

Post-dispersal seed removal rates: the relative roles played by vertebrates and invertebrates along a land-use gradient due to tropical forest degradation in Sabah, Malaysia



**A thesis submitted in partial fulfilment of the requirements for the degree of
Master of Science and the Diploma of Imperial College London**

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DECLARATION OF OWN WORK

I declare that this thesis

Post-dispersal seed removal rates: the relative roles played by vertebrates and invertebrates along a land-use gradient due to tropical forest degradation in Sabah, Malaysia

Is entirely my own work and that where material could be construed as the work of others, it is fully cited and referenced, and/or with the appropriate acknowledgement given.

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List of Acronyms

ANOVA	Analysis of Variance
FQ	Forest Quality
GLM	Generalized Linear Model
GPS	Global Positioning System
Lmer	Linear Mixed Effects Model
SAFE	Stability of Altered Forest Ecosystems project

Abstract

Tropical forests are being continually degraded and converted to plantations, to the detriment of the organisms living within them. Understanding how land use change affects the very processes underpinning ecosystem function is understudied, yet plays a key role in biodiversity conservation. This study used exclosure experiments to quantify the roles played by vertebrates and invertebrates in secondary seed removal, at a site in Northern Borneo. Transects were laid out in unlogged primary forest, twice logged secondary forest and oil palm plantation, all as part of the Stability of Altered Forest Ecosystems project, a large ecological project examining the effects of fragmentation and conversion to monocultural agriculture on forests in Malaysia. The relationship between rates of seed removal and forest quality were investigated. Invertebrates were found to dominate seed removal across all habitats and forest quality levels, with significantly increased vertebrate seed removal in highly degraded forest, which is thought to be linked to higher ground vegetation in these microhabitats. Although seed size and chemistry must play an important role, it appears that invertebrates play a key role in secondary seed predation and dispersal beyond what was assumed for South-East Asian forests.

Word Count: 12,337

Acknowledgements

I would first like to thank the SAFE project, along with its main sponsor the SIME Darby Foundation, for funding this project. Thank you also to Sabah Biodiversity Research Council, for giving me permission to carry out this research, and the Maliau Basin Management Committee for allowing me to sample in their forest reserve. Another thank you should also go to Bakhtair Effendi, my collaborator at Universiti Malaysia Sabah, for kindly meeting me and assisting with my visa, as well as his unbelievably kind colleague Bee, who I never thanked properly for all her help.

A big thanks to Rob Ewers, for picking me to tackle this project and providing me with help and support throughout; including, spending a valuable day with me in the field and discovering a trilobite beetle.

My time in Malaysia was eventful to say the least, so thank you to Maria and Rizma for nursing me in their houses when I was ill at camp. Thank you to Glen Reynolds, for being supportive when I fell ill, and visiting me in hospital. An enormous thank you also needs to go to Simon Amos and his lovely family, for bringing me appetizing food in hospital and then treating me as one of the family throughout my rehabilitation.

To Clare Wilkinson, thank you for being there every step of the way. You were like my sister in the field, and my much needed confidante. Thank you also to all the amazing researchers I met at SAFE who gave me support and advice: Sarah Luke, Terhi Riutta, Timm Dobert, Hayley Brant, Anand Nainar, Dena Clink and Sri Rao. Thank you to Rajeev Pillay for lending me his camera traps. Thank you to all the Malaysian research assistants who helped me in the field at one point or another: Mus, Mai, Harbin, Alex, Denny, Mike and Opong. Thank you to Sarah Watson for running the camp as well as she does, and keeping us topped up with fruit and good sense.

Thanks to David Orme for his help with my analysis, that one hour made all the difference. A big thank you to Sam Jones for taking time out of his hectic schedule to proofread my final draft and contribute valuable suggestions, and also to Billy Fairburn for helping me bind this thesis at the eleventh hour. And thank you to E.J. Milner-Gulland for her help all the way through the course.

Thank you to Gareth Davies, for making sure I applied to this course in the first place, putting up with me living away for a year and out of the country for 3.5 months and never saying a word in complaint; your endless patience and support means the world.

1. INTRODUCTION

Loss of tropical forests continues apace worldwide, causing great concern to conservationists. The principal drivers of this habitat destruction include activities such as slash-and-burn agriculture, managed logging concessions and wide-scale conversion to intensive agricultural land (Laurance, 1999; Sodhi, Koh, Brook & Ng, 2004). High rates of deforestation affect Southeast Asia in particular, a region containing 11% of the world's tropical forests (Iremonger & Ravilious, 1997). Within Southeast Asia, deforestation rates have continued at a rate of c. 1.4% per year in the last decade (Sodhi et al. 2004), which is higher than other species rich tropical regions.

The island of Borneo, widely recognised as a 'Biodiversity Hotspot' (Myers, Mittermeier, Mittermeier, Da Fonseca & Kent, 2000) lies within the Sundaland region of Southeast Asia, and is home to over 3000 tree species, dominated by large and economically valuable dipterocarp trees (family Dipterocarpaceae). Much of the forested landscape in Malaysian Borneo has been selectively logged, in many areas more than once; only 38% of the total remaining forest cover is relatively intact (Bryan et al. 2013). Conversion of landscapes on a large scale can have unexpected consequences for the ecosystems contained within them, due to a number of dynamics such as habitat fragmentation. This can take place through changes in structure and microclimate, resulting in a loss of biodiversity (Ding, Zang, Letcher, Liu & He, 2010; Bihn, Gebauer & Brandl, 2010). There is now a greater need to better understand such changes and their impacts upon other aspects of the ecosystem. To fully evaluate these outcomes, scientists need to understand the processes that underpin biodiversity and associated responses to land-use change and fragmentation.

In recent years, many tropical regions have witnessed a dramatic increase in oil palm cultivation, with the global extent increasing more than 3.5 times in 45 years to 13.2 million ha by 2006 (FAO, 2007). Tropical rainforests in Malaysian and Indonesian Borneo are currently under great pressure to undergo conversion of degraded forests to monoculture oil palm plantation due to rising global demand (Clay, 2004). Many governments view logged (secondary) forest as sufficiently degraded for conversion to this monoculture crop. These countries are currently the two largest palm oil producers worldwide (FAO, 2007).

Forest fragmentation is thought likely to affect key biological processes that support ecosystem functions, such as nutrient cycling, seed predation, decomposition and pollination (Didham, Ghazoul, Stork & Davis, 1996). Seed removal (both predation and dispersal) is an important process regulating both spatial dynamics of forest plant species and composition of plant

communities (Ashton, 1979; Janzen, 1972). Within Southeast Asian forests, seeds already dispersed from the parent tree (or pre-dispersed) are subsequently removed by vertebrate taxa such as bearded pigs (*Sus barbatus*), spiny rats (*Maxomys spp.*), squirrels and various species of bird (Curran & Leighton, 2000) as well as invertebrates such as insects. The effects of forest modification on rates of seed removal, where comparisons are made between unlogged and logged forest, has received little scientific attention; Notman and Gorchov (2001) compared forest with abandoned pasture land in South America, but no research has yet made this comparison for Southeast Asian forests.

1.1 A focus on secondary seed removal rates

As part of the larger SAFE project, this research focuses on secondary seed removal and the relative roles played by vertebrates and invertebrate guilds. Hulme (1998) identified the importance of quantifying the effects of different seed removal guilds as they potentially differ in their temporal and spatial effects, seed species preferences and foraging consequences. Removal rates were studied across three habitat types (see **Appendix 3** for photographs): unlogged primary forest, twice logged forest and oil palm plantation.

To compare these three separate habitats, a novel seed, unfamiliar to all potential seed predators, was used to investigate patterns displayed across the afore-mentioned land-use gradient. In addition, the study used an intermediate sized seed that had the greatest perceived chance of appealing equally to both vertebrates and invertebrate seed predators. The majority of previous work has examined seeds which could bias results too strongly in favour of either guild; seeds which are very small may escape the notice of vertebrates, and seeds which are too large may be too difficult for invertebrates to tackle.

Aside from posing the logistical issue in terms of sourcing a sufficient quantity of naturally-occurring seeds outside of the supra-annual seed masting season (Ashton, Givnish & Appanah, 1988), the habitats studied here (forest and oil palm plantation) share little or none of the same plant species (Danielsen et al. 2008). The use of exclosures is one of the predominant methods used to separate input into various processes by different animals groups (Holmes et al. 1979; Hamilton, Ankney & Bailey, 1994; Heithaus, 1981). To fully investigate the contribution from vertebrates and invertebrates, both guilds were excluded separately rather than relying on post-hoc diagnosis of seed predation through examination of gnaw marks and other indicative traces, which have the potential to bias patterns observed, under or over-estimating the contribution by either group.

1.2 Research aims and objectives

This study uses a modified technique in experimental exclusion of vertebrates and invertebrates from a model seed bait, in order to quantify the relative input from either taxon in secondary seed dispersal and the response of this dynamic to selective logging and conversion to oil palm. Its aims are to:

1. Model the overall level of seed removal across a land-use gradient to assess whether this differs between old growth, logged and agricultural sites.
2. Model the different contribution made by vertebrates and invertebrates across these sites as a function of forest quality.
3. Model the levels of partial seed predation, comparing vertebrate and invertebrate patterns.
4. Determine what factors may be driving these differences and patterns.
5. Critically appraise the use of a novel exclosure design and model seed in determining this.

2 BACKGROUND

2.1 Seed dispersal and predation in tropical forests

Forest ecosystems are underpinned by a number of important ecological processes, such as herbivory, pollination, seed dispersal and predation (Crawley, 1982; Terborgh et al. 2001). Seed production is a key stage of a plant's life cycle and associated predation patterns can be a major component of seed mortality, strongly impacting abundance, community structure, distribution and evolution (Duggan, 1985; Risch & Carroll 1986) as can dispersal patterns (Galetti et al. 2013).

Seed predation can be broadly split into two categories: pre-dispersal and post-dispersal (Janzen 1971a) (alternatively named pre-seedfall and post-seedfall (Kjellsson, 1985)). Pre-dispersal seed predation occurs when seeds are still attached to the parent plant and post-dispersal once they have been shed. Post-dispersal seed predation can occur on a number of substrates, such as soil or animal dung (Zhang, Drummond, Liebman & Hartke, 1997; Slade, Mann, Villanueva & Lewis, 2007) and may account for a high proportion of seed mortality. For instance, post-dispersal seed predation was found to be responsible for 55% of the total seed population of *Carex piluifera* in Denmark during the summer and autumn (Kjellsson, 1985). Predation also has a high impact on seedling recruitment in dipterocarp forests with most seeds killed through either pre- or post-dispersal predation (Maycock, Thewlis, Ghazoul, Nilus & Burslem, 2005).

Post-dispersal (or secondary) removal can exert a significant influence over density and distribution patterns of primary dispersal. McConkey (2005) found post-dispersal events to have a large effect on the seed shadow cast by gibbons in Central Kalimantan, Indonesia. Understanding factors affecting both seed dispersal and predation are important as altered patterns of seed removal could affect the community composition of native flora, potentially contributing to declines within fragmented ecosystems.

2.2 Role of vertebrates and invertebrates in seed predation and dispersal

Comparison between types of seed predators (e.g. large and small mammals) can give rise to general patterns. Broader groups such as vertebrates and invertebrates are viewed as particularly important, as differences between the two are likely to be larger and more consistent (Hammond & Brown, 1996). Ants (Hymenoptera), carabid beetles (family Carabidae)

and rodents are historically the best studied groups of post-dispersal seed predators (Zhang et al. 1997).

Previous work experimentally partitioning the role played by vertebrates and invertebrates has found vertebrates to dominate seed predation. Notman and Gorchov (2001) found over 75% (across a range of seed species), were removed by vertebrates in a Peruvian lowland tropical forest. Vertebrates are also postulated to be a primary selective factor in the evolution of synchronised mast seeding in dipterocarps (Janzen, 1974). However, some research has suggested that they also play important roles in seed dispersal through caching, leaving uneaten seeds (Forget 1991; Brewer & Rejmanek 1999). Other research, however, has found little evidence of scatter-hoarding; Maycock et al. (2005) found as little as 2% of the dipterocarp seeds examined in Sepilok, Sabah were cached, all of which were consumed during the experimental period. Winged dipterocarp seeds are poorly dispersed from the parent tree by gravity (Suzuki & Ashton, 1996), indicating secondary dispersal may be an important mechanism for seedling recruitment in Malaysian forests.

Invertebrates such as ants are commonly regarded as 'ecosystem engineers' (Jones, Lawton & Shachak, 1994) as they exert a high influence over the ecosystems they inhabit. Ants are often viewed as seed dispersers as well as predators, whereas vertebrates are often considered as primarily predators (Zhang et al. 1997). Myrmecochory, or seed dispersal by ants, is a co-evolved feature of many plant species around the globe (Buckley, 1982). Plants produce seeds containing a fleshy and nutritious appendage known as an elaiosome, which induces ants to disperse the diaspore (elaiosome plus seed) whilst consuming only the elaiosome (Handel & Beattie, 1990). This adaptation has been shown to reduce seed predation at the parent plant (Heithaus, 1981). Invertebrates are also considered to be important secondary seed predators as well as dispersal agents, such as in south-eastern Australian woodland (Andersen, 1987), an Israeli desert (Abramsky, 1983) and Costa Rican lowland rainforest (Levey & Byrne, 1993). Whilst both invertebrates and vertebrates can act at both dispersal stages, pre-dispersal predation is generally considered to be dominated by invertebrates, particularly insects (Nakagawa, Takeuchi, Kenta & Nakashizuka, 2005) and post-dispersal predation by vertebrates, such as small mammals (Terborgh et al. 1993; Notman & Gorchov, 2000; Maycock et al. 2005).

Studies have suggested that vertebrates may have greater sensitivity to the effects of human disturbance on animal communities (Wright et al. 2000), however, this was examining poaching levels as opposed to logging intensities. Elsewhere it is posed that invertebrates may be more sensitive to anthropogenic impacts as they have greater sensitivity to abiotic factors such as humidity (Lewis & Basset, 2007). Vertebrates and invertebrates vary greatly in terms of seed

predation behaviour. Species preference, timing and detection ability are all thought to contrast (Abramsky, 1983; Zhang et al. 1997; Rey et al. 2002). Rodents are considered to be more efficient at finding seeds through olfaction, and buried seeds (Zhang et al. 1997). Heithaus (1981) observed ants to steadily forage over a 24 hour period, while mice foraged intensively for shorter time periods, also invertebrates such as ants tend to be diurnal, and vertebrates such as rodents nocturnal (Zhang et al. 1997). Abramsky (1983) recorded rodents to utilise larger seeds before moving onto smaller ones, however, this was demonstrated using a narrow range of seed sizes and the potential bias of this inference must be acknowledged.

Seed size is thought to play an important role in feeding preferences. Larger seeds provide more energy per unit, thus fewer seeds are required by an individual animal (Zhang et al. 1997; Abramsky, 1983). Maycock et al. (2005) found no relationship between seed size and the likelihood of vertebrate predation, however, this was investigating only a small subset of dipterocarp seeds with a range of weights between 1.5 and 31.2 g. Blate, Peart and Leighton, (1998) in contrast, found a negative relationship between predation rates and seed size, coat thickness and hardness (fresh weight range between 0.1g and 11.6 g). Rey et al. (2002) showed granivorous ants in south-eastern Spain were unwilling to remove seeds weighing over 20 mg.

Although there does not appear to be any formal definition of 'large' and 'small' seeds across the available literature, Terborgh et al. (1993) classed their seeds as 'large' at 3-10 cm in size. This overlaps with size classes defined elsewhere; Harrison et al. (2013) defined large seeds as over or equal to 50 mm (5 cm) long. Conversely, Abramsky (1983) classed 'large seeds' as being 0.033 g in weight and 5.2 mm long. This ambiguity over seed size has been a potentially confounding element to the findings of other studies and makes comparison difficult.

2.3 Exclosure techniques

Studies looking at vertebrate and invertebrate driven seed removal have tended to use some form of exclosure. For instance, exclosure based experiments have been used to look at seed removal and functional group richness in dung beetles (Slade et al. 2007). Vertebrates are usually excluded using some form of cage or mesh, and invertebrates a barrier (Notman & Gorchov 2001; Heithaus, 1981; Abramsky, 1983). This barrier has consisted of either a slippery barrier, such as a petri dish (Abramsky, 1983), or a sticky/slippery substance such as Tanglefoot or Fluon applied to another structure (Fedriani et al. 2004; Hulme, 1997). The use of one or the other is allocated on its local appropriateness to the granivorous invertebrate species found in that area. Fewer experiments have excluded both guilds in the same study. This may be

due to the challenges in explicitly excluding invertebrates. Only a handful have compared exclusions for both taxa to a control, allowing access by both or denying access to both (Heithaus, 1981; Hulme, 1997; Fedriani et al. 2004). Terborgh, Losos, Riley and Riley (1993) found mixed results when examining seed removal of five large seeded tree species; most tree species were attacked by vertebrate seed predators, but one species was strongly attacked by bruchid beetles unless the seeds had been scatterhoarded by mammals, indicating a level of dependence on mammals for successful dispersal. In this study, only two forms of enclosure were used, and these were for mammals of different sizes.

Another enclosure study conducted by Nakagawa et al. (2005) investigating pre-dispersal seed predation in Sarawak, Malaysia found that invertebrates dominated predation for a number of dipterocarp species. The authors acknowledged that other work has found vertebrates to be the dominant post-dispersal seed remover, however, did not empirically test this within their habitat of study. Closer to the intended study site, Maycock et al (2005) compared vertebrate and invertebrate seed predation of four dipterocarp species within the Sepilok Forest Reserve, Sabah. Seed weights ranged from 1.5 to over 31 g. Again, vertebrate seed predators seemed to dominate post-dispersal predation.

Further work has shown that the interaction between vertebrate and invertebrate seed removal can significantly impact the fate of typically ant-dispersed (myrmecochorous) seeds. For instance, Heithaus (1981) found (by use of experimental exclusions where ants were excluded) seed-predating vertebrates (small mammals and birds) removed 70% of seeds, but where only ants had access, just 24-39% of seeds were predated.

Previous study has primarily used locally-sourced seeds found naturally within the habitats studied, and either compared removal rates across degraded and pristine habitats (Notman & Gorchov, 2001) or looked at primary forest alone (Heithaus, 1981; Terborgh et al. 1993; Maycock et al. 2005). One study compared seed removal rates of both groups across abandoned pasture, mature forest and treefall gaps in Amazonia (Nepstad, Uhl, Pereira & da Silva, 1996) however this did not experimentally compare the relative input from either taxon. An alternative 'seed' used is a mimic made from another edible substance, such as sieved barley grains (Abramsky, 1983), milled pearl barley (Kaspari & Weiser, 1996) and a corn starch based mixture (Whitford & Steinburger, 2009), where lipid and protein content can be controlled. The advantage of this is that size can be carefully manipulated.

2.4 Study area

2.4.1 The Stability of Altered Forest Ecosystems (SAFE) Project

The SAFE Project is an interdisciplinary, multinational project based in Sabah, Malaysian Borneo. It aims to assess how the impacts of modifying forest ramify across the broader ecological network. Formally established in 2011, it builds on the success of the Biological Dynamics of Forest Fragments project in South America and acts as a next step in large-scale ecological experimentation (Tollefson, 2013). The forest found at SAFE stands in an 8,000 ha block of twice-logged forest which is currently contiguous with a million hectare concession and that has been gazetted for conversion to oil palm plantation for the last 20 years. This plan forms the basis of the project, aiming to take advantage of this planned logging to experimentally monitor the functioning of the forest over a decade, in terms of its ecological processes plus the biological species assemblages both before and after logging takes place.

During the logging process, fragments of forest have been designed to remain so that the effects of fragmentation may be studied. Six landscape blocks will remain, each consisting of one 100 ha, two 10 ha and four 1 ha fragments. Each of these contains forest of varying quality and cover. Sampling is based on a fractal design which will allow comparison of diversity and ecological processes across multiple spatial scales (Ewers et al. 2011).

Logging began in April 2013, so sites were selected that would not yet be affected by the logging activity, and were still situated within continuous forest. Each fragment will gradually become isolated throughout the process, eventually surrounded by a matrix of cultivated oil palm land. The Maliau Basin Conservation Area and the nearby oil palm estate of Selangan Batu will both act as controls, namely primary forest and an established monoculture area, respectively.

2.4.2 Continuous logged forest - Yayasan Sabah Concession Area

The Yayasan Sabah Management Area (4°40'29.70"N, 117°34'44.25"E) is located in Eastern Sabah, comprising of 1 million ha of forest. An area of 750,000 ha is commercially managed, having been selectively logged from the 1970s onwards. Past harvesting methods over the past 30 years have differed in intensity, leading to differing patterns of disturbance and a variety of forest structure and qualities. The majority of areas have experienced two rounds of selective logging. The SAFE project logged forest site lies within the Kalabakan Forest Reserve. The secondary forest sites were selectively logged, taking between 8-15 trees per hectare of >60 cm DBH.

2.4.3 Continuous old growth forest – Maliau Basin Conservation Area (MBCA)

Sampling sites for pristine forest are located both within and directly next to the Maliau Basin Conservation area (5°02'47.40"N, 117°16'02.94"E). Initially gazetted in 1981, the Basin itself encompasses over 390km² of pristine, primary forest. Following a recent addition of 153,000ha totally protected forest to Sabah's patchwork of protected areas in 2012; Maliau now represents 3% of the total protected area landscape. Two of the SAFE Project sampling sites are within the conservation area, and the third is within the water catchment area for the Maliau Basin Field Centre (**Fig. 2.1**). This third site was lightly logged in the 1970s and once more in the 1990s for the construction of the field centre; however the structure and community composition of the forest remains representative of primary forest in the wider region.

2.4.4 Oil Palm Agriculture - Benta Wawasan Oil Palm

Yayasan Sabah granted permission to Benta Wawasan Sdn. Bhd. in 2004 to cultivate 48,800 ha of forest reserve within the Yayasan Concession Area into oil palm (*Elaeis guineensis*) plantation (4°33'50.16"N, 117°28'24.41"E). By the end of 2009, this plantation land formed 11 business estates, containing oil palm plants aged between 7 and 13 years. The SAFE project has three control sites which lie seven kilometres to the west of the main experimental site, within the Selangan Batu estate (**Fig. 2.1**).

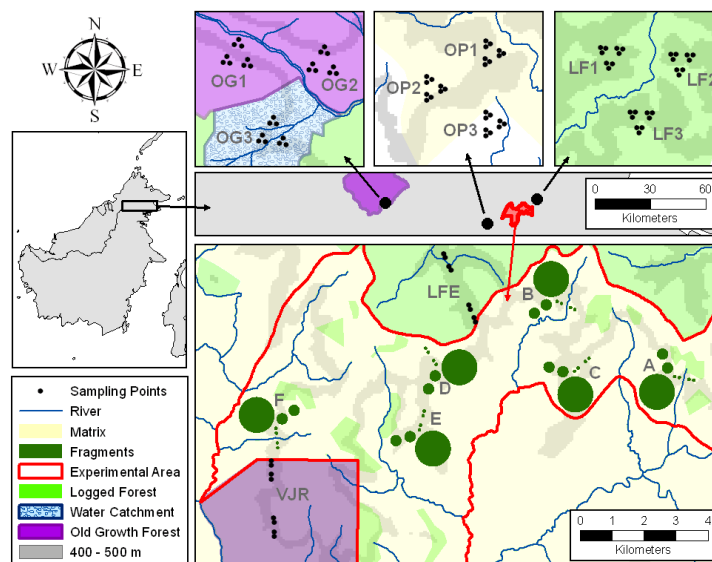


Fig. 2.1. Overview of the SAFE project, including location within Sabah, Northern Borneo. Red line denotes the experimental area. Areas with purple shading and black dots show control areas. Those labelled OG1, OG2 and OG3 area situated inside the Maliau Basin Conservation Area. Palm oil control plots are found west of the principal experimental site, and are labelled as OP1, OP2 and OP3. Sites labelled A-F are planned future fragments, consisting of 100 ha, 10 ha and 1 ha blocks, which are currently contiguous with a larger forest area. Logging began in April 2013, beginning the process of isolating these areas. Other sampling sites include the Virgin Jungle Reserve (VJR), Logged Forest (LF) controls and Logged Forest Edge (LFE). Figure taken from: <http://www.safeproject.net/wp-content/uploads/2010/08/SAFEdesignFigure.png>

3. METHODS

3.1 Data collection

3.1.1. Experimental sampling design and location

Experiments were carried out within the SAFE project experimental area. All planned landscape blocks were designed to minimise potential effects from confounding factors on a larger scale, and control for the effects of slope, distance from forest edge (once land conversion has taken place), latitude and longitude, so this study does not have to explicitly take these into account. Additionally, all blocks were positioned so that a large proportion of sampling points were found within the 400-500m altitude band, thus removing the potentially confounding effect of altitude (Ewers et al. 2011).

The SAFE Project fractal-base sampling design uses points set out in a hierarchy of increasing spatial scales using the same basic triangular pattern (Ewers et al. 2011). First order points are set in clusters of three, and are based a minimum of 56m apart. These are arranged in an equilateral triangle, with their centres forming the individual second order points. The sides of the second order fractal patterns are 178m. These are in turn nested within the patterns of larger third and fourth order fractals (see **Figure 3.1**). The experiment was conducted within all first order points located inside four sampling blocks, representing old growth, twice logged forest and oil palm plantation.

Logged Forest Sites

Sampling occurred along the four transects of block D (see **Appendix 2** for a detailed map of each block). In total, 48 first order points were sampled in this block. First order points were used as this was the smallest sampling scale available. It was judged that this would be most appropriate for the small organisms under study.

A second block (F) was sampled to provide potential contrast to block D, as experimental blocks of logged forest within SAFE varied in terms of forest quality. Although the two blocks have similar levels of canopy cover, F overall contains better quality forest patches (average forest quality in D is 2.06 whereas the average in F is 2.50 – **Table 3.1**; Ewers et al. 2011). A total of 36 first order points were sampled in this block.

Oil Palm Site

OP3 is one of three sampling blocks within SAFE's oil palm control site. This block was planted in 2000, has a closed canopy and lies 1km from the forest edge. Twenty seven first order points were sampled in this block.

Old Growth Site

OG2 is one of three sampling blocks that lies within SAFE's old growth control. It is located within the Maliau Basin Conservation Area itself, more than 500m from the reserve boundary. It has never been logged, with forest cover at 100%. 27 first order points were sampled in this block.

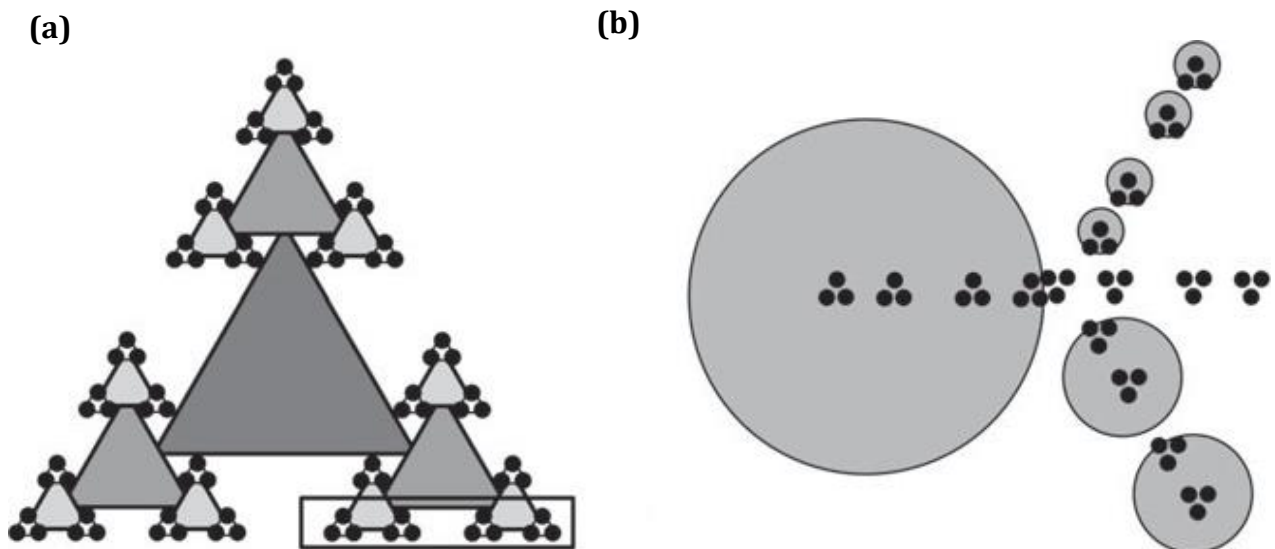


Fig. 3.1. (a) Fractal geometry used by the SAFE project. Black dots represent sampling points, with progressively darker triangles depicting progression from first to fourth order fractal patterns. **(b).** Spatial layout of each transect. Second order points are represented by a black dot. Largest circle is the planned 100ha fragment, two middle circles are 10 ha fragments and the four smallest circles the 1 ha fragments. (Ewers et al. 2011).

3.1.2 Forest quality scores

Data on Forest Quality (FQ) scores were taken from SAFE Project vegetation surveys performed in 2010. These surveys measured a number of parameters at each second order point, totalling 4 per transect within the SAFE Project experimental area (16 per block) and 9 points in each of the three discrete sampling blocks in the Old Growth and Oil Palm sites. FQ is a 6-level

qualitative score giving general information about the level of disturbance a site has undergone (Table 3.1).

Table 3.1. *Standardised forest quality scale as used by the SAFE project.*

Factor Level	Forest Quality	Description of area around sampling point
OP	Oil Palm	Oil palm plantation
1	Very Poor	No 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

Rainfall intensity data was taken on each day, rated between 0 – 5 (0 being no rain and 5 being torrential rain). Scores were based upon rainfall events at the study site lasting 30 minutes or more.

3.1.3 Experimental protocol

Data were collected between May 7th – July 27th 2013 and all specific dates of work were recorded.

The experimental design was based upon the SAFE Project fractal design: 20 seeds were placed at each corner of an equilateral triangle with 4m sides. A first order sampling point formed the centre of each triangle, located using GPS. Where it was impossible to centre the triangle directly over the sampling point (due to dense vegetation, large trees or streams), the triangle was centred as close to the first order point as possible. Each group of seeds would be randomly assigned one of three exclusions.

Seeds were placed upon standardised acrylic 'leaves', at the litter-layer level. All leaves were brown, to mimic the litter layer). Disposable latex gloves were worn when handling seeds, to prevent addition of any olfactory cues which could potentially alter the locating ability or preferences of potential seed predators. Insect repellent was also not worn whilst in the field. All leaves were of the dimensions 80mm x 120mm x 5mm. These were used to control for differences in substrate across the different habitat types, specifically leaf size, colour and chemistry. Leaves were worn with rough sandpaper and scored with a knife to allow

invertebrate seed removers access to the surface (previous work has shown invertebrates displayed behaviour suggesting a smooth leaf surface could act as a deterrent; Boyle, 2012).

Seed type was selected on the basis of size based commonality between ant/invertebrate and mouse/vertebrate seed predators and determined on the basis of field trials. Seeds novel to all three land use types were selected, allowing seeds to be used as a model and ensuring that no seed predators would have prior familiarity with the food source thus potentially skewing results. Dried, unflavoured pumpkin seeds (*Curcubita spp.*) were used and only intact, whole seeds were included in the experiment to prevent false identification of partially eaten seeds. Wet weight of a sample of 30 seeds along with length and width were measured: mean weight (g): 0.128, mean length (cm): 1.373 and mean width (cm): 0.723.

3.1.4 Treatment design

The study made use of enclosure treatments (hereafter 'treatments', designed to differentiate between vertebrate and invertebrate seed removers:

Treatment 1: No exclusion, both groups can access and remove seeds. Seeds placed upon a single leaf. This is a control treatment.

Treatment 2: Vertebrate exclusion: 18 x 18 x 18cm metal wire cage enclosures with a mesh size of 0.5 inch were placed at the litter-layer level, containing seeds placed on a leaf. These were pinned into the ground at the corners.

Treatment 3: Invertebrate exclusion: a layer of non-toxic insect trapping glue applied to a ca. 15cm x 18cm wooden frame, surrounding the leaf platform, nailed to a thin plywood board (**Fig. 3.2**). The board was pinned to the ground with nails.

Polystyrene rain covers (10" plates) were placed over enclosures at a minimum height of 30cm from the ground to ensure all small mammal seed predators could still access the seeds (**Fig. 3.2**). Rain covers were supported by sticks anchored in the ground to prevent rain washing away seeds or leaves forming bridges over the glue barrier in treatment 3. Supportive sticks were obtained from vegetation surrounding each first order point.



(a)



(b)



(c)

Fig. 3.2. Experimental set-up in the field: (a) shows Exclusion 1, (b) shows Exclusion 2 and (c) shows Exclusion 3.

Seeds were placed in the morning and left for 24 hours. Each seed was accounted for and any discovered in a ca. 20 cm radius around the experimental area was closely inspected. Seeds were assigned under a series of categories (**Table 3.2**).

Table 3.2. List of categories each seed was assigned to following a 24 hour period in the field.

Category Number	Seed Category	Description of seed condition
1	Seed remaining and uneaten	Seed is still on the leaf surface and outer coat has no visible holes or tooth marks.
2	Seed removed and uneaten	Seed is off the leaf surface and outer coat has no visible holes or tooth marks. This measure does not differentiate between seeds displaced a short distance or those further away. This includes seeds that have been cached underneath the leaf.
3	Seed remaining and eaten	Seed is still on the leaf surface but has been partially eaten. This ranged from small, visible holes on the seed coat to more substantial damage.
4	Seed removed and eaten	Seed is off the leaf surface and has been partially eaten, as above.
5	Seed removed and unknown	Seed has been removed completely from the experimental area and its ultimate fate (dispersal or predation) is unknown.

On the second day, exclosures within a triangle were re-positioned unidirectionally to an adjacent vertex, each in the same direction (**Fig. 3.3**). Presence/absence of ants at each treatment 1 and 2 site was recorded. Old seeds were removed and disposed of away from the experimental site and replaced with fresh seeds. The exclusion treatment 3 glue barrier was visually inspected for invertebrate by-catch. These were removed and additional glue was applied to the frame if necessary. The second round of seeds was then left for a further 24 hours. The second replicate would then be counted as before, and all equipment and half-eaten seeds removed from the experimental site.

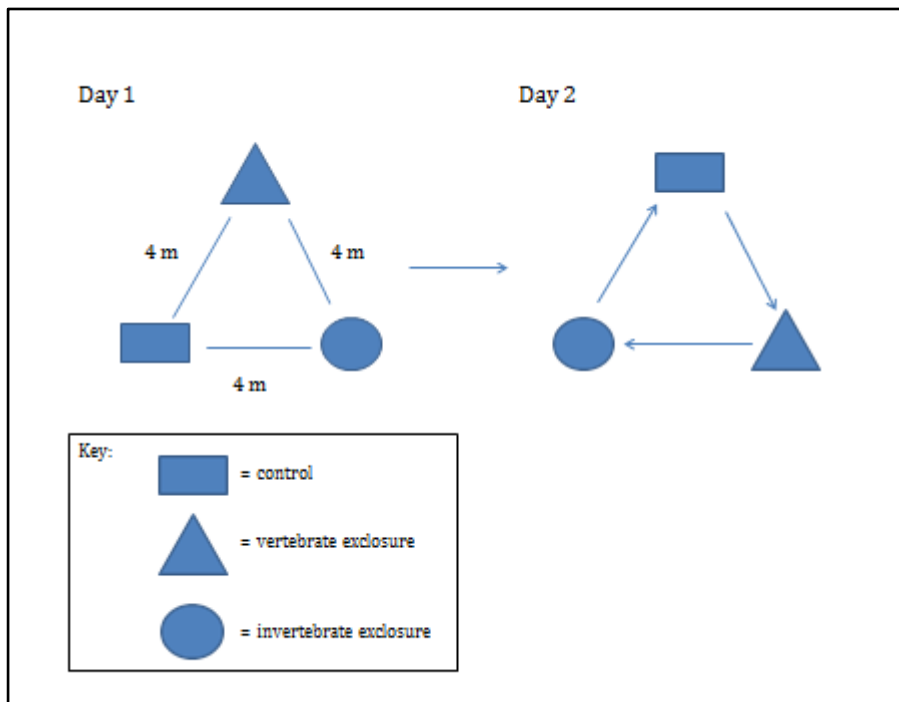


Fig. 3.3. Diagram showing the re-positioning of each exclosure following the first 24 hour period. Arrows denote direction of movement. Each exclosure moves 120 degrees to the adjacent vertex of the triangle.

3.2 Data Analysis

All statistical analyses were carried out in the R 2.15.2 statistical package for Windows (R Core Team, 2013).

The seed count is strictly bounded between 0 and 20, allowing the data to be viewed as proportions (0-1). Initially a generalised linear model (GLM) was used. Seed frequencies (the proportion of seeds removed from the exclosure area) were taken as the response variable, and treatment and forest quality as the categorical explanatory variables. All GLMs used binomial

errors (as errors are non-normal, due to the use of proportion data), except for when data was over-dispersed, in which case a quasi-binomial distribution was used. Model fits were tested with ANOVA, using an F test (for data with quasi-binomial fits). Null and simplified models were run to test the fit of the model to the data.

GLMs cannot include random effects; a linear mixed effect model was run on the same data to explore the random effects of site and date, using the 'lme4' package (Bates et al. 2013). Site was the location of the first order point sampled. The lmer function is able to remove the effect of temporal pseudo-replication generated by non-independent replicates at the same site over 48 hours. Overdispersion cannot be corrected for using the 'lme4' package using 'quasi' distributions as the results were deemed by the function's creator as unreliable. In addition, Bates (2010) does not provide degrees of freedom with his model summary, as he does not believe in the leading paradigm wherein F statistics are computed with a given numerator and denominator d.f., extracted by an approximation. Thus, many outputs quoted within the Results do not contain d.f. The generalised linear model and linear mixed effects models were compared. Results showed high levels of similarity. Lmer models with and without an interaction between fixed effects were tested using ANOVA.

Overdispersion in lmer can sometimes be corrected for by fitting observation level random effects, as demonstrated in Browne, Subramanian, Jones and Goldstein (2005). The resulting outputs had fewer significant results than the standard lmer function, and more closely matched the GLM outputs generated (which also accounts for overdispersion) – see **Appendix 1**.

Covariate FQ had the subset level '4' removed from many of the analyses, owing to the much smaller sample size (just 6 sites were sampled for level 4, in contrast with 101 for subset level 2 and 54 each in old growth and oil palm) and high standard error. This is a reflection of the lack of higher quality forest patches within the logged forest mosaic. A GLM was run also on the combined partially-eaten seed data, plus on each category of seed data (**Table 3.2**).

4 RESULTS

4.1 Seed removal and predation rates

Comparison of lmer models showed a strong interaction between treatment type and FQ level for both seed removal and seed predation (chi-square = 261.62, d.f. = 8, $p < 0.001$; chi-square = 57.323, $p < 0.001$, d.f. = 5). This suggests that seed removal rates were affected more heavily where particular treatment types and areas of forest quality combined. There was a particularly significant and negative interaction where FQ 2 and invertebrates only had access to seeds ($p = 0.004$, $z = -2.825$). For seed predation rates, this also suggests an amplifying effect whereby predation rates were increased more with particular treatment and FQ combinations; invertebrate only sites and degraded FQ level 2 forest had a significantly strong effect ($p < 0.001$, $z = 4.270$).

4.1.1 Seed removal and predation by both taxa (Treatment 1)

Seed removal was significantly higher within each FQ type when both taxa (vertebrates and invertebrates) had access ($p < 0.001$, $z = 3.320$). This was only negligibly higher when compared to when just invertebrates had access to seeds, but significantly higher than when only vertebrates had access ($p > 0.001$, $z = -8.502$). Seed removal rates were highest in the logged forest, changing across the gradient of land use intensity, with 80.28% removed or part-eaten in old growth, 90.34% in twice logged forest and 59.35% in oil palm plantation. Seed predation rates in contrast were higher in oil palm than in logged or old growth forest ($p = 0.01$, $z = 2.548$). Lowest predation rates were observed in sites of FQ 2 and 4, at 7.08% and 4.17% respectively (sample size for FQ 4 was much smaller than for FQ 2, with a higher standard error, thus the results for this may need to be treated with caution). Rates of partial seed predation were similar in logged and old growth forest (average 8.99% and 14.07% respectively), with no significant difference between the two. Seed removal rates were significantly lower in the oil palm than the logged forest and old growth ($p < 0.001$, $z = 3.320$).

4.1.2 Seed removal and predation by invertebrates (Treatment 2)

5,960 seeds placed at 298 exclosures were available exclusively to invertebrates; 3 of these were breached by vertebrates (in all cases, a rat dug underneath the exclosure) and as a result

these data were removed from the analysis. The total sample size in this analysis is therefore 5,900. Seed removal rates as well as seed predation where only invertebrates had access were removed at a similar rate to controls and higher than invertebrate exclusions. Lowest rates of seed removal for treatment 2 were seen in oil palm plantation (61.11%), highest in logged forest (FQ levels 1-4, average 83.76%) and intermediate rates in old growth forest (78.24%) (**Fig. 4.1**). Highest numbers of part-eaten seeds were found in oil palm (29.26%), declining to 25.28% in old growth forest, followed by an average of 23.13% in logged forest. There was however a higher percentage of part-eaten seeds in FQ 1 level sites. There was a negligible difference only between removal rates from control sites and invertebrate only sites, suggesting that invertebrates were the dominant seed removers in this study. The percentage of partially eaten seeds in oil palm at control and invertebrate sites are also highly similar, with 27.59% found at control sites and 29.26% where only invertebrates had access.

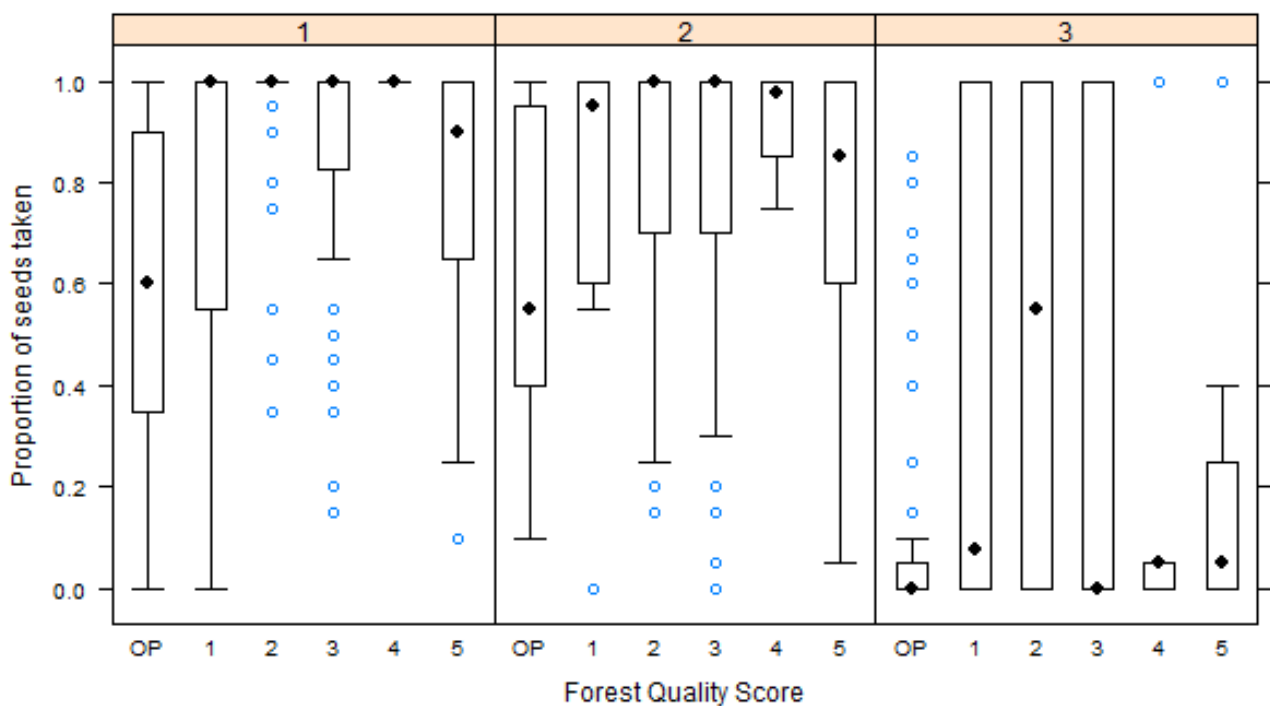


Fig. 4.1. Box and whisker plots showing seed removal rates expressed as a proportion of the initial 20 seeds placed in the experiment. Median = (black dots) and the 25th and 75th percentiles (lower and upper limits of boxes) along with 95% confidence limits (whiskers). Open circles denote outliers. Forest Quality (FQ) as a predictor of seed removal rate from each treatment type (top box): 1 = both taxa, 2 = invertebrates only and 3 = vertebrates only.. OP = Oil Palm, FQ 5 = Old Growth and FQ 1-4 represents the Logged Forest.

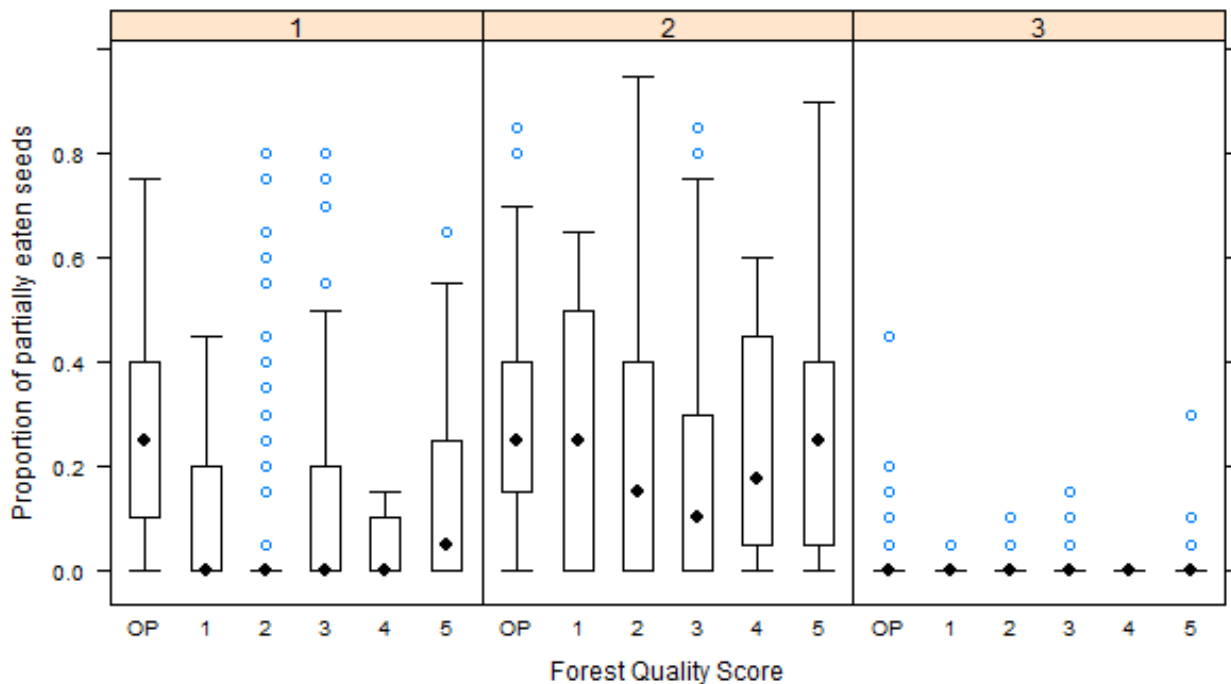


Fig. 4.2. Figure shows the relationship between FQ and the proportion of partially eaten seeds left behind (both on and off the leaf) at each experimental site. Box and whisker plots; the median = black dots, 25th and 75th percentile = lower and upper edges of boxes, 95% confidence limits = whiskers. Outliers are shown by open circles.

4.1.3 Seed removal and predation by vertebrates (Treatment 3)

5,960 seeds placed at 298 exclosures were available exclusively to vertebrates in this study. 49 of these exclosures were breached by invertebrates (either via a leaf or twig forming a bridge over the glue or by heavy rain rendering the glue barrier less sticky). These data points were removed from the analysis, thus the total sample size in this analysis was 4,980, available at 249 exclosures.

Rates for both seed removal and seed predation by vertebrates were significantly lower than for controls and just invertebrates across the habitat gradient ($p = < 0.001$, $z = -8.502$; $p = < 0.001$, $z = -7.002$). Patterns of removal however differed across the FQ gradient. Seed removal rates were lowest in the oil palm plantation (10.43%) and at slightly higher, similar levels in much of the logged forest and old growth (average 35.03% in LF and 22.14% OG). Seed predation rates were consistently low across all FQ levels (**Fig. 4.2**); highest in oil palm (2.31%), next highest in old growth (1.33%) and lowest in logged forest (0-1.18%). There is a sharp rise in removal in FQ 2 (52.24%), suggesting a greater role in seed removal played by vertebrates in disturbed forest where there is higher levels of undergrowth (**Fig. 4.1**).

4.2 Seed Remover Identity

It is not known exactly which specific animals were responsible for seed removal in this study. Ants were commonly observed at both treatment control and vertebrate exclosures, and on a number of occasions breached treatment invertebrate exclosures. Ants were recorded as still present at 36% of treatment control and vertebrate exclusion sites. This is a conservative measure as ants were likely to forage elsewhere once they had exhausted a food source, and many sites had all seeds removed.

Some anecdotal evidence suggests that small mammals were at least partially responsible for seed removal for treatment 3 sites. Rodent hairs and paw prints were observed on several occasions in the glue barrier. In addition, treatment 2 exclosures were breached on two separate occasions by a rat (*Maxomys whiteheadi*) digging underneath.

5 DISCUSSION

5.1 Seed removal across the land-use gradient

The results of this study counter the previous convention that vertebrates dominate most post-dispersal seed removal in tropical forests: invertebrates were found to be the dominant seed removal agent across all levels of the modified habitat gradient. This was highest in logged forest, followed by old growth forest and lowest in oil palm plantation. Most studies partitioning vertebrate and invertebrate-driven secondary seed removal have concluded that this process is overwhelmingly driven by vertebrates such as small mammals (Notman & Gorchoy, 2001; Terborgh et al. 1993; Maycock et al. 2005), particularly in tropical systems.

Lower rates of seed removal were observed in old growth forest than logged forest, despite the higher species diversity of both ants and small mammals and birds recorded in this habitat type (Fayle et al. 2010; Edwards, Edwards, Hamer & Davies, 2013; Bernard, Fjeldså & Mohamed, 2009; Wells, Kalko, Lakim & Pfeiffer, 2007). This may be due in part to sampling occurring during what appeared to be a mini-mast event (*pers. obsv.*), which could be ‘diluting’ the foraging efforts of both taxa. There were a number of dipterocarps producing winged seeds at the Maliau Basin study site at the time of sampling (*pers. obsv.*). Seed removal rates for control exclosures and invertebrates were very similar (78.24% and 80.28%, respectively), suggesting that insects were responsible for most of the removed seeds. Removal rates for vertebrates were 22.14%, suggesting they did still play a role.

A possible explanation for this lies in differences in seed characteristics used in each experiment. The most obvious factor is seed size and weight; where vertebrates are seen to dominate seed removal, seed weight tends to be ca. > 1 g. The mean weight of pumpkin seeds in this experiment came to 0.128 g, which allowed a greater share of input from small invertebrates. Nepstad et al. (1996) postulated that seeds weighing over 0.4g would be too large to be moved by ants, but this is based on the seed species in their study. Indeed, others have pointed out that the limits of what small mammals and ants vertebrates will remove are likely to vary locally, depending on the sizes of members of each group (Abbott & van Heurck, 1985). There is no set consensus across the literature as to what constitutes a 'large' or a 'small' seed; rather, it seems defined more by the local context and sample of seed species used in a study. Furthermore, it seems reasonable to assume that vertebrates would prefer larger seeds, as these provide more food per individual item (Zhang et al. 1997; Abramsky, 1983). Thus, should this experiment be repeated with a large seed species, a different relationship between vertebrate and invertebrate seed removal may be witnessed.

The results observed here do however reflect those found by Alvarez-Buylla and Martínez-Ramos (1990), where it was judged that invertebrates were the primary seed predators of the Mexican tropical pioneer tree *Cecropia obtusifolia*, as their removal rate was equal to those in control plots. Tentative conclusions should be drawn considering that only two enclosure types were utilised: a control (open) type along with an invertebrate-only treatment. Individual seeds were however considered 'small' at 1-2 mm long, so this result may have validity.

Other potential influences on seed preference include hardness, width and nutritive value (Abbott & van Heurck, 1985). The seeds used in this study had their seed coat removed, making them more easily accessible by ants; ease of handling has been put forward as an important factor in seed preferences (Lund & Turpin 1977). Abbott and van Heurck (1985) found that seeds containing the highest relative amounts of nitrogen and phosphorous were most favoured by vertebrates. Myrmecochorous (ant-dispersal) behaviour is thought to be partly stimulated by the composition of fatty acids elaiosomes contain, particularly oleic acid (Brew, O'Dowd & Rae 1989); this substance happens to be one of the dominant fatty acids found in the experimental seeds in this study (Murkovic, Hillebrand, Winkler, Leitner & Pfannhauser, 1996).

Furthermore, a previous study of leaf litter ant diversity within repeatedly logged forest habitats in Sabah, Borneo has been shown there to be over 80% of the species found in unlogged forest (Woodcock et al. 2011). This lends support to the high levels of invertebrate seed removal both logged and unlogged forest contained.

The sharp increase in vertebrate seed removal in forest patches ranked at FQ level two is in line with findings that significantly higher densities of generalist non-volant small mammal species occur in disturbed forest (Bernard, Fjeldsa & Mohammed, 2009). This is thought to be related to structural differences between logged and unlogged habitats, as disturbed habitats contain dense ground level herbaceous cover, plus smaller trees and lianas, which can correlate with the presence of tropical species of rat (Lambert & Adler, 2000). These features typify the poorer quality areas of forest at the SAFE project. Microhabitats of a similar type found within unlogged forest areas have been shown to harbour higher densities of generalist small mammal species (Wells, Pfeiffer, Lakim & Linsenmair, 2004). Similarly, Nepstad et al. (1996) found in Amazonia that rodents were more common in areas of abandoned pasture than mature forest.

Other work suggests that vertebrates play a dominant role in seed removal and predation within disturbed tropical forest habitats (Notman & Gorchov, 2001). However, here they found no consistent difference in seed predation rates (including both vertebrates and invertebrates) between young and mature forest. They also found greater insect-driven seed predation in mature forest, possibly due to differences in abiotic conditions, which is in contrast to this study. However, the principle invertebrate seed removing agents were a species of cricket, rather than ants.

The reduced rates of seed removal within oil palm plantations, found in this study for both vertebrates and invertebrates, are supported by the depauperate nature of oil palm fauna. Fayle et al. (2010) found a significant loss of species richness and relative abundance of leaf litter ants between primary forest and oil palm plantation. Similarly, Bernard et al. (2009) confirmed the impoverished nature of small mammal communities in oil palm.

Rates of seed removal for control and invertebrate sites showed high levels of similarity, indicating that almost all seed removal was carried out by invertebrates. The low levels of seed removal by vertebrates could be due to a number of reasons; oil palm fruits are high in fat content, and abundant throughout plantations, so may represent a preferred food source over the experimental seeds; densities of small mammals may have been low enough that rats never encountered the exclosures. Birds were present in the plantations, and prints and feathers were observed on the glue barrier on an exclosure permitting entry by vertebrates on one occasion (*pers. obs.*). Although granivorous passerines were still found relatively commonly within oil palm (Edwards et al. 2013), they may under-utilising available resources, not encountering the experimental seed or showing preference for more abundant oil palm fruit. Further work leaving seeds out for longer periods may help determine this cause.

5.2 Seed predation

Rates of partial seed predation (seeds both left on and nearby the experimental 'leaf') show clear differences between vertebrates and invertebrates. Invertebrates consistently leave a quantity of partially predated seeds after 24 hours, whereas vertebrates would consume all seeds present if discovered. Heithaus (1981) similarly noticed that mice would finish a depot of seeds once located.

The differing rates are likely to largely reflect the speed with which either group can consume seeds, once found. Alvarez-Buylla and Martinez-Ramos (1990) reported that seed predation rates by ants were bimodal after 4 days of experimentation, thus all seeds were eventually eaten once found; in this study seeds were left out for a quarter of this time.

Ant foraging behaviour varied within this study; some species appeared to prefer removing seeds and caching them beneath the leaf before taking seeds apart gradually and parcelling smaller pieces to their nest (*pers. obsv.*). Others piled soil over the seeds and leaf surface and subsequently broke the seeds down; others cooperatively or singly removed individual seeds along trails, depending on the worker size. Wells and Bagchi (2005) found that part-consumed seeds were still able to germinate but lost viability, only provided the level of consumption was less than half the original seed. These differences could potentially affect dispersal or predation patterns and may be an interesting avenue for further study.

The fact that numbers of partially eaten seeds at the control sites were lower than the invertebrate sites suggests that vertebrates were indeed discovering seeds at the controls, but not all the time. Also, the far lower numbers of partially consumed seeds left in FQ two patches is further evidence that vertebrates were finding seeds in these areas more frequently than in patches of different quality.

That vertebrates did not leave many seed remains or only part-consume them does not tell us anything about the seed's ultimate fate; each seed had the potential to be consumed on the spot, removed and consumed or scatter-hoarded for later. Occasional vertebrate sites suggested at-site consumption: seed husks left behind (*pers. obsv.*). Scatter-hoarding by rodents in tropical forests has been recorded, although it is poorly understood in the paleotropics in comparison to the neotropics (McConkey, 2005); Yasuda, Miura and Nor Azman (2000) reports this behaviour by the brown spiny rat *Maxomys rajah* in Peninsular Malaysia, and McConkey (2005) discusses hoards of a tree seed by the same rodent in central Borneo. However, Maycock et al. (2005) stated that they found little evidence of scatter hoarding by mammals in a forest reserve in Sabah, with just 2% experimental seeds cached, and all of these consumed within the

experimental period. It was also suggested here that secondary dispersal by vertebrates may take on greater importance during general flowering events. Interpreting the consequences of seed removal requires greater knowledge of the species of animal and plant species involved (Hulme & Kollmann, 2005).

These patterns all indicate the disparity in feeding behaviour between vertebrates and invertebrates, but also that this changes very little across habitats. It also suggests that there may be more competition for dispersed seeds between ants and small mammals in highly disturbed forest patches, although the ultimate consequences of this would be challenging to guess without further work.

5.3 Impacts on the ecosystem and conservation implications

The patterns observed in the data have broader implications in terms of the wider ecosystem, particularly in terms of oil palm plantation and logged forest. Logged forest habitats have been shown repeatedly to contain greater densities of generalist small mammal seed predators (Bernard et al. 2009; Cusack, 2011), which could translate to enhanced secondary seed dispersal in some instances but may also lead to more intense seed predation. This may have impacts upon secondary forest regeneration, either in managed logging concessions or areas permanently recovering (such as the newly gazetted extension to the current protected area network in the Yayasan Sabah Management Area). Higher predation rates could slow recovery of forest cover, if low intensity masting events saw little recruitment (Maycock et al. 2005). This may lend support to the need for longer periods between logging rounds to permit recruitment of dipterocarp and other forest seedlings. Evidence of higher mammal abundance negatively affecting seedling recruitment was found within Western Kalimantan (Curran et al. 1999) and Panama (De Steven & Putz, 1984). Selective logging operations should therefore be careful to not over-harvest areas, as this may create patches which favour seed predators which could potentially hamper forest regeneration and the recruitment of valuable hardwood tree species.

A further impact of altered seed predation dynamics in logged forest is on plant community composition, as seed preferences may influence succession patterns. For instance, weed communities were affected by the selective removal of grass seeds by *Pheidole* ants (Risch & Carroll, 1986). Thus, where both vertebrates and invertebrates have seed preferences in heavily disturbed forest sites, high predation levels may drive down recruitment for those species (Heithaus, 1981). In addition, Wells and Bagchi (2005) postulated that certain seeds could be preferentially cached over others, due to factors such as germination speed, which may lead to increased survival.

5.4 Limitations of the study and future research

5.4.1 Overall study design

Unequal sampling effort was given across the various FQ levels, as a result of the natural heterogeneity encountered in the logged forest sites. Most sites within this habitat tended to be at FQ level two or three. Thus it is recommended that additional sampling be carried out at both sites containing more FQ level one and four patches. Measures of FQ were taken separately at individual second order points; however this was not repeated at the finer scale of first order points. Some variation existed in FQ between second order points and their surrounding first order points, which could potentially cause bias within the analysis due to the lack of a finer spatial scale; in practise this is unlikely to have exceeded more than one FQ level and as most sets of sampling points shared highly similar forest quality characteristics, the results are likely to be robust despite this.

5.4.2 Exclosure design

The principal barrier used to repel invertebrate seed removers at treatment 3 exclosures was specialised glue. This glue lost stickiness in heavy rain, rendering it less effective as a barrier to invertebrates such as ants. Although it was clear once this barrier had been breached (ants typically left a soil trail across the barrier – see **Appendix 4**) this ultimately lost data, however not enough to impact on the results. Observations in the field suggested that not all invertebrates were necessarily excluded by treatment three; many sites, and particularly in the oil palm, showed various species of crickets and grasshoppers acted as seed predators. These were also seen to occasionally breach the invertebrate barrier which could have inflated seed predation rates by vertebrates; however many also were caught in the barrier itself. In addition, seed predation by orthoptera was at low intensities, with just one present at a site at any one time, thus they were unlikely to alter the picture of the general vertebrate or invertebrate dynamic. Ants appeared to be the dominant seed predator, although this was only witnessed during the day. However, Heithaus (1981) stated that ants foraged over a 24 hour period.

The glue could potentially be affecting vertebrate willingness to remove seeds, due to its highly sticky nature. In addition, over the course of each 24 hour period the glue gradually gathered increasing numbers of arthropod by-catch as creatures attempted to reach the seeds. It is possible that the odour of dead insects in the glue could attract certain animals. This in turn occasionally attracted small litter dwelling skinks which became stuck in the barrier. Other studies employing exclosure techniques have used a raised pedestal platform, with the insect-

repelling substance applied underneath (Heithaus, 1981) which could solve some of these issues, but could also be more vulnerable to being tipped over by larger animals. Ultimately however, despite these various criticisms, the use of the new method seemed highly successful.

5.4.2 Effect of seed bait

Seed size and chemical composition might potentially have had a disproportionate effect on the likelihood of removal by different animals, making it possible that the picture of the general roles played by vertebrates and invertebrates was distorted. However, this could be a risk with any model seed used, without prior knowledge of the feeding preferences of organisms present in the habitat of study. Plus, the high rates of removal by vertebrates in certain forest areas suggest that the experimental seeds were still appealing to this group as well. Food preference experiments performed with caught small mammal seed predators would give insight into seed choice; such tests performed on *Maxomys* spp. (spiny rats, widespread in Borneo) by Blate et al. (1998) showed these rodents preferred medium sized, soft seeds.

Artificial seeds would control for chemical composition and shape whilst more accurately testing the effect of size. A range of seed sizes could be tested and the dynamics of the relative input by vertebrates and invertebrates examined. Due to the high humidity levels and heavy rainfall in the tropics however, this method would need to ensure high structural integrity of these seeds, which could become soft and fall apart. Seeds of other sizes were compared in trials for this study; smaller sesame seeds (*Sesamum indicum*) also showed lower removal rates for vertebrates than invertebrates, as did the use of larger shelled peanuts (*Arachis hypogaea*). The sesame seeds were generally taken at higher rates than pumpkin seeds for invertebrates, possibly as individual ants were able to remove seeds for a greater number of species (*pers. obsv.*).

The ultimate fate of seeds was unknown, which could have given some further insight into the roles of vertebrates and invertebrates: as dispersers or predators. Other papers do however suggest that most seeds are consumed (Maycock et al. 2005). A number of studies have employed techniques attaching thread to individual seeds to give insight into their fate (Wells & Bagchi, 2005; Guariguata, Adame & Finegan, 2000). Artificial seeds could be unsuitable for that type of study, as it would be reasonable to assume that these would be more likely consumed, due to not possessing any chemical defences against being eaten (which naturally occurring dipterocarp seeds have, Maycock et al. 2005).

5.5 Conclusion

The results of this investigation suggest that ants and other invertebrates can play a leading role in secondary seed removal in South East Asian tropical forests, contrary to previous wisdom, although this will likely depend on seed characteristics. This was consistent across all habitat types examined. In addition, it shows that vertebrates played a far greater role in seed removal in areas of highly disturbed logged forest. This may be related to higher densities of small generalist mammals inhabiting degraded forests. Mammals such as rats and squirrels are often the last remaining in fragments of disturbed forest (Corlett, 1998). Shifts in seed predation and dispersal brought about by anthropogenic changes may be set to become even more important to understand in the face of future tropical landscape patterns.

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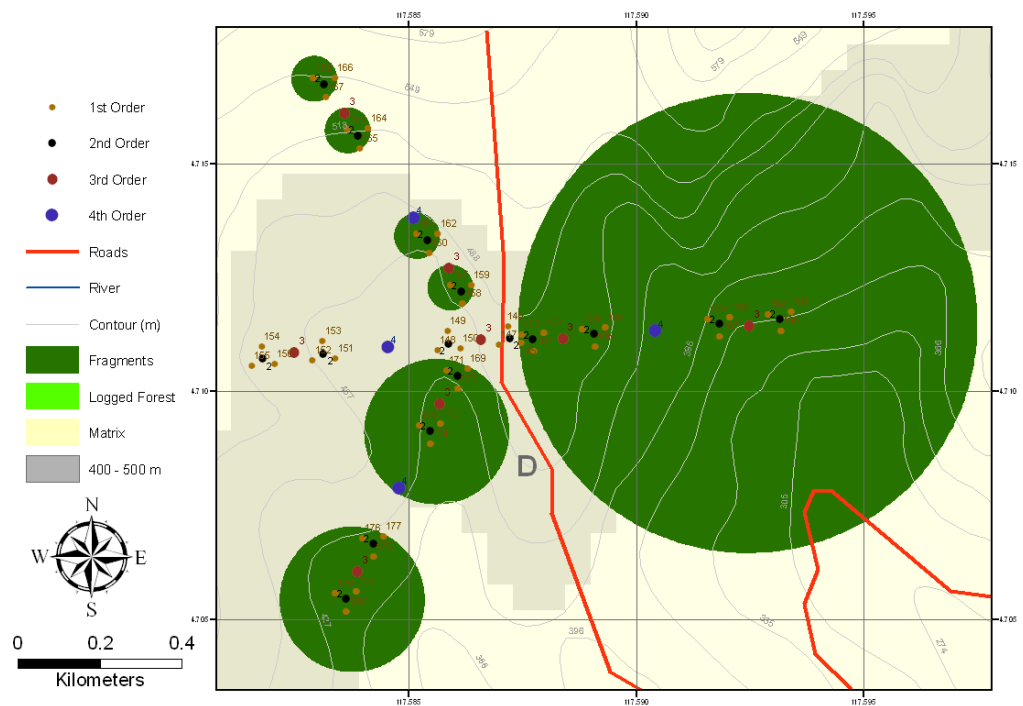
Appendix

Appendix 1 - Model Outputs

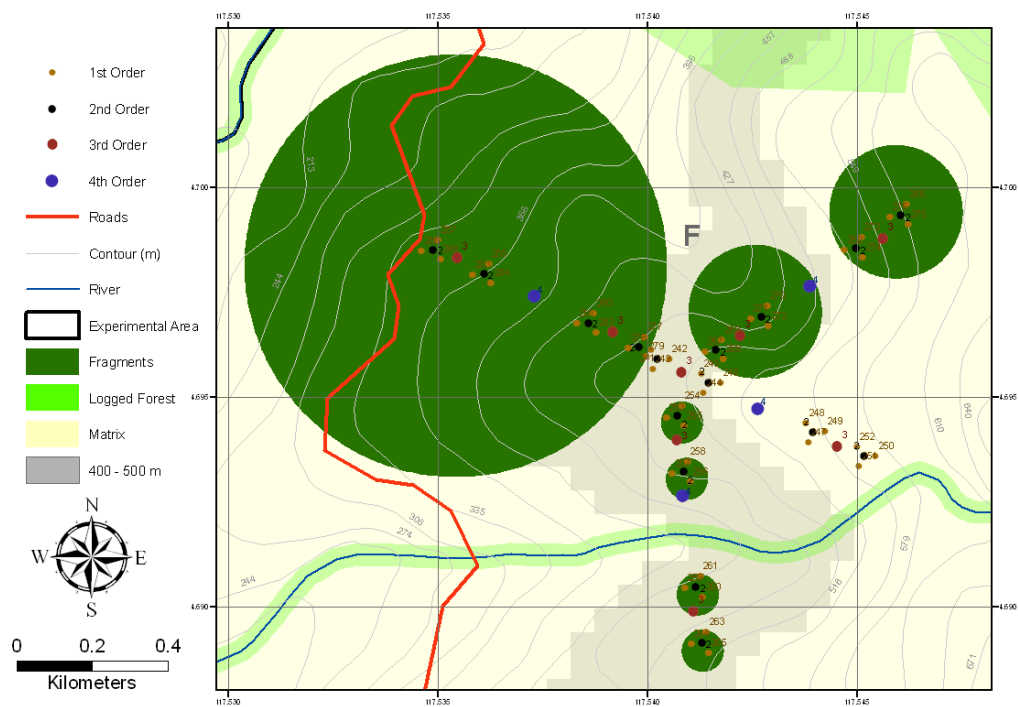
Variable	GLM	LMER	LMER – no overdispersion?
Intercept	$p = 0.06058$, $t = 1.879$, $d.f. = 824$	$p = 0.27625$, $z = 1.089$	$p = 0.000899$ ***, $z = 3.320$
ForestQuality1	$p = 0.10562$, $t = 1.620$, $d.f. = 824$	$p = 0.00256$ **, $z = 3.016$	$p = 0.482594$, $z = 0.702$
ForestQuality2	$p = 5.60e-11$ ***, $t = 6.642$, $d.f. = 824$	$p = 1.20e-10$ ***, $z = 6.440$	$p = 1.32e-05$ ***, $z = 4.356$
ForestQuality3	$p = 3.44e-06$ ***, $t = 4.674$, $d.f. = 824$	$p = 1.74e-08$ ***, $z = 5.636$	$p = 0.014884$ *, $z = 2.435$
ForestQuality5	$p = 0.00141$ **, $t = 3.204$, $d.f. = 824$	$p = 0.02433$ *, $z = 2.252$	$p = 0.238810$, $z = 1.178$
Treatment2	$p = 0.79734$, $t = 0.257$, $d.f. = 824$	$p = 0.36461$, $z = 0.907$	$p = 0.592835$, $z = -0.535$
Treatment3	$p = 1.25e-10$ ***, $t = -6.517$, $d.f. = 824$	$p < 2e-16$ ***, $z = -21.916$	$p < 2e-16$ ***, $z = -8.502$
ForestQuality2:Treatment2	$p = 0.00059$ ***, $t = -3.450$, $d.f. = 824$	$p < 2e-16$ ***, $z = -11.910$	$p = 0.004728$ **, $z = -2.825$
ForestQuality3:Treatment2	$p = 0.23856$, $t = -1.179$, $d.f. = 824$	$p = 1.65e-05$ ***, $z = -4.307$	$p = 0.619835$, $z = 0.496$
ForestQuality1:Treatment3	$p = 0.45612$, $t = 0.746$, $d.f. = 842$	$p = 0.00566$ **, $z = -2.767$	$p = 0.752403$, $z = 0.315$
ForestQuality2:Treatment3	$p = 0.17971$, $t = -1.343$, $d.f. = 842$	$p = 1.12e-07$ ***, $z = -5.306$	$p = 0.411140$, $z = -0.822$
ForestQuality3:Treatment3	$p = 0.63797$, $t = -0.471$, $d.f. = 842$	$p = 5.58e-11$ ***, $z = -6.554$	$p = 0.244108$, $z = -1.165$
ForestQuality5:Treatment3	$p = 0.60001$, $t = -0.525$, $d.f. = 842$	$p = 0.00244$ **, $z = -3.031$	$p = 0.320248$, $z = -0.994$

Model outputs for removed seeds.

Appendix 2 – SAFE sampling blocks



SAFE project sampling block D



SAFE project sampling block F

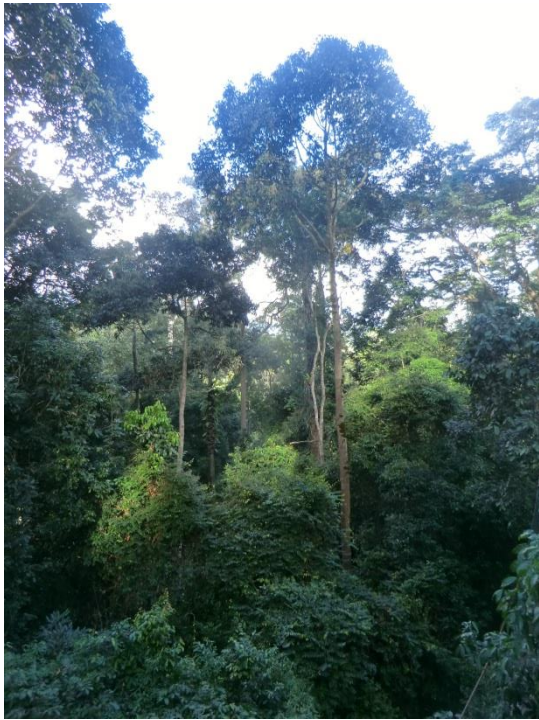
Appendix 3 – Habitat photographs (© Rosalind Gleave)



Oil palm plantation. Interior of the plantation, taken from within sampling block OP3.



Heterogeneous, twice logged forest at the SAFE project experimental site, located near the logged forest edge. Forest has its characteristic broken canopy.



Primary forest, within the Maliau Basin Conservation Area; this is characterised by unbroken canopy cover plus many large trees.

Appendix 4 – Photographs of exclosure breaches (© Rosalind Gleave)



Typical evidence remaining when ants had managed to breach a treatment 3 exclosure; a soil bridge formed over the glue barrier.



Photograph of a treatment 2 exclosure breach by an individual *Maxomys whiteheadi*, or Whitehead's spiny rat. The rat had managed to dig its way under the cage through soft soil.