.4). For adult communities, increasing canopy infestation was associated with greater community weighted wood density and SLA at the block-level (Figure 5.3c and f), and increasing SLA and LNC and declining mature height at the plot-level (Figure 5.4f, i, and l). For juvenile communities, mature height declined with increasing canopy infestation at both the plot- and block-level (Figures 5.3k and 5.4k), with greater community weighted SLA associated with increasing liana loads at the plot-level (Figure 5.3e). For sapling communities, community weighted values of all continuous traits were unrelated to canopy infestation at the plot-level, but with higher leaf nitrogen content associated with increasing liana loads at the block-level (Figure 5.4e).

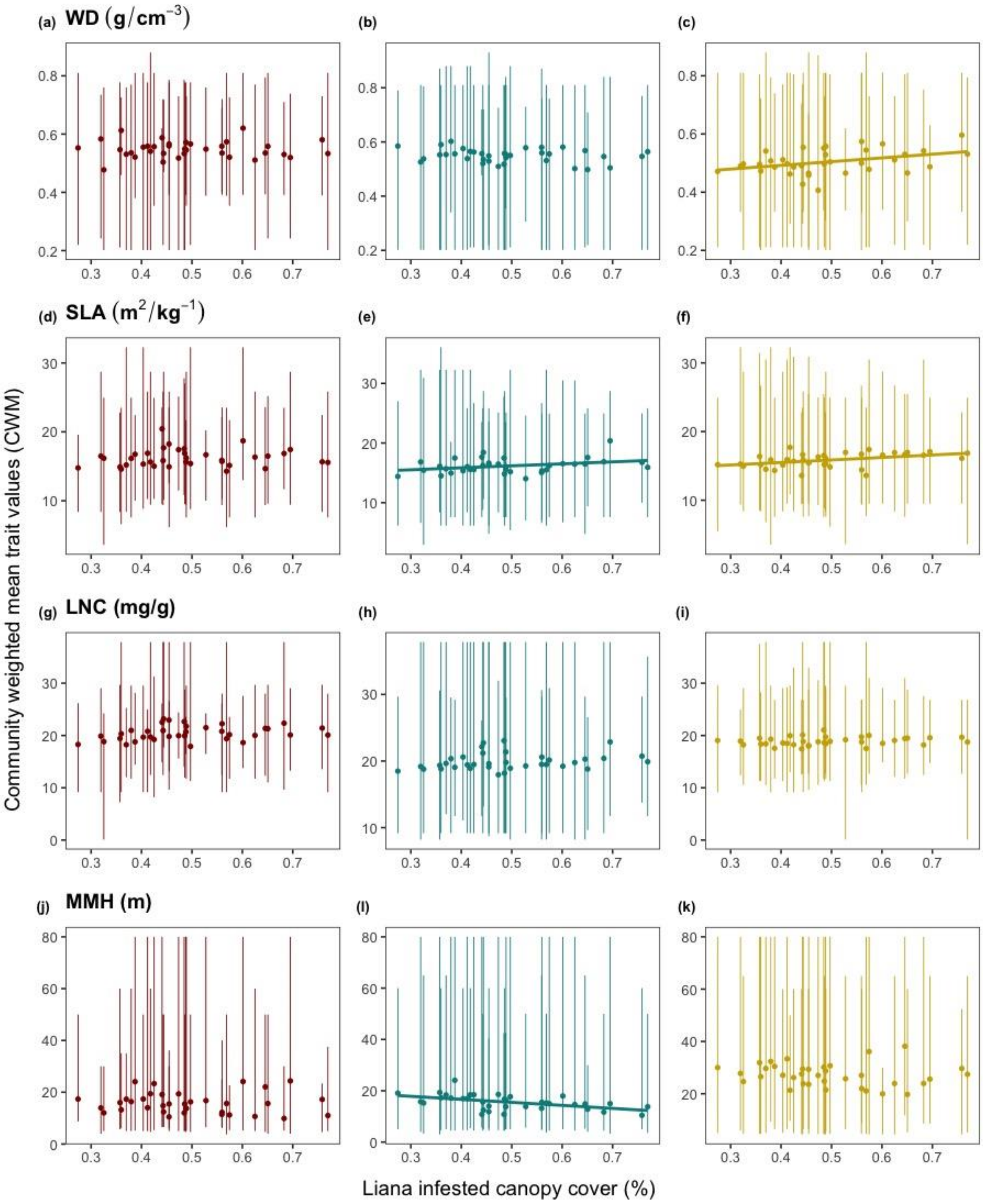

Figure 5. 3. Changes in the community weighted means (CWM) and ranges of individual morphological plant traits at each sample block across gradients of increasing liana infestation. CWM given for saplings (red; a, d, g, and j), juveniles (blue; b, e, h and k), and adults (yellow; c, f, i, and l) separately. Vertical bars indicate the maximum and minimum trait value of each community. Solid horizontal lines indicate significant correlation coefficients (Pearson's: $p < 0.05$). WD = wood density, SLA = specific leaf area, LNC = leaf nitrogen content per leaf dry mass, and MMH = mean mature height.

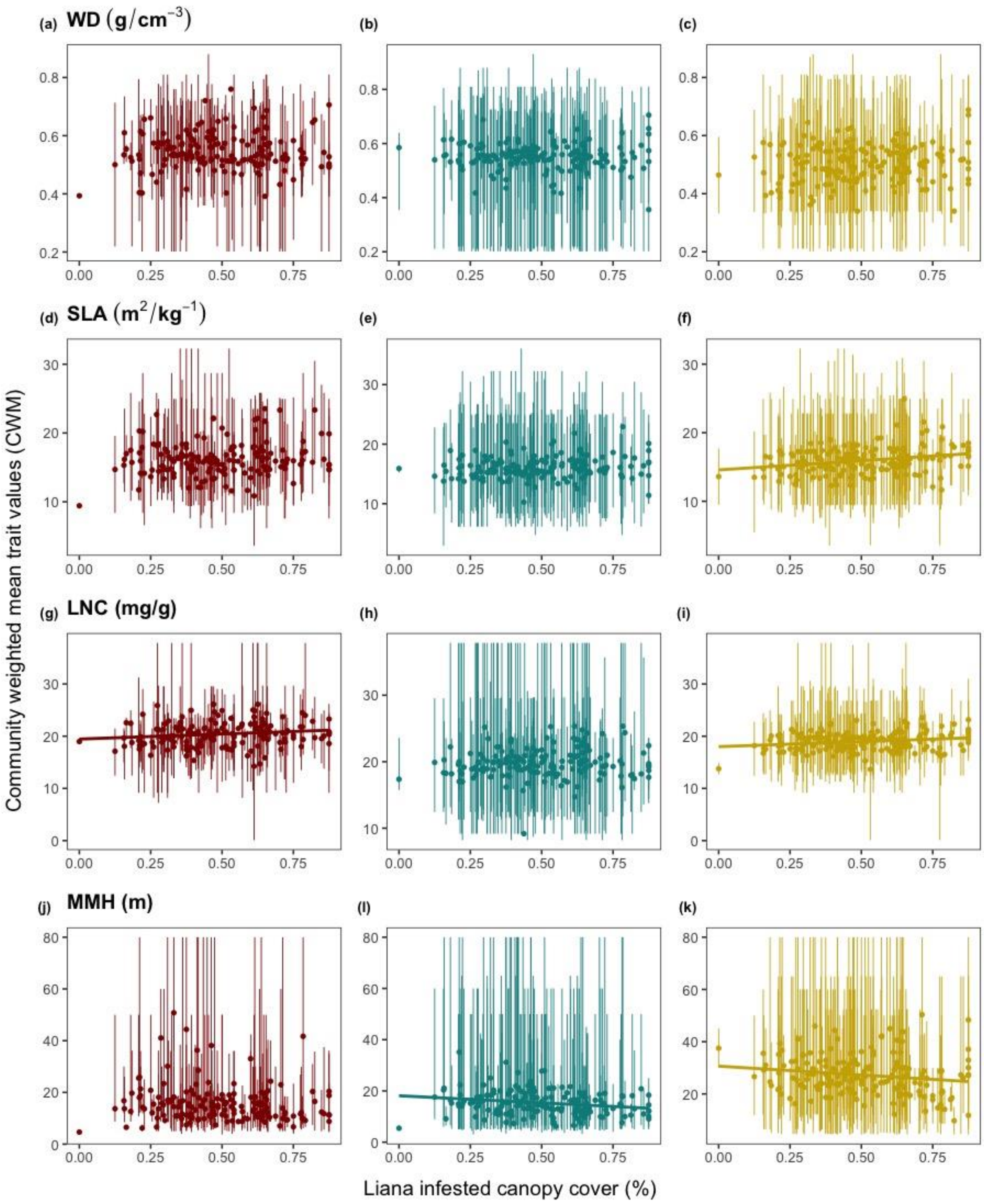

Figure 5. 4. Changes in the community weighted means (CWM) and ranges of individual morphological plant traits at each sample plot across gradients of increasing liana infestation. CWM given for saplings (red; a, d, g, and j), juveniles (blue; b, e, h, and k), and adults (yellow; c, f, i, and l) separately. Vertical bars indicate the maximum and minimum trait value of each community. Solid horizontal lines indicate statistically significant relationships from linear regressions ($p < 0.05$). WD = wood density, SLA = specific leaf area, LNC = leaf nitrogen content per leaf dry mass, and MMH = mean mature height.

Table 5. 4. Pearson's correlation coefficients and associated *p*-values of the relationship between community weighted trait means (CWM) and liana infested canopy cover (liana load) for sapling, juvenile, and adult communities at both the plot- and block-level. Significant terms in bold.

Liana Prevalence		Plot-level		Block-level	
Trait	Life stage	R^2	*P-value*	R^2	*P-value*
Wood density	Adult	0.129	0.084	**0.385**	**0.020**
	Juvenile	-0.028	0.719	-0.238	0.16
	Sapling	0.028	0.716	-0.008	0.962
Specific leaf area	Adult	**0.266**	**0.000**	**0.439**	**0.007**
	Juvenile	0.147	0.052	**0.337**	**0.043**
	Sapling	0.147	0.058	0.072	0.672
Leaf nitrogen content	Adult	**0.210**	**0.004**	0.197	0.247
	Juvenile	0.119	0.116	0.256	0.131
	Sapling	**0.156**	**0.044**	0.289	0.087
Mean mature height	Adult	**-0.171**	**0.021**	-0.160	0.348
	Juvenile	**-0.216**	**0.004**	**-0.506**	**0.001**
	Sapling	-0116	0134	-0.044	0.796

5.5 Discussion

Lianas are an important component of perturbed tropical forests, modifying forest structure, composition, and ecosystem function (Chandler et al., 2021; Magrach et al., 2016; Van Der Heijden et al., 2015; Visser, Muller-Landau, et al., 2018). Increasing liana loads in logged forests have the potential to severely impede the provision of ecosystem services, progression towards forest restoration targets, and contributions to the global carbon cycle (di Porcia e Brugnera et al., 2019; Marshall et al., 2020).

Despite consistent patterns of functional simplification and trait convergence following selective logging in both the Neotropics and Asian tropics (Baraloto et al., 2012; Döbert et al., 2017; Hogan et al., 2018), we find limited evidence that substantial variation in liana infestation following logging operations contributes to patterns of trait similarity in sapling, juvenile, or adult tree communities. Variation in tree community functional composition was similar between life stages and was better explained by spatial variation in sample plots, as opposed to liana infestation. In addition, liana infestation was only associated with modest shifts in community trait values. Our work is the first to specifically examine patterns of trait similarity in tree communities across gradients of liana infestation. We find that, despite the potential importance of lianas in altering forest tree composition (Muller-Landau & Visser, 2019; Visser, Schnitzer, et al., 2018), local-scale patterns of liana infestation do not strongly relate to the simplification of host tree functional composition following logging, suggesting logging intensity represents a significantly more important modifier of tree functional composition.

5.51 Trait divergence following selective logging and across tree life stages

In contrast to previous patterns of trait convergence in plant communities following logging in North-eastern Borneo (Döbert et al., 2017), we found that communities at all life stages are more functionally diverse than expected, with trait divergence greatest in earlier life stages. Consistent with increased diversity following intermediate disturbances (Imai et al., 2016), this finding likely reflects the persistence of reduced abundances of commercial species following extractions, and the increased recruitment of fast-growing and functionally dissimilar pioneer species in the 12 years after logging (Berry et al., 2008). Such findings are supported by our previous work demonstrating persistent patterns of high beta-diversity in tree communities following harvests in the same forest sites (Chapter 4). Moreover, the consistency of trait divergence across tree life stages suggests that commercial species are still present in all life stages, with the greatest trait divergence in sapling communities likely reflecting the faster responses of the earlier life stages of pioneer species to disturbances.

5.52 Influence of lianas on patterns of trait similarity

Consistent with the hypothesis that lianas alter tree composition by differentially effecting species' vital rates and with such effects heavily mediated by host functional traits (Muller-Landau & Visser, 2019; Visser, Schnitzer, et al., 2018), we expected lianas to relate strongly to patterns of trait convergence. Conversely, we found minimal effects of liana prevalence or canopy load on patterns of trait similarity. This finding is likely partly explained by liana infestation and its effects on host composition being both variable and temporally dynamic, with lagged responses between infestation and potential shifts in host composition. For example, although colonization by lianas is lower for hosts possessing liana avoidance traits (Putz, 1980; Sfair et al., 2018; Visser, Muller-Landau, et al., 2018), some will still fail to avoid infestation. Colonization of liana-avoiding species will occur where conditions facilitate proliferation, such as following relative dry periods or severe disturbance (Schnitzer & van der Heijden, 2019), or where infested neighbours enable lateral colonization, bypassing many avoidance strategies (Van der, Geertje, Healey, & Phillips, 2008). In addition, liana prone hosts will not die immediately after infestation, with intraspecific mortality rates varying with species stature (Visser, Schnitzer, et al., 2018). As a result, 'snapshots' of liana infestation will include trees at varying stages of colonization, shedding, and mortality, weakening the signal between local infestation and observed trait similarity.

That liana infestation does not mirror logging activity in its substantial influence on patterns of trait convergence in tree communities likely demonstrates a spatial decoupling between logging activity and liana infestation. For example, lianas do not occur exclusively in areas of logging activity, with natural aggregations at tree fall gaps and forest edges (Campbell et al., 2018; Schnitzer & Bongers, 2002). Additionally, even where logging intensity is high, lianas may not always proliferate. Areas of intensive local logging activity may remain relatively liana-free if fast-growing species possessing liana-avoidance traits remain undamaged and quickly fill the canopy. Models including the spatial arrangement of sample plots explained a greater proportion of variance in trait similarity, suggesting that spatial variation in logging intensity, as opposed to resultant liana infestation, is more important in governing patterns of trait similarity.

5.53 Other processes of community assembly

The composition of complex forest plant communities is modulated by a number of assembly mechanisms and influenced by numerous interacting abiotic and biotic variables (Mayfield & Levine, 2010). Species are filtered across a number of environmental gradients, whilst variation in competitive ability organise species along key resource-use gradients via niche partitioning (Hardin, 1960; Weiher & Keddy, 1995). In addition, processes such as dispersal ability mediate species' responses to seedling density, predation, and herbivore grazing (Muller-Landau & Adler, 2007). These mechanisms have operated before logging and well before the subsequent colonisation of communities by lianas. Consequently, lianas represent just one of a plethora of interacting factors shaping the taxonomic and functional composition of tropical forests. It is perhaps unsurprising, therefore, that we find little evidence of strong signals between infestation and host trait similarity.

Despite the complexity of community assembly mechanisms that structure tree assemblages, community similarity declined with liana infestation for the vast majority life stages and spatial scales. This finding suggests that lianas do, in part, modulate host tree functional composition. However, the overall weak association between liana infestation and patterns of host trait similarity suggests experimental manipulation of liana densities may be required to quantify liana effects on tree composition. Such manipulations have already contributed substantially to our understanding of liana-tree interactions (Estrada-Villegas and Schnitzer, 2018) and may provide additional opportunities to disentangle the interdependencies between liana infestation and tree composition. For example, examining whether lianas infest functionally similar species following removal, reflecting colonization rates mediated by host functional traits.

Lianas themselves represent a highly diverse plant group (Schnitzer & Bongers, 2002), with liana species varying substantially in their detrimental effects on trees and mediated by their functional traits (Ichihashi & Tateno, 2011). Thus, the effects of lianas on hosts and overall rates of infestation likely depend on the functional composition of both lianas and trees, with interactions between the two potentially contributing to differences in tree species niches (Muller-Landau & Visser, 2019). Additionally, lianas and trees respond differently to selective logging (Guo, Zhao, Bu, & Yue, 2019), with potentially detrimental modifications to liana-tree interaction networks (Magrach et al., 2016). Patterns of liana trait similarity may more accurately predict spatial patterns of liana infestation, with important impacts on host composition. For example, disturbances resulting in the dominance of a few functionally similar liana species may coincide with areas of hyperabundant liana infestation. Quantifying the effects of different combinations of lianas and trees species on liana-tree interactions may provide insight into their effects on host functional composition.

5.54 Community trait means & host functional traits

Across life stages, we observed modest shifts in community trait means along gradients of liana infestation. Similar to patterns of community trait similarity, this result likely reflects the novel overall trend of functional diversification at our site, the temporal and spatial variation in liana infestation, and its contribution as just one of many interacting variables that either select or filter species' traits. Additionally, the majority of shifts in community trait values were observed for adult communities, whilst only liana canopy load and not liana prevalence related to declining trait divergence. Such findings are consistent with the idea that lianas predominantly influence adult trees by over-topping adult host leaves (Stewart & Schnitzer, 2017).

Functional diversity indices, and thus conclusions of trait similarity, are partly dependent on their constituent functional traits (Mouchet et al., 2010). Many plant traits directly related to liana infestation, however, are infrequently collected, owing to the overall sparsity of available trait data for the tens of thousands of tropical plant species (Döbert et al., 2017; Slik et al., 2015). For instance, measures of bark texture, growth rate, and branch-free bole-height are absent for the majority of tropical tree species at any one study site, yet are posited to strongly influence rates of liana infestation (Putz, 1980; Van der et al., 2008; Visser, Muller-Landau, et al., 2018). Our selected traits encompass a substantial proportion of variation along key axes of plant ecological strategy, relating to species' growth, survival and reproduction (Díaz et al., 2016). Importantly, traits relating to adult stature (mature height), leaf investment (specific leaf area and nitrogen content), and wood density represent the majority of global variation in plant life history strategies and consistently influence plants competitive interactions (Díaz et al., 2016; Kunstler et al., 2016).

5.6 Conclusion

Overall, we find that selective logging has a diversifying effect on the functional composition of tree communities at all life stages, with observed variation in functional trait similarity only minimally related to strong gradients of local-scale liana infestation. Our study highlights both the complexity of processes that govern the assembly of diverse plant assemblages and the variable and dynamic nature of liana infestation in disturbed forest systems. Further study is required to disentangle the interdependencies of host functional composition and local scale liana infestation, likely requiring the manipulation of liana densities and host composition. Such studies would also benefit from the inclusion of liana species diversity and associated variation in liana-tree interactions, to gain further understanding of the effects of lianas on tree communities and their functional traits.

5.7 Acknowledgements

We thank Datuk Dr Glen Reynolds and the South East Asia Rainforest Research Program (SEARRP), as well as site manager Remmy Murinus and the Malua research team, for research and logistical support. For site access and research permissions, we thank the Sabah Biodiversity Council, Yayasan Sabah and Sabah Forestry Department, Danum Valley Management Committee, the State Secretary, Sabah Chief Minister's Department and the Malaysian Economic Planning Unit. Additionally, we thank research assistants Udin Jaga, Jude, Ridly, Eglie, Japin Rasiun, Vendi Vens Aishiteru, Viddi Saidi, Mohammad Fauzi Osman, Yvonne Koid Qian Qun, Emma Watson, Daniel Simonsen, Lucy Watson, Rob Davies, Gillian Gabriel Gallus Gawis, Grace Juman, Rui Wong Yu, and Frolyin Felix. P.G.C was funded by a PhD studentship from the Leverhulme Trust’s Centre for Advanced Biological Modelling (CABM).

CHAPTER ❻

GENERAL DISCUSSION

6.1 Summary

The conservation of tropical forests is integral to alleviating global forest and biodiversity loss and circumventing a collapse in the Earth's systems (Barlow et al., 2018; D. P. Edwards et al., 2019; Lewis et al., 2015; Malhi et al., 2014). Human-driven land-use change poses the greatest threat to tropical biodiversity, with commercial selective logging the most prevalent tropical land use (Asner et al., 2009; Matthew C. Hansen et al., 2008). The millions of hectares of already selectively logged forest now play a crucial role in tropical conservation, preventing significant further biodiversity losses from forest conversion to farmlands and plantations (D. P. Edwards, Tobias, et al., 2014; Gibson et al., 2011). The continued value of logged forests for tropical conservation is in part dependent on their recovery, with returns to primary forest plant composition predicted to take decades to centuries (Osazuwa-Peters, Jiménez, et al., 2015; Shima et al., 2018). Efforts to conserve tropical forests could be strengthened by a more detailed understanding of how anthropogenic disturbances alter forest diversity and dynamics, including the mechanisms and interactions that maintain diversity. The loss of complex interactions between plants and their natural enemies, for example, could cause the continued degradation of diversity many decades after initial disturbances. Two key areas of remaining research addressed in this thesis, are: 1) the extent to which well-established mechanisms of diversity enhancement are effective in maintaining tropical diversity, and are generalisable for forests outside the Neotropics, and 2) the extent to which selective logging and its associated effects have altered the composition of tropical tree communities, with implications for their long-term recovery.

The main aim of this thesis was to improve our understanding of the dynamics and resulting diversity patterns of the diverse tree assemblages of Borneo's selectively logged forests. First, using a manipulative shadehouse experiment, I found that unlike in Neotropical forests and species, fungal pathogens facilitate only weak negative density-dependent mortality, that is unlikely to promote diversity in Borneo's mast fruiting forests (Cannon et al., 2020). Reviewing recent modelling of coexistence mechanisms, we then found that variation in species' sensitivity to density-dependent mortality, as well as in their 'intrinsic fitness', form a number of scenarios in which C-NDD can degrade, as opposed to promote diversity (Cannon et al., 2021). Importantly, under all scenarios, limited seed dispersal quicky eroded community diversity. To determine how selective logging impacts the composition of diverse plant communities, we examined communities of multiple life stages of trees 12 years after two successive logging events in Borneo. We found evidence that persistent patterns of high spatial turnover in tree communities are the result of greater dispersal limitations from increasingly isolated and aggregated adult trees (Chapter 4). In contrast, increased environmental heterogeneity associated with logging, including variation in liana infestation, only modestly affected the spatial arrangement of tree communities. Consistent with this finding, when combining tree community data and liana infestation rates with freely available tree trait data in Chapter 5, we found that intensified liana infestation gradients were only modestly associated with declining trait similarity of trees following logging.

In the following sections I synthesise the results of the previous chapters to demonstrate how selective logging has impacted the composition of logged forest tree communities and how alterations to diversity enhancing mechanisms may mediate plant communities' responses to forest disturbance. To conclude, I discuss the conservation implications and provide recommendations for forest practitioners, highlighting directions of future work throughout.

6.2 Drivers of altered logged forest composition

It is often assumed that increased environmental heterogeneity resulting from logging facilitates increased spatial turnover of tree communities (Berry et al., 2008). The findings of Chapter 4, however, highlight that such spatial variation in within-forest disturbances is comparatively unimportant in driving compositional turnover relative to increased aggregation and isolation of adult trees following logging. Intensive logging harvests that remove a greater number of adult trees per hectare and result in greater isolation and aggregation of remnant adults could potentially cause longer term shifts in tree composition. As long-lived organisms, the full impacts of selective logging on tree communities will most probably only be realised centuries after logging events, with the continued loss of non-reproductive relics further degrading forest diversity (Rigueira et al., 2013). High spatial turnover of younger tree communities underlines persistent trends of stalled compositional recovery following logging, suggesting that forest communities may now be permanently altered (Chapter 4).

Evidence of the detrimental effects of prolific liana growth following forest disturbance increasingly suggests lianas play a key role in modifying tree composition and delaying forest recovery (Marshall et al., 2020; Visser, Schnitzer, et al., 2018). In Chapter 5, we further examined the role of environmental heterogeneity in modifying tree composition, by examining how gradients of logging-induced liana infestation influenced patterns of tree functional composition using tree functional trait data. Supporting findings of Chapter 4, we found that tree functional composition was largely unrelated to variation in liana infestation and was better explained by the spatial arrangement of plots. Thus, logging intensity may be a more important driver of variation in tree functional composition.

Further research is necessary to determine the timescales of compositional recovery post-logging. Forest models incorporating varying silvicultural practices (Ruslandi et al., 2017), competing vegetation types (di Porcia e Brugnera et al., 2019; Verbeeck & Kearsley, 2016), and changing climate conditions (He, Gustafson, & Lischke, 2017) have already provided valuable insight into forest recovery trajectories. Emphasis of future modelling should be placed on predicting forests comparatively lagged compositional responses to human disturbance.

6.3 Maintenance of tropical diversity

Previously, the vast majority of manipulative studies examining the role of fungal pathogens in maintaining forest diversity came from Neotropical forests, with 35% carried out at just two research stations in Panama and Belize (Appendix A; Table A.2). The findings from Chapter 2 demonstrate the pitfalls of assuming well-established drivers of diversity enhancement in Neotropical forests operate across presently unquantified tropical systems and regions. Diversity maintenance in wider masting systems and tropical montane and peat forests remain comparatively understudied, with studies across all forest types most lacking in African regions and in parts of the Indo-Pacific (Chapter 2).

Chapter 2 focused on empirically testing whether fungal driven C-NDD was present in a previously unquantified forest. However, demonstrating the presence of C-NDD, even across forests pantropically, does not directly test the effectives of C-NDD in promoting forest diversity. In Chapter 3, we highlight that the maintenance of tropical diversity is sensitive to two aspects of species' variation: variation in species' intrinsic fitness (population growth rate), and variation in species' sensitivity to C-NDD. Additionally, we highlight that diversity enhancing mechanisms can degrade, rather than promote diversity, when species experience limited dispersal. We find evidence of such dispersal effects in Chapter 4, with limited dispersal resulting from selective logging likely having shaped the persistent spatial arrangement of logged forest tree diversity. Given the widespread degradation of tropical forests globally (Barlow et al., 2018), how anthropogenic disturbances directly impact mechanisms of diversity maintenance represents a priority research direction. Such work could potentially reveal the mechanisms underpinning the lagged and persistent alterations to disturbed forest communities as well as their potential recovery trajectories.

Currently, little attention has been paid to how forest disturbances effect the mechanisms that prevent competitive exclusion. Forest degradation, however, has the potential to significantly impede the effectiveness of coexistence mechanisms by influencing all three aspects of species' variation highlighted in Chapter 3. Firstly, modified abiotic conditions (altered microclimates) and biotic interactions (liana-tree interactions) following logging can both modify or strengthen competitive differences between cooccurring species (Muller-Landau & Visser, 2019), potentially eroding species richness over time. Forest degradation may also directly interfere with species' sensitivity to C-NDD, as well as the overall strength of C-NDD mortality. For example, declining seasonality and precipitation under future climate change could reduce the capacity for plant pathogens to mediate coexistence mechanisms, with disease transmission dependent on humid forests conditions (Milici et al., 2020;

Swinfield et al., 2012). Such effects are likely heightened in degraded forests and have already been demonstrated in fragmented and edge-affected forests, with weakened activity of fungal pathogens and insect herbivores limiting tree diversity at forest edges (Krishnadas et al., 2018; Krishnadas & Stump, 2021). Coexistence mechanisms are probably similarly affected in severely degraded logged and fire damaged forests but remain untested. Finally, limited seed dispersal can degrade overall community diversity by increasing recruitment advantages for species insensitive to C-NDD (Chapter 3). Whilst we found indirect evidence of dispersal limitations altering patterns of tree diversity following logging (Chapter 4), loss of animal dispersers may also degrade diversity enhancement in over-hunted tropical forests (Caughlin et al., 2014).

Future research needs to address the substantial knowledge gaps surrounding how diversity is maintained, including: 1) assessing the mechanisms and drivers of diversity enhancement in a wider suite of tropical regions and forest types, 2) testing how these mechanisms are influenced by a diverse array of anthropogenic disturbances, and 3) how such disturbances influence the recovery of forest composition post-disturbance. Additionally, these knowledge gaps require ecologists to apply approaches that go beyond merely evidencing the presence of proposed mechanisms of diversity enhancement, and instead test their effectiveness in promoting diversity (Hülsmann et al., 2020) by incorporating variation in species sensitivity to C-NDD and their intrinsic fitness (Chisholm & Fung, 2020; Stump & Comita, 2018). Priority research sites for such work include Papua New Guinea and wider Malesia. Both regions have highly diverse and largely unquantified flora and are facing expanding selective logging operations and oil palm plantations (D. P. Edwards et al., 2019).

6.4 Conservation implications

We find evidence that persistent alterations to logged forest tree composition are the result of greater aggregation and isolation of fewer adult trees (Chapter 4). This finding suggests that the conservation of logged forests should focus on limiting the intensity of future harvests. Leaving a greater number of large, reproductive adult trees, would increase total landscape-scale seed production (Bagchi et al., 2011), and improve the size and potential viability of individual seed crops by increasing cross pollination between a greater number of less isolated remnant trees (Ghazoul et al., 1998; Pillay et al., 2018). Larger seed crops and seedling banks would also limit the concentration of generalist seed predators (Bagchi et al., 2011) that are responsible for the majority of seed mortality but do not contribute to diversity enhancement (Kurten & Carson, 2015).

Limiting the intensity of harvests, however, raises the important question of how current and future timber demands will be met. Although less intensively logged forests can be harvested more frequently, timber and biodiversity will degrade over successive operations, with rapid degradation when prematurely logged (Burivalova et al., 2014). Another option is to log more expansively, thus offsetting lost timber yields per hectare by logging more forest. Expansion of low intensity logging, however, will become increasingly difficult over time as the majority of accessible tropical forest has already been logged (Asner et al., 2009). Additionally, at the landscape-level, such land-sharing logging approaches are increasingly shown to conserve fewer species across taxa than more intensive logging, coupled with protection of spared intact forest (D. P. Edwards, Gilroy, et al., 2014; Griscom, Goodman, Burivalova, & Putz, 2018; Runting et al., 2019). Even low intensity harvests can cause declines in disturbance sensitive species (França, Frazão, Korasaki, Louzada, & Barlow, 2017). Alternatively, land-sparing approaches that retain primary forest reserves can act as refugia for disturbance sensitive species and facilitate recolonisation of seeds and species in to adjacent logged forests (Betts et al., 2021).

The success of land-sparing logging in concurrently meeting timber and biodiversity goals, is dependent on preventing biodiversity losses from logged forest conversion (Griscom et al., 2018; Runting et al., 2019). Unsustainable logging practices increase the risk of reclassification, salvage logging, and eventual conversion once depleted (D. P. Edwards, Tobias, et al., 2014). Secure land tenure, greater application of RIL techniques, and the rotation of intensive logging and restoration practices within larger timber concessions, can all alleviate risk of overharvesting whilst crucially retaining areas of old-growth forest (Betts et al., 2021; Cerullo & Edwards, 2019; D. P. Edwards, Tobias, et al., 2014; Putz et al., 2008). Such practices will likely also limit isolation and aggregation of adult trees and potentially limit interference with mechanisms promoting overall forest diversity. For example, preserving reproductive adults in adjacent primary forest could ensure the delivery of cross pollination services, disperse generalist seed predators, and boost total forest-wide seed production. Reducing overall logging damage could also limit the effects of harsh abiotic conditions on temperature sensitive natural enemies.

The costly adoption of sustainable logging and forest restoration practices, however, will require improvements to current financial incentives. For example at present, Forest Stewardship Certification (FSC) has been granted for less than 2% of tropical forests (D. P. Edwards et al., 2019) and FSC certified forests have similar biodiversity and carbon value and equivalent rates of deforestation as non-certified concessions (Campos-Cerqueira et al., 2020; Panlasigui, Rico-Straffon, Pfaff, Swenson, & Loucks, 2018). In Malaysian Borneo, unattainable carbon prices are currently required to offset ecologically successful restoration activities (Philipson *et al.*, 2020). Consequently, governments, forest practitioners, and conservationists must strive to provide new and improved strategies to incentivise the large-scale adoption of sustainable logging practices.

If land-sparing logging is suitably incentivised, areas of intensive timber extraction must still be minimised, thus simultaneously minimising areas at risk of greater compositional change (Chapter 4). Without a sharp and immediate decline in global timber demands, minimising the extent of intensive logging will likely require large-scale commercial timber plantations now widely advocated as part of emerging global reforestation agendas, such as REDD+ and the Bonn Challenge (Edwards & Cerullo et al., 2021). Robust policy is required to prevent leakage of biodiversity losses, alleviate negative ecological impacts, and ensure new plantations are fostered on abandoned agricultural lands (Betts et al. 2021; Edwards & Cerullo et al., 2021). Triad approaches combining limited and sustainable intensive logging, spared intact forest, and establishment of high-yielding plantations could allow large expanses of already logged forests to recover whilst satisfying global timber demands (Betts et al., 2021) and arguably go some way to mitigating global climate change (Elias et al., 2020; Girardin et al., 2021).

6.5 Conclusion

Explaining how the extraordinary but declining wealth of tropical diversity is maintained remains a central challenge in ecology. The effects of pervasive forest degradation on tropical biodiversity will become increasingly apparent over the next few decades, with the loss of vulnerable tropical biodiversity increasingly impacting human populations. The drivers of forest diversity enhancement vary between regions and forest types, with the effectiveness of mechanisms posited to maintain and structure tropical diversity sensitive to species' variations and vulnerable to anthropogenic disturbance. The severity of selective logging events will likely tightly govern the extent to which forest communities will recover from human perturbation. Conservationists should aim to reduce the impacts of future degradation on the diversity and dynamics of tropical forests to prevent long-term compositional shifts and permanent impairment of diversity enhancing mechanisms. Such an approach will require policy to incentivise the adoption of sustainable forestry and forest restoration practices, and renewed scientific interest in how diversity is maintained, to infer how it can be conserved.

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2

Table A. 1. Description of the eight lowland tree species used in the experiment. Relative abundance and stem densities calculated using data from the 50-Hectare Plot Project Danum Valley, part of the CTFS-ForestGEO network (Anderson-Teixeira et al., 2015).

Species	IUCN red list status	Relative abundance	Stems ha^{-2}	Total number of seedlings
Dryobalanops lanceolata Burck *	LC	0.10	5.26	264
Koompassia excelsa (Becc.) Taub. **	CD	0.01	0.70	264
Parashorea malaanonan Merr. *	LC	0.77	40.28	242
Scaphium macropodum Miq. ***	LC	0.02	1.08	242
Shorea johorensis Foxw. *	CR	0.88	46.70	242
Shorea leprosula Miq. *	NT	0.26	13.90	286
Shorea pauciflora King*	EN	0.09	4.96	264
Shorea symingtonii G.H.S.Wood *	VU	0.17	9.14	176

Tree species family: * *Dipterocarpaceae;* ** *Leguminosae;* *** *Malvaceae.*

1 **Table A. 2.** Tropical studies manipulating seed or seedling densities of trees.

Region	Location	Life stage	Natural enemy tested	No. of species	Species	Study
Neotropics	Barro Colorado Island, Panama	seedling	none	1	*Cordia alliodora*	Downey *et al.*, 2018
	Western Brazil	seed	none	1	*Dypterix alata*	Ragusa-Netto, 2017
	Chiquibul Forest, Belize	seed, seedling	fungal pathogen	5	*Acacia polyphylla,* *Cedrela odorata,* *Cordia alliodora* *Cryosophila stauracantha,* *Terminalia amazonia*	Gripenberg *et al.*, 2014
	Tinigua National Park, Colombia	seed	none	1	*Pachira quinata*	Castellanos and Stevenson, 2011
	Chiquibul Forest, Belize	seedling	fungal pathogen	1	*Pleradenophora longicuspis*	Bagchi *et al.*, 2010
	Pacaya-Samiria Reserve, Peru	seedling	none	2	*Garcinia macrophylla,* *Xylopia micans*	Anderson J. T, 2008

	Chiquibul Forest, Belize	seedling	fungal pathogen	1	*Pleradenophora longicuspis*	Bell, Freckleton and Lewis, 2006
	Barro Colorado Island, Panama	seed, seedling	none	1	*Tachigalia versicolor*	Augspurger and Kitajima, 1992
	Mexico	seed	none	1	*Cymbopetalum baillonii*	Coates-Estrada and Estrada, 1988
	Atlantic lowlands, Costa Rica	seedling	none	1	*Dipteryx panamensis*	Clark and Clark, 1985
	Barro Colorado Island, Panama	seedling	none	13	*Platypodium elegans,* *Lafoensia punicifolia,* *Pseudobombax septenatum,* *Triplaris cumingiana,* *Luehea seemannii,* *Tabebuia rosea,* *Cordia alliodora,* *Aspidosperma cruenata,* *Terminalia oblonga,*	Augspurger and Kelly, 1984

					Terminalia amazonica, *Ochroma pyramidale,* *Cochlospermum vitifolium,* *Ceiba penta*	
Afrotropics	North Eastern Gabon	seed	herbivores	10	*Pycnanthus angolensis,* *Pentaclethra macrophylla,* *Pentaclethra eetveldeana,* *Cylicodiscus gabunensis,* *Pseudospondias microcarpa,* *Diospyros crassiflora,* *Scorodophloeus zenkeri,* *Piptadeniastrum africanum,* *Dacryodes buettneri,* *Pterocarpus soyauxii*	Rosin and Poulsen, 2018
	Republic of Congo	seed, seedling	herbivores	4	*Pancovia laurentii,* *Staudtia kamerunensis,* *Manilkara mabokeensis,*	Clark, Poulsen and Levey, 2012

					Myrianthus arboreus, *Entandophragma utile*	
	Korup National Park, Cameroon	seedling	fungal pathogen	2	*Oubanguia alata,* *Microberlinia bisculcata*	Norghauer *et al.*, 2010
Asian tropics	Western Ghats, India	seedling	fungal pathogen	4	*Toona ciliata,* *Macaranga peltata,* *Olea dioica,* *Heritiera papilio*	Krishnadas and Comita, 2018
	Lambir Hills National Park, Malaysian Borneo	seed	none	2	*Shorea laxa,* *Dipterocarpus tempehes*	Takeuchi and Nakashizuka, 2007
	North Queensland, Australia	seed	none	1	*Normanbya normanbyi*	Lott *et al.*, 1995

Table A. 3. Overall and species-level effects of planting density (high or low), fungicide treatment (+ or -) and the interaction between density and fungicide on seedling mortality. Coefficients estimated using generalized linear mixed models with binomial distribution and log-link function within a hierarchical Bayesian framework allowing for estimation of coefficients despite no mortality recorded within some pots. Random uncorrelated slopes for fungus and density were estimated per species.

Term	**Estimate**	**Error**	**CI 97.5%**	**CI 97.5%**
Across species				
Intercept	-2.87	2.21	-6.98	1.73
Density	-1.27	2.12	-5.70	2.62
Fungicide	0.86	1.39	-1.88	3.62
Density x fungicide	-0.44	1.27	-3.00	2.07
Shorea pauciflora				
Density	-1.20	2.17	-5.82	2.73
Fungicide	1.48	1.38	-1.22	4.25
Shorea leprosula				
Density	-1.88	2.26	-6.69	2.20
Fungicide	1.01	1.40	-1.71	3.84
Shorea johorensis				
Density	-1.39	2.16	-5.93	2.56
Fungicide	0.83	1.40	-1.93	3.60
Shorea symingtonii				
Density	-2.00	2.33	-6.89	2.20
Fungicide	0.24	1.55	-2.91	3.22
Parashorea malaanonan				
Density	-1.50	2.19	-6.14	2.52
Fungicide	0.56	1.44	-2.30	3.40
Dryobalanops lanceolata				

Density	-1.42	2.16	-6.01	2.46
Fungicide	0.86	1.40	-1.91	3.64
Scaphium macropodum				
Density	-0.51	2.06	-4.91	3.28
Fungicide	1.18	1.41	-1.59	3.96
Koompasia excelsa				
Density	-0.31	2.03	-4.61	3.38
Fungicide	0.66	1.45	-2.20	3.53

Table A. 4. Summary of analysis of variance tables of fitted models for seedling height, stem diameter and leaf damage score. Significant terms in bold.

Model	Term	d.f.	Sum sq.	*F* value	*P* value
lm	***Height***				
	Species	**7**	**57746**	**336.74**	**0.000**
	Density	1	5	0.20	0.656
	Fungicide	1	76	3.11	0.076
	Density x fungicide	1	9	0.37	0.539
lm	***Stem diameter***				
	Species	**7**	**328.1**	**122.80**	**0.000**
	Density	1	1.1	2.94	0.094
	Fungicide	1	0.3	0.72	0.406
	Density x fungicide	1	0.6	1.70	
lm	***Leaf damage score***				
	Species	**7**	**186.6**	**10.64**	**0.000**
	Density	1	1.2	0.46	0.498
	Fungicide	1	0.7	0.28	0.596
	Density x fungicide	1	1.3	0.51	0.480

Table A. 5. Analysis of variance table of individual species linear regressions for seedling height. Significant terms in bold.

Term	d.f.	Sums sq	*F* value	*P* value
Shorea pauciflora				
Density	1	0.06	0.48	0.490
Fungicide	1	0.06	0.49	0.488
Density x fungicide	1	0.06	0.47	0.496
Residuals	44	5.82		
Shorea leprosula				
Density	1	0.52	0.27	0.604
Fungicide	1	4.31	2.25	0.140
Density x fungicide	**1**	**42.91**	**22.44**	**0.000**
Residuals	48	91.80		
Shorea johorensis				
Density	1	6.26	0.42	0.521
Fungicide	1	30.79	2.06	0.159
Density x fungicide	1	38.19	2.55	0.118
Residuals	40	597.78		
Shorea symingtonii				
Density	1	0.11	0.09	0.762
Fungicide	**1**	**15.40**	**12.70**	**0.001**
Density x fungicide	1	4.80	4.80	0.056
Residuals	28	33.95	3.96	
Parashorea malaanonan				
Density	1	1.99	0.26	0.616
Fungicide	1	19.24	2.46	0.125

Density x fungicide	1	0.69	0.09	0.767
Residuals	39	305.01		
Dryobalanops lanceolata				
Density	1	3.84	0.17	0.681
Fungicide	1	78.37	3.49	0.068
Density x fungicide	1	28.62	1.28	0.265
Residuals	44			
Scaphium macropodum				
Density	1	14.80	2.78	0.104
Fungicide	1	2.66	0.50	0.484
Density x fungicide	1	0.06	0.01	0.914
Residuals	39	207.62		
Koompasia excelsa				
Density	**1**	**36.18**	**9.14**	**0.004**
Fungicide	1	0.01	0.00	0.959
Density x fungicide	1	0.93	0.23	0.631
Residuals	42	166.27		

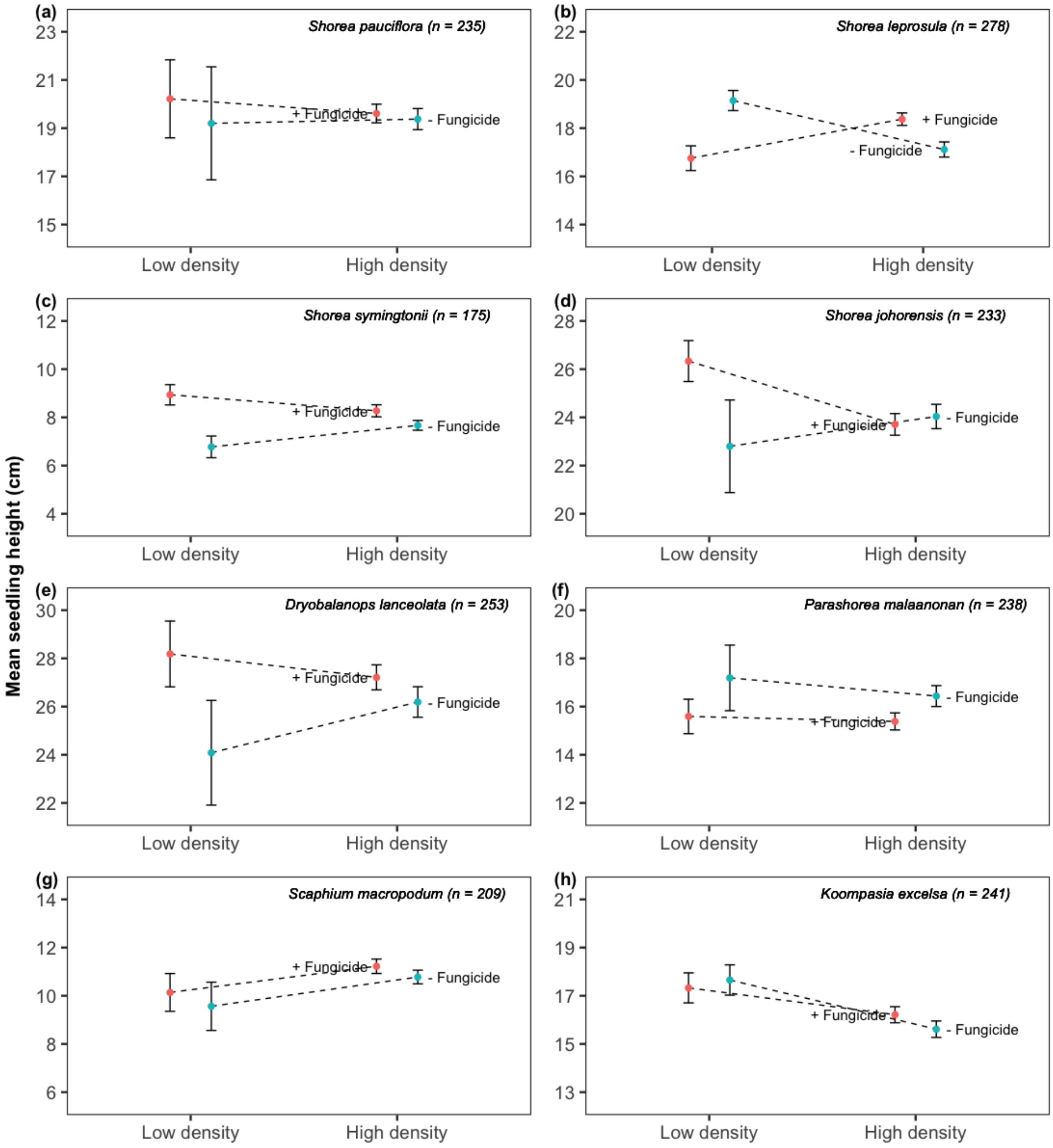

Figure A. 1. Mean seedling height (cm) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error.

Table A. 6. Analysis of variance table of individual species linear regressions for seedling stem diameter. Significant terms in bold.

Term	d.f.	Sums sq	*F* value	*P* value
Shorea pauciflora				
Density	1	0.39	3.84	0.056
Fungicide	1	0.00	0.04	0.844
Density x fungicide	1	0.04	0.38	0.541
Residuals	44	4.46		
Shorea leprosula				
Density	**1**	**0.19**	**4.35**	**0.042**
Fungicide	1	0.02	0.42	0.518
Density x fungicide	1	0.11	2.57	0.115
Residuals	48	2.11		
Shorea johorensis				
Density	1	0.00	0.05	0.817
Fungicide	1	0.09	0.53	0.470
Density x fungicide	1	0.09	0.55	0.463
Residuals	40	6.41		
Shorea symingtonii				
Density	**1**	**0.35**	**5.81**	**0.023**
Fungicide	**1**	**0.30**	**4.90**	**0.035**
Density x fungicide	1	0.13	2.11	0.157
Residuals	28	1.70		
Parashorea malaanonan				
Density	1	0.06	0.26	0.611
Fungicide	1	0.05	0.21	0.649
Density x fungicide	1	0.10	0.41	0.528

Residuals	39	9.15		
Dryobalanops lanceolata				
Density	1	0.02	0.32	0.573
Fungicide	**1**	**0.53**	**7.02**	**0.011**
Density x fungicide	1	0.14	1.82	0.184
Residuals	44	3.30		
Scaphium macropodum				
Density	1	0.02	0.24	0.629
Fungicide	1	0.24	2.87	0.098
Density x fungicide	1	0.32	3.79	0.059
Residuals	39	3.31		
Koompasia excelsa				
Density	1	0.05	0.54	0.465
Fungicide	1	0.01	0.09	0.772
Density x fungicide	1	0.00	0.02	0.886
Residuals	42	4.03		

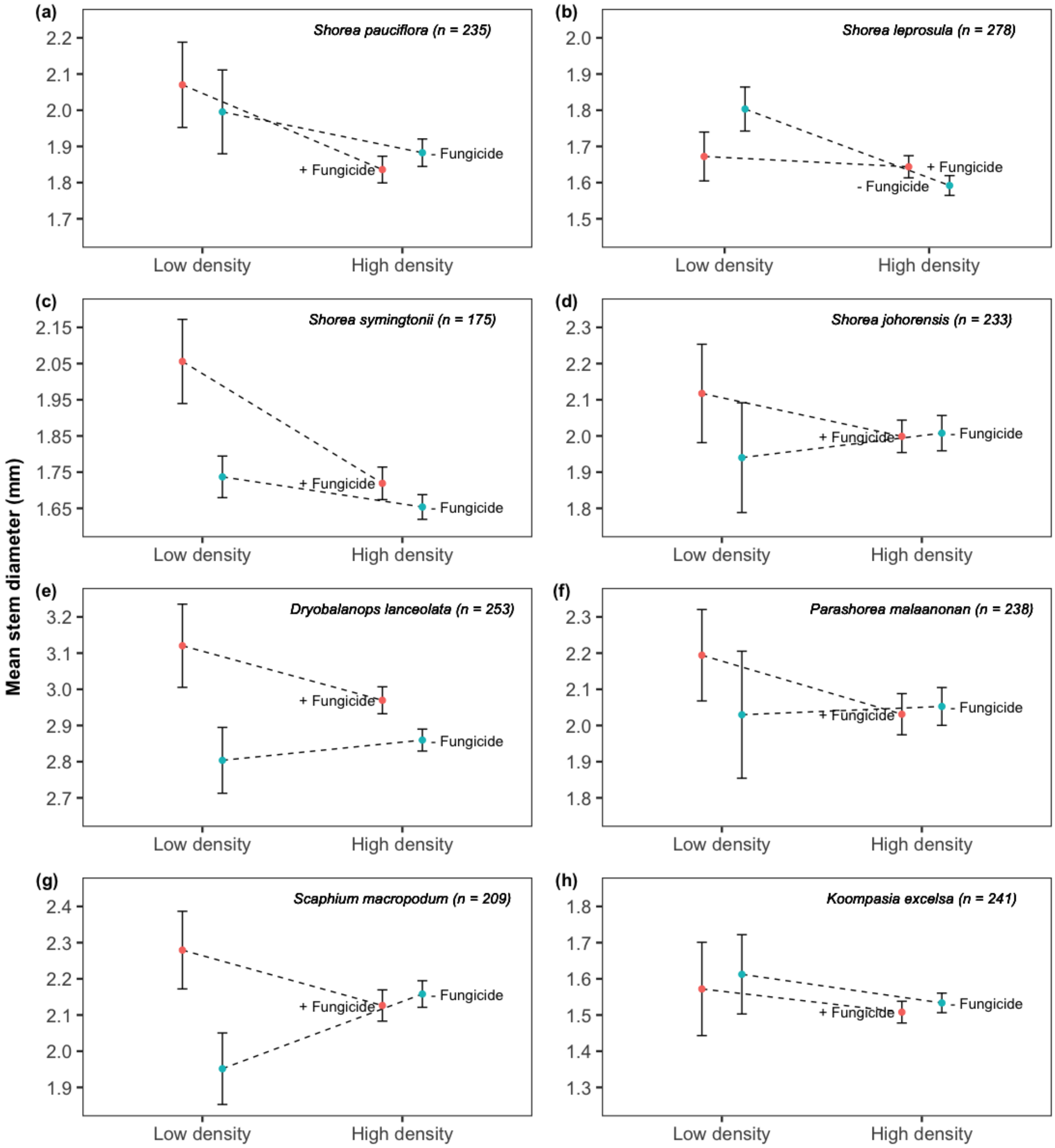

Figure A. 2. Mean stem diameter (mm) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error.

Table A. 7. Individual species analysis of variance table for seedling leaf damage score. Significant terms in bold.

Term	d.f.	Sums sq	*F* value	*P* value
Shorea pauciflora				
Density	1	1.21	0.03	0.856
Fungicide	1	4.09	0.11	0.740
Density x fungicide	1	3.78	0.10	0.749
Residuals	44	1612.1		
Shorea leprosula				
Density	1	0.86	0.14	0.712
Fungicide	**1**	**58.46**	**9.37**	**0.004**
Density x fungicide	**1**	**78.55**	**12.59**	**0.000**
Residuals	48	299.46		
Shorea johorensis				
Density	1	9.67	0.26	0.613
Fungicide	1	0.08	0.00	0.963
Density x fungicide	1	74.37	2.00	0.166
Residuals	40	37.28		
Shorea symingtonii				
Density	1	0.19	0.04	0.852
Fungicide	**1**	**24.42**	**4.63**	**0.040**
Density x fungicide	1	8.82	1.67	0.207
Residuals	28	147.79		
Parashorea malaanonan				
Density	1	3.78	0.14	0.708
Fungicide	1	71.97	2.70	0.108
Density x fungicide	1	1.43	0.05	0.818

Residuals	39	26.66		
Dryobalanops lanceolata				
Density	1	7.06	0.15	0.696
Fungicide	1	109.18	2.39	0.129
Density x fungicide	1	51.46	1.13	0.294
Residuals	44	45.70		
Scaphium macropodum				
Density	1	25.87	1.92	0.174
Fungicide	1	11.03	0.82	0.371
Density x fungicide	1	0.08	0.01	0.939
Residuals	39	13.49		
Koompasia excelsa				
Density	1	50.34	3.31	0.076
Fungicide	1	16.03	1.05	0.310
Density x fungicide	1	4.31	0.28	0.598
Residuals	42	15.21		

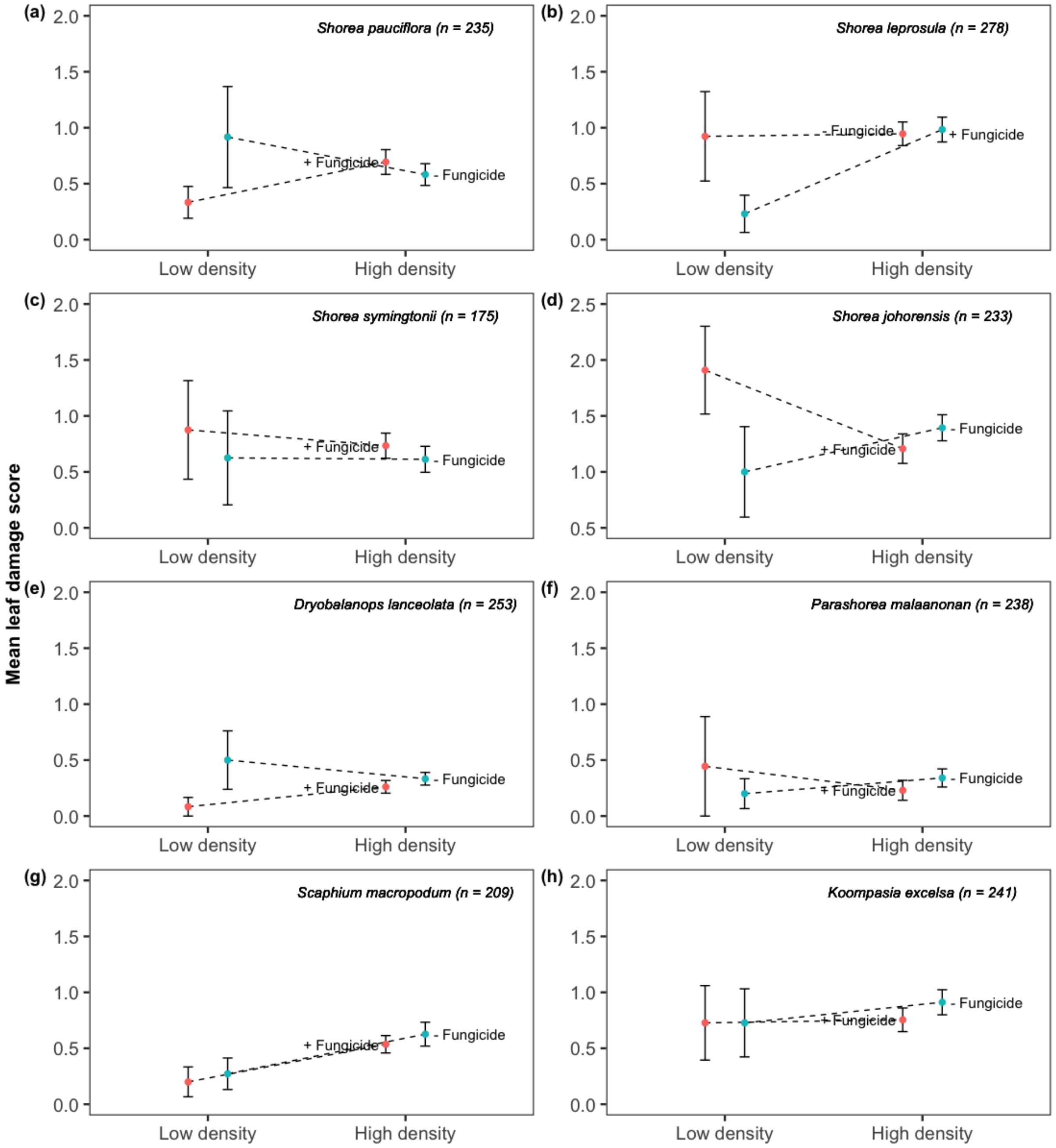

Figure A. 3. Mean leaf damage score (1 to 4 ordinal scale) of 1863 seedlings surviving 60 days after germination between pots planted at high and low density and treated with (+) or without (-) fungicide for each species: (a) *Shorea pauciflora*, (b) *Shorea leprosula*, (c) *Shorea symingtonii*, (d) *Shorea johorensis*, (e) *Dryobalanops lanceolata*, (f) *Parashorea malaanonan*, (g) *Scaphium macropodum*, and (h) *Koompasia exelsa*. Data points represent means across replicates and error bars denote standard error.

SUPPORTING INFORMATION FOR CHAPTER 4

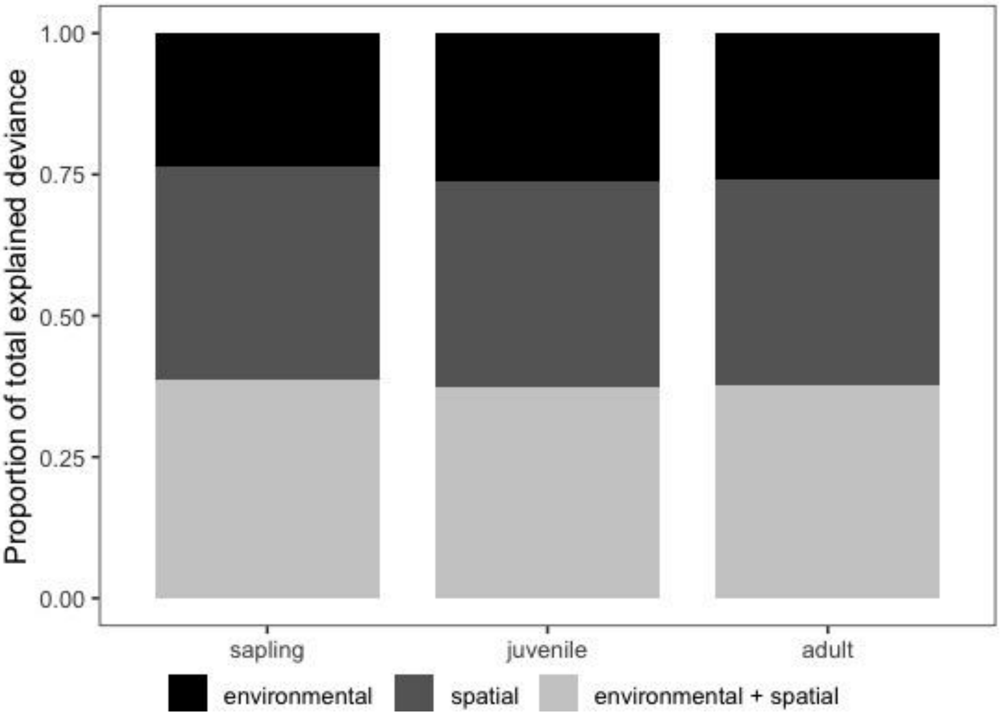

Figure B. 1. Proportions of total explained deviance in observed ß-diversity (Bray-Curtis index) attributed to environmental, spatial, and both environmental and spatial predictors, for each tree life stage. Null community ß-diversity included as a predictor in all GDMs.

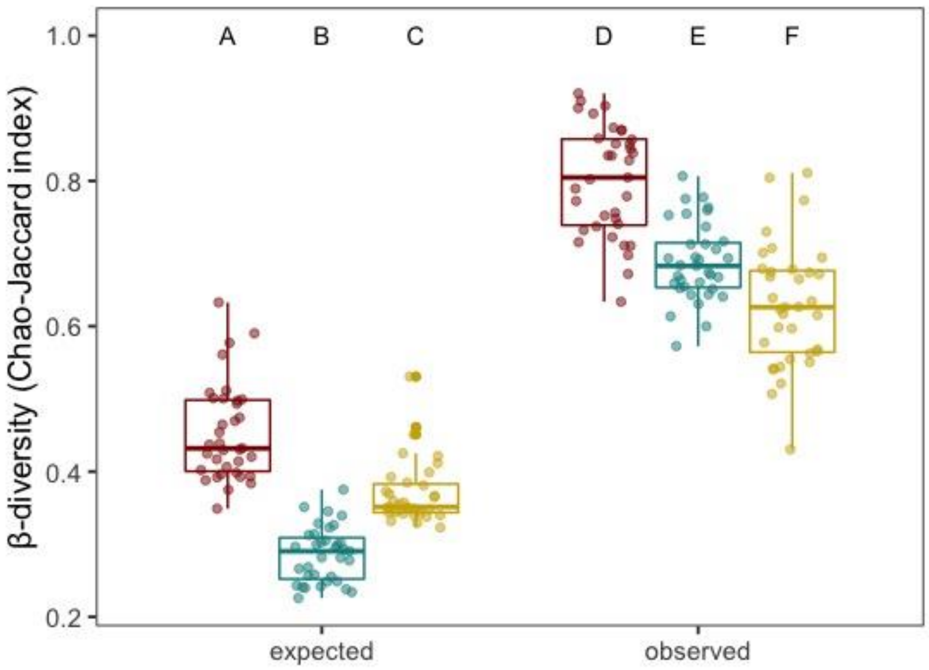

Figure B. 2. ß-diversity (Chao-Jaccard index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test (Life stages ANOVA: $F_{(2,206)} = 87.75$, $p < 0.001$, Null-expected ANOVA: $F_{(1,206)} = 1237.69$, $p < 0.001$).

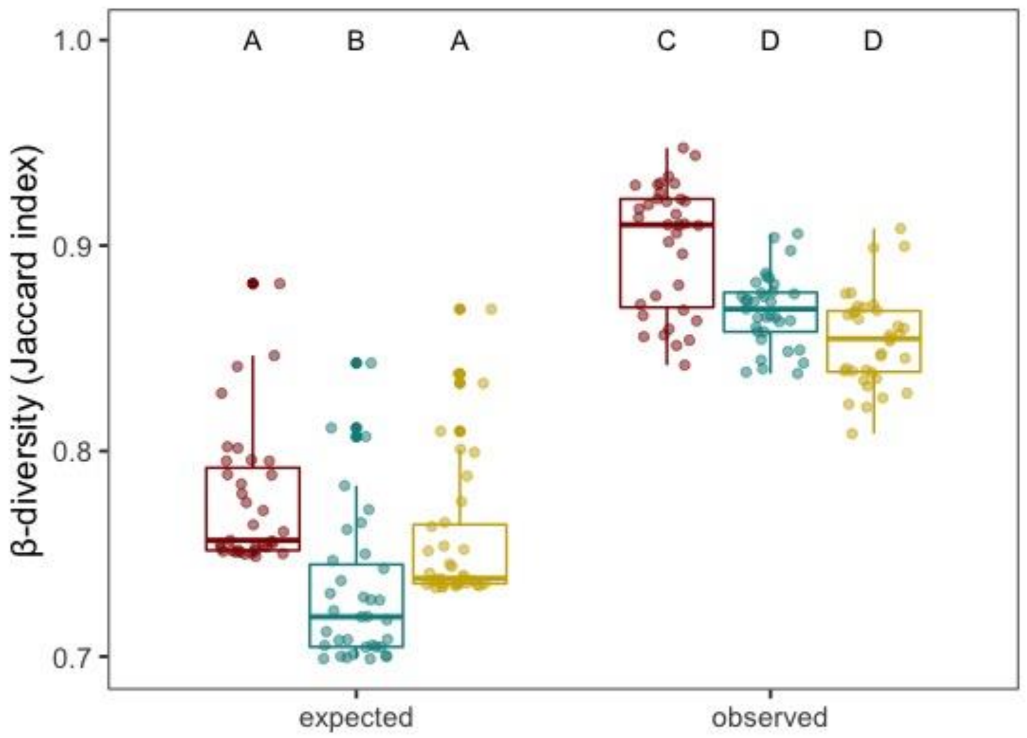

Figure B. 3. ß-diversity (Jaccard index) between life stages for expected and observed communities. Average expected dissimilarity generated from 999 null communities produced by randomising species identities and abundances at each sample point. Boxplots present median dissimilarity between sample points, with upper and lower limits representing 25th and 75th percentiles, and whiskers showing the interquartile range. Significant pairwise comparisons between life stages and observed and null-expected dissimilarity denoted by different letters, comparisons estimated using two-way ANOVA and Tukey's post-hoc test (Life stages ANOVA: $F_{(2,206)} = 30.97$, $p < 0.001$, Null-expected ANOVA: $F_{(1,206)} = 781.17$, $p < 0.001$).

Table B. 1. Relationships of observed dissimilarity in tree community ß-diversity between pairs of life stages. Values represent the sum of coefficients across three I-splines from GDMs with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with community dissimilarity represented by a dash and significant relationships indicated in bold. All models contained geographic distance as a significant predictor.

Gradient	**Sapling vs Adult**	**Juvenile vs Adult**	**Sapling vs Juvenile**
Deviance explained %	28.230	42.234	33.185
Distance (km)	**1.609**	**0.922**	**1.200**
Expected ß-diversity	-	**0.819**	**1.311**

Table B. 2. The relative importance of each environmental variable and geographic distance in explaining nestedness and turnover components of logged forest tree ß-diversity (Bray-Curtis index). Values represent the sum of coefficients across three I-splines from GDMs, with variable significance derived using Monte Carlo permutation (*nperm* = 50). Variables with no relationship with components of ß-diversity represented by a dash and significant relationships indicated in bold. Coefficients of all predictors of GDMs of sapling and adult nestedness equalled zero.

	Nestedness component			Turnover component		
Gradient	**Sapling**	**Juvenile**	**Adult**	**Sapling**	**Juvenile**	**Adult**
Deviance explained %	-	41.428	-	28.980	13.090	10.285
Distance (km)	-	**0.049**	-	**1.654**	**0.664**	**0.650**
Adult abundance	-	0.063	-	0.131	-	-
Basal area (m^2 ha^{-1})	-	0.023	-	0.033	-	-
Canopy openness (%)	-	**0.116**	-	-	0.074	-
Liana Prevalence (%)	-	0.014	-	0.230	-	0.125
Liana Load (%)	-	0.025	-	0.206	0.176	-

APPENDIX C

SUPPORTING INFORMATION FOR CHAPTER 5

C1.1 Supplementary analysis 1. Environmental drivers of liana infestation

We used linear mixed-effects models (LMM) within the LME4 package (Bates et al., 2015) to assess the importance of environmental and forest structural variables in determining plot-level liana load and prevalence. Fixed-predictors included plot-level adult basal area, adult tree abundance, canopy openness and species richness. All predictors were standardised and checked for collinearity (VIF < 3; $r < 0.6$) before inclusion in models. Liana prevalence was log transformed (*log10*) due to being highly negatively skewed (-1.304). Non-linear relationships between liana load and prevalence and adult basal area were added to both models as second-order polynomials. As sample plots were nested with blocks and blocks within sites, we included the spatial arrangement of plots as a nested random effect in all models.

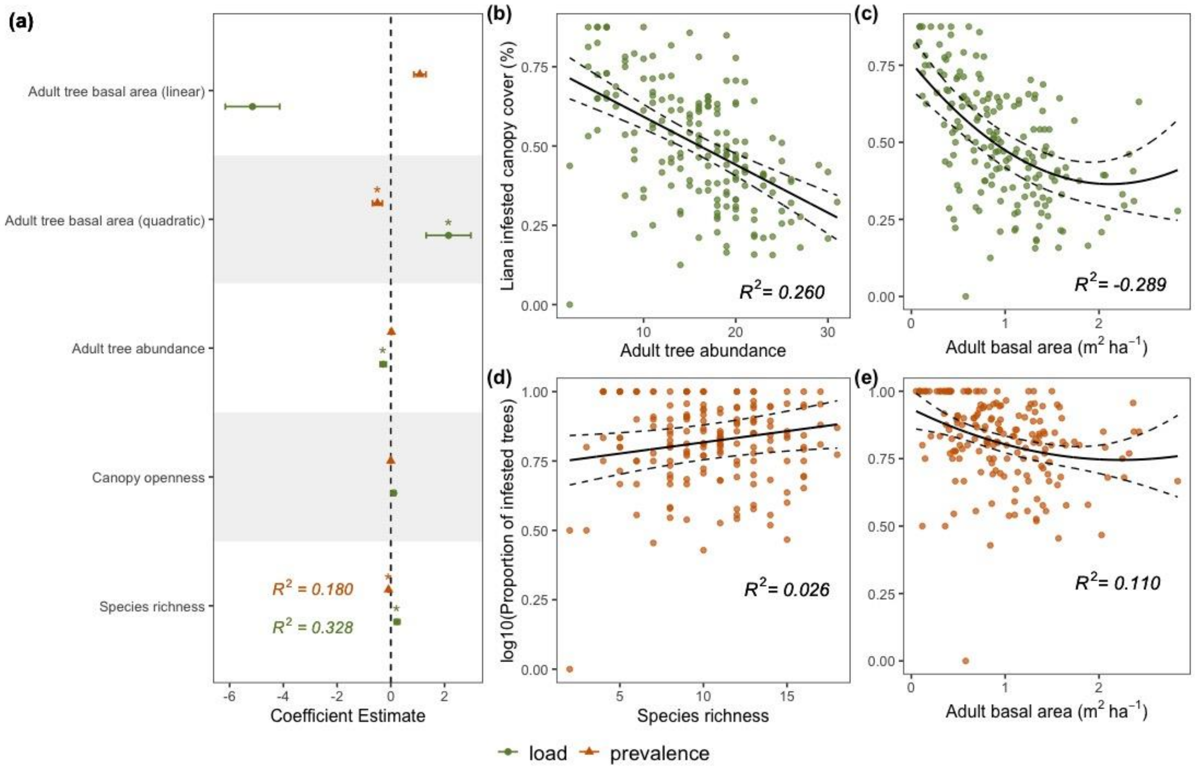

Figure C. 1. Model coefficients of the effects of adult basal area, adult abundance, canopy openness and tree species diversity on plot-level liana infestation (a). Model coefficients estimated using linear mixed models, with nested study design included as random effects. Significant terms denoted by *** ($p < 0.001$), and error bars represent ± 1 SE and marginal R^2 given in text. Relationships between significant variables in linear mixed models and liana load (b & c) and liana prevalence (d & e). Dotted lines represent 95% CIs and marginal R^2 given in text.

Table C. 1. Summary statistics of fixed effects from linear mixed models (LMM) of the relationships between within-forest disturbance measures and liana infestation (load and prevalence) at the plot-level. Both models include sample block and site as a nested random effects structure. Significant terms in bold ($p < 0.05$).

Liana load	*Estimate*	*Std. Error*	*t-value*	*P-value*
Adult tree abundance	**-0.282**	**0.114**	**-2.472**	**0.014**
Species richness	**0.228**	**0.101**	**2.246**	**0.026**
Canopy openness	0.108	0.066	1.645	0.101
Adult basal area (linear term)	**-5.150**	**1.013**	**-5.083**	**0.000**
Adult basal area (quadratic term)	**2.148**	**0.831**	**2.584**	**0.011**
log10(Liana prevalence)	*Estimate*	*Std. Error*	*t-value*	*P-value*
Adult tree abundance	0.022	0.025	0.882	0.379
Species richness	**-0.085**	**0.024**	**-3.832**	**0.000**
Canopy openness	-0.0004	0.014	-0.030	0.976
Adult basal area (linear term)	**1.084**	**0.224**	**4.818**	**0.000**
Adult basal area (quadratic term)	**-0.498**	**0.183**	**-2.715**	**0.007**

Table C. 2. Statistics of phylogenetic signal for the six functional traits.

Trait	*Blomberg's K*	*Pagel's* λ
Dispersal syndrome	-	1.00
Leaf phenology type	-	1.00
Wood density g cm^{-3} (WD)	0.866	-
Specific leaf area m^2 kg^{-1} (SLA)	0.589	-
Leaf nitrogen content per leaf dry mass mg/g (LNC)	0.838	-
Mean mature height m	0.800	-

Table C. 3. Description of plant functional trait matrix with species- and genus-level coverage from which missing species' values were phylogenetically imputed. Trait data was recorded for a total of 5605 species from all 199 genera found in our study data, including 392 of the 503 (77.9%) focal species.

Trait	**Species-level coverage**	**No. species used in imputation**	**Genus-level coverage**	**Range/Categories**
Dispersal syndrome	153 (30.4%)	1055	128 (64.3%)	passive, wind, water, invertebrate, vertebrate, autochory
Leaf phenology type	299 (59.4%)	3409	185 (93.4%)	evergreen, deciduous
Wood density	277 (55.1%)	2770	173 (86.9%)	0.13-1.15 g cm^{-3}
Specific leaf area (SLA)	219 (43.5%)	1594	165 (82.9%)	1.96-139.67 m^2 kg^{-1}
Leaf nitrogen content per leaf dry mass	119 (23.7%)	1239	152 (76.3%)	0.09-51.78 mg/g
Mean mature height	133(26.4%)	1931	163 (81.9%)	2-80 m

The majority trait estimates were obtained from various sources within the online databases; TRY plant trait database (version 4.0, http://www.try-db.org) and Global Wood Density Database (available from: http://datadryad.org/handle/10255/dryad.235) (Jerome Chave et al., 2009; Zanne et al., 2009). Additional data on SLA and dispersal syndrome sourced from Döbert et al., (2017), and tree height from Peñuelas et al., (2013).

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