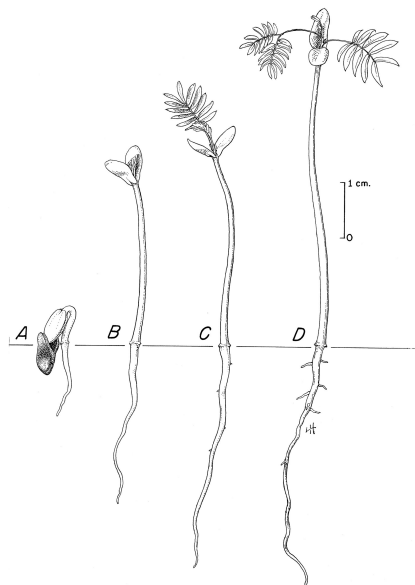


LINKING THE IMPACT OF SELECTIVE
LOGGING WITH SEEDLING RECRUITMENT
DYNAMICS



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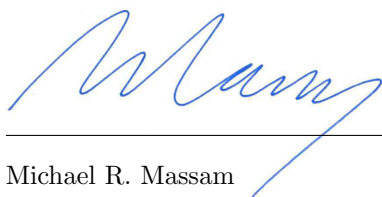
Declaration of Authorship

This thesis is an account of research undertaken between December 2014 and September 2015 at The Department of Life Sciences, Imperial College London, UK.

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- The thesis complies with the relevant word length specified in the College regulations.
- All main sources of help have been appropriately acknowledged.
- No element of this material has been published previously.
- Seedling census data preceding 2015 were collected by Hamzah Bin Tangki. SAFE core data and insect trapping data was collected by Dr. Marion Pfeifer and SAFE research assistants. Microclimate data was collected by Dr. Stephen Hardwick. The remaining data was collected by myself.
- All data processing and analyses were conducted by myself with the exception of some quality control on the raw microclimate data which was conducted by Dr. Stephen Hardwick.
- All empirical models presented were constructed by myself.
- Development of the analyses presented was aided by broad conceptual guidance by my supervisor, Dr. Rob Ewers.

Signed:



Michael R. Massam

September, 2015

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Contents

1	Summary	5
2	Introduction	6
3	Materials and Methods	11
3.1	Study Sites	11
3.2	Seedling census data	12
3.3	Recruitment factor data	13
3.3.1	SAFE core data	13
3.3.2	Microclimate data	14
3.3.3	Beetle abundance data	15
3.3.4	Seedling-plot-specific data	15
3.4	Data Analysis	16
3.4.1	Disturbance Index	16
3.4.2	Recruitment factors on recruitment dynamics	17
3.4.3	Logging disturbance on recruitment factors	18
3.4.4	Logging disturbance on recruitment dynamics	18
4	Results	19
4.1	Disturbance Index	19
4.2	Recruitment factors on recruitment dynamics	19
4.3	Logging disturbance on recruitment factors	20
4.4	Logging disturbance on recruitment dynamics	20
5	Discussion	23
6	Appendices	33
6.1	Appendix 1	33
6.2	Appendix 2	34
6.3	Appendix 3	35
6.4	Appendix 4	37
6.5	Appendix 5	38

1 Summary

1. The natural regeneration of tropical forests is underpinned by successful transition through the recruitment process. Mechanistic forest growth models have received much attention however recruitment at the seedling stage is generally omitted due to a lack of understanding of the physiological mechanisms involved and the vulnerability of seedlings to stochastic events.
2. I examined the growth, mortality and recruitment rates of seedlings in response to recruitment factors across a gradient of logging disturbance in humid tropical forests of Sabah, Malaysian Borneo to elucidate the physiological mechanisms at play.
3. Recruitment was inhibited by competitive interactions which were exacerbated by logging disturbance intensity. This relationship was only weakly observed when not considering the intermediary recruitment factors due to differential impacts of selective logging on aspects of recruitment.
4. *Synthesis.* My results unfurl the mechanisms dictating seedling recruitment while demonstrating the importance of considering the context of logging disturbance when inferring causality on seedling recruitment.

2 Introduction

Humid tropical forests cover 20 million km² of the world's surface and accommodate the highest terrestrial biodiversity of all biomes (Pimm & Sugden, 1994). Tropical forests provide vital ecosystem services, both as a carbon sink (Malhi & Grace, 2000) and as an important source of timber, contributing roughly one eighth of global timber supply. Increasing rates of forest clearing have threatened tropical forests for the last four decades (Lambin *et al.*, 2003) and the resultant fragmentation and habitat loss has major impacts on biodiversity (Gibson *et al.*, 2011; Barlow *et al.*, 2006). Selective logging, the removal of specific timber trees from the forest stand, while comparatively less detrimental (Edwards *et al.*, 2011) can alter community composition and forest structure, cause local extinctions and disrupt ecosystem processes (Thiollay, 1992; Johns, 1988; Schleuning *et al.*, 2011; Ewers *et al.*, 2015).

With 20% of global tropical forests having been subject to selective logging and a further 25% of primary forests set aside for timber extraction (FAO, 2010; Blaser, 2011), selective logging is one of the most widespread instances of human disturbance. With almost half the world's tropical forest set to be subject to logging, it is vital to develop a good understanding of the short and long-term consequences to the health of the forest since this will determine their future ecological and economic importance.

There is an extensive literature on the impact of timber extraction on adult tree growth, mortality and recruitment (van Bodegom & de Graaf, 1991; Rolff & Ågren, 1999; Parrotta *et al.*, 2002), driven by its relevance in informing optimal harvesting intensities and frequencies of silvicultural systems and these relationships have been modelled extensively (Vanclay, 1989; Ong & Kleine, 1996; Phillips *et al.*, 2003; Kariuki *et al.*, 2006; Peng, 2000). However, the vast majority of such recruitment models start at a late stage in the tree life cycle since attempts to build seedling models are hindered by the significant stochasticity in seedling dynamics, the insufficiency of empirical data to fit the model and a lack of knowledge on the physiological processes involved (Vanclay, 1994). Therefore, predictions from natural forest growth models tend to assume that recruitment, growth and mortality at the seedling phase will not significantly impact estimates of forest regeneration. This is unsatisfactory since successful recruitment of seedlings underlies the development and sustainability of tree communities in forest ecosystems (Leck *et al.*, 2008). Seedling growth, survival and recruitment are therefore critical components of forest regeneration and for maintaining healthy forest function.

The seedling stage of a plant's life cycle represents a population bottleneck. The recruitment process requires successful transition through seed production, dispersal, germination, growth and establishment. With strong selection pressures at each of these stages, the probability of a given

seed producing an established tree is very small (Simpson *et al.*, 1985). The factors affecting seedling recruitment, henceforth referred to as recruitment factors, can vary over both spatial and temporal scales, can interact and can be biotic or abiotic, this combined with their high vulnerability, make seedling dynamics highly complex. Biotic factors consist of competition for resources, predation and disease while abiotic factors relate to the environmental constraints imposed by the ecosystem. (Grubb, 1977; Fenner & Thompson, 2005)

Competition for resources with surrounding vegetation is one of the predominant factors capable of inhibiting seedling establishment (Taylor & Aarssen, 1989; Gross, 1980). In forest ecosystems, light limitation by canopy crowns is the major limiting factor for establishment of understory plants (Lorimer *et al.*, 1994) but plants also compete below-ground for water and nutrients (Casper & Jackson, 1997). Successful establishment can also be inhibited by predation of seeds, fruits and leaves by both vertebrate and invertebrate granivores, frugivores and herbivores (Clark & Clark, 1985; Hanley, 1998; Marquis, 1984). In addition to these biotic factors, recruitment is contingent on environmental conditions. Habitat microclimate influences a wide range of ecological processes (Bonan, 2002); extreme temperatures and drought can alter nutrient cycling and photochemical efficiency (Engelbrecht *et al.*, 2007; Jiang & Huang, 2000). Highly acidic or alkaline soils can impede nutrient uptake (Wilkinson, 2000), leaf litter depth can provide a favourable, stable microclimate for germination (Molofsky & Augspurger, 1992) and the density of the top soil layer can influence root penetrability, moisture availability and soil aeration (Lewis & THS, 1991). Simply by virtue of being small, seedlings are also more vulnerable to stochastic events such as damage due to falling litter (Clark & Clark, 1991). Finally, the aforementioned factors can vary in both magnitude and direction of response depending on the traits and tolerances of the species. Tropical tree species are known to respond differently across light and nutrient gradients (Poorter *et al.*, 2005) and across and within life cycle stages (Kitajima, 2002; Myers & Kitajima, 2007), implicating community composition as an important factor in forest regeneration.

Disturbance resulting from logging can modify all such factors. Changes in canopy cover associated with the removal of timber (Pfeifer *et al.*, 2014) and distance to the forest edge are shown to reduce relative humidity and increase air temperature (Hardwick *et al.*, 2015; Pohlman *et al.*, 2007) in the understory. Dense canopies can block 95% of solar radiation (Bonan, 2002), keeping the understory cool and can absorb air momentum (Garratt, 1994), preventing warmer, 'drier' air from mixing with cool, moist air in the understory. Construction of skid roads to transport cultivated timber can cause compaction of soils (Dykstra & Curran, 2000; Jim, 1993; Froehlich, 1979) and increases in soil pH are often also observed (Congdon & Herbohn, 1993; Olander *et al.*, 2005). These disturbances to surface soil can persist for over a decade (McNabb *et al.*, 1997).

Due to the selective nature of logging whereby extraction is based on the traits of the species and individual, selective logging has significant directional impacts on the tree community composition which can persist for a very long time (Chazdon, 2003). This impact is particularly marked in Borneo, where dipterocarps contribute at least 70% (Appanah & Turnbull, 1998; Curran & Leighton, 2000) of canopy biomass and make up 85% of Indonesia's timber exports (Curran *et al.*, 1999). Changes in parent community result in differences in seed production, and ultimately, differences in competitive interactions in altered seedling community composition. This alongside the inherent reduction of canopy cover associated with timber extraction and the concurrent increase in light intensity in the understory, logging can have pronounced consequences to competition for resources in understory vegetation. Beyond changes to tree communities, literature on the impact of logging on community composition and function of other taxa is extensive. Logging can reduce biodiversity by disturbing habitats and resources required by certain species, causing abundance shifts and sometimes local extinctions (Nittérus *et al.*, 2007; Hill & Hamer, 2004; Burivalova *et al.*, 2014; Bennett *et al.*, 2015). Depending on logging intensity and the complexity of the food web (Kondoh, 2003), knock on effects can permeate across all species, many of which are likely to be leaf, seed or fruit predators. The complexity of food webs and trophic interactions makes it difficult to predict how herbivore abundance might respond to logging disturbance (Howlett & Davidson, 2001; Holloway *et al.*, 1992) and will vary between species and food webs. The impact of selective logging on the factors described above combine to affect the seedling recruitment process. In cases where seed availability is insufficient (Curran *et al.*, 1999), excessive damage has been caused to the residual forest stand (Peña-Claros *et al.*, 2008) or canopy cover is depleted to the extent that pioneer species establish and outcompete seedlings, recruitment failure can occur, preventing natural regeneration and restarting the chain of ecological succession (Peña-Claros *et al.*, 2008).

While the impact on factors affecting seedling recruitment are well represented in the literature, some of which assess the relative importance of factors (Toledo *et al.*, 2011), relatively few have looked directly at the impact of logging disturbance on recruitment. Those that have, do not quantify logging intensity according to some disturbance index, instead using ordinal or binary classifications (Valverde-Barrantes & Rocha, 2013; Chapman & Chapman, 1997; Schwartz & Caro, 2003; Guarino & Scariot, 2012; Pinard *et al.*, 1996) which limits comparability between studies. Further, several of these studies offer conflicting results on the impact logging disturbance has on the seedling recruitment process (Valverde-Barrantes & Rocha, 2013; Chapman & Chapman, 1997; Schwartz & Caro, 2003). Others experimentally manipulate seed or seedling presence which does not consider whether it makes sense for it to be there in the first place. Circumstances might dictate that seeds of a certain species could not disperse to the plot or could not germinate within the plot (Guarino & Scariot, 2012; Pinard *et al.*, 1996). Beyond this, no studies have explicitly linked

the effect of selective logging on recruitment factors with the effect of those factors on recruitment within the same experiment. This is unsatisfactory since responses to logging will depend on context, which is the likely explanation for inconsistencies in the literature. Therefore, a deeper understanding of the mechanisms at play is required to infer causality.

Here I attempted to bridge the gap in understanding of the physiological processes involved in seedling recruitment in forest disturbed by selective logging via a three year observational experiment in humid tropical forests of Sabah, Malaysian Borneo. I examine seedling height growth, diameter growth, mortality and recruitment rates across a gradient of forest disturbance using an explicit index of disturbance and measures of competition (basal area, seedling basal area, percentage cover of understory vegetation), predation (abundance of herbivorous beetles, percentage of leaves with signs of herbivory) and environmental constraints (pH, canopy density, temperature, humidity, litter depth, soil depth) to link them. I construct six empirical models that describe seedling growth (height and diameter), mortality and recruitment (germinations, seedlings, juveniles (Bell & Bryan, 2008)), aiming to inform reduced impact logging techniques and improved construction of forest growth models through inclusion of seedling recruitment dynamics.

In accordance with what is known about recruitment factors and what is known about the effects of logging on such factors, I hypothesised that, seedling growth would be most significantly increased by light availability, which may be signalled via canopy density or through variables that act as a metric for competitive interactions with other plants. Further, I hypothesised that rate of herbivory, high temperatures would increase growth rate as well as relative humidity and there might exist an interaction between them whereby temperature increases growth unless humidity is low since dessication may slow the process. I also believed that soil with a deep top layer would facilitate growth by allowing deep penetration of the root system and efficient uptake of nutrients. Density dependence signals were also hypothesised, that the number of seedlings of the same genus would reduce growth through intraspecific competition. I was also interested in looking for an effect of pH although no predictions were made about the directionality of any effect. I predicted the same responses for birth rate although I expected there to be an influence of leaf litter depth by provision of stable, moist soil conditions for optimum germination. Furthermore I expected there to be greater influence of competition on the recruitment process than on growth. Mortality rate was hypothesised to show opposite relationships to recruitment rate but with no signal from leaf litter depth and increased signal from herbivory rate. I further predicted that logging would have major directional impacts on all recruitment factors with the exception of pH, slope and soil depth which are likely to be highly localised at roads. Lastly, I predicted that this link would also transfer to being able to explicitly predict the impact of logging on seedling growth, mortality and

recruitment.

3 Materials and Methods

3.1 Study Sites

Data were collected from Kalabakan Forest Reserve ($4^{\circ}33'N$, $117^{\circ}16'E$) and Maliau Basin Conservation Area ($4^{\circ}49'N$, $116^{\circ}54'E$) in Sabah, Malaysian Borneo, as part of the Stability of Altered Forest Ecosystems (SAFE) project (Fig. 3.1) (Ewers *et al.*, 2011). The Kalabakan Forest Reserve consists of 7200ha of lowland dipterocarp rainforest and has undergone two rotations of logging since 1978; once in the 1970s, removing $113m^3ha^{-1}$, and three times in the second rotation between 2000 and 2008, removing $66m^3ha^{-1}$ (Fisher *et al.*, 2011). Therefore, the forest at these logged sites is heavily degraded and rank among some of the most intensely logged forests in the tropics (Burivalova *et al.*, 2014). Conversely, Maliau Basin Conservation Area has been protected under Malaysian law as a Class 1 Protection Forest Reserve since 1997 and contains large areas of forest that have never been logged.

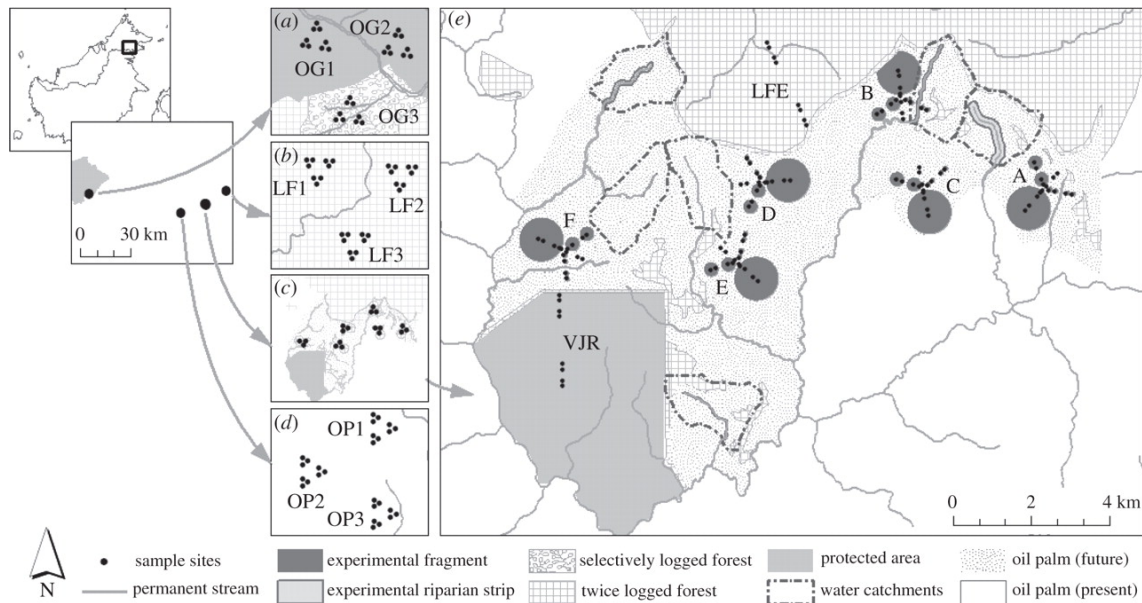


Figure 1: Map of SAFE project sampling sites encompassing a gradient of forest modification, located in Sabah, Malaysian Borneo. Reproduced with permissions of Ewers *et al.* (2011)

The SAFE site sampling design uses a fractal sampling structure (Fig. 3.1) (Marsh & Ewers, 2013) with sampling points located $10^{2-25}m$ apart and nested within 14 forested blocks which are $> 1km$ apart. Primary forest blocks in Maliau Basin Conservation Area are located approximately 65km northwest of the main SAFE site. Blocks are arranged non-randomly to maximise the range of forest cover surrounding sampling points which provides a forest modification gradient across which to examine the impact to seedling growth, mortality and recruitment (Table 1). Further,

the blocks are orientated to minimise change in confounding variables along sampling transects, such as altitude, slope and distance to forest edge. For full details on the nature of the fractal sampling design, see Ewers *et al.* (2011).

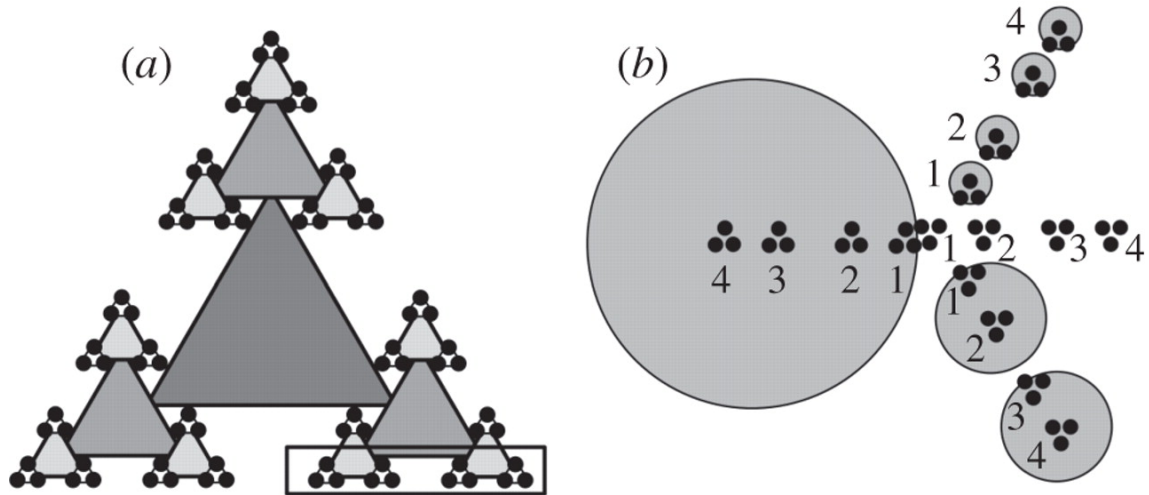


Figure 2: (a) Fractal geometry of the sampling network at SAFE, points on the triangle vertices are sampling points and triangle shading represent progression from first to fourth order of the fractal sampling pattern. (b) Spatial layout of the blocks forming the split-plot design at SAFE. Reproduced with permission from Ewers *et al.* (2011)

I established 84 seedling plots in eight blocks at the center of the northwest quarter of SAFE's 25×25m second-order vegetation plots such that there was a gradient of forest cover across blocks; six located in logged forest (A, C, D, E, LF1 and LF2) and two in unmodified primary forest (OG1 and OG2). A disproportionate number of seedling plots were established in logged forest because leaf area index, which is a measure of forest structure, had higher variance (0.51 versus 0.39) and a greater range (4.73 versus 2.36) in logged versus primary forest (Ewers *et al.*, 2015). Plots consist of a 5×5m plot and a 2×2m sub-plot to record saplings and seedlings respectively.

3.2 Seedling census data

Measurements were recorded from plots in three collection periods in May–June 2012, December 2012 and April–May 2015. At each collection, all tree and liana stems ≥ 50 cm height and ≤ 1 cm DBH were tagged, mapped and identified. In the 2×2m subplot, this was done for stems ≥ 10 cm height. Seedlings which could not be identified in the field were later identified from photos and samples taken from matching species outside the plot. Where matching species were not available, leaf samples were taken from the seedling itself if it was deemed established enough to not be significantly inhibited by leaf loss.

Table 1: The land-use intensity gradient at the SAFE site in order from least to most disturbed, including primary forest to oil palm plantation. Blocks correspond to the sampling sites illustrated in Fig. 3.1

Block	Logging	Forest Cover (%)	Forest Quality (range)
OG1	never	100	4.44 (3–5)
OG2	never	100	4.88 (4–5)
OG3	low intensity	100	4.22 (3–5)
LF1	twice	100	3.22 (3–4)
LF3	twice	76	3.44 (3–4)
LF2	twice	86	3.67 (3–4)
LFE	twice	71	3.25 (2–4)
VJR	variable	61	3.43 (2–5)
B	twice	50	2.75 (2–4)
D	twice	35	2.06 (1–3)
F	twice	34	2.50 (1–3)
A	twice	26	2.25 (1–4)
E	twice	21	1.94 (1–4)
C	twice	16	2.06 (1–4)

Basal diameter point of measurement was marked at 20cm from the ground and two perpendicular measurements taken using digital calipers to give an average. Height of all trees were recorded but omitted for lianas since they often form a branching network along the understory floor or permeate, beyond reach, into the canopy and are therefore troublesome to measure. At the third collection, the number of new germinations within the subplot were counted with no tagging, mapping or identification.

Beyond collection for use as response variables, census data was used to calculate seedling richness and ‘density of seedlings of matching genus’ for each seedling to represent intraspecific competition and density dependence dynamics. Seedling basal area was also taken as a measure of interspecific competition.

3.3 Recruitment factor data

3.3.1 SAFE core data

Measures of soil pH, litter depth, litter dry weight, soil depth, relative ground cover, herbivory, basal area and forest quality were collected at all of SAFE’s vegetation plots in 2011 as part of SAFE’s core data.

Relative cover was estimated as the proportion of ground area covered by ferns, grass, trees, vines,

ginger or being bare as seen from above the centre of the plot. Cover of ferns, grass, vines and ginger were summed to provide a metric for intensity of competition for resources at the understory level.

Litterfall dry weight (g) was collected using a litter trap with a collection area of 1m² stationed at the centre of the plot. Samples were sorted into leaves, wood, seeds and fruit, and were dried in a drying rack until weight ceased to decrease.

Soil pH, soil depth and litter depth were estimated at three randomly chosen points within each vegetation plot. Soil pH was measured using a Kelway © meter (accuracy ± 0.2) and litter depth (cm) with a rule. Soil depth (cm) was quantified as the mean depth of the A-horizon, which is the upper-most layer of humus-rich soil (Foth *et al.*, 1991), using a soil sampling tube and examining the distance to the B-horizon which is characterised by a sharp colour change from dark brown to orange/red (Davies *et al.*, 2003).

Evidence of herbivory was evaluated by examining the percentage of leaves showing signs of insect herbivory. An extensive census of each vegetation plot was conducted where all trees within the 25times25m area ≥ 10 cm DBH were measured. Further, all deadwood was counted, measured and the cause of death assessed. Beyond these quantitative measures, each plot was scored on a qualitative scale of 1–5 as a metric for forest quality. The scoring criteria can be seen in Table 2.

Table 2: Scoring criteria for forest quality

Score	Forest Quality	Forest Description
1	Very poor	No standing trees – open canopy with ginger, vines or low scrub
2	Poor	Open with occasional small trees over ginger/vine layer
3	OK	Small trees fairly abundant/canopy at least partially closed
4	Good	Lots of trees, some large, canopy closed
5	Very good	No evidence of logging at all, closed canopy with large trees

3.3.2 Microclimate data

Air temperature and relative humidity (RH) metrics were recorded using Hydrochron iButtons © (Maxim Integrated SystemsTM, temperature accuracy $< \pm 0.5^\circ\text{C}$; RH accuracy $< \pm 5\%$) from 2011–present. Full details of the materials and methods can be found in Hardwick *et al.* (2015). Where data for a given vegetation plot was not available, temperature and RH from the nearest SAFE first-order point, which was never further than 32m away, was taken as a proxy.

RH readings tended to drift beyond 100% when RH had not fallen below 85% in some time, which is unphysical. Under advice from the manufacturer (Appendix 1), values exceeding 100% were taken to be 100%. Further, readings behaved erratically when batteries began to run out so time series

for each plot were scrutinised and data following erratic behaviour was discarded. While this means data is missing for certain parts of the year, daily meteorological records from the Danum Valley Field Center (~60km from Kalabakan Forest Reserve) show that weather in Sabah is aseasonal (SEARRP: <http://www.searrp.org/danum-valley/the-conservation-area/climate/>) with a range of mean monthly temperature of 0.6°C and RH of 1.6%.

Tropical forests exhibit almost complete RH saturation at night so the mean minimum daily RH was taken as the preferred metric conveying forest quality. Reduced canopy cover also has the effect of higher daily temperature maxima so mean daily maximum temperature is used. This has the added benefit of minimising seasonal temperature differences due to variable temporal spread of available data between plots. (Barry & Chorley, 2009)

3.3.3 Beetle abundance data

Beetle abundance data was collected across six insect trapping sessions between 2011 and 2013 at all vegetation plots. Trapping techniques used modified flight intercept traps at each vegetation plot which were dug into the ground to simultaneously act as pitfall traps. For a more detailed outline of the beetle sampling procedure, see Ewers *et al.* (2015). Mean abundance of herbivorous beetles was taken as a further metric of herbivory rate.

3.3.4 Seedling-plot-specific data

While SAFE core data includes three measures of canopy density (leaf area index, fraction of green vegetation and canopy closure), the forest in logged blocks can be patchy, with some seedling plots located in gaps or on old logging skid roads. Densiometer readings were taken at first collection as a metric of canopy density (Lemmon, 1957). Densiometer readings can suffer to overestimation of canopy density due to the 'angle of view' causing trees to 'fall' towards the centre of the observation area (Korhonen *et al.*, 2006). However they still give values associated with light intensity and can, therefore, justifiably be used as a link to seedling growth and survival (Jennings *et al.*, 1999). Four readings were taken facing north, south, east and west at each seedling plot by the same person to eliminate error introduced by differences in viewpoint (Bunnell & Vales, 1990; Ganey & Block, 1994). These readings were averaged and multiplied by 1.04 to get a reading for canopy closure as is standard (Paletto & Tosi, 2009).

While slope is not expressly effected by logging disturbance, slope has been found to be important in shaping community composition through its influence on soil moisture retention (Engelbrecht *et al.*, 2007). Accordingly, I found it prudent that it be included in the analysis. As with canopy density, slope can vary significantly at a finer scale. Two perpendicular measures of slope were taken at five points (one in the centre and 4 half way between the centre and each respective corner) in seedling plots using the calibrated clinometer mobile application 'Clinometer and Bubble Level'

(plaincodeTM, accuracy $\pm 0.1^\circ$). The perpendicular measures were combined to calculate the slope in the direction where slope was maximal, using;

$$S = \arccos \left(\frac{|\tan \theta_N \cdot \tan \theta_N + \tan \theta_E \cdot \tan \theta_E + 1 \times 10^{30}|}{\sqrt{(\tan \theta_N)^2 + (\tan \theta_E)^2 + 1} \cdot \sqrt{(\tan \theta_N)^2 + (\tan \theta_E)^2 + 1 \times 10^{60}}} \right) \quad (3.1)$$

where S is Slope, θ_N and θ_E denote the recorded angle in radians in the direction of north and east respectively. This equation is derived from the equation to find the angle between two planes (Anton *et al.*, 2002). While aspect can be an important driver of biological patterns in temperate (MCDonald & Urban, 2004) zones, it is of relative unimportance in the tropics so was not considered.

3.4 Data Analysis

Data from the second collection was omitted from this analysis since it was conducted too soon after the first collection for seedlings to exhibit significant differences in growth, mortality or recruitment (6 months). All analyses were conducted using the R statistical computing environment (R Core Team, 2015) with corresponding referenced packages. Prior to analyses, explanatory variables were tested for multicollinearity. Covarying variables were removed from all analyses when their variance inflation factor (VIF) exceeded 5 (O'Brien, 2007). This resulted in the exclusion of all litterfall measures, except for dry weight of leaf litter and removal of percentage cover trees and of bare ground.

3.4.1 Disturbance Index

The disturbance index was calculated to quantify logging intensity as:

$$DI = \frac{n_S}{n_S + n_L} \quad (3.2)$$

where DI , is the disturbance index, n_S denotes the number of logged stumps in the vegetation plot and n_L denotes the number of live trees. This index was a good representation of disturbance in an analysis of deadwood carbon by Pfeifer *et al.* (2015), calculated from the same SAFE core dataset.

To justify the suitability of this index as a metric for logging disturbance, I used ordered logistic regression to check for correspondence with the qualitative forest quality score.

3.4.2 Recruitment factors on recruitment dynamics

I fit generalised linear mixed effects models (GLMMs) with random effects to reflect the spatial nestedness of the sampling design and to account for pseudoreplication at the plot level (multiple observations within plots within blocks within sites) (Millar & Anderson, 2004). Genus was added as a further random effect to remove variance dictated by the traits of a given species in order to elucidate the broad mechanisms at play.

Explanatory variables were centred and scaled with a z -transformation to reduce multicollinearity and improve interpretability of results (Schielzeth, 2010). Occurrence of mortalities, represented as a binary data, were modelled using binomial error distribution. Occurrence of recruitment could not be modelled as binary data, since it requires comparison against non-occurrence of recruitment, therefore, recruitment was represented as count data at the plot level and fit with Poisson distributions. They were further subdivided into three groups, representing new germinations ($< 10\text{cm}$ height), seedling recruits ($< 50\text{cm}$ & $> 10\text{cm}$) and juvenile recruits in accordance with (Bell & Bryan, 2008) on plant life cycles. For abundance-linked response variables, namely mortality and recruitment, seedling basal area and seedling species richness were excluded from the analyses. Mortality would be highly correlated with the number of surrounding seedlings that have not died and recruitment with the number that have successfully recruited but these are not signals of interest. Similarly, species richness was excluded since high seedling richness is likely to be a sampling artefact of high abundance. (Kutner *et al.*, 2004).

The relative diameter growth rate (RGDR) of a seedling was calculated as:

$$RGDR = \frac{\log(D_k/D_0)}{t} \quad (3.3)$$

where D_k denotes the diameter of the seedling at the final collection and D_0 is the initial diameter in May–June 2012. Similarly, relative height growth rate was calculated as:

$$RGHR = \frac{\log(H_k/H_0)}{t} \quad (3.4)$$

where H_k denotes the height at third collection and H_0 denotes height at first collection (Bowman *et al.*, 2013). Growth models were fit with Gaussian errors and left untransformed as normality was within acceptable bounds. Models were fit using the lme4 package (Bates *et al.*, 2013). The proportion of variance explained by fixed factors ($R^2_{GLMM(m)}$) and by both fixed and random factors ($R^2_{GLMM(c)}$) are calculated according to Nakagawa & Schielzeth (2013).

Candidate models were compared using Akaike information criterion (AIC) since the use of p -values

in GLMMs is unsound (Bates *et al.*, 2014). Models were selected using multimodel inference since it is preferred over iterative stepwise approaches which generally cannot be expected to converge to the same model (Grafen *et al.*, 2002; Venables & Ripley, 2013). From a candidate set of the 100 ‘best’ models, model averaging was done over the best minimal n models for which the cumulative Akaike weights exceeded 0.9. In this way, candidate sets of models with no clear subset of ‘best’ models were averaged over a greater number of candidate models than cases where small set of models were clearly ‘better’ than the others. This minimises model uncertainty which can result in overestimation of model parameter precision and cause inference to be overly specific to the given dataset (Burnham & Anderson, 2002). The importance of reducing specificity to context is especially highlighted in this case by numbers of conflicting results in the literature (Valverde-Barrantes & Rocha, 2013; Chapman & Chapman, 1997; Schwartz & Caro, 2003). A given variable was included in the final model when their model-averaged importance was at least 0.8, i.e. the variable appeared in 80% or more of the ‘best’ models.

The model selection process for each model was conducted using the `glmulti` package in R using a genetic algorithm to minimise the computational load associated with comparing models with a high number of explanatory variables and their interactions. An immigration factor of 0.5 was used to prevent the algorithm getting ‘stuck’ at a suboptimal but locally stable state. The algorithm has been demonstrated to perform accurately in replicating the results of an exhaustive screen of variable combinations (Calcagno *et al.*, 2010) but each run was replicated 3 times to ensure convergence was consistent. On no occasion were discrepancies found so this matter is not discussed further.

3.4.3 Logging disturbance on recruitment factors

The impact of logging on recruitment factors was assessed by fitting generalised linear models to each recruitment factor used in the previous analysis in response to disturbance intensity. Mixed effects models were not used in this instance since the logging intensity gradient present at SAFE is the experimental treatment itself. Therefore, spatial variation and logging intensity are confounded when regarding solely disturbance intensity as an explanatory variable.

3.4.4 Logging disturbance on recruitment dynamics

To examine the extent to which the effects of logging intensity transfer through from recruitment factors to seedling growth, mortality and recruitment, further generalised mixed effects models were fit, with DI as the only explanatory variable. Significance here was tested using log-likelihood ratios.

4 Results

4.1 Disturbance Index

The disturbance index, used to provide a continuous variable for intensity of logging disturbance, was found to accurately predict qualitative classifications of forest quality. Disturbance index was zero for all plots with a forest quality of 5 and the difference between each score was significant with the exception of between scores of 3 and 4.

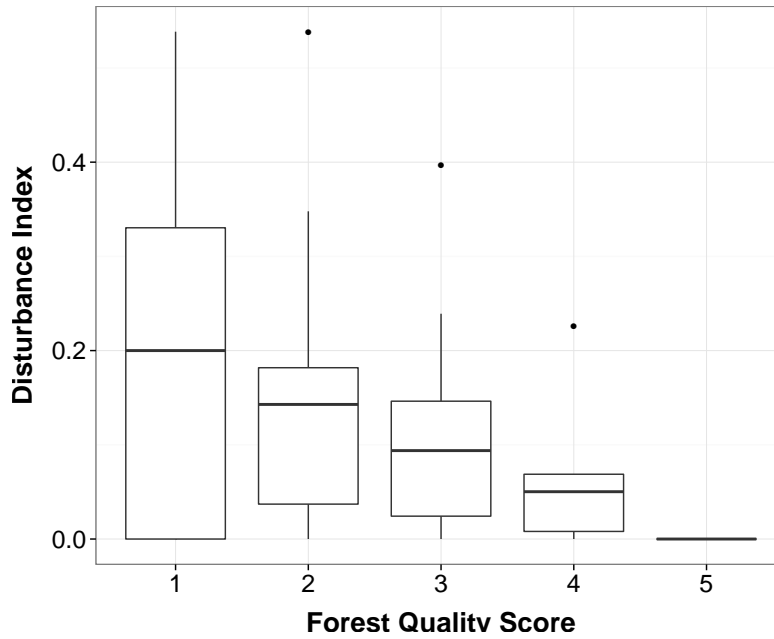


Figure 3: Disturbance intensity index accurately represents forest quality in stands of humid tropical forest, Sabah, Malaysian Borneo (regression coefficient = -8.7 ± 1.9 , $z = -4.5$, $p < 0.001$). See Equation 3.2 for quantification of the disturbance index (DI) and Table 2 for classification of forest quality scores)

4.2 Recruitment factors on recruitment dynamics

All runs of each genetic algorithm in glmulti converged to the same model, for which the full parameter estimates can be seen in Appendix 6.3. Diameter growth rate was decreased in plots which had high canopy density, high density of competing seedlings and alkaline soils but increased with increasing soil depth. Height growth rate experienced the same negative impact of canopy density, seedling density and pH but in contrast to diameter growth rate, soil depth was not predictive, but instead basal area of the surrounding adult tree community. In both cases canopy closure played the biggest role by some way.

Mortality rate was greatly increased by the percentage cover of understory vegetation, but was

Table 3: Generalised Linear model statistics for analyses of the effect of logging disturbance on recruitment factors

Variable	<i>df</i>	<i>t</i>	<i>p</i>	Residual <i>df</i>	<i>R</i> ²
Vegetation cover	2	27.62	<0.001	58	0.32
Adult basal area	2	15.40	<0.001	82	0.16
Canopy closure	2	9.79	<0.01	82	0.11
Herbivorous beetle abundance	2	9.74	<0.01	82	0.11
Seedling basal area	2	8.55	<0.01	82	0.09
Seedling Richness	2	7.39	<0.01	82	0.08
Mean daily maximum temperature	2	4.56	<0.05	73	0.06

alleviated by high canopy density, the size of the individual and the depth of litter.

The rate of germination was found to increase with the average maximum daily temperature experienced in a plot but germination rate was seen to decrease in plots with high vegetation cover, alkaline soils and interestingly, leaf litterfall weight. The ability of such new germinations to be recruited to the seedling phase of the tree life cycle was influenced similarly, however seedling recruitment was also reduced by canopy density and an interaction with vegetation cover whereby dense canopies and understory vegetation prevented recruitment, except where both were high, in which case seedling recruitment was facilitated. For larger, juvenile trees and vines, both the temperature and humidity facilitated successful recruitment to the juvenile phase when they were high yet again were negatively impacted by leaf litterfall and the percentage cover of vegetation.

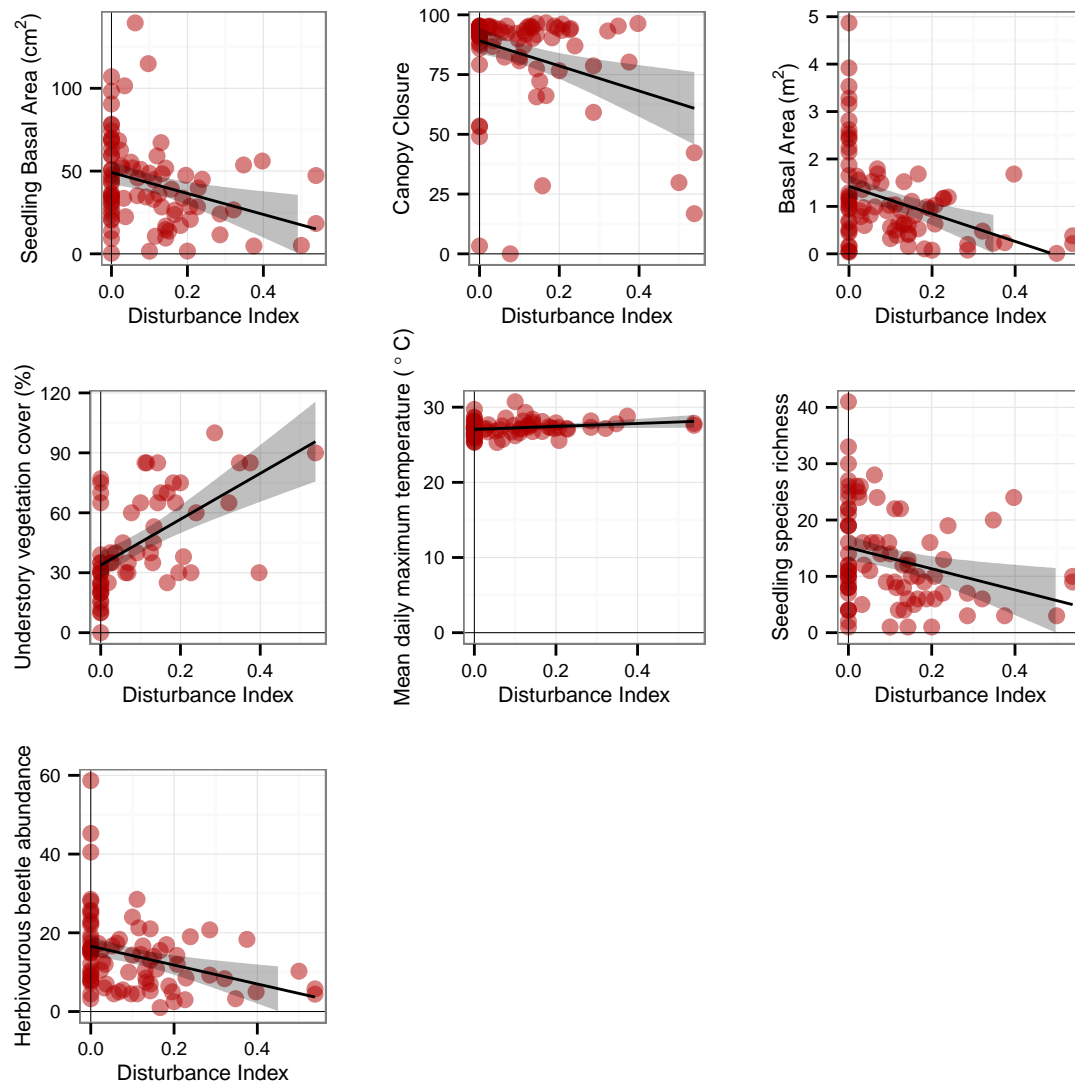
4.3 Logging disturbance on recruitment factors

Results from generalised linear models show that logging disturbance intensity was a significant predictor of the percentage cover of understory vegetation, unsurprisingly basal area and canopy closure, abundance of herbivorous beetles, seedling richness and density and the mean maximum daily temperature within plots (Fig. 4.3). Percentage vegetation cover was by far the most affected (Table 3) by logging while temperature and seedling richness were subject to low effect sizes. The full set of test statistics including factors which were not significantly affected by logging disturbance can be seen in Appendix 6.4.

4.4 Logging disturbance on recruitment dynamics

The impact of logging disturbance was surprisingly only found to significantly affect the recruitment rate of seedlings (-3.8 ± 1.23 , $\chi^2_1 = 11.8$, $p < 0.001$, $N = 84$) and juveniles (-1.6 ± 0.59 , $\chi^2_1 = 8.0$, $p < 0.01$, $N = 84$) (Fig. 4.4). All other aspects of recruitment dynamics remained unaffected (see

Figure 4: Logging disturbance has a significant effect on seedling density and richness, canopy density, basal area, understory vegetation cover and maximum daily temperature and abundance of herbivorous beetles in humid tropical rainforests of Sabah, Malaysian Borneo.



Appendix ??)

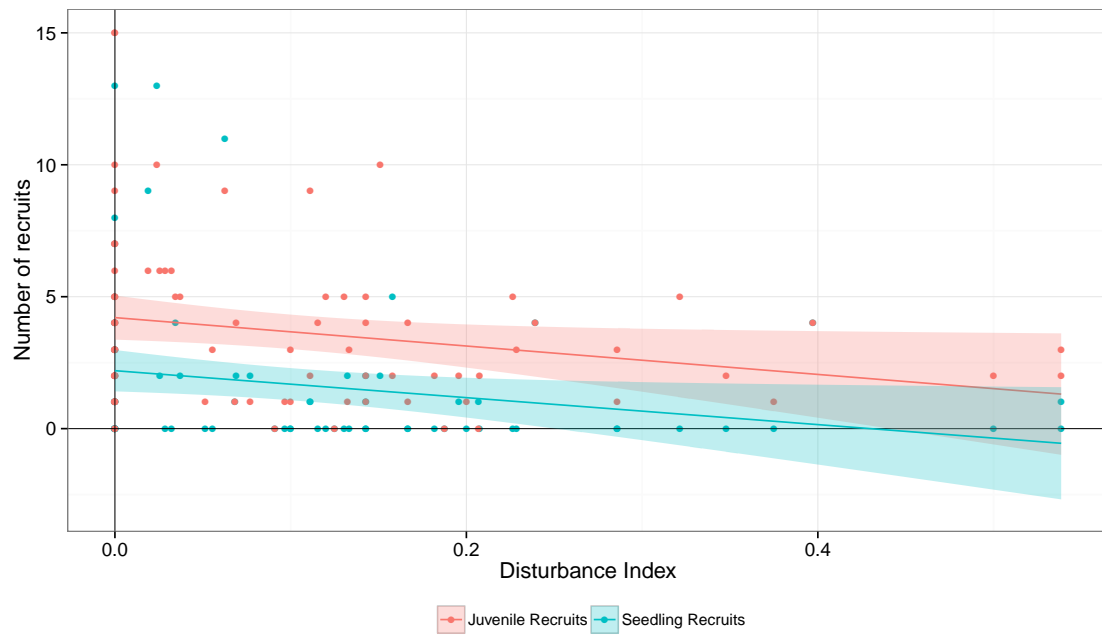


Figure 5: Logging intensity negatively impacts the recruitment rates of seedlings at two phases of their life cycle in humid tropical forests of Sabah, Malaysian Borneo.

5 Discussion

I showed that the major recruitment factors involved in shaping seedling recruitment dynamics relate to light intensity and competition for that light and other below ground resources. The empirical models developed through model averaging consistently identified the percentage cover of vegetation, canopy closure and basal area measures as important factors in effecting seedling recruitment. Directionality of these effects tended to be coherent too, vegetation cover hindered growth rate, increased mortality and reduced recruitment rate through all stages, producing an overall negative impact on seedling recovery. This is in line with what we would expect, since ferns, grasses and ginger are fast growing plants which impart a shade at a low level to the ground, creating a dense shade which will strongly outcompete woody slow growing plants. Equally, canopy closure affects the seedling recruitment process in line with what we would expect. Dense canopies hinder growth through limitation of the rate of photosynthesis, but does so at the canopy level which does not create such a dense shade as other vegetation. This explains why we see canopy closure reduce mortality rate while vegetation cover increases it. Vegetation cover is explicitly related to competition whereas canopy closure represents a limited resource. Seedling density within the plot was also seen to reduce growth rate. Since seedlings do not tend to create a dense shade on the understory floor, there is an indication here that growth rate may be impeded by competition for below ground resources. A surprising finding was the persistence in which leaf litterfall weight negatively impacted the rate of recruitment through each stage of the life cycle. Furthermore, the effect size of leaf litterfall increases through the recruitment process. My original hypothesis states that litter would provide a moist, stable environment to promote germination and some positive ‘hangover’ on growth might still be signalled in later phases but a reduction in recruitment was unexpected. One potential explanation is that litterfall damage may play a role in preventing recruitment between phases, however some studies have shown that litterfall damage can actually increase seedling growth rate Gillman *et al.* (2003) and this would not explain why the effect became larger as seedlings grew and became inherently more . Even more curious is that litter depth reduced mortality, in complete contrast to litter leaf weight. There is clearly some difference between these two metrics of leaf abundance, possibly relating to decomposition, however the exact mechanism remains elusive. It quite possible that this signal is false and arises through covariation with some other effect.

While disturbance intensity was shown to significantly impact many of the recruitment factors presented, examining the R^2 values shows that even for observational tropical ecology studies, the proportion of variance explained by each model is extremely low. The effect of logging on vegetation ground cover is the only variable that has a satisfactory R^2 for this field. Nevertheless, logging intensity is shown to have at least some impact on many of these factors. Interesting to note was the fact that herbivorous beetle abundance showed significant reduction with logging.

This is as one might expect with reduced food resources that is inherent with logging, however no affect of herbivory on seedling dynamics was apparent. This both highlights the complex nature of food webs and calls for an improved metric of herbivory rate.

Given that vegetation cover was strongly influenced by logging disturbance and was a strong predictor of recruitment rates, it is not of huge surprise that logging intensity strongly associated with reduced rates of recruitment. It is somewhat more surprising however that logging was not seen to directly affect mortality or growth rates. This could well be a symptom of logging having affects on sets of recruitment factors which vary in their effect on seedling dynamics. For example logging was seen to affect canopy closure and vegetation percentage which seen to have opposite implications to seedling mortality rate. This important point highlights the failure inherent in studies that attempt to study the effect of logging on seedling recruitment without considering the underlying mechanisms.

While previous studies have fallen foul to these issues, this study also falls foul to the large amount of stochasticity involved in seedling dynamics. While an extensive set of environmental and abiotic variables have been collated here, there still goes a large amount of unexplained variance. Improvements required to this study to elucidate the finer details of seedling dynamics include the need to collect data at a finer temporal resolution to adequately track growth through time since two data points is not sufficient to conclude significant findings on growth. Furthermore, the poor temporal resolution results in missing seedlings which are recruited and die in that time gap. There is also a call for better metrics for some of the recruitment factors examined here. Herbivorous beetle abundance and evidence of herbivory on leaves are crude metrics for herbivory rate. I suspect that herbivory plays a much larger role in the seedling recruitment process than is represented here. Lois Kineen currently at SAFE is explicitly studying the effects of logging on herbivory rates and Dr. Ollie Wearn's studies on animal abundances could prove fruitful opportunities for collaboration in quantifying herbivory.

Although, many of the intricacies involved in seedling recruitment have been elusive here, we have shown how deadwood can be used as reliable metric for disturbance intensity and for the first time have highlighted some of the mechanisms by which logging affects seedling recruitment which has potential in informing reduced impact logging practises and recruitment models for silvicultural harvest models.

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6 Appendices

6.1 Appendix 1

```

=====
| Staff Comment          2015-08-17 22:34:13 PST
| By: Feng G
|
| Thank you for contacting with Maxim Technical Support.
|
| We recommend to consider the value larger than 100% to be 100%,
| and keep the value less than 100% as it is.
|
| Thanks
|
=====
| Submit Request         2015-08-17 20:27:21 PST
| By: michael.massam11@imperial.ac.uk
|
| Hi
|
| I am using data collected from Hydrochron iButtons to determine
| the effect of humidity on seedling growth, recruitment and
| mortality in tropical rainforests. The data collected from these
| iButtons seems to behave strangely and regularly exceed 100%
| humidity. This happens for nearly all iButtons used. I am
| trying to make sense of the data here by scaling the data such
| that the maximum humidity is set to 100% but I am unsure on the
| mechanics of the iButton so was hoping you could answer some
| questions.
|
| Is this error a magnitude or a proportion of the measured value.
| i.e. if 106% is recorded, when humidity is 100%, would the same
| iButton record 0% or 6% in 0% humidity?
|
| It is generally well regarded that the humidity of the forest is
| 100% at night, yet many iButtons appear to have many levels of
| plateau. For example, see attachment 1, there are multiple
| 'levels' of above-100% humidity. The maximum humidity across this
| time is a peak in the month of December and only occurs in one
| instance, meaning if I was to scale by this value, all other
| nights would be below 100% relative humidity which is highly
| unlikely.
|
| Since you would know more about how the iButtons function and
| behave, what do you think the best way to treat this data is?
| Regard all recordings above 100% as 100% or to rescale them?
| Rescale by subtracting the difference or by dividing by
| (maximum/100)?
|
| Would really appreciate your input on this.
|
| Cheers,
| Mike

```

Figure 6: Personal communication with staff of Maxim, justifying treatment of RH values above 100%, as 100% with no scaling necessary

6.2 Appendix 2

Table 4: Test statistics for ordered logistic regression of forest quality in response to disturbance intensity index. Significance of regression coefficient is inferred with a z test

		Regression coefficient (\pm SE)	z	p
Disturbance Index		-8.7 ± 1.9	-4.5	<0.001
Forest quality score intercept:	1—2	-3.3 ± 0.5	-6.6	<0.001
	2—3	-1.8 ± 0.4	-5.0	<0.001
	3—4	0.3 ± 0.3	1.1	0.29
	4—5	0.8 ± 0.3	2.6	<0.05

6.3 Appendix 3

Table 5: Parameters for empirical averaged models for relative diameter growth rate (RGDR), relative height growth rate (RGHR), mortality rate, new germination rate, seedling recruitment rate and juvenile recruitment rate. Important model terms are understory vegetation cover (VegC, %), canopy closure (CClosure, %), seedling basal area (sBA, cm²), , basal area (BA, cm²), pH, soil depth (SoilD, cm), diameter of seedling at point of measurement (DPOM, mm), litter depth (LitterD, cm), leaf litterfall dry weight (LittF, g), mean daily maximum temperature (MaxTemp, °) and mean daily minimim relative humidity (MinRH, %)

Model	Estimate	Unconditional Variance	N_b	Importance	95% confidence interval	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Seedling recruits							
Intercept	0.056	1.479792	16	1.00	2.385		
VegC	-1.748	0.183235	16	1.00	0.839		
LitterF	-0.345	0.020867	16	1.00	0.283		
CClosure	-0.052	0.187315	16	1.00	0.848		
MaxTemp	1.010	0.051588	16	1.00	0.445		
CClosure \times VegC	1.539	0.294824	2	0.91	1.064		
Juvenile recruits							
Intercept	1.134	0.008987	60	1.00	0.186		
LitterF	-0.457	0.011840	60	1.00	0.213		
VegC	-0.197	0.011434	60	1.00	0.210		
MaxTemp	0.301	0.026355	60	1.00	0.318		
MinRH	0.423	0.023031	60	1.00	0.297		

Table 6: continued from Table 5

Model	Estimate	Unconditional Variance	N_b	Importance	95% confidence interval	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
RGDR						0.08922	0.24553
Intercept	0.060	0.000047	68	1.00	0.013		
CClosure	-0.019	0.000031	68	1.00	0.011		
sBA	-0.013	0.000027	68	1.00	0.010		
pH	-0.009	0.000030	66	0.97	0.011		
SoilD	0.007	0.000030	64	0.85	0.011		
RGHR						0.04328	0.20168
Intercept	0.063	0.000056	81	1.00	0.015		
VegC	-0.021	0.000068	81	1.00	0.016		
pH	-0.008	0.000049	75	0.92	0.014		
sBA	-0.009	0.000057	70	0.86	0.015		
BA	0.008	0.000058	72	0.85	0.015		
Mortality							
Intercept	-0.041	0.045129	86	1.00	0.416		
VegC	0.604	0.024569	86	1.00	0.307		
CClosure	-0.310	0.047297	86	1.00	0.426		
DPOM	-0.076	0.000260	86	1.00	0.032		
LitterD	-0.356	0.072926	79	0.90	0.529		
New Germinations							
Intercept	0.393	0.520495	60	1.00	1.414		
VegC	-0.559	0.026698	60	1.00	0.320		
LitterF	-0.186	0.016428	60	1.00	0.251		
MaxTemp	0.312	0.013516	60	1.00	0.228		
pH	-0.339	0.010347	60	1.00	0.199		

6.4 Appendix 4

Table 7: Test statistics for generalised linear regressions for each recruitment factor in response to disturbance intensity

Response	Intercept	Slope	<i>df</i>	<i>t</i>	<i>p</i>	Residual <i>df</i>	<i>R</i> ²
Vegetation ground cover	34 ± 3.4	110 ± 22	2	5.3	<0.001	58	0.32
Adult basal area	1.4 ± 0.12	-2.9 ± 0.74	2	-3.9	<0.001	82	0.16
Canopy closure	89 ± 2.8	-52 ± 17	2	-3.1	<0.01	82	0.11
Herbivorous beetle abundance	17 ± 1.3	-24 ± 7.7	2	-3.1	<0.01	82	0.11
Seedling basal area	49 ± 3.6	-63 ± 22	2	-2.9	<0.01	82	0.09
Seedling Richness	15 ± 1.1	-19 ± 6.9	2	-2.7	<0.01	82	0.08
Mean daily maximum temperature	27 ± 0.14	2 ± 0.92	2	2.1	<0.05	73	0.06
Mean daily minimum RH	89 ± 0.68	-4.8 ± 4.2	2	-1.1	0.2544	73	0.02
Leaf litter dry weight	32 ± 3.1	-17 ± 18	2	-0.9	0.3513	62	0.01
pH	6 ± 0.06	0.13 ± 0.36	2	0.4	0.357591	82	0
Litter Depth	2.2 ± 0.29	0.54 ± 1.7	2	0.3	0.7577	82	0
Evidence of herbivory	7.5 ± 0.61	0.79 ± 3.6	2	0.2	0.8297	79	0
Soil depth	2.9 ± 0.18	0.2 ± 1.1	2	0.2	0.8568	82	0
Beetle diversity	1.2 ± 0.034	0.007 ± 0.21	2	0.0	0.9732	82	0

6.5 Appendix 5

app:app5

Table 8: Test statistics for generalised linear mixed effects models on the impact of logging on germination, seedling recruitment, juvenile recruitment, mortality and relative diameter and height growth rates (RDGR & RHGR). Significance is inferred by log likelihood ratios

Response	Intercept	Slope	χ^2	df	p	N
Number of seedling recruits	0.77 ± 0.59	-3.8 ± 1.2323	11.8	1	<0.001	84
Number of juvenile recruits	1.5 ± 0.18	-1.59 ± 0.59	8.0	1	<0.01	84
Mortality rate	-0.81 ± 0.25	1.6 ± 0.97	2.6	1	0.11	2597
RDGR	0.049 ± 0.011	0.058 ± 0.049	1.5	1	0.23	1252
Number of new germinations	1.1 ± 0.38	-0.81 ± 0.79	1.1	1	0.29	84
RHGR	0.056 ± 0.0091	0.024 ± 0.062	0.2	1	0.69	891