Assessing biodiversity and ecosystem functioning in fragmented tropical landscapes

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Abstract

Agricultural expansion and logging are resulting in habitat degradation and fragmentation, especially in tropical regions. In Southeast Asia oil palm agriculture and commercial logging are the main threats to rainforest biodiversity, and I assessed the impacts of forest disturbance and land-use change on species composition and ecosystem functioning. I explored the role of the High Conservation Value (HCV) approach for biodiversity conservation in tropical agricultural landscapes and concluded that better knowledge exchange between scientists and HCV users is needed to improve biodiversity conservation in managed landscapes. I carried out a meta-analysis to examine the responses of birds, ants and beetles to the conversion of rainforest to oil palm which revealed that species in plantations were generally small-bodied species from lower trophic levels that had low abundances in forest. I collected new field data from Sabah (Malaysian Borneo) on dung beetle diversity and ecosystem functioning in undisturbed forest, selectively logged forest and forest fragments (5-3,529 ha). Dung beetle diversity was adversely affected by forest fragmentation, but not by selective logging. Larger fragments with better quality forest supported similar species assemblages to continuous forest, including functionally important dung beetle species. Dung removal, seed burial and seed dispersal were maintained in selectively logged forest, but were reduced by >50% in forest fragments. Dung removal in forest fragments was dependent on a few large, disturbance-tolerant species, which resulted in highly variable rates of functioning in fragments. Consistently high rates of dung removal and seed dispersal required high species richness as well as high biomass of dung beetles. Overall, forest fragmentation adversely affected diversity and ecosystem functioning, although fragments >100 ha maintained some dung beetle diversity and ecosystem functions. By contrast, degraded logged forest was functionally similar to undisturbed forest and thus should receive higher protection.

Contents

Chapter 3 - Trait-dependent declines of species following conversion of rain forest to oil palm plantations 50

Chapter 4 - Sampling dung beetles and their ecosystem functions in fragmented and degraded rainforest 73

Chapter 6 - Ecosystem functioning in fragmented rainforest 165

List of Tables

List of Figures

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Author's declaration

I declare that the work presented in this thesis is my own, and is written by me except where outlined below:

Chapter 2

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Chapter 3

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Chapter 1 - Introduction

1.1 Biodiversity

1.1.1 Defining and measuring biodiversity

The term ‘biodiversity’ is now firmly established in ecological parlance, and an ISI Web of Knowledge search reveals that in 2013 alone 1,060 papers contained the word in their title. However, biodiversity is a relatively recent term that was first used in the 1980s as an abbreviation of ‘biological diversity’ (Wilson & Peter 1988; Magurran 2004). The most widely used definition is that of the United Nations Environmental Programme (UNEP) (Heywood 1995; www.cbd.int):

“The variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic systems, and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”

This broad definition encompasses variation ranging from individuals to ecosystems, but the term is most commonly used in reference to species richness (Hubbell 2001). Species richness is the number of species in a given area and was used for a long time by conservationists as a criterion to identify high diversity areas worthy of protection (Prendergast et al. 1993; Gotelli & Colwell 2001). However, species richness is now rarely used on its own as it does not capture the full variation in species diversity, endemism and abundance in space and time (e.g. Petchey & Gaston 2002).

In all ecosystems, individual species vary greatly in their relative abundances at a given point in time and space (Fisher et al. 1943a), and even more so across space and time (Preston 1960). Therefore, species diversity can be separated into alpha, beta and gamma diversity to represent diversity measured at increasingly large spatial scales (Anderson et al. 2011), or can be broken down into richness and evenness components to compare the rarity of different species (Magurran 2004). Considering these different components of diversity improves our understanding of species distribution patterns and of how different species use resources in space and time. Assessing species' resource use improves our knowledge of ecosystem functioning and measures of functional diversity have been developed to explain how species traits relate to their potential roles in ecosystem functioning (Petchey & Gaston 2002, 2006). Functional diversity can be measured either using quantitative indices representing a range of functional traits or by directly analysing the relationship between individual functional traits and ecosystem functioning (Bello et al. 2010). Trait analyses can then be used to assess the impacts of biodiversity losses on ecosystem function, and different measures of diversity to better understand the consequences of disturbances for conservation.

1.1.2 Global biodiversity

Along with efforts to define different components of diversity, much ecological research has also focussed on quantifying global diversity patterns (Stork 1993; Mora et al. 2011; Costello et al. 2012). Recent estimates suggest that there may be 8.7 million terrestrial and marine eukaryotic species (Mora et al. 2011), although only around 1.5 million of these have been described to date (May 2011). The taxonomic distribution of these species is uneven and is dominated by the class Insecta, which represent 50-90% of all species (Gaston 1991). Diversity patterns also vary spatially across the globe. The greatest spatial pattern is the latitudinal richness gradient, which leads to an increase in species richness from the poles to the equator (Willig et al. 2003; Brown 2014). Different hypotheses have been proposed for this gradient, including the suggestion that low soil fertility and high humidity drive high diversity in the tropics (Rohde 1992). However, there is a growing consensus that this gradient is caused by high tropical temperatures driving faster metabolic and evolutionary rates, and leading to rapid speciation and greater competition (Brown 2014). However, the extraordinarily high diversity in the tropics is under increasing threat from human activity, leading to research seeking to identify and prioritise areas most in need of protection. For example, 'biodiversity hotspots' are areas with high rates of vertebrate and plant endemism that are undergoing severe habitat loss, such as the ‘Sundaland’ hotspot in Southeast Asia (Myers et al. 2000).

1.1.3 Southeast Asian biodiversity

Biodiversity in Southeast Asia is generally lower than in the Neotropics, but the ‘Sundaland’ biodiversity hotspot supports 5% of global plant species and 3% of vertebrate species (Myers et al. 2000). This high diversity and endemism is the result of the latitudinal temperature gradient and a regional biogeographic history involving shifting species distributions in response to changing rainfall and sea levels (Woodruff 2010). The dominant lowland ecosystem in Southeast Asia is tropical rain forest. Tropical rain forests are defined by a climate where mean monthly temperatures exceed 18^{o}C, annual rainfall is greater than 2000 mm and there are fewer than four months with less than 100 mm rainfall (Richards 1996). These conditions mean that the biomass and diversity of tropical rain forests is unrivalled, and 50 ha of forest in Pasoh, Malaysia supports over 800 tree species, compared to just 50 species across the whole of Europe (Whitmore 1998).

The dominant forest type in Southeast Asia is lowland mixed Dipterocarp forest (LMDF). LMDF is a type of tropical rain forest and is the dominant lowland (<500 m a.s.l.) forest type on Borneo, especially on clay and loam soil types (Whitmore 1984; Richards 1996). This forest is dominated by tree species of the Dipterocarpaceae family. Dipterocarp species comprise up to 75% of all trees and 45% of basal area within these forests, although this dominance varies across the island (Richards 1996). In the undisturbed, continuous forest sites considered in this thesis, Dipterocarps make up around 88% of the timber volume of large trees and 49% of basal area (Marsh & Greer 1992; Newbery et al. 1992). These large Dipterocarp trees dominate the canopy and emergent strata of undisturbed forest, resulting in these forests being the tallest tropical rain forests globally, with the canopy reaching 30-40 m and emergent trees up to 50-70 m (Richards 1996). These Southeast Asian rainforests are also characterised by intermittent mass flowering events of Dipterocarps, and many other tree families, at intervals of multiple years (Appanah 1985; Sakai 2002). Canopy trees, such as Dipterocarps, have evolved long, straight boles, as an effective evolutionary strategy to maximise tree height and so increase access to photosynthetically active radiation. However, these long, branchless boles and the hardwood qualities of many Dipterocarps that make them so functionally dominant also means that they are of high commercial timber value (Meijaard et al. 2006; Basuki et al. 2009).

1.2 Ecosystem functioning

Functional ecology aims to understand longer term consequences of biodiversity losses and impacts on ecosystem services (Reiss et al. 2009; Peh & Lewis 2012). Functional ecology assesses the contribution of individual species to ecosystem functions or processes and ecosystem functioning, where ecosystem functions are “changes in matter and energy over time through biological activity” and all functions combined are required to sustain overall ecosystem functioning (Millennium Ecosystem Assessment 2005; Reiss et al. 2009). Products of ecosystem functioning that are of value to humanity are referred to as ecosystem services, and can be broken down into provisioning, regulating, supporting and cultural services (Millennium Ecosystem Assessment 2005). For example, nutrient cycling, primary productivity and decomposition are ecosystem processes that contribute to regulating and supporting ecosystem services such as flood control, climate regulation and soil formation (Millennium Ecosystem Assessment 2005). Ecosystem functions, and ultimately ecosystem services, result from individual species interacting with biotic and abiotic ecosystem components (Reiss et al. 2009). As species grow and reproduce, their use of biotic and abiotic resources leads to the transfer of energy or matter through ecosystems.

The dependence of ecosystem functioning on the activity of individual species means that studying the relationship between biodiversity and functioning is crucial. It was originally proposed that there may be a linear positive relationship between species richness and ecosystem function, as a result of the complementary use of resources by species with non-overlapping niches (Schulze & Mooney 1994). A strict linear relationship is rarely true in reality, where species interactions, trait variation, resource use efficiencies and abundances in space and time all lead to interspecific differences in contributions to ecosystem functions (Hooper et al. 2005; Yachi & Loreau 2007; Bello et al. 2010). For example, common and large-bodied species can be competitively and functionally dominant (Smith & Knapp 2003; Woodward et al. 2005). However, increased species richness does lead to increased ecosystem functioning, especially over broader spatial and temporal scales and following disturbance. For example, although domesticated honey bees can be efficient pollinators in typical weather conditions, a high diversity of wild pollinator species leads to increased flower visitation and pollination of almond trees under high wind conditions (Brittain et al. 2013).

1.3 Dung beetles

Dung beetles are not an especially speciose group, numbering approximately 5,000 species globally in the main subfamily Scarabaeinae (Family Scarabaeidae), and 120 species on the island of Borneo (Davis & Scholtz 2001). Nonetheless, they have long been of ecological interest because of their specialisation on vertebrate dung, parental care, resource competition and reliance on ephemeral resources (Hanski & Cambefort 1991; Davis & Scholtz 2001). Intense competition for ephemeral resources has led to the evolution of large variation in dung beetle morphologies and behaviour (Monaghan et al. 2007). This variation is characterised by the nesting behaviour of dung beetles, which splits them into four main groups: tunnellers (paracoprids), rollers (telecoprids), dwellers (endocoprids) and kleptoparasites (Hanski & Cambefort 1991). Tunnellers and rollers are considered 'true' dung beetles because they form nests and make brood balls and comprise the dominant groups in biomass and species richness, especially in the tropics (Hanski & Cambefort 1991). Tunnellers bury their brood ball directly underneath the dung pile, whilst rollers form a ball that is rolled away from the dung pile before being buried at a shallower depth than is the case for tunnellers. Rollers are characterised by more compact, rounded body shapes, curved hind tibia and longer femurs (Figure 1.1) than tunnellers that have broader and longer bodies with short hind tibia and broader ‘spade-like’ fore tibia (Figure 1.2; Inward et al. 2011). Neither dwellers nor kleptoparasites are abundant or functionally important in Southeast Asia and so receive little attention in this thesis (Hanski & Cambefort 1991).

*Figure 1.1. Roller dung beetle (*Paragymnopleurus sparsus *Sharp). Note the long hind legs that aid dung ball-rolling, and the flatter and more circular body shape than the tunneller in Figure 1.2.*

*Figure 1.2. Tunneller dung beetle (*Catharsius dayacus *Lansberge). Note the shorter limbs and broad ‘spade-like’ fore tibia evolved for digging.*

In addition to diverse nesting behaviour, dung beetles also exhibit diet and habitat specialisation. Southeast Asian dung beetle assemblages include carrion and fruit-feeding specialists, but omnivore dung attracts most species and can be removed by beetles within a few hours (Hanski 1983; Hanski & Cambefort 1991). More species are typically associated with abundant dung resources, such as omnivore and herbivore dung, where competitive exclusion is rare (Hanski & Cambefort 1991). Forest dung beetle species are commonly stenotopic (confined to a narrow range of environmental conditions). For example, riverine and edge forest habitats in Sabah, Malaysia support different species assemblages to interior forest, and the assemblages of selectively logged forest resemble those found in riverine and edge habitats (Davis et al. 2001). Furthermore, the study of a savannah-forest ecotone in Bolivia revealed only two shared species between the habitats (Spector & Ayzama 2003). This habitat specialisation and reliance on vertebrate dung means dung beetles can be used as indicators of habitat disturbance and the mammalian fauna (Spector 2006; Nichols et al. 2009).

In recent decades there has been a growing interest in the functional ecology of dung beetles, because of their roles in nutrient cycling, parasite suppression and secondary seed dispersal (Nichols et al. 2008). As a by-product of burying their brood balls, dung beetles bury dung and seeds in the soil which returns nitrogen to the soil and can aid seedling germination (Andresen & Feer 2005; Nichols et al. 2008). For example, dung burial by beetles makes nitrogen available to plants through mineralisation (Nichols et al. 2008) leading to increased plant productivity and growth (Bang et al. 2005), and seed burial reduces seed predation and increases seedling establishment (Andresen 2001). Dung beetles can also reduce the density of seedlings (Lawson et al. 2012), which is crucial for reducing density-dependent seed and seedling mortality and maintaining seedling diversity (Bagchi et al. 2014). These functional roles and the ecological responses of dung beetles to spatially and temporally patchy dung resources makes them an excellent focal taxon for assessing the impacts of land use change on biodiversity and ecosystem function.

1.4 Threats to tropical biodiversity

Human population growth and rising per capita consumption are increasing demand for food, fuel and timber (Butchart et al. 2010; Pereira et al. 2010). This is driving habitat and biodiversity losses, especially in the tropics where biodiversity is highest and development fastest (Gibson et al. 2011; Phalan et al. 2013). Within the tropics, Southeast Asia has experienced the highest rates of habitat and biodiversity loss driven primarily by commercial logging and oil palm (*Elaeis guineensis* Jacq) expansion (Sodhi et al. 2010). For example, oil palm plantations in Malaysia and Indonesia expanded from 2.4 million ha in 1990 to 7.2 million ha in 2012, and 55-59% of this expansion replaced native tropical forest (Koh & Wilcove 2008). Furthermore, of the remaining 18.6 million ha of native forest in Malaysia in 2010, only 3.8 million ha were undisturbed primary forest, less than the area under oil palm cultivation (4.4 million ha) (FAO 2010). This pattern of land-use change is typical of Southeast Asia, where the majority of lowland forest has been subject to commercial selective logging (Edwards et al. 2011b).

Commercial selective logging and oil palm expansion cause forest degradation, habitat fragmentation and habitat conversion, all of which have adverse impacts on Southeast Asian biodiversity (Fahrig 2003; Fitzherbert et al. 2008; Edwards et al. 2011b). All of these disturbances cause reductions in species richness and abundance, and changes in species composition in relation to intact primary forest (Fahrig 2003; Gibson et al. 2011). However, selective commercial logging is generally less detrimental than forest fragmentation, which in turn is less damaging to biodiversity than conversion of forest to agriculture (Fitzherbert et al. 2008; Berry et al. 2010; Edwards et al. 2010). In fact, analyses of multiple taxa revealed that ~90% of primary forest species persist after one logging rotation, and >75% after two rotations of high-intensity selective logging (Berry et al. 2010; Edwards et al. 2011b). The value of forest fragments for biodiversity depends greatly on their size and isolation from continuous forest, but even relatively small fragments <300 ha in oil palm plantations have been shown to protect range-restricted populations of forest dependent butterfly and bat species (Benedick et al. 2006; Struebig et al. 2008). Conversely, oil palm plantations support highly depauperate species assemblages (Fitzherbert et al. 2008). The impacts of logging, fragmentation and oil palm conversion on species richness and abundance, are now well established, but studies are lacking on their effects on functionally important taxa, such as dung beetles.

1.4.1 Land use change in Sabah, Malaysia

The Malaysian state of Sabah is the country's most easterly State and is situated on the island of Borneo (Figure 4.1). In 2010, Sabah had a population of 3.2 million people at a density of ~40 people km^{-2}, making it relatively sparsely populated by Southeast Asian standards (Reynolds et al. 2011). The majority of the population lives in the cities of Kota Kinabalu, Sandakan and Tawau, with much of the state remaining largely rural, with 51% (3.8 million ha) of the State covered by forest and 19% (1.4 million ha) by oil palm plantations (Reynolds et al. 2011). However, approximately 73% of Sabah's forested area has been selectively logged at least twice and is now highly degraded. Much of the remaining undisturbed primary forest now persists in the highlands of Sabah and it is estimated that only 70,000 ha of undisturbed primary lowland forest remain in the State (Reynolds et al. 2011). Sabah's three main lowland conservation areas, Danum Valley, Imbak Canyon and Maliau Basin, account for about 50,000 ha of the remaining primary lowland forest and the rest persists almost entirely in the State's other protected areas, including Virgin Jungle Reserves (Reynolds et al. 2011). This loss of primary lowland forest started in 1890 when the British North Borneo company began logging the area's forests for timber, and converting forest to expand tobacco and rubber plantations. This logging and agricultural expansion continued following Malaysia's independence in 1963, and at a higher intensity associated with the increasing mechanisation of logging. Timber production in Sabah plateaued in the 1970s and 1980s, and subsequent declining timber yields led to increased forest conversion for oil palm plantations. Some oil palm expansion replaced existing rubber and cocoa plantations, but the vast majority (~80%) replaced natural forest (McMorrow & Talip 2001; Reynolds et al. 2011). Consequently, virtually all lowland forest in Sabah is now either heavily degraded or persists in forest fragments within landscapes dominated by oil palm plantations.

1.4.2 Oil palm agriculture and the Roundtable on Sustainable Palm Oil

The African oil palm (*Elaeis guineensis* Jacq) is by far the highest yielding commercial vegetable oil crop, producing ~3.7 tonnes of oil ha^{-1} y^{-1}, which is over six times the yield of soybean, sunflower or rapeseed oil (Basiron 2007). This remarkable productivity means that palm oil is now the cheapest and most used vegetable oil and it represents 35% of global vegetable oil production (USDA 2014). Two oil types are extracted from the African oil palm: palm oil from the fruit mesocarp and palm kernel oil from the kernel (Corley & Tinker 2008). Palm oil is used primarily for food whilst the kernel oil is used in cosmetics and toiletries (Basiron 2007). The African oil palm has been used by humans for thousands of years, but the first large plantations of oil palm were developed in Indonesia and Malaysia as early as 1911 and major expansion of the industry occurred in Southeast Asia after 1970 (Corley & Tinker 2008). Consequently, Malaysia and Indonesia are responsible for approximately 86% of current oil palm production, but the crop’s profitability has led to continuing global expansion with an increasing focus on West Africa and Latin America (Butler et al. 2009; Phalan et al. 2013).

Over the last 15 years, as the oil palm industry has become increasingly global, concerns have been raised over the industry’s environmental impact. Consumer groups highlighted the widespread loss of tropical forests and biodiversity associated with oil palm expansion (Edwards et al. 2012b). As a result, the Roundtable on Sustainable Palm Oil (RSPO) was formally established in 2004 to address these negative environmental impacts, as well as adverse social impacts such as land grabbing, low wages and minimal labour rights (Paoli et al. 2010; RSPO 2012a). The RSPO is a multi-stakeholder membership organisation formed of oil palm growers, processors, traders and retailers, social and environmental NGOs and investors. It aims to ensure the sustainable economic, social and environmental production of palm oil (RSPO 2012b).

A key component of the RSPO's principles and criteria for sustainability is the requirement for certified plantations to maintain and enhance areas of High Conservation Value (HCV). The HCV approach consists of six values that aim to protect unique and threatened biodiversity, ecosystems and social sites or resources (www.hcvnetwork.org). New oil palm plantations seeking certification by the RSPO must carry out an HCV assessment prior to developing the land (Brown et al. 2013). However, the effectiveness of the HCV approach for biodiversity conservation has been questioned because of inconsistent HCV assessments and doubts as to whether HCV areas will protect biodiversity in the long term (Paoli & Harjanthi 2011; Edwards et al. 2012b). There are also few studies which consider the effectiveness of the HCV approach, and so further research is required to compare strategies for biodiversity conservation within oil palm plantations and to improve the evidence base of the HCV approach.

1.5 Understanding and addressing the ecological impacts of land use change

Commercial selective logging, forest fragmentation and conversion of forest to oil palm plantations have different impacts on biodiversity and comparing the ecological mechanisms behind these impacts can help to minimise losses of functionally important species and species of conservation value.

1.5.1 Habitat fragmentation

The effects of fragmentation on biodiversity are underpinned by established ecological concepts, including the Species-Area Relationship (SAR) and the Theory of Island Biogeography. First proposed by Preston in the 1960s, the SAR describes the concave, curvilinear increase in the number of species found in increasingly larger areas of habitat (Preston 1960, 1962). Subsequently, ecologists have to sought to understand the mechanisms behind the SAR, and the Theory of Island Biogeography was one of the first mechanisms proposed by MacArthur and Wilson (MacArthur & Wilson 1967). This theory proposes that the number of species on an oceanic island is determined by the rate at which species go extinct versus colonise the island. The number of species present on an island becomes constant over time as extinction and colonisation rates reach equilibrium. Therefore, larger and less isolated islands support more species because they have higher rates of colonisation and lower rates of extinction.

This theory is supported by numerous empirical datasets (e.g. Simberloff & Wilson 1969), and has evolved to incorporate habitat islands and single species' metapopulation dynamics (Levins 1969). It is now established that individual species vary greatly in their dispersal and colonisation ability, which affects their ability to survive in fragmented landscapes (e.g. Warren et al. 2001). Furthermore, the quality of matrix habitat and time-since-isolation also affect the species that can persist in isolated habitat fragments. For example, extinction debt means that some species can take hundreds of years to go extinct following fragmentation (Brook et al. 2003), but relaxation times can be less than 25 years in forest fragments smaller than 100 hectares (Gibson et al. 2013). Matrix quality is crucial for dung beetle communities in Amazonian forest fragments, with fragments surrounded by regenerating secondary forest supporting species assemblages similar to those in continuous forest, whereas fragments surrounded by pasture support impoverished species communities (Quintero & Roslin 2010).

1.5.2 Habitat quality and complexity

The quality of habitat within fragments, in addition to fragment size and isolation, is important for species persistence. High quality habitat prevents species populations declining, and stable population trends can be a prerequisite for species dispersal (Mair et al. 2014). However, forest fragmentation can reduce habitat quality through edge effects and increased encroachment, such as illegal logging (Laurance et al. 2002). Edge effects alter vegetation structure in forest fragments by increasing ground cover, tree mortality and temperatures, and these changes have been shown to greatly alter the abundance of tropical forest insects, such as beetles (Didham et al. 1998; Didham & Lawton 1999). These changes to habitat quality can have considerable impacts in tropical forests given their high habitat heterogeneity, both vertically through the forest strata and horizontally in relation to natural disturbance and topography (Williams et al. 2002; Dent & Wright 2009).

Selective logging and conversion to oil palm alters habitat quality. Selective logging removes large canopy trees, but it has collateral impacts resulting from climbers bringing down other trees, transporting timber and access trails. For example, in Bornean Dipterocarp forests, logging alters plant diversity, increases the frequency of canopy gaps and linear gaps, such as skid trails, and reduces canopy height and cover (Okuda et al. 2003). Such changes to habitat structure have been shown to alter assemblages of multiple forest taxa, such as dung beetles, butterflies and ants, and can lead to the loss of primary forest specialists that are dependent on closed canopy forest (Davis et al. 1998; Dumbrell & Hill 2005; Woodcock et al. 2011). The conversion of forest to oil palm leads to a much greater loss in habitat heterogeneity than selective logging (Foster et al. 2011). Oil palm plantations are highly ordered monocultures, and although the palm trunks and understory layers provide some habitat variability this is very low in comparison with logged and unlogged tropical forest (Foster et al. 2011; Luskin & Potts 2011). This habitat simplification in plantations also leads to changes in microclimate, with oil palm plantations ~4°C hotter and less humid than Dipterocarp forest (Luskin & Potts 2011). Therefore, forest fragments, logged forests and oil palm plantations have altered habitat structures and microclimates compared to unlogged forest, and this affects the type of species able to persist in these habitats.

1.5.3 Conservation strategies

There has been much debate about the best strategies for conserving biodiversity in tropical agricultural landscapes in the face of land scarcity and the need to maximise agricultural yields. This debate is largely focussed on comparing land sharing and land sparing conservation strategies. Land sharing conservation is when low-intensity agriculture is combined with conservation strategies, such as small riparian buffers or forest fragments, in the same landscape. Conversely, land sparing is when high-intensity agriculture is kept separate from fewer but larger blocks of conservation land (Phalan et al. 2011). These strategies have evolved from the "SLOSS" debate on whether conservation strategies should spread risks across multiple sites with smaller, potentially more vulnerable species populations, or focus on fewer, larger sites that support larger populations (Fischer et al. 2014). Multiple studies in tropical ecosystems, including forest-oil palm landscapes, have shown that land sparing strategies support more species of birds, beetles, trees and ants than land sharing strategies (Phalan et al. 2011; Edwards et al. 2014). However, these studies have focussed on measures of species richness and abundance, and generally ignored practical difficulties of implementing these different land sparing/sharing strategies (Fischer et al. 2014). Research is needed to assess how these strategies will affect ecosystem functioning, a critical concern in agricultural landscapes (Foster et al. 2011). There is also a need for analyses that specifically address the quality and size of shared and spared conservation areas, i.e. the size of fragments in shared landscapes or 'continuous' forest in spared areas.

1.6 Thesis rationale and objectives

This thesis aims to improve our understanding of biodiversity and ecosystem functioning in oil palm dominated landscapes, and to provide an evidence-base for conservation strategies in tropical landscapes. The relative impacts of selective logging, forest fragmentation and oil palm conversion on biodiversity and ecosystem functioning are compared using dung beetles as a focal taxon.

Chapter 2 discusses the role of the HCV approach for biodiversity conservation in tropical agricultural systems. The chapter describes the origins, advantages and disadvantages of the HCV approach and the steps involved in an HCV assessment. It concludes by identifying strategies for improving the scientific evidence base of the HCV approach.

Chapter 3 assesses the impacts of converting tropical forest to oil palm plantations on birds, ants and beetles in relation to their feeding guild, body size, population size and geographic range. I test the hypothesis that locally rare, range-restricted, predatory and large-bodied species show the greatest declines in abundance following conversion. The results are related to resource availability in oil palm plantations and potential conservation and functional consequences are discussed.

Chapter 4 introduces the study sites in Sabah, Malaysia and explains how fieldwork methods used in subsequent chapters were developed in order to sample dung beetles and quantify their ecosystem functions in this thesis. It presents analyses assessing inter-annual variation in dung beetle assemblages and compares assemblages sampled with cattle and human dung baits.

Chapter 5 analyses the impacts of selective logging and forest fragmentation on dung beetle species richness, abundance, biomass and species composition. Separate analyses are conducted to examine diversity changes in functionally important roller and tunneller species, and it tests the hypothesis that species richness, abundance and biomass decline and species assemblages are altered following fragmentation, but not selective logging. I also test the hypothesis that large-bodied species decline more in abundance and biomass following fragmentation than small-bodied species.

Chapter 6 compares rates of dung beetle ecosystem functions (dung removal, seed burial and seed dispersal) in unlogged continuous forest, twice-logged continuous forest and forest fragments. It tests the hypothesis that dung beetle functions are reduced in fragments compared to continuous forest, but are little affected by selective logging. Among fragments, I test the hypothesis that seed dispersal, but not dung removal or seed burial, declines with fragment area.

Chapter 7 relates changes in dung beetle composition with ecosystem functioning to assess the roles of species richness and biomass in maintaining dung beetle ecosystem functions. It also considers the potential importance of a few dominant species for functioning following fragmentation. It tests the hypothesis that biomass is a more important predictor of dung beetle functions than species richness.

Chapter 8 summarises findings from Chapters 2-7. It compares the value of unlogged continuous forest, logged continuous forest and forest fragments of different size, quality and isolation for dung beetle diversity and functioning. I discuss the wider implications of my results for the maintenance of ecosystem functioning and conservation in tropical agricultural landscapes.

Chapter 2 - Improving the effectiveness of the 'High Conservation Value' (HCV) process for biodiversity conservation in managed tropical landscapes

2.1 Abstract

Land-use change is a major driver of tropical biodiversity declines, associated with crops such as oil palm and soya, and with commercial logging. A common feature of many voluntary sustainability standards for mitigating the negative impacts of land-use change within production landscapes is the 'High Conservation Value' (HCV) approach for protecting exceptional environmental and social values. The HCV approach is widely used for land management and land-use planning, in certification schemes (e.g. FSC, RSPO), and by companies with responsible sourcing policies. However, the HCV approach is little known in academia and the scientific evidence-base supporting it is not well developed. By raising the profile of the HCV approach, we hope to instigate new research to examine and enhance the impact of the HCV process on biodiversity conservation. We argue for better knowledge exchange between scientists, policy makers and HCV users, sharing of existing information and consideration of the practical constraints within which HCV users and commodity producers operate. Given the continuing loss and degradation of tropical rainforests, such strategies are required urgently to reduce biodiversity losses in managed landscapes.

2.2 Introduction

Agricultural expansion and timber extraction account for 80% of global deforestation and 70% of global forest degradation respectively (Kissinger et al. 2012). In turn this habitat loss and degradation drives biodiversity loss, particularly in the tropics (e.g. Green et al. 2005; Fitzherbert et al. 2008; Gibson et al. 2011). As a result of this habitat degradation, and social concerns about human rights breaches, the past few decades have seen increasing public concern about the production of timber and crops, such as oil palm and soy. Resulting consumer pressure has led to the development of voluntary sustainability standards (e.g. the Forestry Stewardship Council (FSC) and the Roundtable on Sustainable Palm Oil (RSPO)) aimed at mitigating the negative environmental and social impacts associated with timber and crop production. Given that there are over 49 million km^2 of crop land and 12 million km^2 of production forest globally (“FAOSTAT” 2012), these standards offer opportunities for biodiversity conservation.

A key component of the major sustainability standards (FSC, RSPO, Roundtable on Responsible Soy (RTRS), Bonsucro) is the High Conservation Value (HCV) approach, a tool designed to maintain and enhance critical environmental and social values that may be affected by agricultural or forestry developments (Figure 2.1). Most of these schemes require that new agricultural and forestry developments carry out an HCV assessment to identify any areas of HCV that should be conserved before land development begins. Management and monitoring to maintain and enhance these HCV areas must then be implemented.

HCV 1: Species diversity.
Concentrations of biological diversity including endemic species and rare, threatened or endangered species, that are significant at global, regional or national levels.

HCV 2: Landscape-level ecosystems and mosaics.
Large landscape-level ecosystems and ecosystem mosaics that are significant at global, regional or national levels, and that contain viable populations of the great majority of the naturally occurring species in natural patterns of distribution and abundance.

HCV 3: Ecosystems and habitats.
Rare, threatened or endangered ecosystems, habitats or refugia.

HCV 4: Critical ecosystem services.
Basic ecosystem services in critical situations, including protection of watercatchments and control of erosion of vulnerable soils and slopes.

HCV 5: Community needs.
Sites and resources fundamental for satisfying the basic necessities of local communities or indigenous peoples (for livelihoods, health, nutrition, water, etc.), identified through engagement with these communities or indigenous peoples.

HCV 6: Cultural values.
Sites, resources, habitats and landscapes of global or national cultural, archaeological or historical significance, and/or of critical cultural, ecological, economic or religious/sacred importance for the traditional cultures of local communities or indigenous peoples, identified through engagement with these local communities or indigenous peoples.

Figure 2.1. The six High Conservation Values (taken from Brown et al. 2013).

Many conservation practitioners and commodity producers see the HCV approach as a practical and accessible tool for mitigating the negative impacts of crop and timber production. However, as the scope of the approach has expanded from its original use in forestry to include agricultural land uses, its effectiveness for biodiversity conservation has come under scrutiny, particularly in relation to the palm oil sector (Edwards et al. 2010, 2012b; Paoli & Harjanthi 2011). This scrutiny is vital for ensuring that the HCV approach fulfils its aim of identifying critical environmental and social values and, more widely, for assessing the robustness of voluntary sustainability standards, an issue rarely covered in the scientific literature (Blackman & Rivera 2011). Criticism of the HCV approach has also come from HCV users such as agricultural producers and HCV assessors themselves (e.g. Paoli & Harjanthi 2011). In fact, discussions between NGOs and private sector representatives about the inconsistent application of the HCV approach in agricultural landscapes led to the formation of the HCV Resource Network (HCVRN) in 2006 (www.hcvnetwork.org), to support the continued use and robust application of the HCV approach.

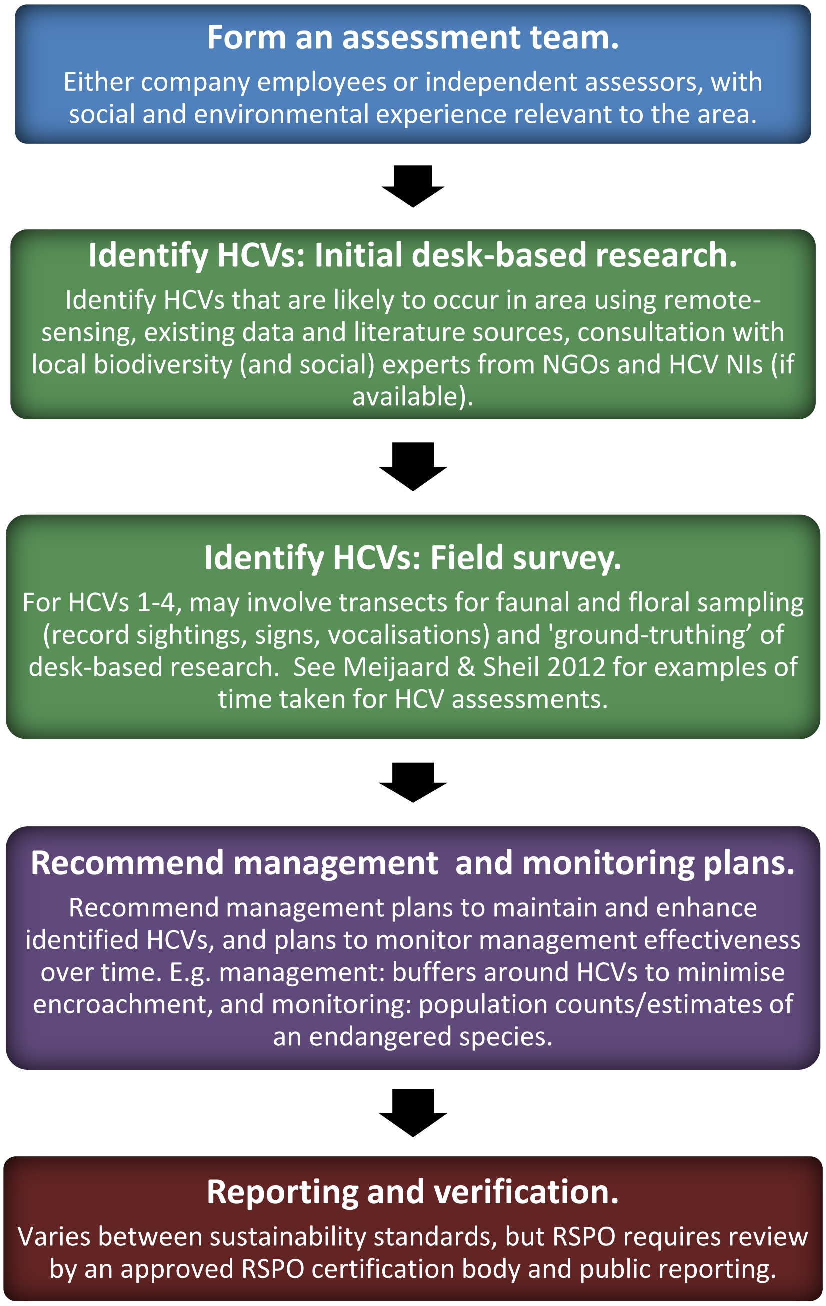
Yet despite being so widely used, the HCV approach is rarely discussed in academic literature in relation to biodiversity conservation. Furthermore, the few papers that do consider the HCV approach in tropical agricultural landscapes (Edwards et al. 2010, 2011a, 2012b; Edwards & Laurance 2012) conclude that the HCV approach provides insufficient protection for biodiversity. Thus there is an apparent disconnect between HCV users and academics; the HCV approach continues to be widely used as a conservation tool in production landscapes and yet there is little scientific investigation of its effectiveness. Given the urgent need to improve biodiversity conservation in managed landscapes, we argue for increased engagement of scientists with the HCV assessment process.

First, we describe the HCV approach, discuss its scope, and the steps involved in an HCV assessment. We highlight the advantages that have led to it being so widely used and argue that the HCV approach remains one of the best practical tools for biodiversity conservation in agricultural landscapes, but that improvements are vital. We then consider evidence for the effectiveness of the HCV approach for conserving tropical biodiversity, and conclude that continued improvements to the guidance and monitoring of the HCV assessment process and a stronger scientific evidence-base are required. We conclude by suggesting new solutions for strengthening the scientific evidence-base, focused on increasing knowledge exchange between HCV users, researchers and policy makers, increasing research and data sharing, and improving the communication of research findings and their implications. We consider those aspects of the HCV approach pertinent to biodiversity conservation, and focus particularly on oil palm, as this is a heavily scrutinised sector, although many of the issues we discuss also apply to other sectors.

2.3 What is the HCV approach?

The HCV approach is based on six values that aim to protect exceptional biodiversity, social and cultural identity, and ecosystem services (Figure 2.1). The approach was first developed in the context of sustainable forestry, and incorporated into the Forest Stewardship Council (FSC) standard in 1999. It has since been adopted by major agricultural sustainability standards (RSPO, RTRS, Bonsucro), as well as in a number of corporations' purchasing and investment policies (see http://www.hcvnetwork.org/about-hcvf/hcv-in-natural-resource-certification for a more detailed list of uses). The HCVs that incorporate biodiversity conservation (the focus of this paper) are HCVs 1-4, which aim to protect sites with high species diversity (HCV 1), landscape-level ecosystems and mosaics (HCV 2), rare, threatened or endangered ('RTE') habitats (HCV3), and critical ecosystem services (HCV 4). HCV values 5 and 6 cover community needs and cultural values, and so not all HCV areas are intended to protect biodiversity. HCVs can be terrestrial, freshwater or marine values likely to be affected by a development.

The HCV assessment process identifies values and recommends management and monitoring plans for a particular development (see Appendix A1.1 for definitions). The first step is to identify if any of the six values (Figure 2.2) are present at a site before any development or land clearance starts. If any HCVs are identified then an HCV area is defined as the area required to maintain these values. To qualify as an HCV area, there must be at least one value that is nationally, regionally or globally significant, or critically important at the local level. Throughout the HCV assessment process, assessors are expected to consider the scale and context of the proposed development, how this might affect threats to the identified HCVs, as well as potential conflict between HCVs, for example if subsistence hunting threatens an endangered species (Edwards & Laurance 2012; Brown et al. 2013). Final decisions on which HCVs are present and their management and monitoring follow consultation with stakeholders (e.g. communities, NGOs, research institutions, local authorities), and consider the wider landscape affected by the development. They are also guided by the precautionary principle (Brown et al. 2013) in recognition of difficulties in detecting many tropical species (Meijaard & Sheil 2012), and so assessments take longer for higher risk developments.



Form an assessment team.

Either company employees or independent assessors, with social and environmental experience relevant to the area.

Identify HCVs: Initial desk-based research.

Identify HCVs that are likely to occur in area using remote-sensing, existing data and literature sources, consultation with local biodiversity (and social) experts from NGOs and HCV NIs (if available).

Identify HCVs: Field survey.

For HCVs 1-4, may involve transects for faunal and floral sampling (record sightings, signs, vocalisations) and 'ground-truthing' of desk-based research. See Meijaard & Sheil 2012 for examples of time taken for HCV assessments.

Recommend management and monitoring plans.

Recommend management plans to maintain and enhance identified HCVs, and plans to monitor management effectiveness over time. E.g. management: buffers around HCVs to minimise encroachment, and monitoring: population counts/estimates of an endangered species.

Reporting and verification.

Varies between sustainability standards, but RSPO requires review by an approved RSPO certification body and public reporting.

Figure 2.2. The steps in an HCV assessment. This should apply to any use of the HCV approach although the steps here are specific to the HCV assessment process for RSPO certification. An HCV assessment should always be conducted prior to any land clearance or development (see Brown et al. 2013 for more details).

The HCV approach was first developed in a production context and so does not prohibit development. It is not intended to be a policy for zero deforestation or zero local biodiversity loss, rather a tool for protecting exceptional social and environmental values. An HCV assessment is only one of many steps for achieving sustainable certification, and depending on the certification standard, producer companies may need to comply with additional requirements that go beyond protecting HCV areas (e.g. environmental best practice such as erosion control). After initial certification, companies also have to undergo regular audits to retain their certification status, during which the management and monitoring of HCV areas are a key consideration (see Appendix A1.2).

2.4 Advantages of the HCV approach

The HCV approach is widely supported by environmental and social NGOs and members of the private sector, who jointly developed the approach. This cross-sector collaboration means that the HCV approach included values important to a wide range of stakeholders. It aims to be inclusive, practical and affordable, compared to comprehensive biodiversity or social assessments that can take years to carry out (Meijaard & Sheil 2012). By allowing land development with safeguards that protect exceptional environmental and social values, the HCV approach has been widely adopted by voluntary sustainability standards such as the RSPO, who wish to encourage producers and users to participate (Meijaard & Sheil 2012). As a consequence of being used by certification standards and being monitored by the HCVRN, the HCV approach also has the advantage of added scrutiny and robustness. FSC certified forests and plantations cover >180 million ha (www.fsc.org), and RSPO certified plantations cover >1 million ha (www.rspo.org).

The widespread application of the HCV approach highlights its potential importance for conservation, the importance of evaluating the robustness of the HCV process, and ensuring its effectiveness in conserving tropical biodiversity is maximised. However, the HCV assessment process is little known in the scientific community and research on the effectiveness of HCV areas for protecting biodiversity is lacking. Also, the HCV approach has only been used in agricultural contexts for <10 yrs, and has often been misapplied, leading to poor quality HCV assessments (Paoli & Harjanthi 2011). This makes it difficult to separate criticism of the approach from criticism of its application.

2.5 Improving the HCV approach for conserving tropical biodiversity

Both HCV users (Paoli & Harjanthi 2011) and academics (Edwards et al. 2012b) have criticised the inconsistency of HCV assessments. This inconsistency has been attributed to ambiguous and subjective terms used in HCV guidance documents, that depend too heavily on the discretion of individual assessors (Edwards et al. 2012b). For example, to qualify as HCV 1 the “concentration of endemic or RTE species must be globally, regionally or nationally significant”, yet guidelines for assessing significance are not always clear (but see page 27 of Brown et al. 2013 for more detail). Definitions for the HCV approach need to be broad if they are to be applied across ecosystems, countries and sectors, but this has led to their misinterpretation by HCV assessors (Paoli & Harjanthi 2011).

Guidance and monitoring of the HCV assessment process have been introduced to address problems of misinterpretation. Firstly, HCV national interpretations (NIs) provide greater detail to be used in local contexts (see Appendix A1.1 for more detail). However, not all countries have HCV NIs and, of those that do, many are outdated, specific to just one commodity or insufficiently detailed. Furthermore, many NIs still contain ambiguous language, e.g. leaving assessors to decide what classifies as a nationally significant population of species. Whilst setting thresholds for significant populations is not straightforward, lessons may be learned from previous experiences of setting thresholds for other conservation tools, such as the IUCN Red List. Setting clearer thresholds could help to clarify the ‘critical values’ that the HCV approach is designed to identify and protect, thus helping to eliminate criticism resulting from differing expectations of the approach. Overall, there is a need to develop more, and better, HCV NIs that provide more specific information for all countries.

Secondly, a peer review process allows independent evaluation of HCV assessments (see Appendix A1.1 for more detail). These reviews are conducted by HCV experts recognised by the HCVRN and allow serious methodological flaws in HCV assessments to be identified prior to development, preventing developments that are environmentally or socially irresponsible from getting certified by sustainability standards. In principle, this should require companies seeking certification to conduct new HCV assessments and agree to appropriate HCV management practices. However, peer reviews are relatively rare in practice and are limited by cost.

Finally, the HCVRN is introducing an independent HCV Assessor Licensing Scheme, to ensure quality control of HCV assessor qualifications and to promote consistency in HCV assessment reporting. This new scheme aims to eliminate much of the inconsistency in the quality of HCV assessments. The RSPO has endorsed the scheme and their ultimate aim is for all HCV assessment team leaders to be licensed.

2.6 Knowledge sharing between HCV users, scientists and policy makers

There is a lack of information on the effectiveness of HCV areas for protecting biodiversity. HCV assessors require information to help guide and improve their ability to identify HCV areas and to make robust management recommendations (Meijaard & Sheil 2012). At the same time, many scientists are unaware of the HCV assessment process and of the practical constraints faced by assessors. For example, HCV assessors often have to carry out assessments and make management recommendations based on limited data that are supplemented with expert opinion and rapid field surveys (Edwards & Laurance 2012; Meijaard & Sheil 2012). Locally, some easily accessible guidance has been produced by NGOs to help HCV assessors and oil palm managers manage and monitor areas of HCV (e.g. ZSL 2011, 2013), but increasing knowledge exchange between researchers and assessors would ensure that scientific findings contribute towards improving the HCV process and help to identify knowledge gaps where more research is needed. For example, data are lacking on whether or not HCV areas are sufficiently large to conserve HCV species in the long term (e.g. Wearn et al. 2012), whether HCV areas can act as stepping stone habitats connecting larger tracts of forest (Saura et al. 2013), or whether areas intended to maintain HCVs 5 or 6 could also benefit biodiversity.

Transparency and data sharing by plantation companies and assessors is improving the HCV process, but more research is needed. Improvements to the reliability of species' detection rates in HCV assessments are required, and new technologies such as drones (http://conservationdrones.org/) or acoustic monitoring (Depraetere et al. 2012) might aid the development of quick but reliable measures of diversity for some taxa in megadiverse and remote tropical areas.

Existing research is of relevance to HCV assessors. For example, much research has been done on the impact of rainforest fragmentation and disturbance on biodiversity, but this information is often not in a suitable form for use by HCV assessors. The many dimensions of biodiversity research mean that there may be few simple and universally applicable rules, but rules of thumb could be developed. For example, if assessors are interested in particular threatened vertebrate species then range size and population viability estimates may already exist (e.g. for orang-utan *Pongo pygmaeus*, Singleton et al. 2009). Similarly, data on the proportion of primary forest species protected in different sized fragments are available for many taxa (e.g. for birds in SE Asia, Edwards et al. 2010). These data could be used to inform management recommendations on the minimum size of HCV areas for conserving particular species or communities, and in different agricultural contexts. The SAFE (www.safeproject.net) and SEnSOR (http://sensorproject.net/) research programmes are providing added momentum in this area and will provide independent evidence relevant to maintaining HCVs in oil palm landscapes. Similar projects are needed for other commodities in other geographic regions.

It is vital that research findings are communicated to practitioners through appropriate channels and in appropriate language (Sutherland et al. 2004). This could involve existing web resources (www.ConservationEvidence.com, www.ibatforbusiness.org), or new, more targeted approaches that feed into HCV NIs or a dedicated HCVRN working group. This knowledge exchange needs to include scientists, HCV users and also policy makers. It must also be flexible, with different strategies for small-holders and large, private companies. Small-holders make up over 40% of oil palm production area in Malaysia and Indonesia (FSG 2010), but often lack the technical expertise and funds to carry out comprehensive HCV assessments or to effectively manage HCV areas.

Policy makers have a key role in the promotion of larger scale and longer term conservation goals (such as landscape corridors), which fall outside the control of individual producers (especially smallholders), but can be influenced by national or regional planning (Edwards & Laurance 2012). Better knowledge exchange would help scientists communicate their findings with HCV users and policy makers, and HCV users and producers to share HCV management challenges with scientists and policy makers. Scientists and HCV users also need to be aware of legislative barriers and corruption that may prevent or slow implementation of policy changes in some countries (Smith et al. 2003; Rands et al. 2010).

Improving the relevance of scientific research will benefit from access to HCV management data. Data sharing and transparency are part of the HCV assessment process and the requirements of sustainability standards. For example, RSPO Criterion 1.2 states that management documents on HCV (including monitoring reports) are publicly available (RSPO 2013), and HCV assessment reports for new RSPO plantings must be posted online for public consultation, but there is currently no repository for monitoring reports.

The data currently contained in HCV monitoring reports are often of limited use to academic researchers; monitoring reports will need to contain more detailed, long-term data, including population estimates and details of monitoring protocols, if the effectiveness of HCV areas for biodiversity conservation is to be assessed.

2.7 Solutions to improve the HCV evidence base

We suggest the following practical solutions: to identify knowledge gaps, carry out research to fill gaps, and disseminate information to stakeholders. We hope that a better understanding of the HCV assessment process will stimulate further knowledge exchange, ensure that HCV assessments are based on the best possible scientific evidence and that scientists are aware of key management questions. Possible solutions might be to have more scientists on the HCVRN Technical Panel, or to set up an HCV 'science evidence base' working group to engage researchers with HCV users.

Greater sharing of HCV management and monitoring data would allow the overall benefits of the HCV approach to be quantified. This would not be constrained by commercial sensitivities of producers, given current trends for increasing transparency within standards such as the RSPO. There are likely to be financial and logistical limits to the quality and quantity of data that producers and HCV assessors can collect, but current data already collected for HCV assessments and during HCV monitoring could be useful for academic research if coupled with remote-sensing or modelling data. A starting point could be to share details of existing HCV areas in repositories hosted either by the HCVRN or by individual certification schemes (for the RSPO this could be an extension of the existing report repository for new plantings). Agreements would be needed in terms of reuse of data, metadata standards, and quality control of the data deposited, but such data could be used to examine the importance of HCV areas for species persistence across the wider landscape, and to assess the long term viability of HCV management areas under future land use or climate changes.

Finally, improving communication of research findings would ensure that the implications of the research reach both policy makers and the HCV user community in appropriate, non-technical language. This could begin with workshops that bring together HCV users, scientists and policy makers to discuss knowledge gaps, management and policy challenges and stimulate necessary policy changes. A repository could include findings from published peer-reviewed studies as well as information from reports and the grey literature. Such a database could be used directly by HCV assessors when carrying out assessments, as well as informing the development of thresholds and more refined definitions in HCV NIs of use to assessors. We suggest that these measures would make the HCV evidence-base more robust and lead to improvements in the assessment process. It is vital that the overall effectiveness of the HCV approach is evaluated to improve the conservation of tropical biodiversity in production landscapes.

2.8 Acknowledgements

We thank Anders Lindhe and Jennifer Lucey for comments.

Chapter 3 - Trait-dependent declines of species following conversion of rain forest to oil palm plantations

3.1 Abstract

Conversion of natural habitats to agriculture reduces species richness, particularly in highly diverse tropical regions, but its effects on species composition are less well-studied. The conversion of rain forest to oil palm is of particular conservation concern globally, and we examined how it affects the abundance of birds, beetles, and ants according to their local population size, body size, geographical range size, and feeding guild or trophic position. We re-analysed data from six published studies representing 487 species/genera to assess the relative importance of these traits in explaining changes in abundance following forest conversion. We found consistent patterns across all three taxa, with large-bodied, abundant forest species from higher trophic levels, declining most in abundance following conversion of forest to oil palm. Best-fitting models explained 39%-66% of the variation in abundance changes for the three taxa, and included all ecological traits that we considered. Across the three taxa, those few species found in oil palm tended to be small-bodied species, from lower trophic levels, that had low local abundances in forest. These species were often hyper-abundant in oil palm plantations. These results provide empirical evidence of consistent responses to land-use change among taxonomic groups in relation to ecological traits.

3.2 Introduction

Agriculture is the main driver of tropical deforestation (Kissinger et al. 2012), and the expansion of oil palm plantations threatens tropical forests in Asia, Latin America and Africa (Butler & Laurance 2008; Laurance et al. 2010; Wilcove & Koh 2010). Conversion of forest to oil palm plantation reduces species richness and abundance, and alters species composition in a range of taxa (Fitzherbert et al. 2008; Danielsen et al. 2009; Sodhi et al. 2010). Previous studies have suggested that habitat- and diet-specialist, and restricted-range species may be most at risk from conversion of tropical forest to oil palm (Danielsen & Heegaard 1995; Aratrakorn et al. 2006; Khen 2006; Peh et al. 2006; Fitzherbert et al. 2008), but it is unclear whether there is any consensus in such patterns among major taxonomic groups. Integrated analyses of existing data provide the potential to obtain new insights, and to examine ecological and phylogenetic variables known to be important for explaining species' responses to land-use change (McKinney 1997; Henle et al. 2004).

Ecological response traits (henceforth termed 'ecological traits'), such as body size and feeding guild, group species together according to shared responses to environmental disturbances and are often strongly associated with functional effect traits (henceforth termed 'functional traits'), which classify species based on their shared effects on particular ecosystem functions (Lavorel & Garnier 2002). Consequently, assessing how different ecological traits are affected by land-use changes can reveal concurrent impacts on ecosystem functioning (Hooper et al. 2005; Bello et al. 2010). More directly, response traits can help to understand mechanisms driving species declines and aid conservation efforts by predicting species groups at greatest risk from land-use changes (McGill et al. 2006; Williams et al. 2010). For example, studies have demonstrated that certain feeding guilds are more sensitive to habitat disturbance than others (Gray et al. 2007; Attwood et al. 2008), and predatory species, particularly large-bodied or specialist predators, are especially sensitive to disturbance and land-use changes (e.g. Kareiva 1987; McKinney 1997). Other species traits associated with vulnerability to extinction following habitat fragmentation, land-use change and disturbance include local rarity, large body size, and small geographic range size (e.g. Terborgh 1974; McKinney 1997; Henle et al. 2004). Conversely, omnivores tend to be more resilient to land-use changes (e.g. McKinney 1997; Henle et al. 2004). Mechanisms underlying these trait sensitivities include a reliance on highly specialised resources, and greater energy requirements resulting in low population densities and the need for larger home ranges (e.g. Damuth 1981; Henle et al. 2004).

In cases where ecological traits are associated with functional traits, it is possible to infer direct relationships between declining traits and ecosystem processes. For example, Larsen *et al.* (2005) showed that larger-bodied dung beetles were more susceptible to extinction following habitat loss and were more functionally efficient than smaller-bodied beetles. Declines in larger-bodied beetles following habitat loss reduced rates of dung burial, an important ecosystem function. The same study also showed that declines in bee abundance and species richness following habitat disturbance reduced pollination rates (Larsen et al. 2005b). For vertebrates, long-distance seed dispersal depends disproportionately on a few larger-bodied frugivorous birds and mammals, with decreased abundances of frugivorous birds directly reducing rates of seed dispersal (Moran et al. 2009; Velho et al. 2012). Furthermore, the loss of top predators can cause trophic cascades through food-webs, leading to a hyper-abundance of seed predators and herbivores, and subsequent reductions of seedling and sapling density (Terborgh et al. 2001). Comparison of species responses across different taxonomic and functional groups may thus help to predict ecological consequences of land-use change for ecosystem functioning (Lewis 2009; Morris 2010; Sodhi et al. 2010).

Ecological traits have been widely used to study land-use changes, but very few studies have used them to assess the impacts of converting rain forest to oil palm, and none of these have considered multiple ecological traits across several taxonomic groups. In this study, we assess (i) the relative importance of different ecological traits for explaining changes in abundance following conversion to oil palm, and (ii) the congruence of trait-specific responses across different taxonomic groups. We use a multi-taxon approach, focusing on birds, ants and beetles, which provides greater insight into community level effects than would a single taxon study (Fazey et al. 2005). We use abundance data extracted from published studies to test the hypothesis that, across the three taxonomic groups, species vary in their sensitivity to the conversion of forest to oil palm, and that locally rare, range-restricted, predatory, and large-bodied species show the greatest declines in abundance following the conversion of forest to oil palm. For birds, we account for potential confounding effects of phylogeny (Sibley & Ahlquist 1990) by using phylogenetically independent analyses, but suitable phylogenetic information is not currently available for ants or beetles.

3.3 Methods

We focused on birds, ants and beetles as three ecologically diverse taxa, thereby including vertebrates and invertebrates, social and non-social insects, and taxa representing a range of different feeding groups. We excluded taxa which contain only a single feeding group (e.g. herbivorous Lepidoptera), as it is not possible to quantitatively compare changes in abundance between guilds in such taxa. We searched ISI Web of Knowledge (WoK) for studies examining changes in abundance in forest and large-scale, mature (>10 years) oil palm habitats. We used the following key words: (‘oil palm’) AND ((‘biodiversity’) OR (‘bird(s)’) OR (‘avian’) OR (‘ant(s)’) OR (‘beetle(s)’) OR (‘coleoptera’) OR (‘species richness’) OR (‘composition’) OR (‘abundance’) OR (‘forest’)). We also searched reference lists and citations of studies found from these searches. To ensure our quantitative analyses were robust, we limited our search to peer-reviewed literature. Four otherwise suitable studies had to be excluded from analyses because abundance data for individual species or genera were unavailable (Danielsen & Heegaard 1995; Aratrakorn et al. 2006; Turner & Foster 2009; Bruhl & Eltz 2010).

The final dataset used for analysis was from six published studies which compared extensive tracts of selectively logged, or in one case unlogged, forest with oil palm sites in SE Asia (Malaysia). Studies were limited to those from SE Asia to avoid biogeographical differences in species responses (e.g. Gray et al. 2007). Studies comparing forest and oil palm at more than one location contributed more than one dataset to the analyses (Peh et al. 2006) and so these studies provided a total of seven datasets for analysis; four for birds (total of 188 species), two for ants (207 species) and one for beetles (91 genera). For those studies with unequal sampling effort in different habitats, we randomly selected an equal number of samples from each habitat for analysis (Peh et al. 2006; Sheldon et al. 2010). We excluded species or genera recorded only as singletons from the analyses to avoid errors due to insufficient sampling. This cut-off value was chosen to maximise the number of species/genera analysed, and followed sensitivity analyses that showed that findings were qualitatively similar for thresholds of two, five or ten individuals per species or genus.

We analysed ant data averaged across the two studies comparing oil palm to unlogged forest (Fayle et al. 2010) and to logged forest (Lucey & Hill 2012). To examine whether combining data from logged and unlogged forest sites affected our findings, we compared final parameter estimates from analyses of the combined ant dataset (n=207 species) with those from just the selectively logged forest dataset (n=92 species). The parameter estimates were not qualitatively different between these analyses, and so the combined dataset was used to maximise the number of ant species analysed. This approach of combining the two studies is supported by recent studies showing little difference between species assemblages in unlogged and selectively logged forest (Berry et al. 2010; Edwards et al. 2011b; Woodcock et al. 2011).

Bird names were assigned according to Sibley and Monroe (1990), ants according to Bolton et al. (2006), and beetles according to Bouchard et al. (2011) and the Universal Biological Indexer and Organizer project (www.ubio.org). Ant analyses included morphospecies that represent unique species, but that have not yet been ascribed to known species. However, because morphospecies were not named consistently across studies, we analysed morphospecies data from only the most species-rich dataset (Fayle et al. 2010) to avoid pseudoreplication.

3.3.1 Traits examined and guild classification

We examined the traits of body size, local population size, geographic range size, and trophic position or feeding group classifications of species (hence forth termed ‘feeding guild’). Data on bird body mass and ant body size were from Dunning (2009) and antweb.org, respectively and average values by genus were used if species-level values were unavailable (birds: 6/188 species, and ants 175/207 species); data on bird geographic range sizes were from Birdlife International (2010); local population size was calculated as the mean total abundance of species/genera in forest sites. Our measure of ant abundance (see ‘**Analyses**’ below) gives a robust measure of population size that is independent of colony size. There were no data available for ant or beetle geographical range sizes, or for beetle body sizes.

Birds were assigned to one of six feeding guilds based on Wong (1986), Lambert (1992), Jeyarajasingam & Pearson (1999), Mackinnon & Phillipps (1999), Cleary et al. (2007) and Phillipps & Phillipps (2009) (Table 3.1). Beetles were assigned to guilds based on classifications in Hunt et al. (2007). Three bird species and 14 beetle genera were excluded from analyses, due to a lack of consensus in feeding guild assignment (birds), or where feeding guild was unknown (beetles).

Table 3.1. Species were assigned to feeding guilds based on information in published studies. [a]Lambert (1992) was not used to classify granivores or frugivores as it did not differentiate between seed and fruit eaters, classifying both as frugivores. [b]Hunt et al. (2007) included moss-feeding Byrrhidae, genera of which are included in the beetle dataset from this study, in the algivore guild.

Feeding guild	Description	Food source
Birds		
Carnivore	Carnivore, raptor	Vertebrates (inc. fish), carrion
Frugivore[a]	Frugivore	Fruit, berries
Granivore[a]	Granivore, seed eater	Seeds, grain (not fruit)
Insectivore	Insectivore	Insects, invertebrates
Nectarivore	Nectarivore	Nectar, pollen
Omnivore	Omnivore, opportunist	Combination of other guilds, with no single primary food source
Beetles		
Algivore[b]	Algivores, bryophages	Algae, lichen, and mosses
Fungivore	Fungivore	Fungi
Herbivore	Herbivore, xylophage	Any living plant matter
Saprophage	Saprophage, coprophage	Dung, carrion, dead organisms but not fungi
Predator	Predator	Living invertebrates (and vertebrates)

Assigning species or genera to feeding guilds is possible for well-studied groups, such as birds. However, for hyper-diverse and poorly studied rainforest taxa, assigning guilds is challenging and often impractical (Blüthgen et al. 2003), particularly given that feeding habits of many species do not fall into discrete categories (Petchey & Gaston 2002). However, it is possible to examine the feeding habits of species using analysis of stable isotope ratios (Layman et al. 2007). Nitrogen isotope ratios (^{15}N:^{14}N, expressed as $\delta^{15}N$ values) are particularly useful in determining trophic positions because $\delta^{15}N$ values increase by approximately 2.5-3.5% during each trophic transfer (Vanderklift & Ponsard 2003). $\delta^{15}N$ values can therefore be converted into direct measures of trophic position (Post 2002), with trophic positions of approximately 2 indicating a plant-based diet and a trophic position ≥4 likely to indicate an entirely carnivorous diet. Ants were assigned trophic positions according to stable isotope data from Woodcock (2011a), based on ants sampled from continuous primary forest in Sabah, Malaysia (see Woodcock et al. 2012 for details on methodology). Differences in morphospecies classifications meant that for most ants (178/207 species) species-level data on trophic position were not available, and so species were assigned average values by genus, following Gibb & Cunningham (2011). Six ant species were excluded from analyses because data were not available for any members of the genus. This genus-averaging approach is supported by the observation that, for adequately sampled taxa, the standard deviation of trophic level for different species within each genus (mean $\sigma = 0.31$) was only fractionally higher than the standard deviation for different colonies of each species (mean $\sigma = 0.27$) (Woodcock 2011).

3.3.2 Analyses

Analyses were conducted separately for bird species (four datasets), ant species (two datasets), and beetle genera (one dataset). Ants may form large nests of thousands of individuals, and so individuals sampled at the same sampling point are unlikely to provide independent data. We thus analysed the incidence of species at sites (henceforth termed 'abundance'), based on their presence or absence at individual sampling points within sites (e.g. Woodcock et al. 2011). Beetle analyses were conducted at the genus level, in line with the predominantly genus level identification in the original study (Chung et al. 2000). We computed changes in the abundance of species (birds and ants) or genera (beetles) between sampling locations in forest and oil palm. Following Gray et al. (2007), the mean change in abundance per guild was calculated as:

$$\frac{\sum_{i=1}^{S_g} \frac{n_{op} - n_f}{n_{op} + n_f}}{S_g}$$

Equation 3.1. Mean change in abundance per guild.

where *S* = number of species/genera in the guild, *g*, and *n* = abundance of a species/genus (*i*) in oil palm (*op*) and forest (*f*). For 29 bird species and 20 ant species recorded in multiple studies, we computed the average change in abundance across studies. Data were then standardised according to total abundance of species/genera in forest and oil palm. Thus equation 3.1 weights all species/genera equally according to abundance with possible values ranging from +1, when all individuals are found only in oil palm, to -1 when all individuals are found only in forest.

We conducted separate analyses for the three taxa, containing the following variables; for birds: feeding guild (categorical), local population size (continuous), body mass (continuous) and geographical range size (continuous); for ants: trophic position, local population size and body size (all variables continuous); for beetles: feeding guild (categorical), and local population size (continuous).

We employed an information-theoretic approach to identify and select the best models for explaining changes in abundance in each of our three taxa. For each taxon, we constructed models with all possible combinations of the variables described above. We then fitted general linear models to the data for ants and beetles and phylogenetic generalised linear models

(PGLS, see Freckleton et al. 2002) to the data for birds. The PGLS analysis was carried out using the most extensive estimate of avian phylogeny (Sibley & Ahlquist 1990). It is based on Pagel's (1999) measure of phylogenetic independence (λ), which unlike many other statistical phylogenetic approaches, allows continuous and categorical variables to be analysed together (Pagel 1999). The PGLS method determines a maximum likelihood value for λ, which is then used to correct for phylogenetic non-independence in the data. λ ranges from 0 to 1, where 0 indicates the relationship between traits to be independent of phylogeny and 1 signifying that more closely related species are more likely to have the same trait values.

Prior to final analyses, model diagnostic plots were checked for homogeneity of variance and normality of residuals, following Faraway (2006). Non-homogeneous variances and non-normal residuals were corrected by the following transformations: $\log_{10}$ (bird geographical range size and body mass, ant body size and population size, and beetle population size), $\log_{10}$ square-root (ant change in abundance) and cube root transformation (bird population sizes). After transformation, all continuous predictor variables were standardised to equivalent scales by subtracting the mean value and dividing by twice the standard deviation (Grueber et al. 2011). This means that effect sizes can be used to directly compare the relative importance of each predictor variable for explaining changes in abundance, and that main effect estimates are still interpretable for models that included interaction terms (Schielzeth 2010; Grueber et al. 2011).

Models were ranked according to their $AIC_{c,}$ values (Burnham & Anderson 2002; Mazerolle 2006), which are commonly used for model selection and account for potential biases due to small sample sizes. The smaller the AIC_c value, the better the model's fit (Burnham & Anderson 2002). We calculated the difference in $AIC_{c,}$ value between each model and the best model (delta AIC: Δ_i). Best models were selected as those with Δ_i values <2. If there were multiple models with Δ_i values <2, we carried out model-averaging across these models or, if no other model had a Δ_i value <2, we used the parameters estimates from the single best model (Burnham & Anderson 2002). This allowed estimation of effect sizes and confidence intervals (CIs) for each predictor variable: effect sizes for continuous variables were slope estimates, whereas estimates for categorical feeding guilds were mean changes in abundance for each guild. To assess the overall goodness-of-fit of best models, adjusted R^2 values are presented.

3.4 Results

From six published studies we extracted seven datasets, allowing us to analyse responses of 188 bird species, 207 ant species, and 91 beetle genera, which ranged from endemic to ubiquitous taxa. Birds and beetles spanned 10 feeding guilds, and ant species ranged from herbivorous species (trophic position=2.0) to entirely carnivorous species (trophic position=4.7). Ant body lengths varied from 0.5 – 8.0 mm and bird body masses from 5.6 g – 2.9 kg.

For birds, overall species richness in forest declined by 43% following conversion to oil palm (175 species in forest versus 99 in oil palm), and abundance declined by 18% following conversion (3,812 individuals in forest versus 3,122 in oil palm). For ants, both species richness and abundance declined by 61% following conversion (190 species and 1,003 incidences in forest versus 74 species and 388 incidences in oil palm) and for beetles there was a 52% decline in generic richness (85 genera in forest versus 41 in oil palm) and a 54% decline in abundance (984 individuals in forest versus 450 in oil palm) following conversion.

3.4.1 Selection of best models and model confidence

All the ecological variables we examined were present in the best models for all three taxa (Table 3.2). For birds, the model with the lowest $AIC_{c,}$ value contained the ecological predictor variables of feeding guild, body size, local population size, and geographical range, without any interactions. Both of the best ant models contained all three predictor variables of trophic position, body size, and local population size, as well as an interaction between trophic position and body size. The best beetle model also contained both predictor variables of feeding guild and local population size. Overall model confidence was high for all three taxa, with 43% of the variation in the data set explained in the best bird model, 39% in the best ant model and 66% in the best beetle model (Table 3.2).

Table 3.2. Best models were selected based on AIC_c *values. We computed parameter estimates by using model-averaging across the best models listed below. For each taxon, best models were those with* $\Delta_i < 2$*. Column headings are defined as follows: Log-likelihood = the overall model fit with no adjustment for the number of parameters, K = the number of parameter estimates in the model,* w_i *= the Akaike weight, representing the model's relative strength compared to other best models, and* w_j *= the evidence ratio of the best models compared to the top-ranked model.* AIC_c *and* Δ_i *are explained in METHODS. Abbreviations as follows: mass: body mass, pop: local population size, range: geographic range, trophic: trophic position, and size: body size.*

Model	**Log-lik**	**K**	**AICc**	**Δ_i**	**Rank**	**$\exp(-\Delta_i/2)$**	**w_i**	**w_j**	**Adj R^2**
Birds									
Mass + pop + range + guild	-144.53	9	308.07	0.0	1	1.00	0.31	1.00	0.43
Guild + pop + range	-145.72	8	308.25	0.2	2	0.91	0.28	1.10	0.42
Mass + guild + pop*range	-144.01	10	309.27	1.2	3	0.55	0.17	1.82	0.43
Guild + pop*range	-145.44	9	309.88	1.8	4	0.40	0.12	2.47	0.42
Guild + range + mass*pop	-144.33	10	309.91	1.8	5	0.40	0.12	2.50	0.43
Ants									
Pop + trophic*size	-115.81	4	241.91	0.0	1	1.00	0.65	1.00	0.39
Trophic*size + trophic*pop	-115.36	5	243.13	1.2	2	0.54	0.35	1.84	0.39
Beetles									
Guild + pop	-11.29	6	37.94	0.0	1	1.00	1.00	1.00	0.66

3.4.2 Best predictors of sensitivity to conversion

Presented below are effect sizes and 95% confidence intervals for each variable included in best models. Effect sizes for continuous variables are slope estimates of the variable against change in abundance, whereas estimates for categorical feeding guilds are mean changes in abundance for each guild. Parameter estimates from bird analyses indicated that different feeding guilds varied in their sensitivity to the conversion of forest to oil palm, although some guilds had low sample sizes (Figure 3.1). Insectivores (effect size: -0.48; 95% CIs: -0.63, -0.34) and frugivores (effect size: -0.55; CIs: -0.76, -0.34) declined most in abundance following forest conversion, whilst nectarivores showed smaller declines (effect size: -0.40; CIs: -0.77, -0.026). In contrast, omnivores (effect size: -0.21; CIs: -0.46, 0.045) showed no significant decline in abundance following conversion of forest to oil palm.

Local population size, body mass and geographical range size all had significant effects on the change in abundance of bird species following conversion to oil palm. Local population size had by far the greatest relative impact, with an estimated effect size of -0.75 (CIs: -0.92, -0.59), followed by geographic range size with an estimated effect size of 0.36 (CIs: 0.20, 0.53), and body mass had the smallest relative impact on change in abundance with an estimated effect size of -0.19 (CIs: -0.37, -0.010). Therefore, in decreasing order of importance, bird species with large local population sizes in forest, small geographic ranges, and large bodies declined most in abundance following conversion to oil palm (Figure 3.1).

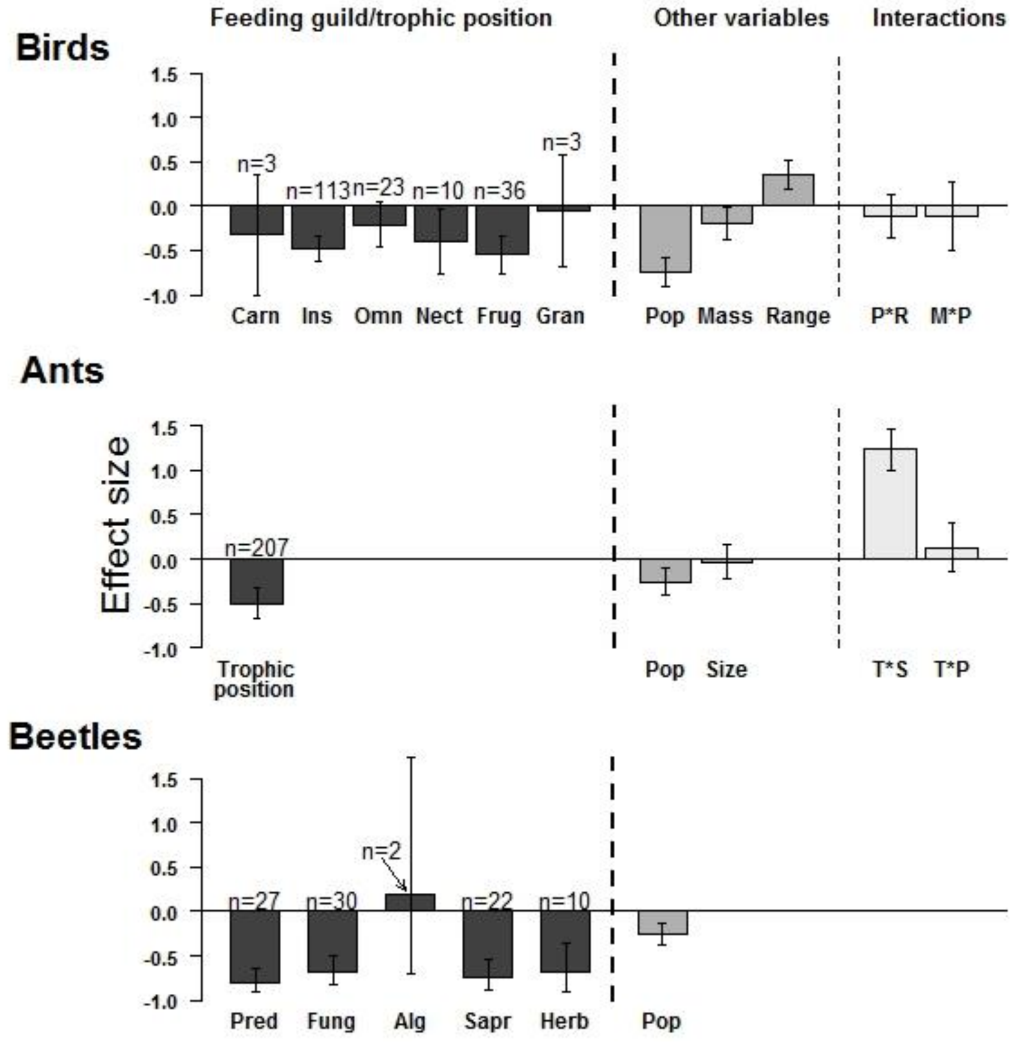


*Figure 3.1. Model-averaged effect sizes of different predictor variables for abundance change of (A) birds, (B) ants, and (C) beetles between forest and oil palm. We present model-averaged effect sizes for all variables included in the best models. Effect sizes for continuous variables and interactions are estimated slope values of standardised variables/interactions against abundance change. Effect sizes for categorical feeding guilds are estimated mean abundance changes of each bird and beetle feeding guild. N.B. Ants were not classified into trophic categories and so the effect size plotted is for the continuous variable trophic position. Sample sizes for the number of species/genera in each feeding guild are shown. For all estimates, error bars give model-averaged 95% confidence intervals. Abbreviations as follows: Trophic: trophic position, Pop: population size, Mass: body mass, Range: geographic range, M*R: body mass*geographic range, M*P: body mass*population size, T*S: trophic position*body size and T*P: trophic position*population size, Carn:*

carnivores, Ins: insectivores, Omn: omnivores, Frug: frugivores, Gran: granivores and Nect: nectarivores, Pred: predators, Fung: fungivores, Alg: algivores, Sapr: saprophages, and Herb: herbivores

In ant analyses, trophic position and local population size both had significant impacts on change in abundance. In addition, the highly significant positive interaction between trophic position and body size (effect size: 1.23, CIs: 1.01, 1.46) was by far the most important factor explaining changes in ant abundance, suggesting that large-bodied, carnivorous ants declined most in oil palm (Figure 3.1). Trophic position was the second best predictor of change in abundance (effect size: -0.50, CIs: -0.66,-0.33), followed by local population size (effect size: -0.26, CIs: -0.41, -0.11). The effect of body size on its own was not significantly different from zero (effect size: -0.03, CIs: -0.22, 0.16). Therefore, in decreasing order of importance, large-bodied ants with more carnivorous diets, carnivorous ants in general, and ants with large local population sizes in forest were particularly vulnerable to conversion to oil palm.

The beetle analyses suggest that feeding guild was not as important for predicting abundance change as for birds and ants, with all guilds except for algivores declining similarly in oil palm. Algivores appear to be more abundant in oil palm than in forest but there were only two genera in this guild, resulting in large confidence intervals (effect size: 0.20, CIs: -0.71, 1.73). All other guilds declined in abundance following conversion. The largest decline was for predators with an effect size of-0.80 (CIs: -0.91, -0.64), followed by saprophages (effect size: -0.73; CIs: -0.88, -0.53), fungivores (effect size: -0.69; CIs: -0.83, -0.50) and herbivores (effect size: -0.69; CIs: -0.91, -0.35). Whilst this suggests that predators may have declined slightly more than other guilds following conversion, population size appeared to be a better predictor of vulnerability for beetles (estimate: -0.25, CIs: -0.37, -0.13). Therefore, genera with large local population sizes in forest declined most in abundance in oil palm.

3.4.3 Similarity of responses among taxa

Across taxonomic groups, there were consistent declines in the abundance of large-bodied and locally abundant forest species, and of species from higher trophic levels following conversion of forest to oil palm. Therefore, species occurring at highest abundances in oil palm plantations tended to be small-bodied species, from lower trophic levels, that are locally rare in forest. Following land-use conversion, relative abundance patterns of species/genera were also less evenly distributed within the three taxa. In each taxon, a small number of species/genera were dominant and became hyper-abundant in oil palm (See Appendix 2, Figure A2.1).

3.4.4 Influence of phylogeny

Comparison of phylogenetic and non-phylogenetic bird analyses revealed little difference in estimated variable parameters (Figure 3.2). Model selection in the non-phylogenetic analyses identified a set of three best models, which were the first, third and fifth best models in the phylogenetic analyses. In the phylogenetic bird analyses, the maximum likelihood value of λ for each of the five best models deviated significantly from 1 ($p<0.0001$ in all cases) but not from 0 ($p>0.16$ in all cases). Thus, there was little evidence that any of the traits considered were related to phylogeny. Although caution is required when extrapolating trends across taxa, the phylogenetic independence of bird analyses may lend support to the validity of the non-phylogenetically adjusted ant and beetle analyses.

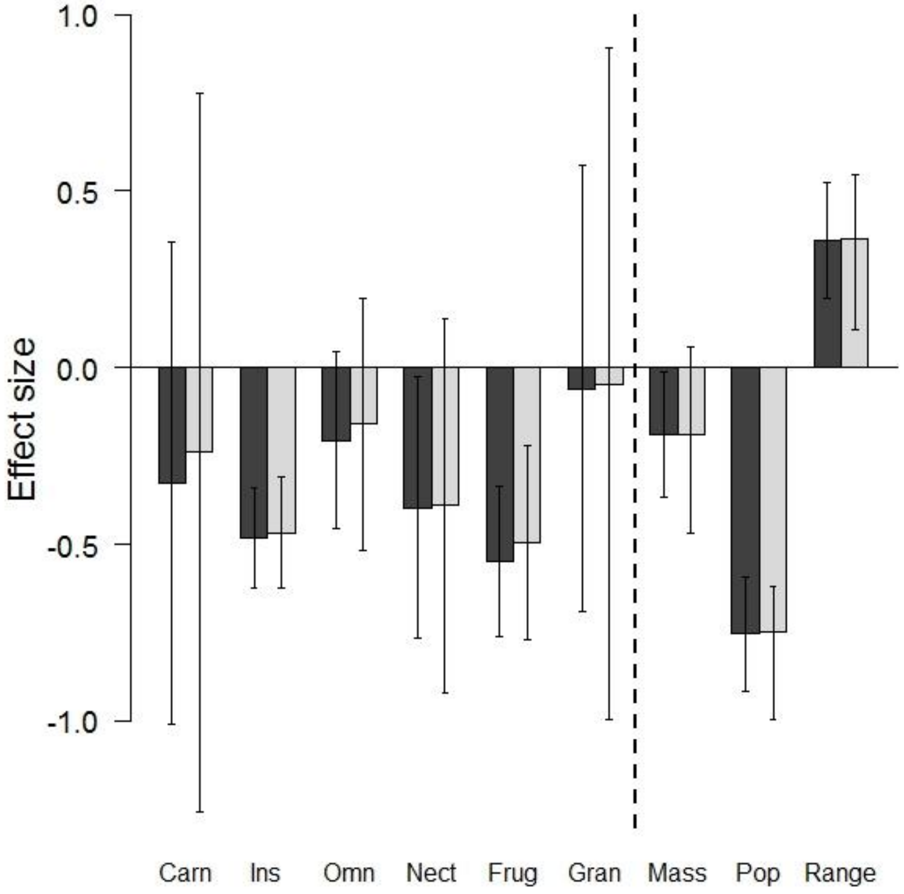


Figure 3.2. Effect sizes of predictor variables from bird analyses with (dark grey bars), and without (light grey bars) adjustment for phylogeny. Effect sizes and CIs for continuous and categorical variables, number of species in each guild, and guild abbreviations as in Figure 3.1.

3.6 Discussion

3.6.1 Conserved trait declines

Our results showed consistent responses across taxa in terms of which ecological traits were most affected by conversion of forest to oil palm. The most abundant species in oil palm tended to occur at very low abundances or be absent in forest, and large-bodied species and those from higher trophic levels also occurred at much lower abundances in oil palm than in forest. This study provides quantitative evidence for consistent patterns in the sensitivity of ecological traits across different taxonomic groups following the conversion of forest to oil palm. Our results show that across three ecologically diverse taxonomic groups, species found in oil palm plantations consistently tend to be small-bodied species, from lower trophic levels, that are locally rare in forest.

3.6.2 Drivers of trait declines

Our results on consistent patterns of declines in traits in different taxa following conversion of forest to oil palm suggest that there may be consistent extinction drivers acting across taxonomic groups. In tropical forest habitats, very high plant diversity supports high structural diversity, which underpins high animal diversity (Novotny et al. 2006). The structurally simple oil palm environment with very low non-palm plant diversity (largely restricted to herbaceous ground cover and epiphytic ferns e.g. Foster et al. 2011) may drive many specialised species extinct and favour more generalist and disturbance-tolerant species that occur at only low abundances in forest. This shift from habitat complexity to simplicity could explain the declines in frugivorous and insectivorous birds. These were the most species rich guilds in our analyses (insectivores: 107 species, frugivores: 35 species) and, thus might be expected to exhibit the greatest niche specialisation in forest (e.g., to avoid competition). The declines of these guilds following habitat conversion may be explained by this specialisation, and by the lack of suitable fruit-bearing trees and invertebrate-rich vegetation layers in the homogenous oil palm environment. Declines of large-bodied and higher trophic level species in oil palm may be explained by cascading bottom-up effects of reduced resource availability disproportionally affecting the species with greater energy requirements and lower population densities (e.g. Damuth 1981).

Our finding that abundant forest species decline most in oil palm does not agree with previous studies showing high vulnerability of rare species (e.g. McKinney 1997; Henle et al. 2004), but this is likely to be explained by two factors. Firstly, the scale at which rarity is defined is critical in explaining whether “rare” species are shown to be more or less vulnerable to extinction following habitat disturbances (McKinney 1997). For example, whilst you would expect high vulnerability of rare species defined by restricted geographic distributions or IUCN Red Listings, our definition of rare species as those with small local population sizes in forest may include geographically widespread, disturbance-associated taxa that occur at low abundances in forest. Indeed, this is supported by our results showing that bird species with smaller geographic ranges declined more in abundance following conversion of forest to oil palm.

Secondly, much of the earlier evidence on the vulnerability of rare species is from studies of forest disturbance and fragmentation (McKinney 1997; Henle et al. 2004), which compare the same habitats under varying levels of disturbance. By contrast, forest and oil palm are distinct habitats, and our results demonstrate that many relatively common forest species cannot persist in oil palm habitats.

We maximised the number of species in our analyses by including all species occurring more than once. However, when only forest species were included in analyses we still found declines of abundant forest species following conversion. Given that the majority of species declined in abundance following conversion, the slope of the relationship between population size and change in abundance is likely to be driven by those few species that increase in abundance in oil palm and so our findings do not preclude the loss of rare forest species, as well as the loss of more abundant forest species, in plantations. In oil palm, the small-bodied species from lower trophic levels, that tended to be locally rare in forest, but that dominated these agricultural sites were probably able to exploit the few crop-associated resources found in the plantations. Similarly, widespread and omnivorous bird species that are not reliant on a single food source were also more abundant in plantations (Gregory & Gaston 2000; Walker 2006).

3.6.3 Hyper-abundance of species on plantations

We observed a few species reaching very high abundances in oil palm sites in all three taxa (see Appendix 2, Figure A2.1). For example, most insectivorous and frugivorous bird species declined in plantations, although some species, such as *Macronous gularis* (Striped Tit-babbler), *Orthotomus sericeus* (Rufous-tailed tailorbird), and *Psitticula longicauda* (Long-tailed parakeet) were highly abundant in oil palm plantations. Similar patterns have also been shown in butterflies (Lucey & Hill 2012), moths (Khen 2006), termites (Hassall et al. 2006), rats (Wood & Fee 2003; Bernard et al. 2009), and frugivorous bats (Danielsen & Heegaard 1995), whereby oil palm plantations typically support a small number of species that occur at much higher abundances than observed in forest habitats. For example, Lucey and Hill (2012) showed that plantations support just 54% of forest species, yet overall butterfly abundance was >3.5 times higher in plantations than in forest. The same trends have also been observed following other land-use changes (e.g. Terborgh et al. 2001; Laurance et al. 2002; Feeley & Terborgh 2006; Gardner et al. 2007; Nichols et al. 2007). Oil palm monocultures can provide a hyper-abundance of just a few resources (e.g. palm fruit and palm fronds) that can be exploited by a few species, which can subsequently achieve very high abundances. However, the restricted range of resources present in plantations means that most resources required to support forest species are absent.

Our results illustrate substantial turnover of species with different ecological traits between forest and oil palm. Many of the traits considered are also functional traits (e.g. body size, feeding guild), implying inherent differences in the way that the forest and plantation systems function ecologically. Essential ecosystem functions in forest may not be important in oil palm plantations, either because they are replaced by plantation management practices, for example the addition of fertilisers in place of natural nutrient cycling, or because there is little requirement for them in monoculture plantations (e.g. seed dispersal). However, in plantations, there may still be risks associated with a reliance on a few numerically dominant species for ecosystem functioning, and more data are required on whether or not a few dominant species in oil palm plantations can compensate for the loss of many specialised forest species (e.g. Loreau et al. 2001; Foster et al. 2011; Peh & Lewis 2012).

3.6.4 Conclusions

Our results show that across three ecologically diverse taxonomic groups there were consistent patterns in the sensitivity of species to land-use change, and that species occurring in oil palm plantations were more likely to be small-bodied species, from lower trophic levels that are present at very low abundances in forest. All three taxonomic groups contained a few species that were hyper-abundant in oil palm, presumably because they could exploit the few highly abundant crop-associated resources present in plantations. Observed declines of large-bodied, higher trophic level, forest species may be a response to the low diversity of available resources in homogenous plantations. Consistent responses to land-use change among the three taxonomic groups in relation to species' ecological traits imply that similar mechanistic drivers affect species' responses to land-use conversion, and infer differences in ecosystem functioning between forest and oil palm habitats.

3.8 Acknowledgments

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Chapter 4 - Sampling dung beetles and their ecosystem functions in fragmented and degraded rainforest

4.1 Abstract

Dung beetles can be sampled efficiently using baited traps and have key functional roles within ecosystems, making them an excellent study taxon for assessing the impacts of tropical forest fragmentation and degradation on ecosystem functioning and species diversity. This chapter provides information about my study sites and their disturbance history, and describes methods for quantifying forest quality across sites. In this thesis, dung beetles were sampled with human dung-baited pitfall traps and data are presented to show that 48 hours of sampling effort was sufficient to characterise dung beetle assemblages at each site. Annual variation in dung beetle richness and abundance from surveys of three sites over three years was low, indicating that comparisons of dung beetle samples and ecosystem functioning measurements between different years were robust. I developed novel methods to measure dung removal and seed dispersal by tunneller and roller dung beetles, which are outlined. Dung removal and seed dispersal were measured using cattle dung rather than human dung which was used for beetle sampling. However, both baits attracted similar species assemblages, including all functionally important large roller and tunneller species, supporting the use of different bait types for species richness and functioning investigations.

4.2 Study location

Fieldwork was carried out from May to August 2011, from March to August 2012, and from June to September 2013 in eastern Sabah, Malaysia (Figure 4.1). I sampled at 18 field sites consisting of two continuous forest sites and 16 forest fragments within oil palm plantations (Figure 4.2). All of these sites were in lowland mixed Dipterocarp forest below 300 m elevation. The forest fragments ranged in size from 5 to 3,529 ha and had been isolated within oil palm plantations for at least 19 years at the time of sampling, and possibly much longer (see Table 4.1 and section for 4.2.3 full details). Fragments were between 0.2 and 46.7 km from the nearest stretch of continuous forest and varied considerably in vegetation quality and management histories (see sections 4.2.3 and 4.3.6). The two continuous forest sites were unlogged forest in Danum Valley Conservation Area and twice-logged forest in the Ulu-Segama Malua Forest Reserve (Table 4.1). Both of these continuous forest sites are within Sabah's largest remaining block of continuous forest of approximately 1 million ha (Figure 4.1). This large area of forest is managed by the Yayasan Sabah Foundation on behalf of the Sabah Forestry Department (Reynolds et al. 2011).

At least 12 of the forest sites sampled in this study had been selectively logged >7 years prior to this study (Table 4.1), and exhibited differences in plant species composition and vegetation structure when compared to undisturbed forest (Figure 4.7). These differences in forest structure are described in greater detail in section 4.3.6. Dipterocarp forest is the predominant forest type in Borneo, but there are also tracts of Kerangas forest and limestone forest in Sabah that were represented in some of the forest sites sampled in this study (Table 4.1). In order to prevent confounding the effects of fragmentation with differences in forest type, transects sampled only Dipterocarp forest.

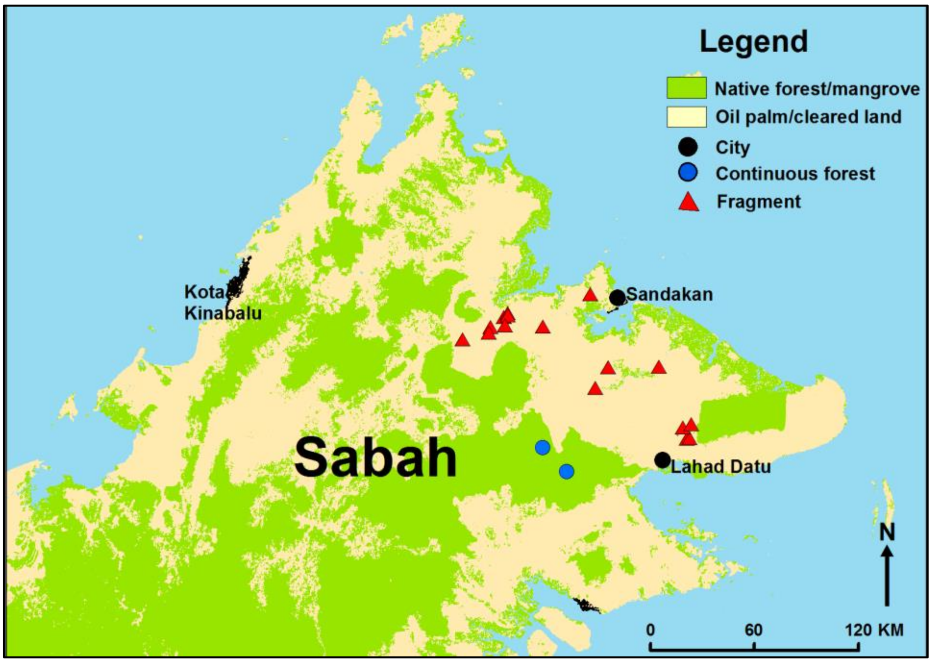

Figure 4.1. Land cover map of Sabah showing study site locations. Land cover classifications are for 2010 and are simplified categories based on Miettinen et al. 2011. *The 'native forest/mangrove' category combines degraded and intact mangrove, peatswamp, and lowland-upper montane forest categories, and 'oil palm/cleared land' combines mosaic and open habitats, large scale palm plantations and plantation/regrowth categories.*

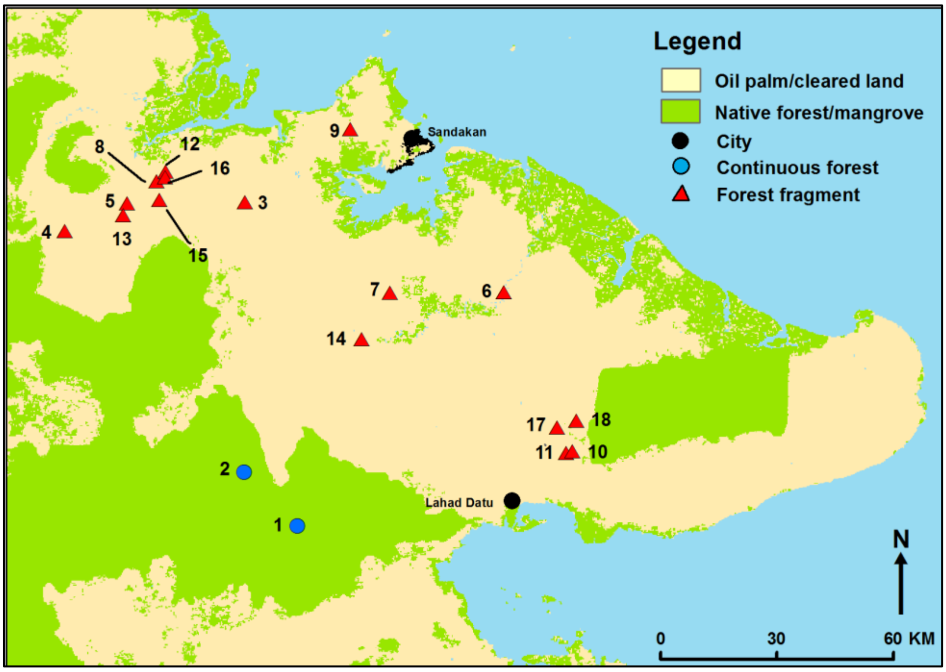

Figure 4.2. Higher resolution map of field site locations in eastern Sabah, Malaysia.

*Table 4.1. Field sites. Site numbers are ranked by forest size and numbers are subsequently used throughout the thesis when referring to individual sites. Site locations are shown on Figure 4.2. *See section 4.2.3 for full details on logging intensity and isolation history. Abbreviations and sites names as follows: U = unlogged, L = logged, 1 = Danum Valley Conservation Area, 2 = Ulu-Segama Malua Forest Reserve, 3 = Lungmanis VJR, 4 = Ulu Sapa Payau VJR, 5 = Sungai Sapi C VJR, 6 = Materis VJR, 7 = Keruak VJR, 8 = 'Watercatchment' HCV area, 9 = Labuk Road VJR, 10 = 'Sabahsar' HCV area, 11 = 'Rekasar' HCV area, 12 = 'Yongpeng' HCV area, 13 = Sungai Sapi A VJR, 14 = Pin Supu forest, 15 = Meranti' HCV area, '16 = 'Jatu' HCV area, 17 = 'Lunpadas' HCV area, and 18 = 'Delilah' HCV area. HCV = High Conservation Value; VJR = Virgin Jungle Reserve.*

Site no.	Size (ha)	Isolation distance (km)	Years since isolation at time of study*	Logging history*	Number of sampling stations	Shortest distance from station to forest edge (m)
1	-	-	-	U	10	100
2	-	-	-	L	10	100
3	3,529	10.1	28	L	10	100
4	720	3.3	28	U	10	100
5	500	13	28	U	10	100
6	250	34.3	28	L	10	100
7	225	32.6	28	L	10	100
8	120	12.6	21	L	10	100
9	120	46.7	28	U	10	100
10	88	2.2	19	L	8	100
11	85	15.1	21	L	7	100
12	57	3.9	19	L	10	100
13	45	10.8	28	U	10	100
14	39	21.9	28	U	5	100
15	30	14.5	21	L	3	60 (1 of 3 traps)
16	12	8.8	21	L	3	100
17	11	5	19	L	4	40 (2 of 4 traps)
18	5	0.2	19	L	3	40 (all 3 traps)

4.2.1 Local Fauna

There are over 200 native land mammal species in Borneo, including at least 90 bat species (Payne et al. 1998), and at least 120 mammal species have been recorded in the unlogged continuous forest site sampled in this study (site 1: Danum Valley Conservation Area) (Marsh & Greer 1992; Hazebroek et al. 2013). Both the unlogged and twice-logged (site 2: Ulu-Segama Malua Forest Reserve) continuous forest sites sampled in this study support the vast majority of Borneo's larger species, including at least 9 primate species, all of Borneo's five felid species and populations of Borneo's largest mammal species, Bornean elephants (*Elephas maximus borneensis*) and Banteng (*Bos javanicus lowi*). Danum Valley Conservation Area is also thought to support some of the last surviving individuals of the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) (Goossens et al. 2013). There has been little quantitative research on Borneo's mammal species in forest fragments, but it is likely that the 16 forest fragments sampled in this study support an impoverished mammalian community compared to that of the continuous forest sites of Danum Valley and Ulu-Segama Malua. Large-bodied species, wide ranging species and those susceptible to hunting often go extinct in forest fragments (Michalski & Peres 2007) and are unlikely to persist in the fragments surveyed in this study. For example, Bornean elephants (*Elephas maximus borneensis*) and Banteng (*Bos javanicus lowi*) are known to be absent from the forest fragments in Sabah (Timmins et al. 2008; Alfred et al. 2010). However, a number of generalist and disturbance-tolerant species, such as Long-tailed macaques (*Macaca fascicularis*), Sambar deer (*Rusa unicolor*) and Bearded pigs (*Sus barbatus*), persist even in the smallest forest fragments sampled in this study (pers. obs.).

4.2.2 Climate

Eastern Sabah experiences a largely aseasonal moist tropical climate, with mean daily temperatures throughout the year of between 24 and 28 °C and mean monthly rainfall consistently in excess of 100 mm (Hazebroek et al. 2013). Climatic records from a small meteorological station at the Danum Valley Field Centre, dating back to 1985, represent typical climatic patterns for the region, indicating that mean annual rainfall is approximately 2800 mm and mean daily temperature is approximately 27 °C (Figure 4.3). There is some weak seasonal variation in rainfall and temperature in Sabah with a slightly drier and hotter season that typically extends from March-September (Hamer et al. 2005), and for this study, all sampling was conducted during this “drier season”. El Niño-Southern Oscillation (ENSO) events also affect the climate of Borneo, leading to reduced rainfall and droughts, especially in Eastern Borneo (Richards 1996). However, no strong ENSO events occurred between 2011 and 2013 when the fieldwork for this study was conducted (NOAA/National Weather Service 2014).

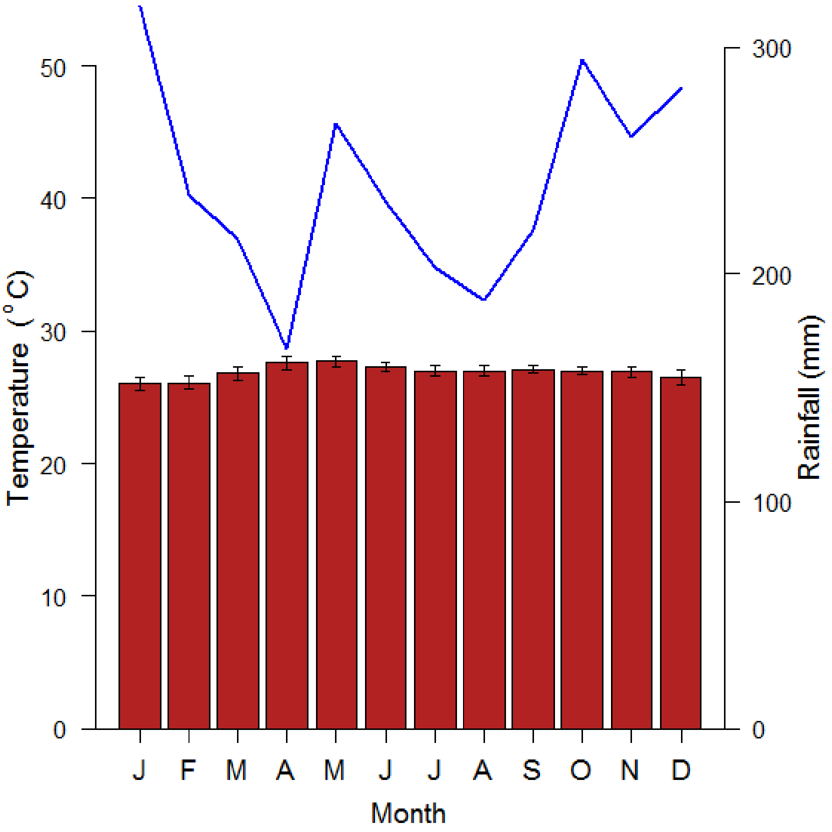

Figure 4.3. Plot showing mean monthly rainfall (blue line) and temperature (red bars) at Danum Valley Field Centre, averaged across years 1985-2011. Data are taken from http://www.searrp.org/danum-valley/the-conservation-area/climate/.

Climatic conditions are broadly similar across eastern Sabah, where my study sites were located, although the east coast of the State receives slightly lower annual rainfall than the central area around the Danum Valley Conservation Area (Sites 1 and 2) (Marsh & Greer 1992). To account for potential variation in climate across study sites, temperature and soil moisture data were recorded. Soil moisture was used as a proxy for relative humidity (see section 4.3.6 for methodological details). These data revealed no relationship of soil moisture or temperature with site longitude or fragment area (regression output: $t_{1,14} < 1.74$, $p > 0.1$). However, temperature was significantly negatively related to ‘forest quality’ (regression output: $t_{1,14} = -3.16$, $p < 0.01$), and more disturbed sites were hotter (see section 4.3.6 for definition of forest quality) (Figure 4.4). Overall, these analyses showed little evidence of climatic differences among sites in relation to their geographic locations, but revealed the potential impacts of fragmentation and disturbance on local microclimate. It should also be noted that the temperatures reported for the Danum Valley Field Centre meteorological station are higher than those recorded during this study, probably because the Danum meteorological station is in a clearing whilst the dataloggers used for this study were placed in the forest.

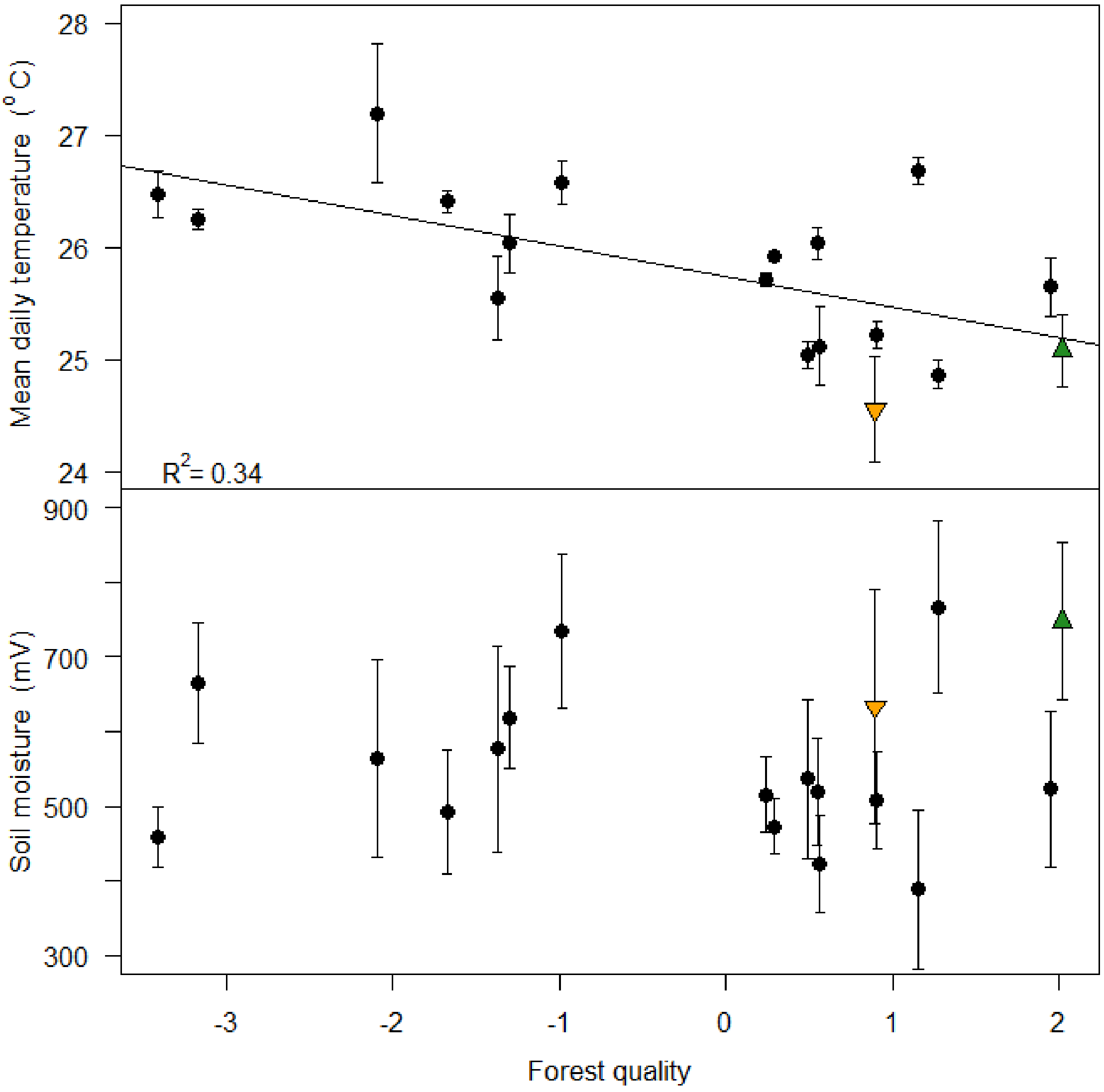

Figure 4.4. Scatter plots of mean daily temperature and mean soil moisture content against forest quality. Error bars show standard deviations. Line of best fit is shown for the significant relationship between temperature and forest quality. There was no significant relationship between forest quality and soil moisture content. Data were collected during sampling at each site (see section 4.3.6 for methods for measuring forest quality). Triangles and green fill represent undisturbed continuous forest sites/stations, triangles and yellow fill represent twice-logged continuous forest sites/stations, and circles and black fill represent forest fragments. Soil moisture content is measured in millivolts. Millivolts are an appropriate measurement unit for soil moisture when detailed soil type data are unavailable, as was the case here (Delta-T Devices Ltd 2013).

4.2.3 Management history

Both of the continuous forest sites sampled in this study (sites 1 and 2) were listed as protected forest reserves at the time of sampling. Danum Valley Conservation Area (site 1) has never been logged and has been officially protected in some capacity since 1980 (Figure 4.5). It is currently listed as a Class I Protection Forest Reserve, which is designed to maintain watershed, climatic and environmental stability (McMorrow & Talip 2001). This is the highest level of forest protection in Sabah (Marsh & Greer 1992; Reynolds et al. 2011). Ulu Segama-Malua (USM) Forest Reserve (site 2) was formerly production forest and classified as a Class II Commercial Forest Reserve, but in 2007 was set-aside as an area of sustainable forest management to rehabilitate the forest. USM Forest Reserve was selectively logged twice, between 1976 and 1991 and then again between 2001 and 2007. The first logging rotation in the area was of an extremely high intensity, with ~120 $m^3 ha^{-1}$ of timber removed, focussed on Dipterocarps larger than 60 cm diameter at breast height (dbh). At the time, this volume of timber extraction was higher than in any other tropical forest globally (Marsh & Greer 1992) and left the forest highly degraded, especially on steep slopes, with a high frequency of skid trails, secondary haulage roads and log-landing sites. The second logging rotation extracted timber above a cutting limit of 40 cm dbh, and focussed on a wider range of target species, including non-Dipterocarps. Approximately 35 $m^3 ha^{-1}$ of timber were extracted in this second rotation and, after completion, the forest canopy in the USM Forest Reserve consisted primarily of pioneer species and very few Dipterocarps (Reynolds et al. 2011).

Figure 4.5. Undisturbed primary dipterocarp forest in Danum Valley Conservation Area (site 1). The three large trees are Dipterocarps.

Eight of the fragments sampled in this study were Virgin Jungle Reserves (VJRs) owned and managed by the Sabah Forestry Department (39-3,529 ha). The remaining eight fragment sites were owned and managed as High Conservation Value (HCV) areas within plantations owned by PPB Group Berhad (Wilmar International) (5-120 ha, henceforth termed 'plantation fragments').These PPB plantations are RSPO certified and so PPB are required to protect HCV species and habitats in their concessions. These HCV study areas were established before 2005, and requirements are more stringent for newer plantations established after 2005 that have to carry out an HCV assessment prior to any forest conversion and then actively protect and manage any HCVs found. However, plantations established before 2005 had typically already cleared forest in their concessions without any assessments and only retained natural forest in areas that were not economically viable to plant with oil palms, such as on steep slopes or waterlogged areas. Therefore, the plantation fragments (HCVs) sampled in this study may not be comparable with HCV areas in new post-2005 plantings.

VJRs were set aside in the 1980s for research purposes and conservation of plant genetic resources, and logging is prohibited, although at least three of the VJRs sampled in this study had been previously logged to some extent prior to gazettement as VJRs in the 1980s (McMorrow & Talip 2001; Sabah Forestry Department 2005). Detailed logging histories were not available for the VJRs considered in this study, but sites 3, 6 and 7 (Lungmanis, Materis and Keruak VJRs) had all been subject to low-intensity selective logging prior to gazettement as VJRs (Sabah Forestry Department 2005). Illegal, small-scale timber extraction was also observed whilst sampling in site 7 during this study. By contrast, all eight plantation fragments were heavily-logged production forest prior to fragmentation in the 1990s (Mr Frederick Chok (manager of Sabahmas estate) and Mr Foo Koh Fei (manager of Reka Halus estate) pers. comm.). There was heterogeneity in forest quality among fragments (Figure 4.6), but in general the intensity of logging in plantation fragments greatly exceeded that in the twice-logged continuous forest site and VJRs, and very few large trees remained (Figure 4.7).

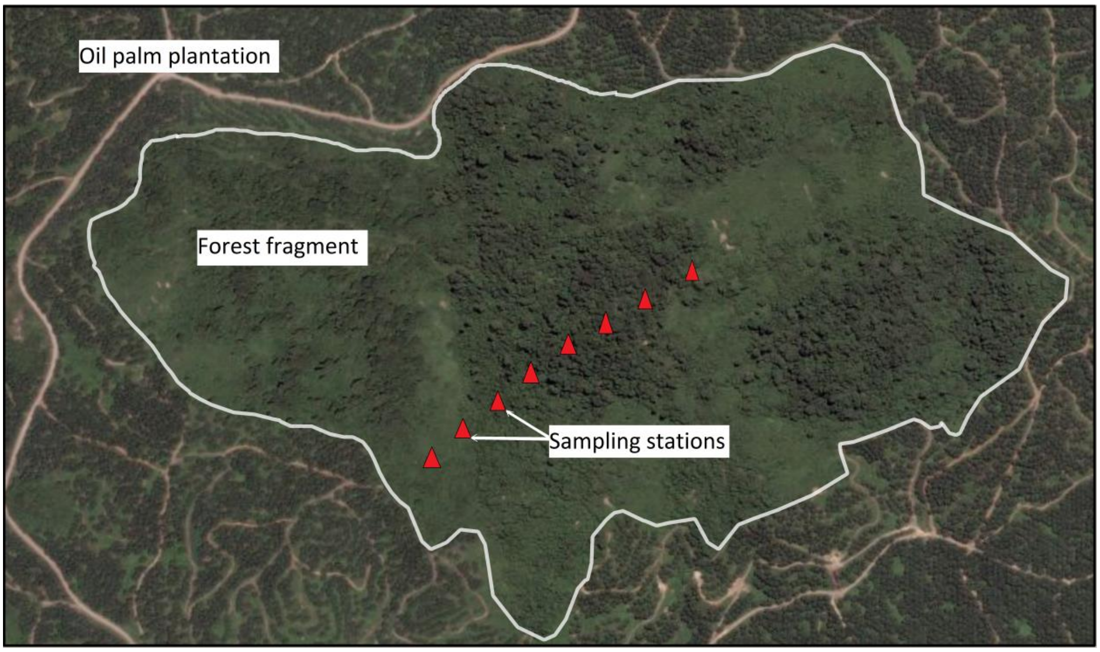

Figure 4.6. High resolution satellite imagery (© ESRI) of site 10, a plantation fragment surrounded by an oil palm plantation. Note the degree of habitat heterogeneity within the fragment with the central area containing relatively intact, closed-canopy forest compared to parts of the fragment's periphery where few trees remain.

Figure 4.7. Low canopy with tangled vines in site 8 (120 ha), showing vegetation structure typical of plantation fragments. Photo courtesy of Benny Yeong.

All of the fragments sampled in this study were first isolated at least 19 years prior to dung beetle sampling in 2012 (Table 4.1). Isolation year is defined as the year when the forest surrounding the site was converted to agriculture. The plantation fragments were first isolated between 1991 and 1993, when the surrounded land was leased to oil palm growers and cleared for planting (Frederick Chok & Foo Koh Fei pers. comm.). Precise isolation dates were not available for the VJR fragments, but VJRs probably became isolated fragments shortly after 1984, when they received their final gazettement as VJRs. This estimation is supported by the fact that the majority of VJRs sampled were surrounded by mature oil palms (>20 years old) (pers. obs.).

4.3 Sampling protocols

At all 18 study sites dung beetles and their ecosystem functions were sampled at 3-10 sampling stations per site, with stations placed at 100 m intervals along 0.3-1 km linear transects (1 transect per site). The number of sampling stations and transect lengths varied among sites because it was not possible to fit 1 km transects into some small fragments (Table 4.1). Establishing transects up to 1 km in length was designed to ensure sampling of the range of habitat heterogeneity present within sites. Spacing between sampling stations was kept constant at 100 m to retain trap independence among stations (Larsen & Forsyth 2005). Sampling stations were placed at least 100 m from the edge of the fragment to avoid edge effects (Laurance et al. 2002), although this was not possible in three of the smallest fragments due to their shape and size. In these fragments sampling stations were at least 40 m from the forest edge (Table 4.1).

4.3.1 Dung beetle sampling

Dung beetles (Coleoptera, Scarabaeidae: Scarabaeinae) were sampled at all 18 study sites between April and August 2012 using human dung-baited pitfall traps (Figure 4.8). Human dung is similar to the dung of other omnivorous species, including other primates, and so attracts a wide range of species including generalists and more specialist species attracted to herbivore dung and carrion (Davis et al. 2001). Pitfall traps consisted of a

500 ml plastic cup buried flush with the soil surface. To prevent traps from being flooded by rain, soil around traps was elevated slightly to prevent water from flowing into the trap and traps were covered with a polystyrene plate. Approximately ~20 g of fresh human dung was suspended above the trap in muslin cloth (Figure 4.8). Traps were filled with ~200 ml of salt water with a small amount of detergent. The salt water acted as a killing fluid and as a mild preservative while the detergent reduced surface tension to prevent beetles from climbing out of the traps. Traps were left out for 48 hours at each site, and were emptied and re-baited daily.

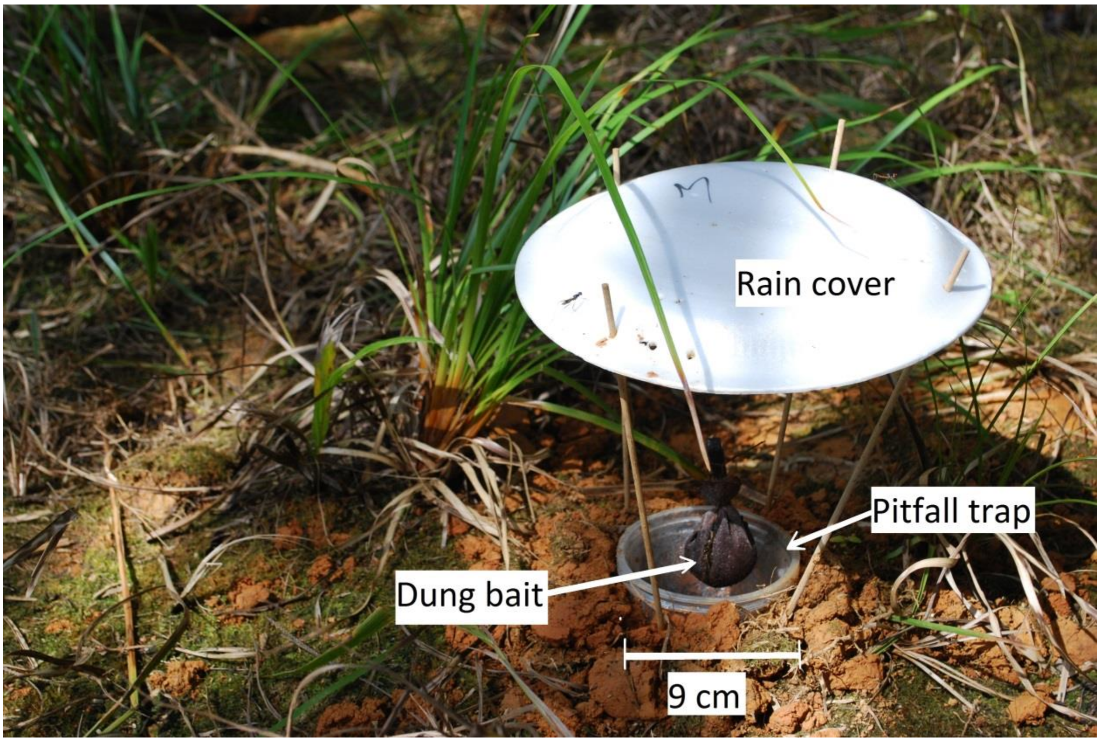

Figure 4.8. Human dung-baited pitfall trap.

4.3.2 Species identification and biomass calculations

Dung beetles were sorted and identified whilst in Sabah using an optical microscope (Figure 4.9), and species identities were determined based on reference collections of Felicity Edwards (Department of Biology, University of Leeds) and Trond Larsen (Conservation International). Species nomenclature was verified by Darren Mann (Oxford University Museum of Natural History). All individuals were identified to species level, and if the species name was not known a unique morphospecies ID was given. Only beetle species in the Scarabaeinae subfamily (‘true dung beetles’) were subsequently considered in analyses. Species identities were used to calculate dung beetle abundance, biomass and species richness at each sampling station.

Figure 4.9. Example of a sample of beetles caught in one pitfall trap in 24 hours in unlogged continuous forest.

Biomass estimates for each sampling station were calculated as the number of individuals of each species trapped at a sampling station multiplied by the mean dry mass of that species. It was not feasible to dry individuals from all 60 beetle species collected and so the majority of species’ dry masses were estimated based on extrapolation from a regression of species length (elytra and pronotum, excluding head; Figure 4.10) against dried mass calculated for 10 species (n = 15-25 individuals per species). The individuals from these 10 species were dried to constant mass (to the nearest 0.0001 g) in an oven at 60°C, and their lengths were measured (to the nearest 0.1 mm) using callipers. A linear regression was then fitted for $\log_e$ length against $\log_e$ dry mass that gave a very strong relationship (Adj-$R^2 = 0.94$; Figure 4.11). The dry masses of the remaining 50 species were then estimated by incorporating data from the measured lengths of each of the species (n=1-25 individuals per species) into this regression. To avoid potential size differences associated with different habitats affecting estimates of biomass, where possible the individuals used for this regression were taken from undisturbed forest samples.

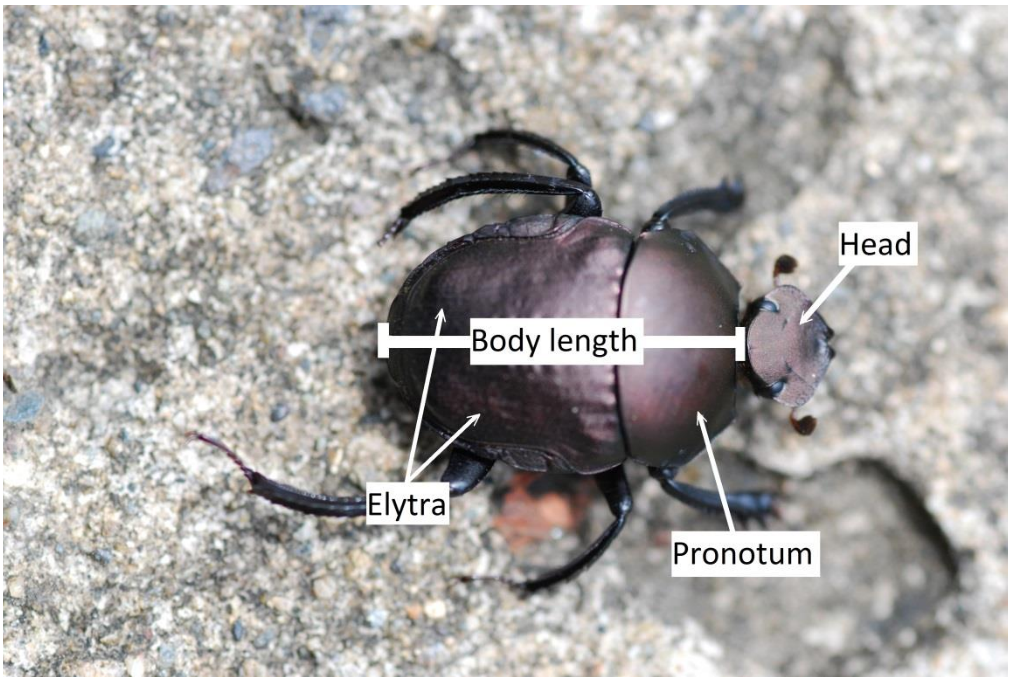

Figure 4.10. Diagram of basic dung beetle anatomy showing how body length was measured.

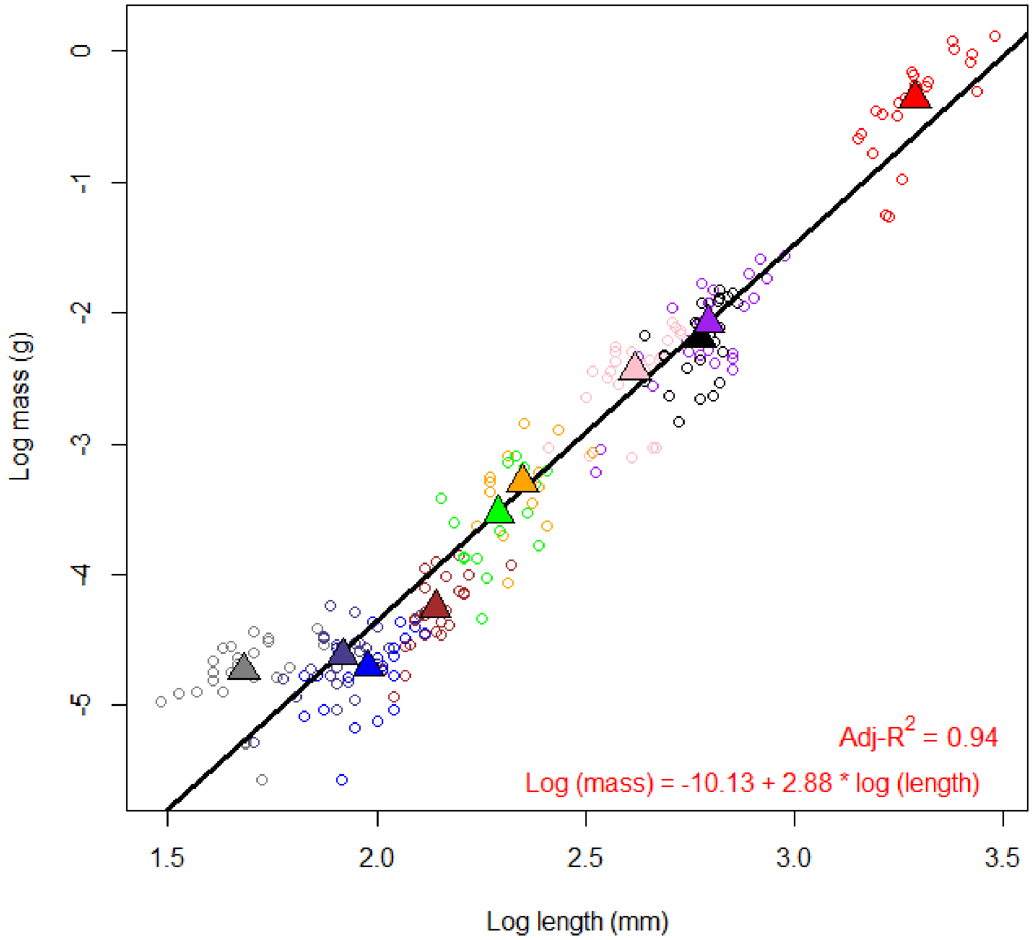

Figure 4.11. Regression of log length (mm) against log dry mass (g) for 10 beetle species. The different species are plotted in different colours, with means for each species plotted as large triangles. Regression line was fitted to individual data.

4.3.3 Robustness of sampling

The completeness of dung beetle sampling at each site was tested by examining species accumulation curves. Furthermore, species assemblages of some tropical insect taxa exhibit large temporal variation (e.g. Hamer et al. 2005) and because dung beetles in the main study were sampled in a single year I tested for potential inter-annual variation in dung beetle species assemblages. To do this, dung beetles were sampled in each of three years (2011, 2012 and 2013) at a sub-set of three sites (sites 1, 6 and 13) using human dung-baited pitfall traps spaced by 100-200 m along 0.5-1 km transects. In order to span the range of fragment sizes of sites used in

Chapters 5-7, the three sites chosen included two forest fragments (45 and 250 ha) and one unlogged continuous forest site. In all three years, the three sites were sampled during the drier months from April and August, to avoid potential intra-annual variation in climate. Rainfall records from site 1 showed that there were climatic differences between years, with 2011 (3899.7 mm yr^{-1}) being 22% wetter than 2012 (3188.2 mm yr^{-1}) and 17% wetter than 2013 (3332.6 mm yr^{-1}), which may have affected beetle assemblages although all three years were wetter than average for the site (2880.7 mm yr^{-1}).

Generalised Linear Mixed Models (GLMMs) were used to test for differences in species richness, abundance and biomass between years. The use of GLMMs accounted for unequal trap spacing and trap numbers across years by fitting site as a random effect. Significant differences in species richness, abundance or biomass across years were defined as when 95% confidence intervals of yearly richness, abundance or biomass values were non-overlapping. Large rollers and large tunnellers are key functional groups for seed dispersal and dung removal, and so I separately tested for differences in the biomass of these groups between years using GLMMs. Non-Metric multiDimensional Scaling (NMDS) and linear vector fitting were used to examine differences in beetle assemblage composition among years. NMDS was fitted using the Bray-Curtis similarity index which clusters sites closer together if they support more similar species assemblages. Linear vector fitting used 100 Monte Carlo permutations to test for significant differences in species assemblages between years.

For all sites, species accumulation curves were increasing only slightly at the end of sampling and for the majority of sites, species richness appeared to be reaching an asymptote (Figure 4.12). Curves were more asymptotic in the larger sites, and more individuals were collected from these sites. The relatively low rates of species accumulation observed across sites suggest that curves would have been unlikely to intersect with further sampling and that two days of sampling was sufficient to compare dung beetle assemblages across sites.

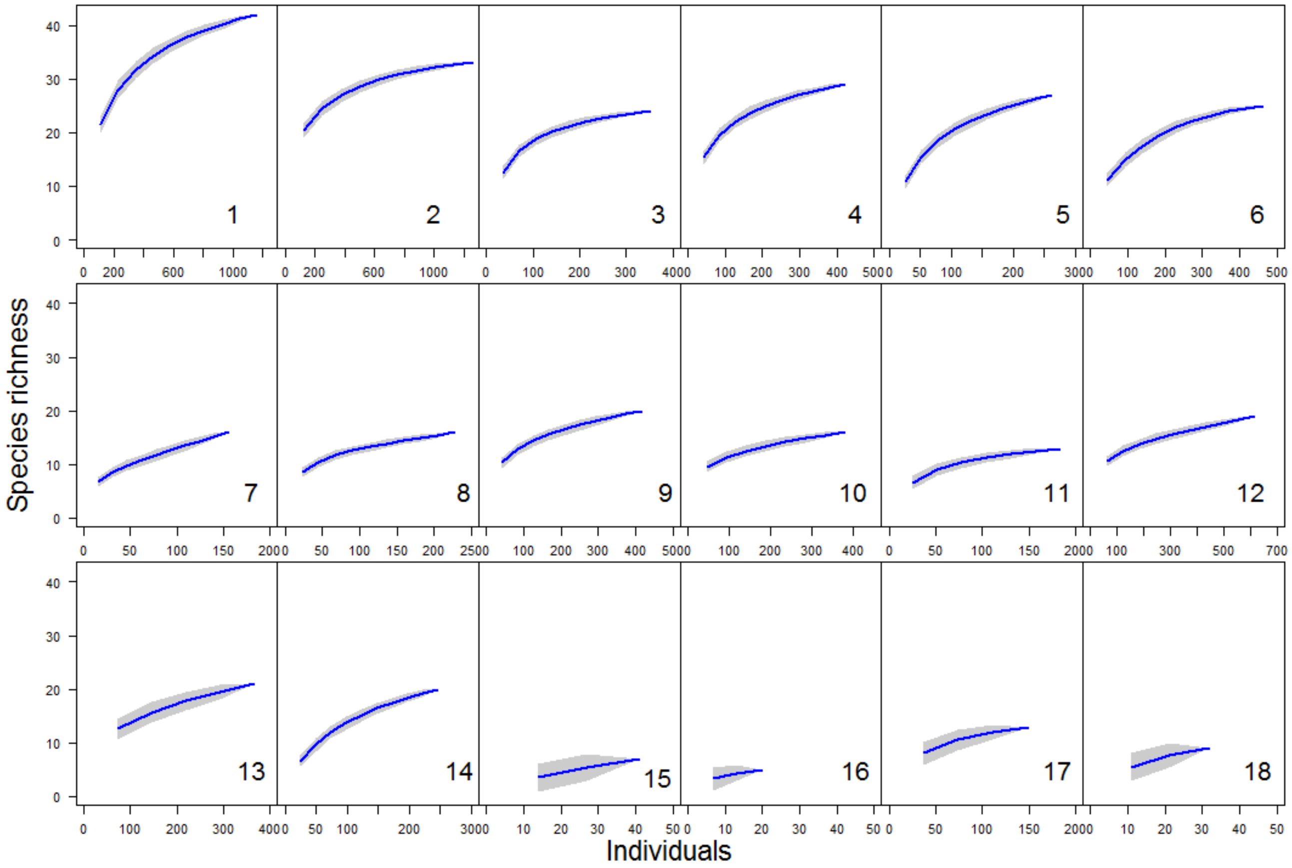

Figure 4.12. Species accumulation curves for all 18 study sites. Species are plotted against the number of individuals sampled. The y-axes for all plots are on the same scale but x-axes are on different scales representing large differences in beetle abundance among sites. Blue lines represent recorded species richness and grey shading show 95% confidence intervals.

Analyses of inter-annual variation revealed no significant differences in species richness, abundance, biomass, large roller biomass, or large tunneller biomass across the 3 years (Figure 4.13; GLMM output: 95% CIs for all variables overlapping across years). Vector fitting also revealed little difference in species assemblages across the 3 years (Figure 4.14; Goodness of fit: $R^2 = 0.0297$, $p = 0.92$). Overall, variation in dung beetle assemblages among sites was consistently greater than variation among years, showing little evidence for inter-annual variation in dung beetle assemblages. This was despite rainfall being ~20% higher in 2011 than in the other years. There was some variation in roller and tunneller biomass between years, but this was exceeded by differences in biomass between the three sites (Figure 4.13). For example, site 6 had consistently lower biomass than either site 1 or 13, perhaps as a result of low mammal abundance and limited dung resources in this fragment. There may be temporal variation in dung beetle assemblages between wet and dry seasons, as observed for butterflies in Sabah (Hamer et al. 2005), but I avoided this possibility by collecting the data for Chapters 5-7 in the drier months from March to September. Thus I conclude that comparing data sets collected in different years in this study is likely to be robust.

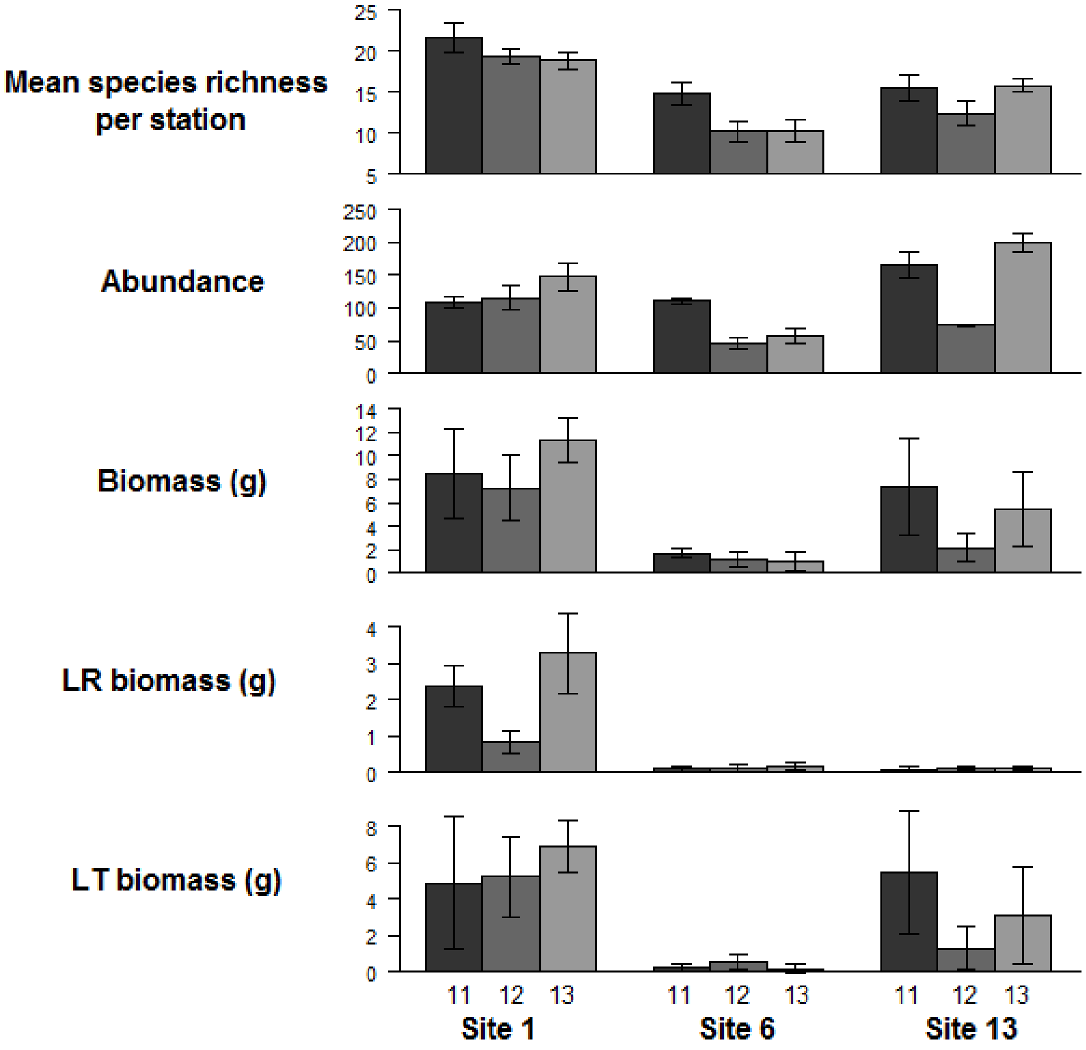

Figure 4.13. Barplots comparing species richness, abundance, total biomass, roller biomass and large tunneller biomass in three years (2011-2013) at three sites (1 (unlogged continuous forest), 6 (250 ha) and 13 (45 ha)). Values shown are means per sampling station and standard deviations. Darker to lighter fill bars represent samples from 2011 to 2013.

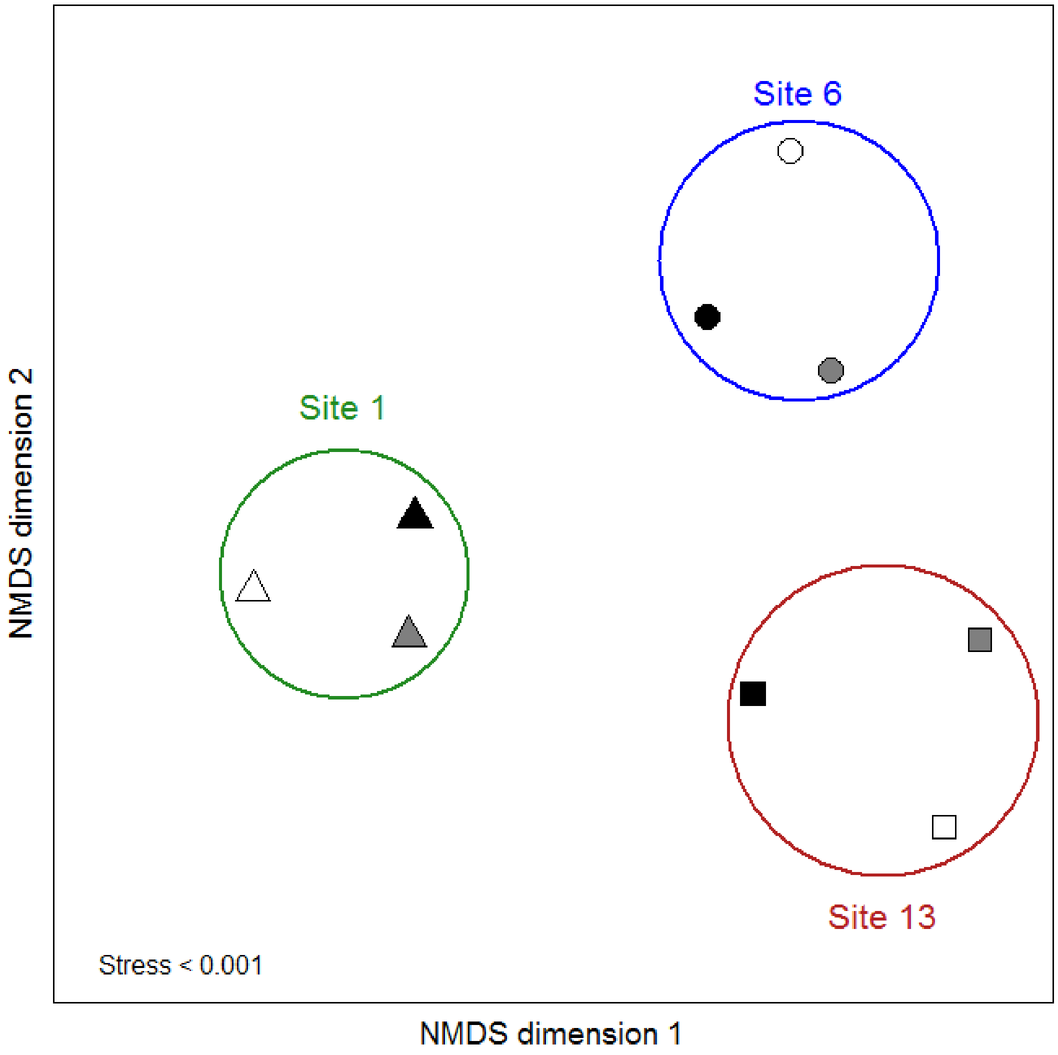

Figure 4.14. NMDS plot (Bray-Curtis method) comparing species assemblages across three years in sites 1 (triangles in the green circle), 6 (circles in the blue circle) and 13 (squares in the red circle). Each data point represents a site in a given year and points that are closer together support more similar species assemblages. Samples from 2011 have black fill, from 2012 have grey fill and from 2013 have white fill. In this analysis, the stress value for the NMDS ordination was approaching zero, indicating a very reliable configuration of sites and no effect of year (Zuur et al. 2007).

4.3.4 Comparing bait types in assessment of dung beetle assemblages

At all 18 field sites, dung removal and secondary seed dispersal by dung beetles were measured between July and September 2013. These functions were measured at the same sampling stations at which dung beetles were sampled in 2012, to allow analyses comparing dung beetle assemblage composition with rates of ecosystem function (Chapter 7).

Dung beetle ecosystem functioning measurements were conducted using cattle dung for logistical reasons, because it was much easier to obtain in the larger quantities needed for these experiments (~7.5 kg dung needed per study site per day). Previous studies in Sabah have shown that cattle dung baits can attract similar dung beetle species assemblages to human dung baits (Slade et al. 2011; Gray et al. 2014), and I compared species assemblages sampled with human versus cattle dung-baited pitfall traps in unlogged, continuous forest (site 1; n= 10 traps per bait type). To avoid differences due to forest type, traps were placed at the same sampling stations that were 100 m apart along the same 1 km transect used in the main study. Samples with the cattle baits were collected a month before those with human baits to avoid interference and possible trapping out effects. All other aspects of trap design were the same for the two bait types (4.3.1; Figure 4.8), with ~20 g baits used for each bait type. Traps were left out for 48 hrs and emptied and re-baited daily. Species richness, abundance and biomass collected with the two bait types were compared using one-way ANOVA fitted as a linear model, with data analysed by station/trap. Separate one-way ANOVAs were also conducted for functionally important rollers and large tunnellers to compare abundance and biomass of these species sampled with human and cow dung baits. Species assemblages sampled with the two baits were compared using NMDS and vector fitting.

Cattle dung attracted 15% fewer species and 50% lower biomass of beetles (for both species richness and biomass: $t_{1,18} > 2.35$, $p < 0.05$), but a similar abundance to human dung (Figure 4.15; $t_{1,18} = -0.9$, $p = 0.38$). Species assemblages were significantly different between baits (Goodness of fit: R^2

$= 0.27$, $p < 0.01$), but functionally important large rollers and large tunnellers, were caught with equal abundance in both bait types (Figure 4.16). The biomass collected with the two baits did differ, primarily because cattle dung attracted fewer large tunneller species. However, these differences are likely to be less marked for functioning experiments where larger cattle dung piles are used, because previous studies have shown that larger cattle dung piles attract very similar species assemblages to human dung-baited pitfall traps (Gray et al. 2014). Furthermore, cattle and human dung both attracted all functionally important large tunneller and roller species, suggesting that functioning experiments will be comparable to species composition samples.

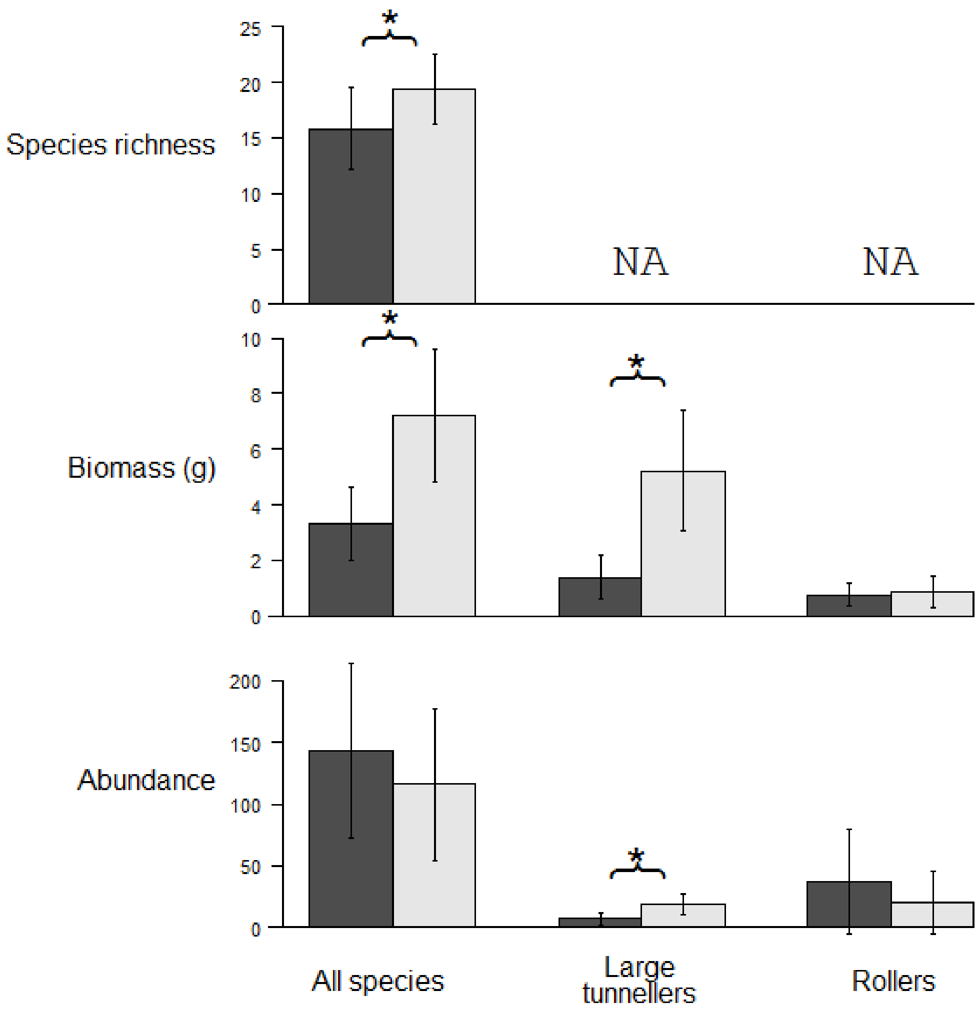

Figure 4.15. Barplots comparing species richness, biomass and abundance of dung beetles sampled with cattle (dark bars) and human dung (light bars). Values plotted are means per sampling station and error bars show standard deviation. Brackets and asterisks indicate significant differences between cow and human dung-baited samples, based on ANOVA fitted as linear models. Species richness of large tunnellers and rollers are not plotted (NA written instead) because there are very few species in these functional groups and all species were collected with both baits.

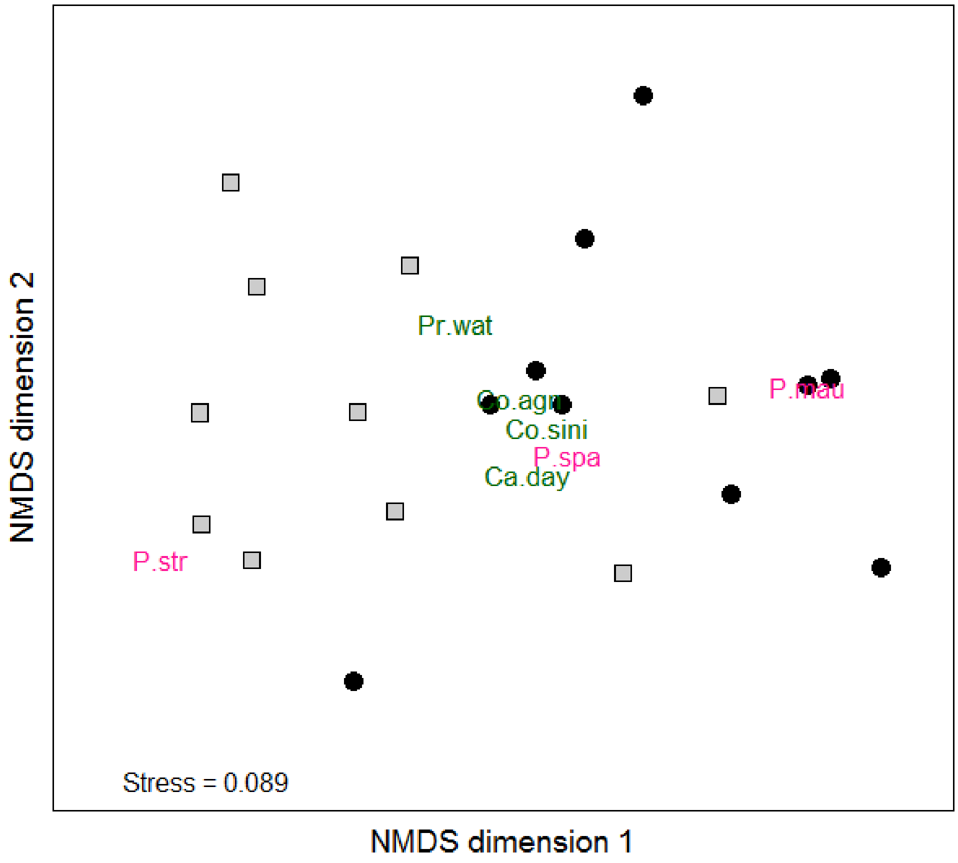

Figure 4.16. NMDS plot (Bray-Curtis method) comparing species assemblages sampled in unlogged continuous forest with cow dung (black circles) and human dung (grey squares). Each data point represents an individual site and points that are closer together support more similar species assemblages. This analysis included all species occurring at ≥2 sites as ≥2 individuals, but results were very similar when different abundance thresholds were used. The scores of key functional species have been plotted, with large tunnellers in green font and large rollers in pink font. Note that 5/7 key functional species are plotted in the middle of cattle and human dung samples suggesting they were equally abundant in the two baits. In this analysis, the stress value for the NMDS ordination was 0.089, indicating a very reliable configuration of points (Zuur et al. 2007).

4.3.5 Measuring ecosystem functions of dung beetles

4.3.5.i Dung removal

At all 18 study sites, dung removal was measured using 630g treatment piles of fresh cattle dung placed at each sampling station (3-10 piles per site, Figure 4.17). Two 630g evaporation control dung piles were also placed at the first two sampling stations at each site (Figure 4.18) to control for effects of evapotranspiration on dung wet mass. Dung piles of 630 g were used as this was the maximum amount of dung removed in 24 hours across six study sites during dung removal trials in 2012, and this size is broadly consistent with the size of dung piles produced by the study region's large herbivores, such as Banteng (*Bos javanicus lowi*). Fresh cattle dung was collected the night before sampling and stored overnight in an icebox. The evaporation control piles were enclosed within 1 mm wire mesh cage that excluded all beetles from accessing the dung, but allowed water loss by evaporation. Dung piles were placed on a raised mound of earth and covered with polystyrene plates (~15 cm above the dung) to protect them from rain. All treatment and control dung piles were collected after 24 hours and change in wet masses of treatment piles were estimated relative to control dung piles after 24 hours to account for mass changes due to water loss:

$$DR_i\ (\%) = \frac{100\ \times\ (treatment\ mass_i - mean\ control\ mass)}{mean\ control\ mass}$$

Equation 4.1. Equation for calculating the percentage of dung removed at each sampling station ($_i$). All mass values used are those after 24 hours. DR = dung removed.

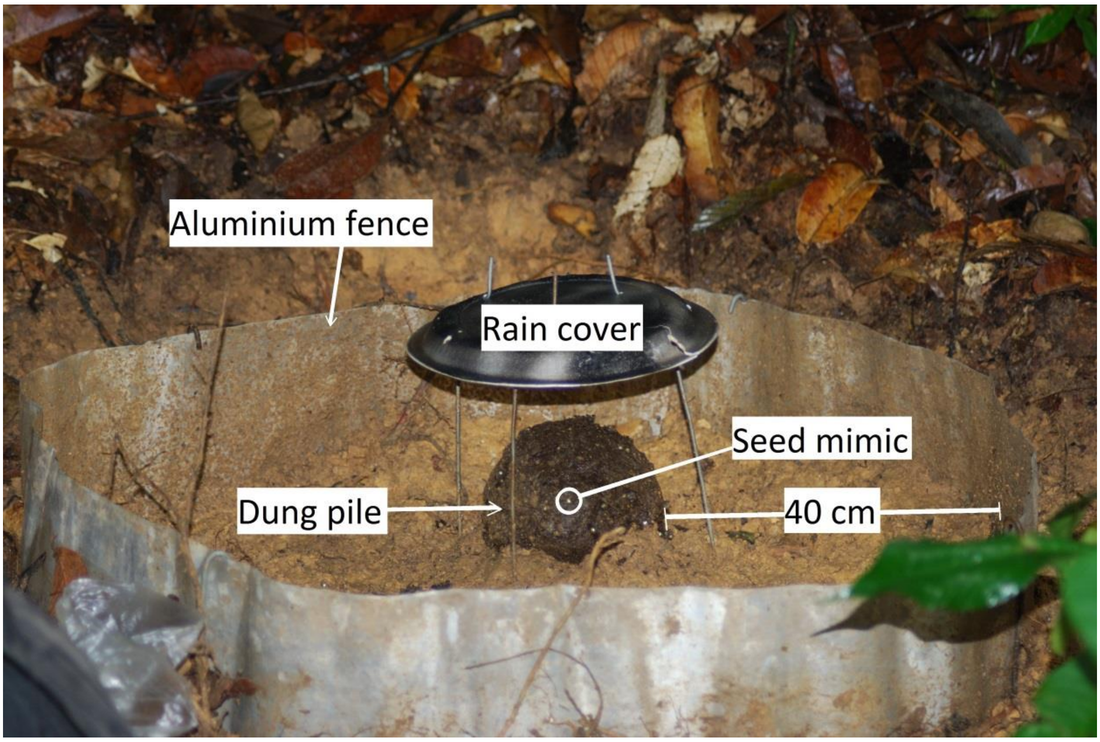

Figure 4.17. Example of a dung removal and seed dispersal replicate at the start of the experiment. The polystyrene plate above the dung pile protected the dung from rain. Dung pile contained 300 x 0.5 cm aluminium balls as seed mimics. The aluminium fence was 10cm high with another 5 cm buried into the soil to prevent rollers digging underneath. The fence formed a circle of 40 cm radius around the dung pile.

Figure 4.18. The evaporation control apparatus (2 per transect). The mesh was opened at the top to allow dung piles to be inserted and removed, and this opening was then sealed with fishing line during sampling. The mesh prevented access to the dung by beetles and so allowed estimates of dung mass loss due to evaporation. The apparatus was covered with a polystyrene plate to protect against rain and left in the field during the experiments.

4.3.5.ii Secondary seed dispersal

Secondary seed dispersal was measured at the same time and stations as dung removal. This was done by placing 300 aluminium beads (0.5 cm diameter) inside each treatment dung pile as seed mimics. Beads were mixed thoroughly into the dung to ensure an even distribution. Beads of 0.5 cm diameter were chosen as seed mimics because this was the minimum size detectable by a handheld metal detector (Garrett Pro-pointer P/N 1166000), and because seeds of this size are consumed and excreted by a range of frugivorous mammals (primary dispersers) in the region (Corlett 1998). After 24 hours, I then counted the number of beads that: 1) remained unburied on the soil surface or in dung on the soil surface, 2) had been dispersed horizontally by roller dung beetles, and 3) were buried in the soil by tunneller dung beetles (Figure 4.19):

1) Unburied beads were defined as any beads still in the dung pile or that were visible on the soil surface. Beads in the dung were recovered by wet sieving the dung after weighing, and beads on the soil surface were located by eye and using a handheld metal detector.

2) Horizontally dispersed beads were defined as those moved to the circular fence of sheet aluminium (radius 40 cm, height 10 cm) placed around each treatment dung pile (Figure 4.19). These beads were recovered by eye and with the assistance of a handheld metal detector. To prevent rolled beads being lost, the fence was buried into the soil to a depth of 5 cm and secured with metal pegs to prevent beetles from digging underneath. A radius of 40 cm was chosen as the optimal distance for detecting beads moved by large roller species, but excluding beads buried by tunnellers. Separate trials with no aluminium fence showed that large roller species rolled their dung balls on average 1.35 m (SD: 0.45, minimum = 0.55 m, n = 17), indicating that rollers would abandon their dung balls at the fence. This confirmed that all beads moved by rollers should be left at the aluminium fence. The action of large tunneller species, especially when they are highly abundant, can result in dung being scattered from its initial dung pile but separate trials at the site with highest abundance of large tunnellers showed that tunnellers never moved dung more than 30 cm from the dung pile on flat ground. Hence, the placement of the aluminium fence allowed beads moved by rollers and by tunnellers to be distinguished. To prevent beads from accidentally rolling or being moved downhill by tunnellers the soil within the aluminium fence was levelled. Trials revealed that tunneller species sometimes stole and buried roller dung balls abandoned next to the fence, and so to account for this I dug down to the

bottom of any burial tunnels near the fence to recover any beads. These were counted as horizontally dispersed beads, because they would have been buried by rollers in the absence of the aluminium fence.

3) Beads buried by tunnellers were defined as those remaining after the unburied and rolled beads had been recovered, which by a process of elimination had to have been buried.

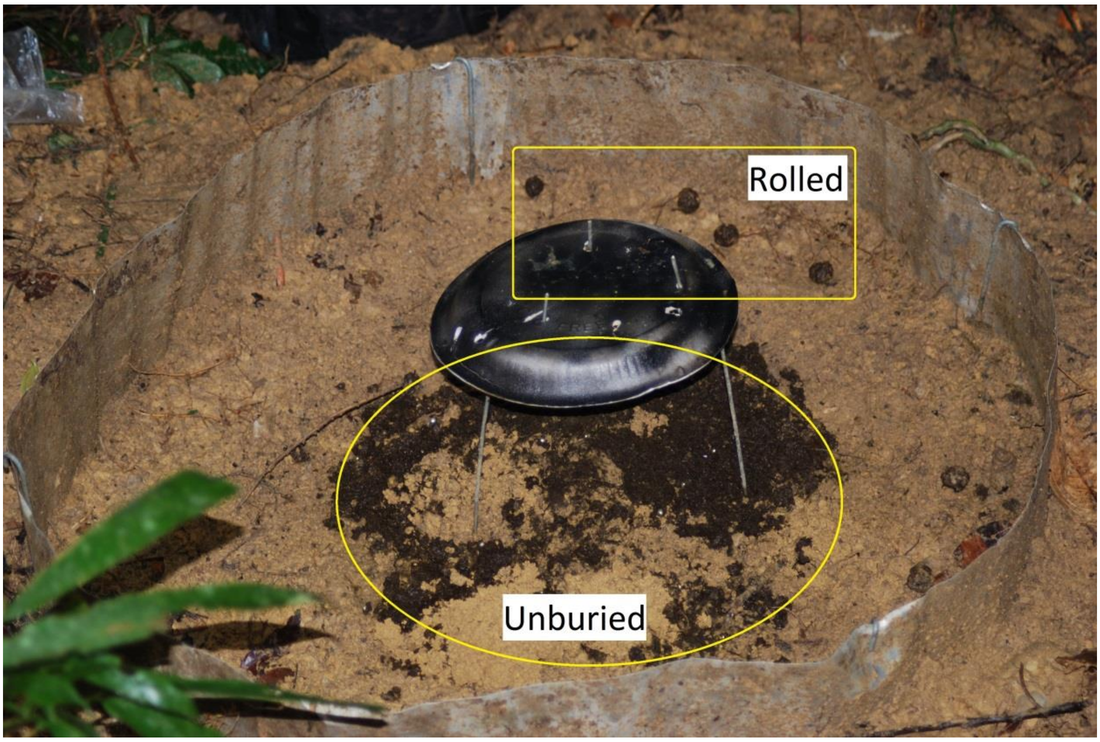

Figure 4.19. Example of dung removal from a dung pile after 24 hours, with rolled and unburied dung highlighted. Some unburied aluminium beads can be seen.

4.3.5.iii Experimental exclusion of Catharsius species

Across all 18 study sites, the large tunneller genus *Catharsius spp*. made up a large proportion of total dung beetle biomass (Figure 4.20). The two species in this genus are the largest dung beetle species at the study site with body length averaging 27 mm (Figure 4.21). This varied across sites from about 50% of biomass in continuous forest sites to 0 - 95% of biomass in fragment sites (Figure 4.20). This dominance of *Catharsius spp*. is supported by Slade et al (2007), and suggests that these species are likely to be extremely important for dung removal.

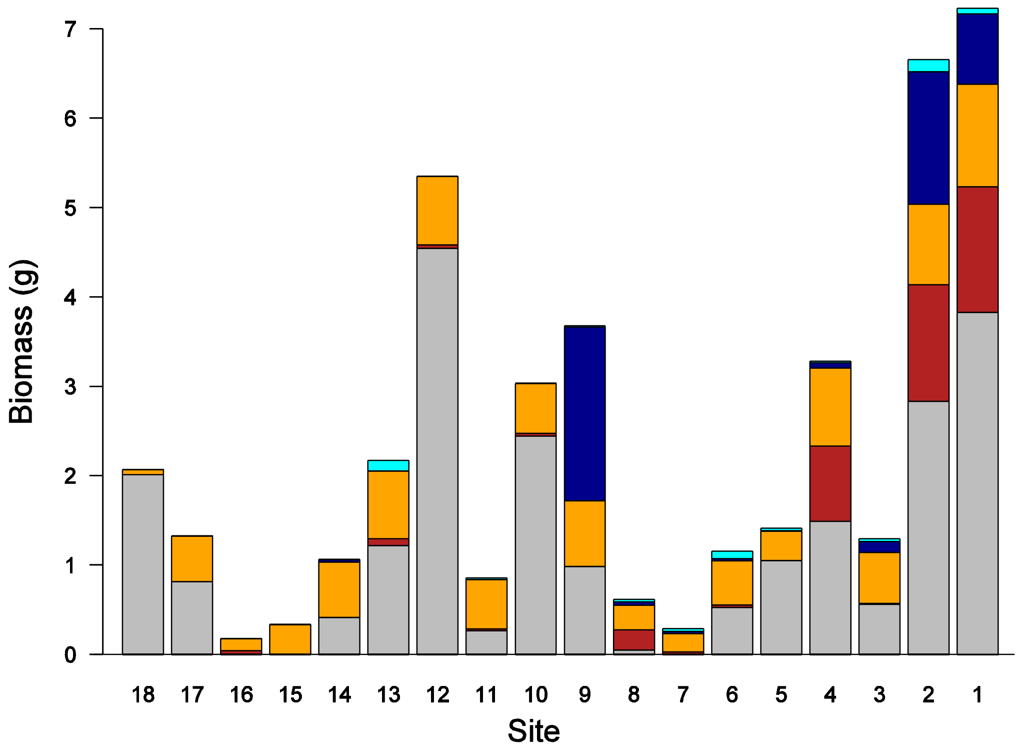

Figure 4.20. Barplot showing the proportion of total dung beetle biomass made up by Catharsius spp *(grey), other large tunnellers (maroon), small tunnellers (orange), large rollers (dark blue) and small rollers (light blue) across study sites. Error bars are not plotted for ease of interpretation.*

Figure 4.21. Picture of a Catharsius dayacus *male. Body length of this individual is ~27 mm.*

To assess the importance of *Catharsius* spp. for dung removal in Chapter 7, additional dung removal experiments were set up but with *Catharsius* spp. excluded. The experimental protocol was identical to that outlined in section 4.3.5, except that a 60 x 60 cm square of wire mesh (1.2 cm mesh size) was placed under treatment dung piles (Figure 4.22). Trials showed that this size of mesh allowed all species, except those in the *Catharsius* genus, to access the dung pile and bury (other tunnellers) or roll (rollers) dung. As with the main dung removal experiment, polystyrene plates were used to protect the dung from rainfall, evaporation controls were used, and dung piles were collected after 24 hours (Figure 4.23).

Figure 4.22. Example of Catharsius *spp. exclusion experiment, showing the wire mesh underneath the dung pile.*

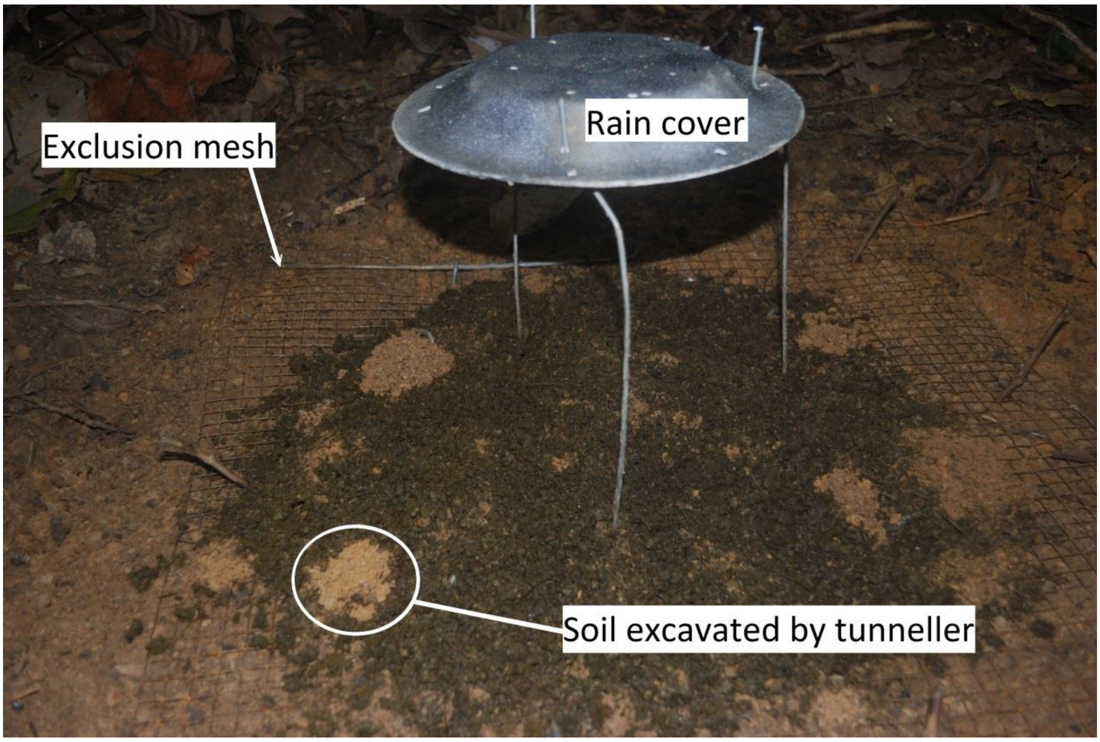

Figure 4.23. Example of a Catharsius *spp. exclusion replicate after 24 hours in the forest showing that some dung was removed by non-Catharsius spp. The aluminium fence was not used for this experiment which focussed on dung removal, not seed dispersal and burial.*

4.3.6 Vegetation structure and microclimate measurements

Vegetation structure and microhabitat can influence dung beetle faunal composition (Davis et al. 1998; Feer 2008; Slade et al. 2011) and so vegetation variables were recorded within a circle of 30 m radius, centred on each sampling station and divided into four quadrants based on the cardinal compass bearings (modified from Hamer et al. 2003).

In each quadrant I measured 10 variables (Table 4.2). I measured the girth (to nearest cm), point of inversion (POI; by eye to nearest metre), and identity (Dipterocarpaceae or not) of the two closest trees (≥60 cm gbh) and the girth of the two closest saplings (10-60 cm gbh) in each quadrant. The total number of saplings (within 10m radius of the sampling station) and trees (within 30m radius of the sampling station) in each quadrant were counted to estimate tree and sapling density. Leaf litter depth (to nearest 0.5 cm) was measured at each station using a ruler, based on the mean of 10 readings (on random compass bearings) at one (n=5) and two (n=5) metres from the sampling station. Percentage ground cover (by eye to nearest 5%) and canopy cover (both by spectral densiometer (henceforth called 'vegetation cover') and by eye (henceforth called 'canopy cover') to nearest 5%) were estimated for an area of 10 m radius around each sampling station. Canopy and ground cover estimates were based on the mean of four readings on the cardinal compass bearings. Canopy cover was estimated by eye and provided a different measure to densiometer readings which recorded all vegetation cover above the recorder, from all forest strata, whereas estimates by eye are specific to the canopy level. Estimates by eye of POI, canopy cover, and ground cover were taken by the same recorder to avoid recorder biases. Means per sampling station were then taken for each of these 10 vegetation variables.

Air temperature and soil moisture (as a proxy for humidity) were recorded at each sampling station because abiotic variables can influence dung beetle activity (Landin 1968). Soil moisture was used as a proxy for relative air humidity, because transpiration and evapotranspiration rates drive relative humidity and are correlated with soil water availability (Richards 1996). Furthermore, relative humidity varies depending on the time of day, whilst soil moisture shows less daily variation (e.g. Roxy et al. 2010). A HOBO® Pendant Temperature Data Logger data logger (Onset Computer Corporation) was fastened to a sapling at approximately 1m height and out of direct sunlight at each sampling station. Data loggers recorded temperature every 30 minutes during the 48 hour sampling period. Soil moisture was recorded at each sampling station at the start of the sampling period using an HH2 Moisture Meter (Delta-T Devices Ltd). Soil moisture measures were taken at 15 cm soil depth to exclude the influence of recent rain in surface soil and to estimate overall site humidity. Soil moisture was the mean of five measurements: one at the sampling station and four (on random compass bearings) at 1 m from the sampling station.

Table 4.2. Summary of mean vegetation measurements across sites. Mean values averaged across sampling stations are presented. Tree and sapling density are stems per hectare. Column headings with grey shading show variables used to quantify forest quality in Principal Components Analysis. Abbreviations as follows: GBH = girth at breast height, mV = millivolts, Prop. = proportion and Veg. = vegetation.

Site	Leaf litter depth (cm)	Veg. cover (%)	Canopy cover (%)	Ground cover (%)	Tree GBH (cm)	POI (m)	Tree density	Prop. of Dipterocarps	Sapling GBH (cm)	Sapling density	Temp. (^{O}C)	Soil moisture (mV)
1	2.4	92.2	59.3	55.4	123.6	13.4	110.4	0.3	21.7	1241.4	25.1	747.6
2	1.3	93.3	62.1	28.9	104.0	12.3	109.3	0.2	17.9	1279.6	24.6	633.3
3	1.8	90.4	35.8	37.0	109.6	10.0	87.0	0.4	15.5	1098.2	25.2	508.1
4	2.1	92.8	64.1	29.1	106.2	10.3	72.5	0.4	18.1	1276.4	24.9	766.8
5	1.5	91.5	49.4	51.3	97.1	10.3	93.7	0.4	14.8	751.8	25.0	536.8
6	1.0	94.1	30.3	27.4	78.2	7.3	54.1	0.1	14.7	604.7	26.0	618.8
7	1.0	95.4	29.4	27.6	78.4	7.3	53.1	0.2	15.0	1196.9	26.6	734.2
8	1.5	88.3	4.1	47.6	81.9	6.5	61.2	0.0	21.2	738.5	26.4	492.7
9	1.8	92.9	59.9	31.8	132.5	12.4	119.9	0.3	19.4	1687.0	25.7	523.6
10	0.6	86.0	17.2	32.8	121.5	8.3	37.1	0.1	18.2	923.1	25.6	576.9
11	1.5	88.9	45.5	38.8	91.6	8.3	193.0	0.0	19.0	1828.0	26.0	519.5
12	0.5	84.3	51.6	47.4	70.9	4.6	79.9	0.0	16.4	811.7	27.2	563.8
13	1.4	91.3	42.5	48.0	89.6	11.7	66.5	0.4	15.3	1126.8	25.7	516.0
14	2.8	94.3	65.1	39.4	95.0	10.4	87.7	0.4	14.5	853.1	26.7	388.7
15	2.1	90.8	44.6	33.3	87.1	7.7	143.8	0.0	16.5	1114.1	25.9	473.5
16	2.0	91.9	24.6	48.3	110.3	10.2	82.5	0.2	17.8	1135.3	25.1	422.8
17	0.6	91.6	0.0	42.2	71.1	4.0	20.3	0.0	16.0	827.6	26.5	458.6
18	0.5	94.1	0.0	21.7	76.1	3.8	23.6	0.0	23.5	1082.3	26.3	665.1

4.3.6.i Quantifying forest quality

To quantify forest quality at each of the study sites the 10 non-independent vegetation variables outlined above were combined into a single independent measure of forest quality for each sampling station. This was done using a Principal Components Analysis (PCA), to combine non-independent vegetation variables into an independent factor (Principal Component) representing forest quality. Examination of a correlation matrix showed that most of the variables were at least weakly correlated (Figure 4.24) and so all of the vegetation variables were incorporated into the PCA. Environmental variables (temperature and soil moisture; Table 4.2) were not included in the PCA, however, these data are used to inform discussion and are plotted in relation to forest quality in Figure 4.4. To ensure normality and homogeneity of error of vegetation variables prior to carrying out the PCA, they were transformed as follows: square root (leaf litter depth, tree density, and sapling density), logged (ground cover, POI, and sapling GBH), double logged (tree GBH), arcsine transformed (canopy cover, and proportion of Dipterocarps), and logit transformed (vegetation cover). As the variables were measured on different scales the PCA was conducted on the correlation matrix of standardised variables (mean = 0, SD = 1) (Kenkel 2006).

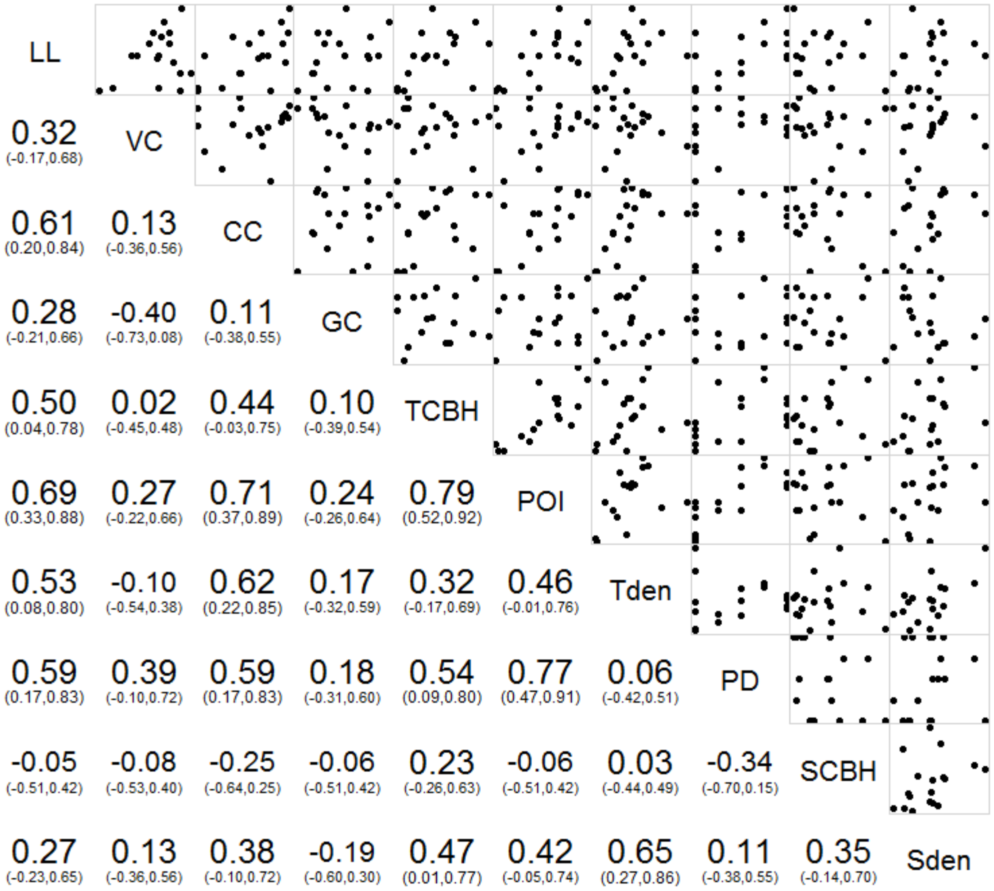

Figure 4.24. Correlation matrix of all vegetation variables included in the Principal Components Analysis. Top right panels show scatter plots and bottom left give Pearson's correlation coefficients and 95% confidence intervals. LL = leaf litter, VC = vegetation cover, CC = canopy cover, GC - ground cover, TCBH = tree girth, POI = point of inversion, Tden = tree density, PD = proportion of Dipterocarps, SCBH = sapling girth and Sden = sapling density.

The first principal component (PC) of the analysis explained 33% of variation in the data set and was characterised by a high density of large, tall Dipterocarps, a high canopy cover and deep leaf litter (Table 4.3). This PC score was therefore used as an index of forest quality because these attributes are associated with undisturbed forest (Figure 4.25). Sensitivity analyses of the PCA excluding each of the 10 vegetation variables in turn produced similar principal component scores for each site, and did not qualitatively change the final results, suggesting that differences in forest quality between sites were robustly captured by the PCA and that individual vegetation variables were not biasing the PCA.

Table 4.3. Contribution of the 10 vegetation variables to all principal components with eigenvalues >1. Only PC1 was used as a measure of quality and so the largest loadings for this are printed in bold. Larger loadings (+ or -) indicate a larger contribution to the first principal component.

		PC1	**PC2**	**PC3**	**PC4**
Eigenvalue		1.35	1.14	1.06	1.00
Variable	**Leaf litter**	**0.37**	0.04	0.22	-0.17
	Vegetation cover	0.07	-0.60	0.02	0.11
	Canopy cover	**0.39**	-0.10	-0.10	-0.30
	Ground cover	-0.03	0.46	0.31	-0.53
	Tree girth	**0.42**	0.26	0.02	0.34
	POI	**0.47**	0.07	0.17	0.20
	Tree density	**0.35**	0.01	-0.33	-0.48
	Proportion of Dipterocarps	**0.34**	-0.18	0.47	0.20
	Sapling girth	0.05	0.54	-0.30	0.42
	Sapling density	0.25	-0.12	-0.63	0.00

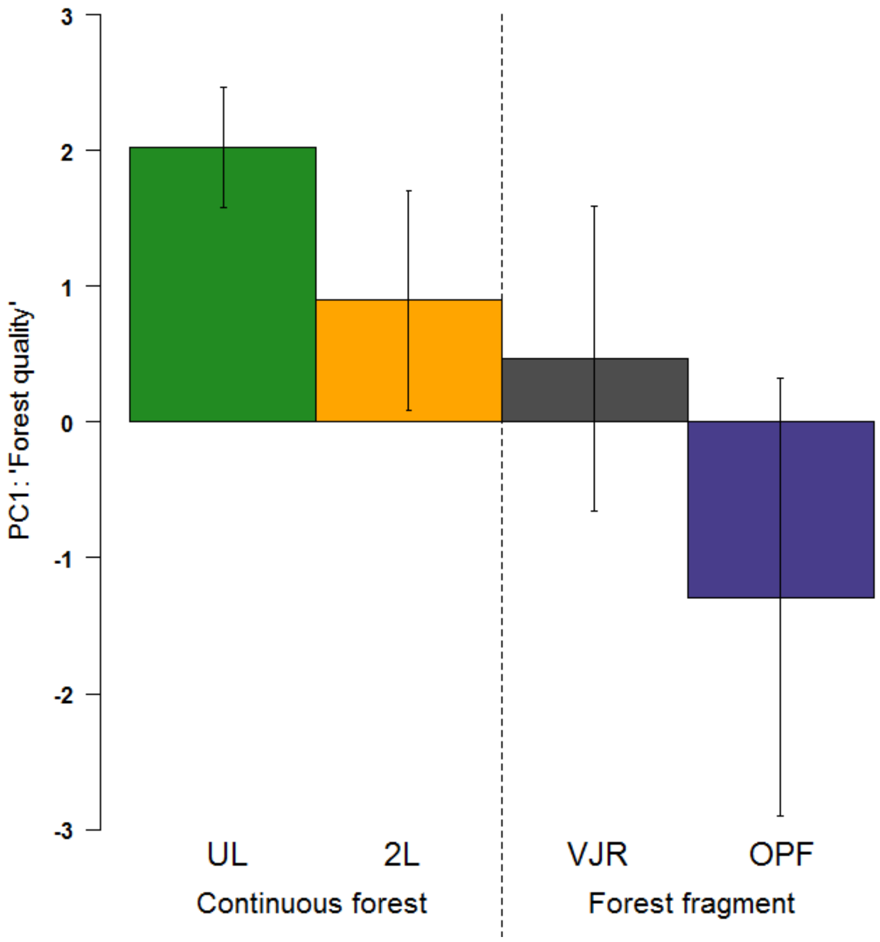

Figure 4.25. Barplot comparing mean forest quality (PC1) scores in unlogged continuous forest sites (UL), twice-logged continuous forest sites (2L), VJR fragment sites and plantation fragment sites (OPF). Values shown are mean and standard deviations. Dotted line separate continuous and fragmented sites

4.4 Statistical Analyses

4.4.1 Calculating site characteristics

Chapters 5, 6 and 7 assess differences in dung beetle assemblages and ecosystem functions between continuous forest and fragments and among fragments in relation to fragment size, forest quality and isolation distance. The forest fragment sizes were taken from Sabah Forestry Department (Sabah Forestry Department 2005) and PPB Group Berhad (Wilmar International) statistics. Isolation distances were defined as the straight-line distance from the edge of the fragment to the boundary of the nearest tract of continuous forest (non-mangrove forest >10,000 ha). Forest quality was defined as outlined above (section 4.3.6.i).

4.4.2 Measures of species richness

In Chapters 5-7 raw species richness per station is used to measure dung beetle species diversity at sites. To ensure that raw species richness represented the diversity of species assemblages at each study site, I compared species richness results to those of two other commonly used diversity indices, Simpson’s 1/D and Fisher’s alpha. Comparison of these measures revealed that all indices were highly positively correlated (Figure 4.26), suggesting that raw species richness is a robust and unbiased measure of diversity. Simpson’s 1/D and Fisher’s alpha also gave qualitatively similar results to species richness in subsequent analyses. Therefore, raw species richness was used in preference to the two other indices, as it was the simplest and most interpretable measure of species diversity, representing the number of species recorded.

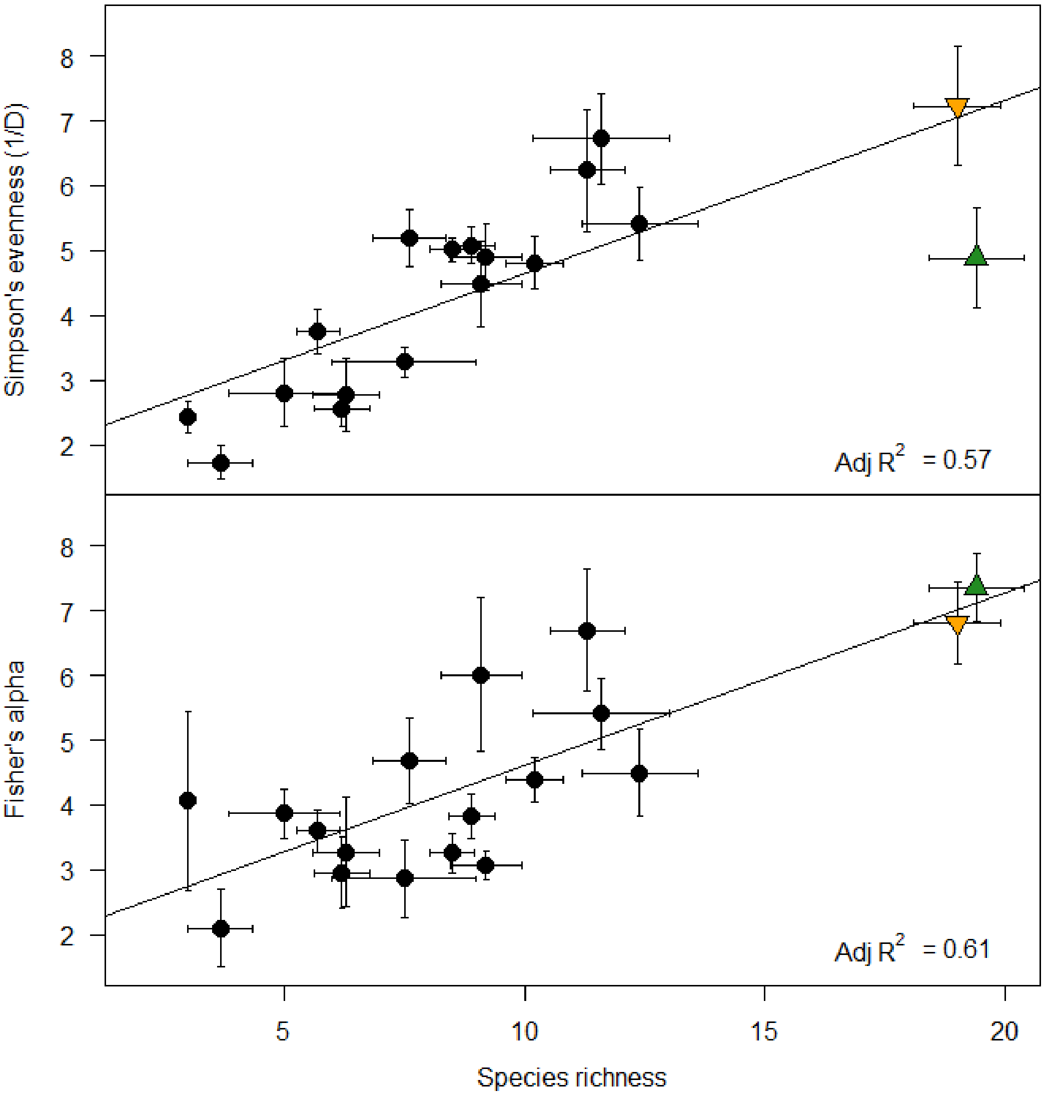

Figure 4.26. Scatterplots comparing species richness to Simpson's evenness and Fisher's alpha at the site level. Best lines are plotted for both highly significant relationships based on linear regression (for both regressions, $t_{1,14} > 4.9$, $p < 0.001$). Green triangles represent unlogged continuous forest, orange triangles twice-logged continuous forest and circles forest fragments.

4.4.3 Information theory and linear mixed models

In this thesis, analyses examining the effects of fragmentation on dung beetles and their functions are carried out primarily using an information theoretic approach, rather than a traditional frequentist (null hypothesis testing) approach (Burnham & Anderson 2002). The frequentist approach uses single models to test hypotheses against a 95% probability threshold.

Conversely, information theory ranks a series of models, using an information criterion such as Akaike's Information Criterion (AIC), to give a weighted quantitative assessment of various competing hypotheses. Information theory does not use p-values for model inference (Grueber et al. 2011). The information theoretic approach incorporates uncertainty from multiple models, as opposed to just one as is typical of the frequentist approach, and so allows better estimation of model parameters and their uncertainty (Burnham & Anderson 2002; Grueber et al. 2011). Throughout this thesis, AIC_c is used to rank models and the best models are defined as those within 2 AIC_c values of the best model with the lowest AIC_c value (Burnham & Anderson 2002). In cases where model ranking identifies more than one 'best' model, then parameter estimates and uncertainty are extracted by averaging across the 'best models'. AIC assesses the goodness of model fit while adjusting for the number of model parameters and AIC_c is a variant of AIC that accounts for biases due to small sample size (Bolker et al. 2009). Following model ranking using AIC, model inferences were made using parameter estimates and 95% confidence intervals based on the best models (Burnham & Anderson 2002; Bolker et al. 2009). Confidence intervals (CIs) can be broadly used to assess the importance of a parameter. For example, important continuous variables are those whose 95% CIs do not overlap zero, and for categorical variables when the CIs of factor levels are non-overlapping.

In Chapters 5-7 I applied the information theoretic approach with generalised linear mixed models. Linear mixed models (LMMs) allow researchers to account for unbalanced sampling designs and for non-independent replicates. LMMs use pseudo Generalised-Least Squares methods for parameter estimation and so provide less biased estimates than linear models for unbalanced data (Bolker et al. 2009). Generalised linear mixed models (GLMMs) are an extension of LMMs that can include non-normal data distributions (Bolker et al. 2009). Ecological datasets are commonly non-normal, as was the case in this thesis. For example, count data are typically Poisson distributed or overdispersed and other data, such as percentage dung removal, are proportional. Traditional linear models deal with non-normality by transforming data, or by using non-parametric statistics. However, non-parametric analyses and transformations are not suitable for all data distributions and often ignore random effects (Bolker et al. 2009). GLMMs can incorporate random effects and use link functions and diverse error distributions, so addressing both of the problems described above. GLMMs are used in this thesis because sampling stations at a site may not be strictly independent of one another, but data from all stations can be used in GLMMs to inform model fit without pseudoreplication. Throughout Chapters 5-7 GLMMs were fitted with study site as a random effect, to account for the unbalanced number of sampling stations per site. Thus analyses were effectively conducted at the site level but using variation among sampling stations to inform model fitting.

Chapter 5 - The response of dung beetle assemblages to forest fragmentation: effects of fragment area, forest quality and isolation

5.1 Abstract

Expansion of crops is a major driver of tropical deforestation and initiatives such as the Roundtable on Sustainable Palm Oil (RSPO) have been developed to mitigate environmental impacts. RSPO certified companies are expected to reduce biodiversity losses by maintaining High Conservation Value (HCV) forest areas within their concessions. I assessed how the size, forest quality and isolation of these forest fragments affected biodiversity by collecting data on dung beetle assemblages from 16 forest fragments and two continuous forest ‘control’ sites in eastern Sabah (Malaysian Borneo). Dung beetle species richness, abundance and assemblage composition were very similar in pristine and twice-logged continuous forest, but forest fragments (5 ha – 3,529 ha) supported over 50% fewer species and individuals than did continuous forest sites. Among fragments, fragment area had the greatest impact on dung beetle species richness, but differences in species turnover between sites were best explained by differences in forest quality. Overall abundance and biomass of dung beetles varied little among fragments, but the abundance and biomass of rollers (a group important for secondary seed dispersal) declined with fragment area and large rollers were absent from the smallest fragments. The abundance and biomass of large (>10 mm) tunnellers, the group most important for dung burial, was not affected by fragment area or forest quality, but decreased slightly with isolation. Avoiding the conversion of continuous forest to fragments is key to reducing biodiversity losses. However, following fragmentation, maximising the size of HCV areas will support more species and maintain populations of functionally important large rollers and large tunnellers. Improving forest quality in smaller HCV areas could allow these sites to support similar species assemblages to continuous forest.

5.2 Introduction

Across the tropics, agricultural expansion is a major cause of deforestation (Kissinger et al. 2012). This deforestation and concurrent biodiversity losses have led to negative publicity for tropical agricultural commodities, such as palm oil (*Elaeis guineensis Jacq.*). In response to this, initiatives such as the Roundtable on Sustainable Palm Oil (RSPO) and the Roundtable on Responsible Soy have been developed to mitigate the environmental and social impacts of agricultural expansion. In the case of oil palm agriculture, the RSPO uses the High Conservation Value (HCV) approach to reduce biodiversity losses associated with oil palm expansion. Plantations established before 2005 and seeking RSPO-certification are required to identify, maintain, and enhance areas of HCV habitat within their concessions, and new oil palm concessions seeking certification cannot convert HCV forest (RSPO 2013).

Recent research has questioned the use of the HCV approach for biodiversity conservation in oil palm plantations (Edwards et al. 2010, 2012) suggesting that HCV areas tend to be small forest fragments supporting low species richness and abundances. Significantly though, this criticism focussed on small (<100 ha in size), logged forest patches in plantations established before 2005 and the patches that were studied were not originally identified as HCV areas. The requirement for new oil palm plantings is that HCV areas are identified in concessions before the land is cleared for planting, and these areas should be as large as is necessary to maintain any identified HCVs (Chapter 2, Brown et al. 2013). However, HCV assessors are in need of guidance to help them identify HCV areas and to develop appropriate management plans (Chapter 2, Meijaard & Sheil 2012), and so there is an urgent need to measure biodiversity and ecosystem functioning in fragments and to examine the importance of fragment size and forest quality. There is also a need to move beyond measures of species richness and abundance, to assessing the maintenance of key ecosystem functions, such as decomposition and seed dispersal (Reiss et al. 2009) in HCV areas. These functions underpin the functioning of the entire ecosystem by maintaining abiotic conditions and biotic processes necessary for species persistence (Millennium Ecosystem Assessment 2005; Hooper et al. 2012). Given that oil palm agriculture is continuing to expand (Butler et al. 2009; Laurance et al. 2010), it is vital to assess the effectiveness of HCV areas for maintaining both biodiversity and ecosystem functioning within oil palm landscapes.

HCV assessments for new oil palm concessions identify HCV areas to be protected from conversion and maintained over time. However, concessions often replace continuous, albeit highly degraded, forest and so these HCVs are identified in continuous forest, but then typically protected as isolated HCV areas within the concession area. The fragmentation literature can provide insight into the value of these fragments for conservation. Fragmentation can affect biodiversity through habitat loss and the breaking apart of habitat, such as changes in the isolation, size and shape of habitat patches (Fahrig 2003). Habitat loss causes species extinctions, as explained by the theory of island biogeography (MacArthur & Wilson 1967), and the independent impacts of the breaking apart of habitat (henceforth ‘fragmentation’) are also becoming clearer. For example, fragmentation causes invasion of non-native species, increased edge effects and increased prevalence of hunting, fires and logging (Turner 1996; Laurance et al. 2013). These pressures mean that equivalent areas of continuous and fragmented forest support very different species assemblages, irrespective of the size and distribution of the fragmented forest (e.g. Nichols et al. 2007). These effects of fragmentation are also key arguments in favour of a ‘land sparing’ approach to conservation, which focuses on protecting larger, pristine natural habitats separately to areas of intensive agriculture, in place of the ‘land sharing’ approach that integrates conservation and agriculture in the same landscape using wildlife-friendly farming (Phalan et al. 2011). Therefore, comparing biodiversity in continuous and fragmented forest is crucial to assessing whether identified HCVs can be maintained in forest fragments, and also to identify the attributes of forest fragments that will best protect biodiversity values found in continuous forest.

Based on evidence from island biogeography and metapopulation dynamics, the effectiveness of HCV areas for biodiversity conservation is likely to depend on their size, isolation from other forest habitat, and the quality of forest they comprise. Species richness and abundance tend to be positively correlated with fragment size, and weakly negatively correlated with fragment isolation across a variety of taxa (e.g. Laurance et al. 2002; Watling & Donnelly 2006; Benedick et al. 2006; Nichols et al. 2007; Edwards et al. 2010). Furthermore, forest fragments are prone to changes in vegetation structure through disturbance, such as logging, increased human encroachment, and edge effects; these changes can alter species richness, abundances and composition through the loss of interior forest specialists, or increases in disturbance-tolerant species (Laurance et al. 2002; Ewers et al. 2007). Independent of fragmentation, changes in forest quality following logging have also been shown to reduce species richness and abundance (Edwards et al. 2011b). Despite these impacts, forest quality is considered in fragmentation studies far less frequently than area or isolation (Nichols et al. 2007), perhaps because of the challenges of separating the confounding impacts of these variables on biodiversity (Ewers & Didham 2006). Nonetheless, comparison of fragment area, isolation and forest quality within the same study could provide greater insight into the effects of fragmentation on biodiversity.

Additionally to the effects of fragmentation, logging is also a widespread threat to biodiversity, especially in the timber-rich forests of Southeast Asia (Edwards et al. 2011b). Logging can reduce forest quality by changing vegetation structure, altering microclimates and reducing habitat heterogeneity, which can in turn influence species richness, abundance and assemblage composition (Hamer et al. 2003). For example, microhabitats such as forest gaps are more common in logged forest and some species of dung beetle and butterfly are associated with particular microhabitats, such as forest gaps or riverine vegetation (Davis et al. 1998; Hamer et al. 2003). Previous research in Southeast Asia has revealed that species richness and abundance decline after two, but not one, logging rotations, but one logging rotation is enough to cause significant changes in species composition (Hamer et al. 2003; Benedick et al. 2006; Edwards et al.

2011b; Woodcock et al. 2011). However, in Southeast Asia the impacts of logging and fragmentation on biodiversity have not been considered together in the same study. Doing this will allow the relative impacts of logging and fragmentation on different aspects of diversity to be compared.

Changes in the composition of species assemblages is a less-studied aspect of diversity in fragmentation studies, but may be crucial for determining effects of fragmentation on ecosystem functioning and species of conservation concern (Tilman et al. 1997). In pristine habitats, protecting sites that maximise beta diversity by protecting the most complementary set of species may enable more efficient use of limited conservation resources (Margules & Pressey 2000). However, most ecosystems are subject to disturbances, such as logging and fragmentation, which may drive species extinctions, and so conservation often focusses on supporting species assemblages most similar to those in pristine ecosystems (Holloway et al. 1992; Dent & Wright 2009). Logging and fragmentation cause distinct changes in forest quality, fragment area or isolation, that can have differing impacts on species assemblages. For example, reduced forest quality and altered microclimate in response to logging adversely affects forest specialists (Edwards et al. 2013), declining fragment area negatively affects species with larger ranges, and increased fragment isolation negatively impacts dispersal-limited species (Hill et al. 2011). Therefore, assessing turnover in species assemblages in response to changes in forest quality, area and isolation can help to identify extinction mechanisms, and also to evaluate whether the size, quality or isolation of HCV areas has the greatest impact on species assemblages. Similarity indices are widely used to assess spatial turnover in species assemblages and identify sites of conservation value (Su et al. 2004), and when coupled with gradient analysis, can be used to relate turnover in species assemblages to environmental gradients, such as forest quality, fragment area and isolation (R. H. Jongman, C. J. F. ter Braak 1995). Such analyses can also be used to assess how changes in species assemblages following logging and fragmentation affect ecosystem functioning.

Within a taxon, species' traits can be defined as functional effect traits (henceforth termed 'functional traits') which group species together based on their shared effects on certain ecosystem functions, and/or as 'response traits' that group species together based on shared responses to disturbances (Lavorel & Garnier 2002). If a functional trait is not a response trait then this suggests that the ecosystem function performed by species with that trait will be robust to disturbance. However, if species have traits that are both functional and response traits then assessing species' responses to disturbance can be used to predict changes in functioning in response to disturbance (Larsen et al. 2005b). Dung beetles have crucial roles in ecosystem functions such as nutrient cycling, and seed dispersal, and exhibit large trait variation in relation to their dung processing behaviour and body size (Chapter 1 and 4, Nichols et al. 2008). Both dung processing behaviour and body size are functional traits for dung beetles, with large tunnellers being especially important for dung burial and hence nutrient cycling (Larsen et al. 2005b; Slade et al. 2007b; Dangles et al. 2012), and large rollers for horizontal secondary seed dispersal (henceforth 'secondary seed dispersal') (Andresen & Feer 2005). Therefore, assessing whether dung beetle functional group type and body size are response traits to logging and fragmentation will help predict changes in nutrient cycling and seed dispersal.

There is currently no evidence that dung beetle functional group is a key response trait to fragmentation (Larsen et al. 2008), but dung beetle size is an important response trait, with larger species being particularly vulnerable to extinction in fragments (Larsen et al. 2005b). Neither functional group nor body size are important response traits to logging or declining forest quality (Slade et al. 2011; Edwards et al. 2013). Thus in this study, rollers and tunnellers might be expected to show similar responses to fragmentation, but large species of dung beetles would be expected to show greater declines compared with small species.

I sampled dung beetles in Sabah, Malaysia from 16 forest fragments, and twice-logged and pristine continuous forest. In addition to their functional importance, dung beetles are also useful ecological indicators of mammalian assemblages and forest quality because of their reliance on dung resources and habitat specialisation (Davis et al. 2001; Spector 2006; Nichols et al. 2009). This habitat specificity and their reliance on spatially and temporally patchy resources (Feer & Hingrat 2005) also makes them an excellent focal taxon for studying extinction dynamics. This chapter compares dung beetle diversity in pristine and twice-logged continuous forest sites (Hypothesis 1), in continuous forest sites and forest fragments (Hypothesis 2), and among forest fragments in relation to fragment area, forest quality and isolation (Hypothesis 3). I also compared turnover in species assemblages across all fragments and continuous forest sites (Hypothesis 4). These hypotheses are as follows:

Hypothesis 1. Dung beetle species richness, abundance and biomass are lower in twice-logged than pristine continuous forest. There is no difference in the response of species in relation to functional group or body size.

Hypothesis 2. Dung beetle species richness, abundance and biomass are lower in forest fragments than in continuous forest. Large-bodied species decline more than small species, whilst there is no difference in the response of rollers and tunnellers.

Hypothesis 3. In fragments, dung beetle species richness, abundance and biomass decline in relation to fragment area, forest quality and isolation. Larger species show greater declines than smaller species, but roller and tunneller species show similar responses.

Hypothesis 4. Species assemblages in continuous forest are significantly different from those in forest fragments, and among fragments are more similar in sites with similar area, forest quality and isolation.

5.3 Methods

5.3.1 Study sites

Dung beetles were sampled in two continuous forest ‘control’ sites and 16 forest fragments in eastern Sabah, Malaysia (5 °N, 117 °E, Chapter 4). All sampling took place during the ‘drier’ season between April and August 2012. The continuous forest sites were in undisturbed, primary forest (Danum Valley Conservation Area) and in twice-logged production forest (Ulu-Segama Malua Forest Reserve). Ulu-Segama Malua Forest Reserve was first logged between 1976 and 1991 (~120 m^3 ha^{-1} of timber removed), and then again between 2001 and 2007 (~35 m^3 ha^{-1} of timber removed) (Edwards et al. 2011b; Reynolds et al. 2011). The forest fragments varied in size from 5 to 3,529 ha, and varied in degree of isolation from the nearest continuous forest by 0.2 to 46.7 km. All fragments had been isolated within oil palm plantations for at least 15 years at the time of sampling. The fragments varied in their history of disturbance and forest management, with at least 11 of the fragments having been selectively logged prior to study (Chapter 4). Eight fragments were managed by the Sabah Forestry Department (38-3,529 ha, Sites 3-7, 9, 13-14) and eight fragments by PPB (Wilmar International) oil palm plantations (5-120 ha, Sites 8, 10, 12, 15-18). I quantified forest quality at each site by recording ground cover, canopy cover, vegetation cover (above 2m), leaf litter depth, tree density, girth, identity (Dipterocarpaceae or not) and point of inversion, sapling density and girth at each station (see Chapter 4 for more details). These non-independent variables were combined into independent measures of forest quality for each forest site using a Principal Components Analysis (PCA), and the first principal component was extracted as a measure of forest quality (Figure 5.1). This principal component explained 33% of variation in vegetation variables, revealed large differences in forest quality among sites (Figure 5.1), and was characterised by a high density of large, tall Dipterocarp trees, a high canopy cover and deep leaf litter (Chapter 4 Table 4.2). Fragment areas were taken from Sabah Forestry Department and PPB plantations statistics, and isolation distances calculated in ArcMap as the straight-line distance from the edge of the fragment to the boundary of the nearest tract of continuous forest (defined as non-mangrove forest >10,000 ha). Fragment area, isolation and forest quality were considered together in this study after correlation matrices revealed no significant relationships between the variables (Figure 5.2).

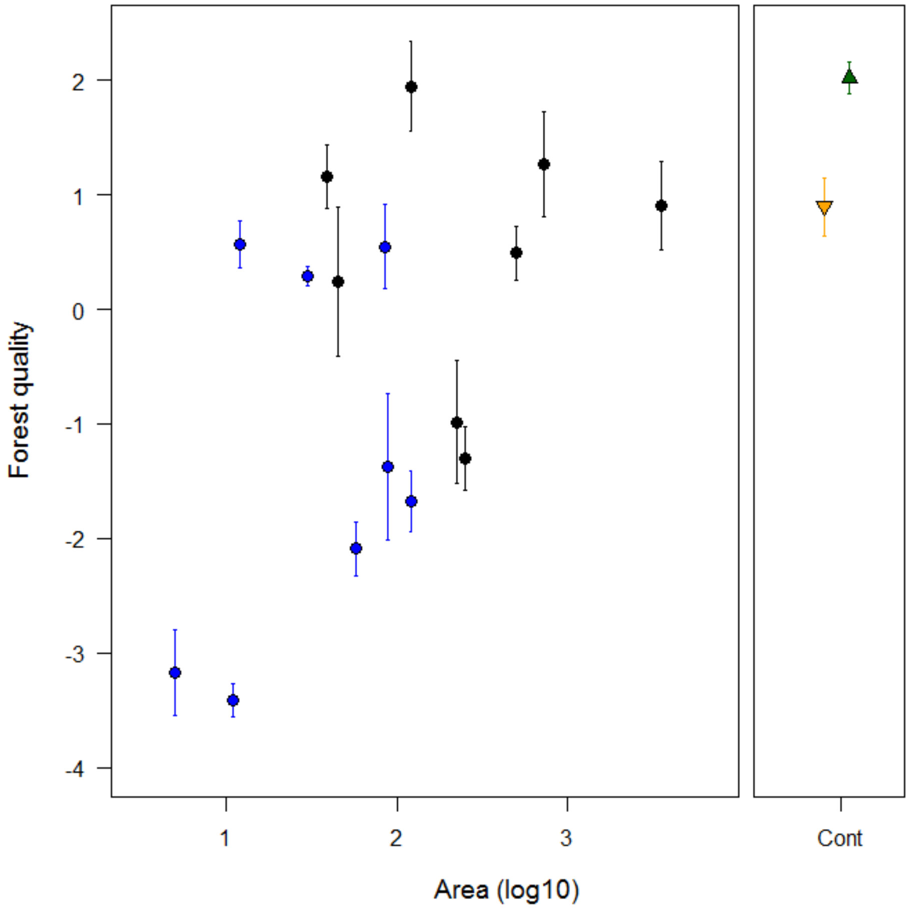

Figure 5.1. Plot of log10 area against forest quality (PC1 scores) with standard error. Green triangles are continuous forest sites, black circles are fragments managed by the Sabah Forestry Department, and blue circles are fragments managed by PPB oil palm plantations. There was no significant relationship between area and forest quality (Pearson's R = 0.47 (-0.03,0.78)).

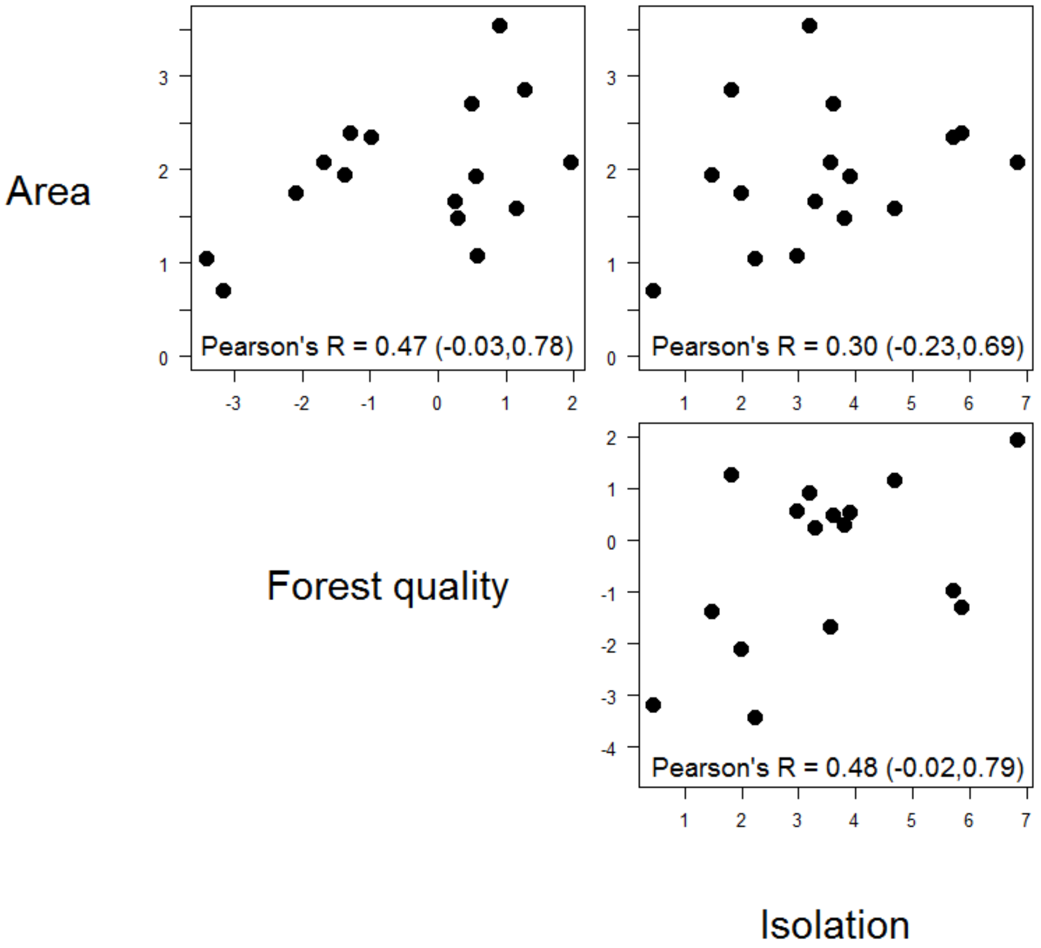

Figure 5.2. Correlation matrix comparing fragment area, forest quality and isolation for the 16 forest fragments. Area values are log10 transformed and isolation values square root transformed. Pearson's correlation coefficient (R) and 95% confidence intervals are shown.

5.3.2 Dung beetle sampling

At each site, dung beetles were sampled with pitfall traps at stations placed at 100 m intervals along transects 0.3-1 km in length (1 transect per site, 3-10 stations per transect depending on fragment size and shape, n = 143 stations in total: 123 in fragments, 20 in continuous forest sites). Trap spacing of 100 m has been shown to be sufficient to ensure independence of samples in tropical forests (Larsen & Forsyth 2005). Pitfall traps were placed at each station (1 per station), and baited with human dung. Pitfall traps were left out for 48 hours and were emptied and re-baited daily. Beetles were sorted and identified whilst in Sabah using an optical microscope. I identified species based on reference collections of Felicity Edwards (University of Leeds) and Trond Larsen (Conservation International), and species identifications were verified by Darren Mann (Oxford University Museum of Natural History). For more details on locations of study sites, sampling methods and species identification see Chapter 4.

5.3.3 Analysis

Following species identification, I calculated species richness, abundance and biomass (dry mass, g) of all species for each station at all sites (see Chapter 4 for details). Biomass was included in analyses as well as abundance as it is more directly related to rates of dung burial than is abundance (Doube 1990; Larsen et al. 2005b). Raw species richness was used as the measure of diversity after sensitivity analyses comparing this to Fisher's Alpha diversity, and Simpson's 1/D yielded qualitatively similar results (full comparison in Chapter 4). I separately calculated abundance and biomass of small rollers, small tunnellers, large rollers and large tunnellers, to assess how dung beetle functional group and body size affected responses to fragmentation. In Sabah, the dweller functional group comprises only a very small proportion of the community (<1% of all individuals collected in this study) and so was removed from subsequent analyses. I examined the effect of body size by splitting rollers and tunnellers into large and small species. In Sabah, there is only one genus of large rollers (*Paragymnopleurus*), comprising three species 13 - 17 mm in length, and two small roller genera (*Sisyphus* and *Ochicanthon*) 3.5 - 6 mm in length. These data were used to define large and small species as those larger or smaller than 10 mm in length. Furthermore, species smaller than 10 mm make only negligible contributions to dung removal (Slade et al. 2007b), and so this size threshold also separates beetles according to their functional importance.

5.3.3.i Differences in dung beetle diversity between twice-logged and pristine continuous forest (Hypothesis 1)

T-tests were used to compare dung beetle species richness, abundance and biomass in pristine and twice-logged continuous forest sites. Separate tests were also conducted for the abundance and biomass of small rollers, large rollers, small tunnellers and large tunnellers. Data from the 20 sampling stations (ten per habitat) were used as replicates in this analysis.

5.3.3.ii Differences in dung beetle diversity between continuous forest and fragments (Hypothesis 2)

I used Generalised Linear Mixed Models (GLMMs) to examine differences in species richness, abundance and biomass between continuous forest sites and forest fragments. Data from all 143 sampling stations across the two continuous forest sites (20 stations) and 16 fragments (123 stations) were analysed, with forest type (continuous or fragment) as a categorical fixed effect and site as a random effect, meaning that analyses were effectively conducted at the site level but using the variation between sampling stations to inform model fitting. Fitting site as a random effect accounted for the unbalanced number of sampling stations at each site and also prevented pseudoreplication. GLMMs use pseudo Generalised-Least Squares methods for parameter estimation and so provide less biased estimates than linear models for unbalanced data, they can also account for non-normal data distributions (Bolker et al. 2009).

Seven separate analyses (for seven response variables) were conducted to compare differences between continuous forest and forest fragments in total species richness, total abundance, total biomass, small roller biomass, large roller biomass, small tunneller biomass and large tunneller biomass. I also analysed differences in the abundance of the four functional groups between fragments and continuous forest, but for brevity these results are presented only in the Appendix (Appendix 3 tables A3.1-2). For each of the seven analyses, models containing ‘forest type’ were compared to models containing just the random effect of ‘site’ (‘null model’) using AIC_C values, to test whether differences between forest types exceeded those within sites and so assessing variation within sites. In each analysis, the model with the lowest AIC_c value was the best fitting. Means and 95% confidence intervals of the seven response variables were extracted for continuous forest and fragment sites. A significant difference between habitat types was assumed if confidence intervals of continuous forest sites and fragment sites did not overlap, and if the 'null model' had a higher AIC_c value than the model containing forest type.

Before carrying out analyses, parametric assumptions of data were tested and appropriate error distributions chosen to ensure assumptions were met (Table 5.1). I also tested for the influence of outliers by calculating Cook's distances, to identify individual points with large residuals and high leverage in the model. I removed data points with Cook's distance values greater than 4/N (i.e. 4/143 = 0.026) (Bollen & Jackman 1990), and so for analyses of large roller abundance and biomass models 11 data points were removed from analyses (all ten stations from one outlying site and one outlying station from a different site). To assess the overall goodness-of-fit of models I also calculated marginal (fixed effects only) and conditional (fixed and random effects) R^2 values for each model (sensu Nakagawa & Schielzeth 2013). It is not currently possible to calculate R^2 values for models with negative-binomial distributions and so R^2 values are not presented for these models. The conditional R^2 value quantified variation within sites, relative to the variation explained by forest type. GLMMs were fitted with R package "lme4" using the function '(g)lmer'.

Table 5.1. List of response variables analysed, along with the data distribution family, and transformation of the response variable used in analyses. The abundance of each of the four functional groups was also analysed, and is presented in Appendix 3 (Tables A3.1,2,5).

Response variable	Distribution family (and link)	Transformation
Species richness	Poisson (log)	None
Abundance	Negative-binomial (log)	None
Biomass	Gaussian (identity)	Log10
Small roller biomass	Poisson (log)	Log10
Large roller biomass	Poisson (log)	Log10
Small tunneller biomass	Poisson (log)	None
Large tunneller biomass	Poisson (log)	None

5.3.3.iii Effects of fragment area, forest quality, and isolation on dung beetle diversity (Hypothesis 3)

GLMMs were also used to examine differences in species richness, abundance and biomass among fragments in relation to fragment area, forest quality and isolation. Continuous forest sites were excluded from these analyses because they cannot be given area or isolation values. Data from all 123 sampling stations across the 16 forest fragment sites were analysed. Fragment area, forest quality and isolation were fitted as fixed effects and site was fitted as a random effect, meaning that analyses were effectively conducted at the site level but using the variation among sampling stations to inform model fitting. The same 11 outlying stations were removed and the same error distributions fitted as described in section 5.3.3.ii (Table 5.1).

Seven separate analyses (for seven response variables) were conducted to compare differences in total species richness, total abundance, total biomass, small roller biomass, large roller biomass, small tunneller biomass and large tunneller biomass among forest fragments. For each of these response variables, models were constructed with all possible combinations of fragment area, forest quality and isolation (explanatory variables) as well as two-way interactions and second-order polynomials (to test for curvilinear relationships and threshold effects). Three-way interactions were excluded from models to avoid over-fitting. A 'null model' was also included containing just the random effect of site, to test the overall goodness of fit of the models and to test whether differences among sites exceeded those within sites. For each of the response variables, all models were then ranked according to their AIC_c values to compare the relative importance of forest fragment area, forest quality and isolation. The best model was defined as that with the lowest AIC_c value, and the best model set as any models with AIC_c values within 2 units ($\Delta_i < 2$) of the best model (Bolker et al. 2009). Coefficients and 95% confidence intervals were then extracted from the single best model, or averaged across the set of best models. A significant relationship was assumed if 95% confidence intervals did not overlap zero. Conditional and marginal R^2 values were calculated.

5.3.3.iv Turnover of dung beetle species assemblages among sites (Hypothesis 4)

To examine differences in the turnover of species assemblages among all sites (continuous and fragment sites), I used Non-Metric multiDimensional Scaling (NMDS). Mixed model structures accounting for the unbalanced number of sample stations across sites are not possible in multivariate analyses and so NMDS analyses were carried out on mean species abundances per site (i.e. total number of individuals of the species at a site/number of stations at a site). This also reduced incidences of shared "double zero" species abundances between stations that complicate the interpretation of multivariate analysis output (Zuur et al. 2010). I conducted two analyses, one including data from all sites (n=18 sites) and one only with data from fragments (n=16 sites). NMDS was carried out using the Bray-Curtis dissimilarity index, after sensitivity analyses comparing this with Morisita Horn and Chao-Jaccard revealed no qualitative differences (see Appendix 3 Table A3.6). In NMDS, species scores at sites are calculated as weighted averages of their abundances at each site (Oksanen et al. 2007). These species scores can be plotted on NMDS plots allowing species associations with particular sites to be identified graphically. Linear vector fitting methods and significance tests based on 1000 Monte Carlo permutations were used to test for significant differences in species assemblages explained by fragment area, isolation and forest quality in the analysis of fragments, and differences explained by forest quality and forest type (continuous versus forest fragment) in the analysis of all sites. NMDS with vector fitting was chosen over constrained ordination analyses because it allows a range of similarity indices to be used and it is better able to handle species abundance data that are typically non-normally distributed (R. H. Jongman, C. J. F. ter Braak 1995; Zuur et al. 2007).

Species found only at a single site are of little use for comparing species assemblages across sites and so highly localised species sampled only at one site were removed from these analyses (Cao et al. 2001). Furthermore, to ensure that incompletely sampled rare species did not unduly influence these analyses, species were included only if two or more individuals were sampled at a site (n = 42/60 species (analysis of all sites), n = 35/60 species (analysis of fragments)). In order to test the sensitivity of results to this selection criterion, I also repeated analyses with more stringent selection criteria, by restricting analyses to only those species where five or more individuals were recorded at a site (n = 34/60 species (analysis of all sites), n = 24/60 species (analysis of fragments)), and to species with at least two individuals at ≥5 sites (n = 22/60 species for both analyses). However, there was no qualitative difference between these three analyses and so I only present results of the analysis using 42 (all sites) and 35 (fragments) species to maximise the sample size of species analysed (see Table A3.6 in Appendix 3).

Sites that are closer together geographically tend to have more similar species assemblages than those that are further apart, as a result of environmental filtering and dispersal limitation (Ramage et al. 2013). Therefore, the impacts of area, forest quality, and isolation could be masked by spatial autocorrelation and similarities in species assemblages that were present prior to fragmentation. Partial Mantel tests were used to assess whether differences in species assemblages explained by area, forest quality, and isolation were present after accounting for geographic proximity of sites. Partial Mantel tests extract residuals of any correlation between geographic Euclidean distance and species abundance matrices (including only those species with >2 individuals recorded at sites; n = 35/60 species). The residuals were then used to test for any remaining correlation between species abundances and matrices of area, forest quality and isolation differences between sites. Significance values of correlations between the different matrices were calculated based on 1000 permutation tests. Pearson's correlation coefficients were also calculated. The matrix of species assemblages was based on the Bray-Curtis dissimilarity index. Sensitivity analyses comparing this with Morisita Horn and Chao-Jaccard indices revealed qualitatively similar relationships (see Appendix 3, Table A3.6 for comparison). All of the above analyses on turnover in species assemblages were conducted in R using the package "vegan" (Oksanen et al. 2013).

5.4 Results

Across all 18 sites I collected a total of 6,706 individuals from 60 species in 288 trap days. Across all sites, the mean capture rate per trap day was 23.4 individuals (SD = 20.5), with small tunnellers making up 70% (n=48 species, mean length = 6.9 mm, SD = 2.6), small rollers 14% (n=4 species, mean length= 5.2 mm, SD= 1.06), large tunnellers 11% (n=5 species, mean length= 20.3 mm, SD= 5.4), and large rollers 6% (n=3 species, mean length= 16.2 mm, SD= 2.2) of all individuals. Dwellers made up <1% of all individuals collected and so were not considered in subsequent functional analyses (tables of raw data of species richness, abundance and biomass in Appendix 3, Table A3.3 & A3.4).

5.4.1 Differences in dung beetle diversity between twice-logged and pristine continuous forest (Hypothesis 1)

There was little difference in dung beetle diversity between pristine and twice-logged continuous forest sites. T-tests revealed no significant differences in species richness, abundance, total biomass, small tunneller biomass or large tunneller biomass between pristine and twice-logged continuous forest (t-test, $t < 1.31$, $df = 18$, $p > 0.26$). Large and small roller biomass were slightly higher in twice-logged continuous forest than pristine continuous forest, and t-tests revealed this difference to be close to significance (large rollers: t= 1.97, df = 18, p = 0.06, small rollers: t= 1.94, df = 18, p = 0.07). This similarity of pristine and twice-logged continuous forest sites is probably because the forest was of higher quality in the twice-logged continuous site than in the majority of fragments, despite two logging rotations (Figure 5.1). Overall, dung beetle diversity and species composition (Figure 5.8) were similar in pristine and twice-logged continuous forest, and so data from the two continuous forest sites were combined for subsequent analyses comparing continuous forest with forest fragments.

5.4.2 Differences in dung beetle diversity between continuous forest and forest fragments (Hypothesis 2)

Dung beetle species richness, abundance and biomass were significantly higher in continuous forest than in fragments (Table 5.2, Figure 5.3). Thus there were considerable impacts of fragmentation, and mean species richness, abundance and biomass was 250-500% higher in continuous forest than in fragments and over 30% higher than in the fragments with the highest biomass, abundance and species richness (Sites 13 and 11). Large roller and large tunneller biomass were also significantly higher in continuous forest than in fragments (700% and 300% higher respectively), although there was no significant difference in small roller and small tunneller biomass between continuous forest and fragments (Table 5.2, Figure 5.4).

Table 5.2. Table comparing means and 95% confidence intervals of species richness, abundance and biomass in continuous forest and fragments. Non-overlapping confidence intervals indicate a significant difference between means, and are indicated by an asterisk (*). The means and confidence intervals presented are back-transformed to their original scales.

Response variable	**Mean (and 95% CIs)**	
	Continuous forest	**Fragments**
Species richness*	19.1 (13.1,27.9)	7.8 (6.7,9.0)
Abundance*	119.1 (56.8,247.6)	28.8 (22.1,37.7)
Biomass*	6.5 (2.1,20.4)	1.0 (0.7,1.5)
Large roller biomass (g)*	0.8 (0.4,3.1)	0.1 (0.1,0.1)
Small roller biomass (g)	0.02 (0.005,0.6)	0.004 (0.003,0.007)
Large tunneller biomass (g)*	4.6 (1.3,16.4)	0.73 (0.4,1.2)
Small tunneller biomass (g)	1.0 (0.7,1.6)	0.5 (0.4,0.7)

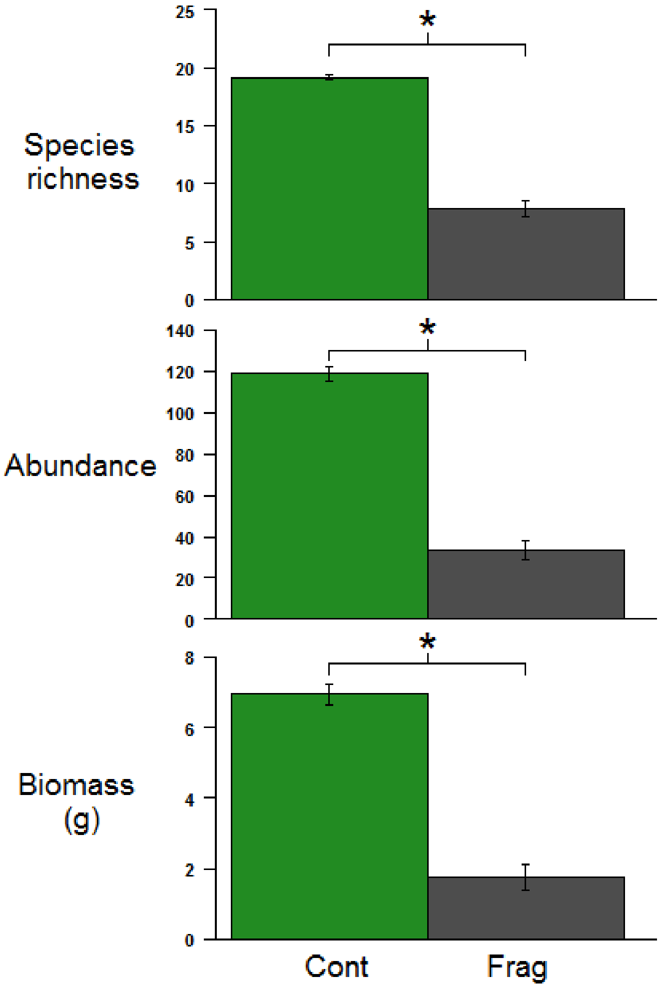

Figure 5.3. Mean species richness, abundance and biomass in continuous forest (n = 2 sites) and fragments (n =16 sites). To account for different numbers of stations sampled at each site, values plotted are mean values per site averaged across forest type with standard errors. Mean values for continuous forest were significantly higher for all variables according to GLMMs, as indicated by the asterisks (*). Cont = continuous forest and Frag = forest fragments. Error bars show standard error.

AIC_c values of GLMMs containing forest type were at least two points lower than models without forest type for all response variables analysed, except for small roller biomass (Appendix 3 table A3.1). Therefore, differences between continuous forest and fragment sites exceeded differences within sites for all variables, except for small roller biomass. For example, the mean within-site range in species richness was 6.4 species, versus the mean difference in species richness between continuous forest and fragments of 11.3 species, whereas for small roller biomass the mean within site range was 0.076 g, compared to the mean difference of 0.072 g between continuous forest and fragments. Therefore, with the exception of small roller biomass, differences between continuous forest and fragments were more important determinants of dung beetle diversity than within site variation (e.g. in resource availability, microhabitat or habitat heterogeneity).

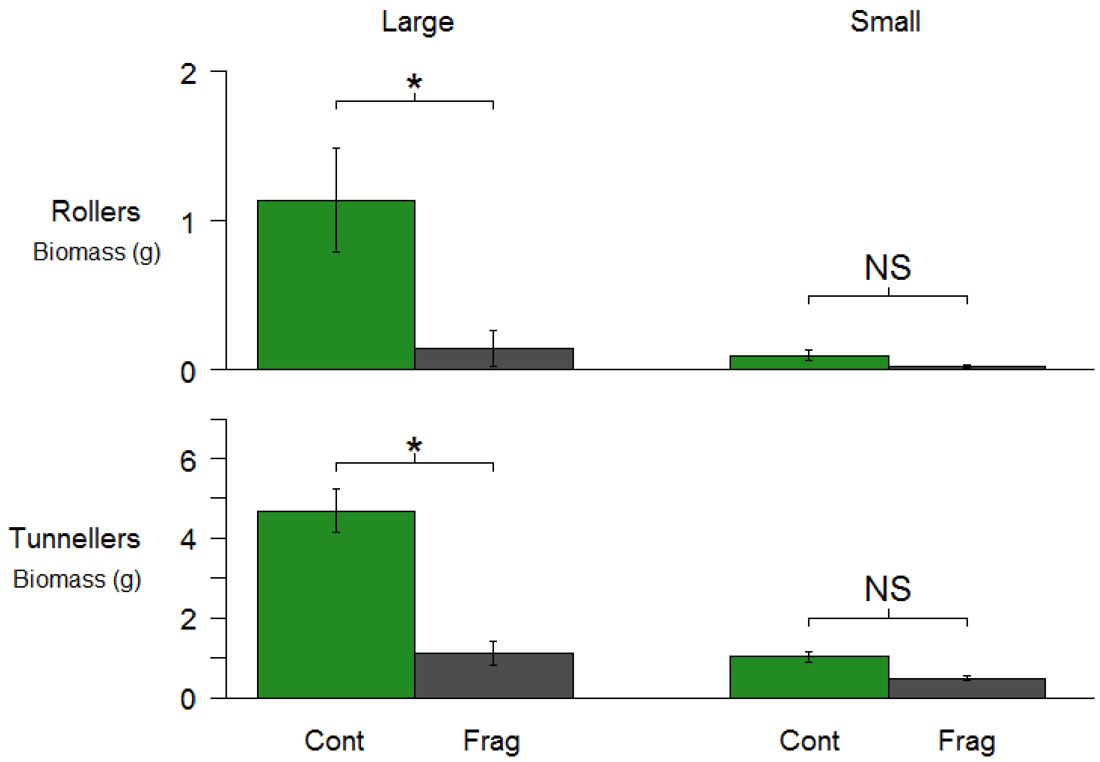

Figure 5.4. Comparisons of large (≥10 mm length) and small (<10 mm length), roller and tunneller biomass in continuous forest (n = 2 sites) and fragments (n =16 sites). To account for different numbers of stations sampled at each site, values plotted are mean values per site averaged across forest type, with standard errors. Mean values for continuous forest were significantly higher than those for forest fragments for large rollers and tunnellers, but not for small rollers and tunnellers according to GLMMs. Asterisks (*) indicate significant difference and "NS" no significant difference. Cont = continuous forest (green shading) and Frag = fragments (black shading). Note that y axes are scaled differently. The maximum number of species in each functional group was as follows: small rollers: n=4, small tunnellers: n=54, large rollers: n=3, large tunnellers: n=5.

5.4.3 Effects of fragment area, forest quality, and isolation on dung beetle diversity (Hypotheses 3)

Overall, the decline in dung beetle abundance and biomass following fragmentation far exceeded any subsequent effects of declining fragment area, forest quality or isolation among fragments. Dung beetle abundance and biomass were about 70% lower in fragments (mean abundance per station = 33 individuals, mean biomass = 1.8 g) than in continuous forest (mean abundance per station = 119 individuals, mean biomass = 6.9 g), but there was no further decline as fragment size decreased (Figure 5.5). Species richness declined following fragmentation, but also decreased significantly with decreasing forest area (Figure 5.5; slope estimate= 0.31, 95% CIs 0.12, 0.50). Species richness in the largest fragment was about 40% lower (11 species per station) than in continuous forest (mean = 19 species per station), and on average one species was lost for every 500 ha reduction in fragment area. Neither species richness, abundance nor biomass were significantly affected by changes in isolation of fragments, and only biomass was significantly related to forest quality, with a significant positive quadratic relationship (slope estimate= 2.40, 95% CIs 0.24, 4.55). Plots revealed that dung beetle biomass was highest in fragments with the worst and best forest quality, but lower in fragments of intermediate forest quality. However, this relationship only became significant in models containing fragment area, where variation due to area was already accounted for (Figure 5.5). Total biomass varied little in response to changing fragment area, quality and isolation, but separate analyses of the biomass of the four functional groups revealed differing responses to fragment area.

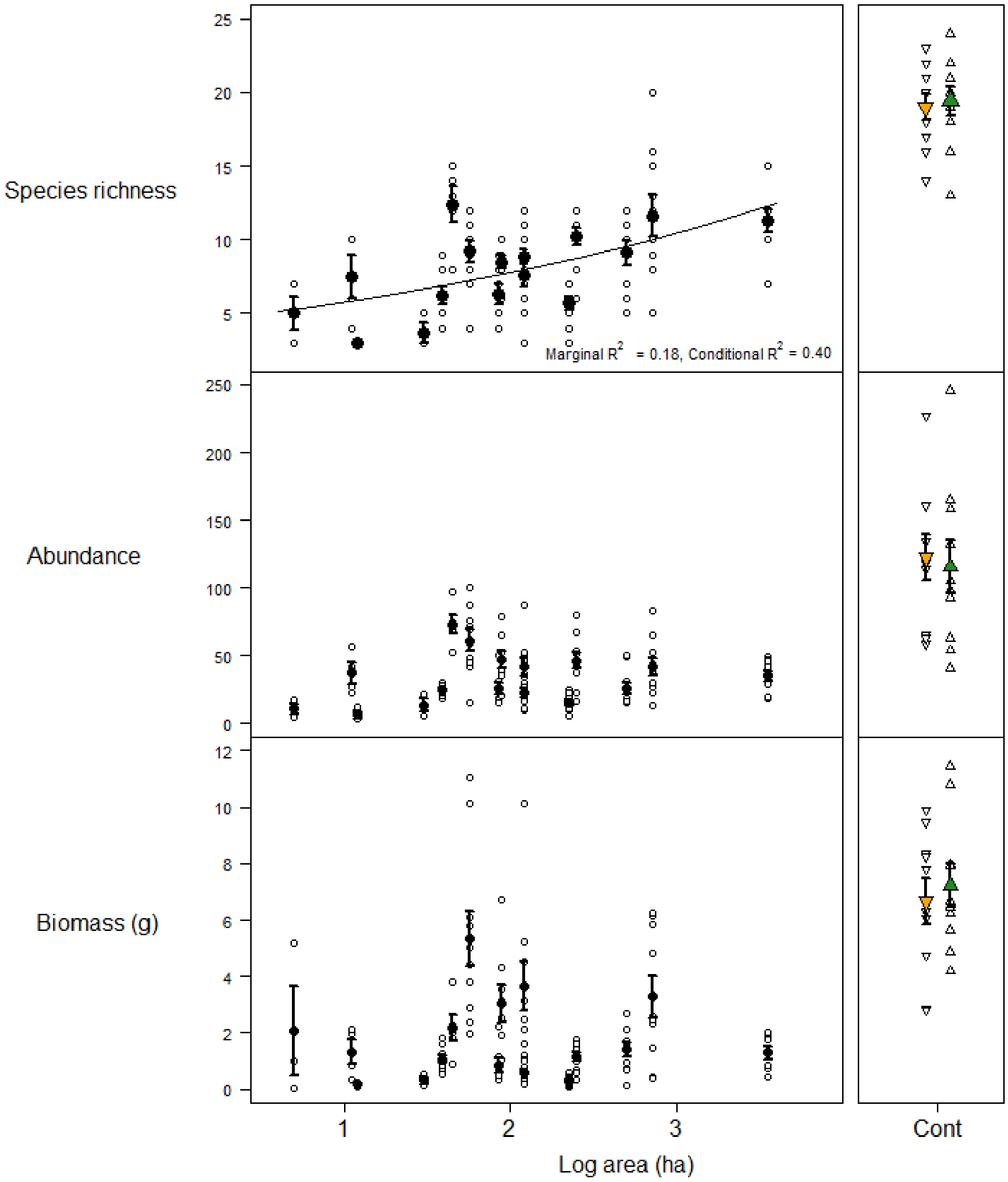

Figure 5.5. Abundance, biomass and species richness in relation to fragment area. Area values are logged (log10). Line of best fit for species richness is taken from GLMM and is only plotted when the slope is significantly different from zero. Hollow symbols are individual station-level values, whilst filled symbols are mean values for each site. Error bars for mean values show standard errors. Triangles and green fill represent undisturbed continuous forest sites/stations, triangles and yellow fill represent twice-logged continuous forest sites/stations, and circles and black fill fragment sites/stations.

Large and small roller biomass declined significantly with declining fragment area, with the decline being slightly steeper for large rollers than for small rollers (large rollers, slope estimate = 1.70, CIs 0.36, 3.04; small rollers, slope = 0.51, CIs 0.11, 0.92). Large rollers occurred in only one fragment smaller than 100 ha. By contrast, small rollers were present in the smallest fragments although their biomass was generally only about 10% of that in the largest fragments (Figure 5.6). Small roller biomass also showed a weak but significant positive linear relationship (slope estimate= 0.18, CIs 0.09, 0.34) and negative curvilinear relationship (slope estimate= -3.37, CIs -6.65, -0.09) with isolation, suggesting that small roller biomass slightly increased initially with increasing fragment isolation, but then remained constant in more isolated sites. However, this relationship was only significant when the strong relationship with area was already accounted for. Neither large nor small roller biomass was significantly related to changes in forest quality.

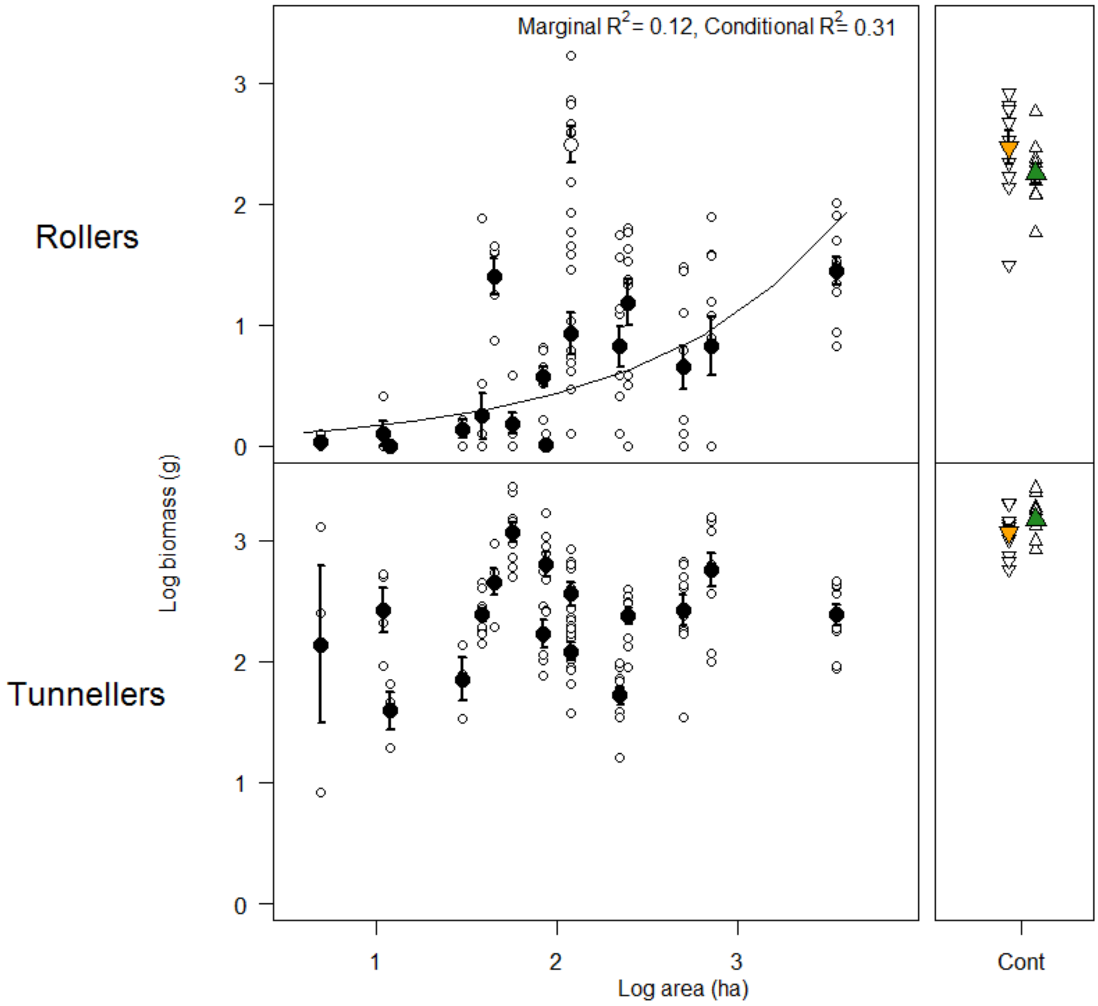

Figure 5.6. Relationships between fragment size and biomass of roller and tunneller guilds. Both graphs show log10 biomass and are plotted on the same scale for ease of interpretation. Error bars show standard errors. Line of best fit for rollers is taken from a GLMM where the slope was significantly different from zero. This best fit line is based on a model excluding one outlying site (plotted as a large hollow circle above) and another outlying station. Triangles and green fill represent undisturbed continuous forest sites/stations, triangles and yellow fill represent twice-logged continuous forest sites/stations, and circles and black fill fragment sites/stations.

By contrast with rollers, fragmentation had little effect on tunneller biomass. Small tunneller biomass was not significantly affected by fragment area, forest quality or isolation, and large tunneller biomass showed only weak curvilinear relationships with area (slope estimate = -4.18, CIs -7.76, -0.61) and isolation (slope estimate = 4.73, CIs 1.03, 8.43). This suggests that in the smallest fragments large tunneller biomass initially increased with increasing area, but then did not show any further increase in larger fragments. Fragment area only had an effect on biomass when isolation was also included in the model, suggesting a relatively weak effect. Large tunneller biomass declined with increasing fragment isolation, but more steeply for less isolated sites and was significant even when it was the only explanatory variable, suggesting that large tunneller biomass was more strongly affected by changes in isolation than by fragment area. Analyses were also carried out on the abundance of the four functional groups but did not reveal any new findings and so for brevity are reported in Appendix 3 (Table 5, Figure A3.1). Overall, biomass of both large and small rollers decreased with decreasing fragment area, but biomass of tunnellers was generally not affected by fragmentation (Figure 5.6).

A comparison of best models sets for all seven response variables revealed that fragment area was significantly related to 4/7 response variables and was in the best model sets (as a linear predictor or second-order polynomial) for all seven response variables (Figure 5.7,Table 5.3). By contrast, isolation and forest quality occurred in the best models for 6/7 and 5/7 response variables respectively, but explained significant relationships for only 2/7 and 1/7 response variables. This indicates that fragment area was a more important predictor of changes in species richness, abundance and biomass (overall and by functional group), than either forest quality or isolation.

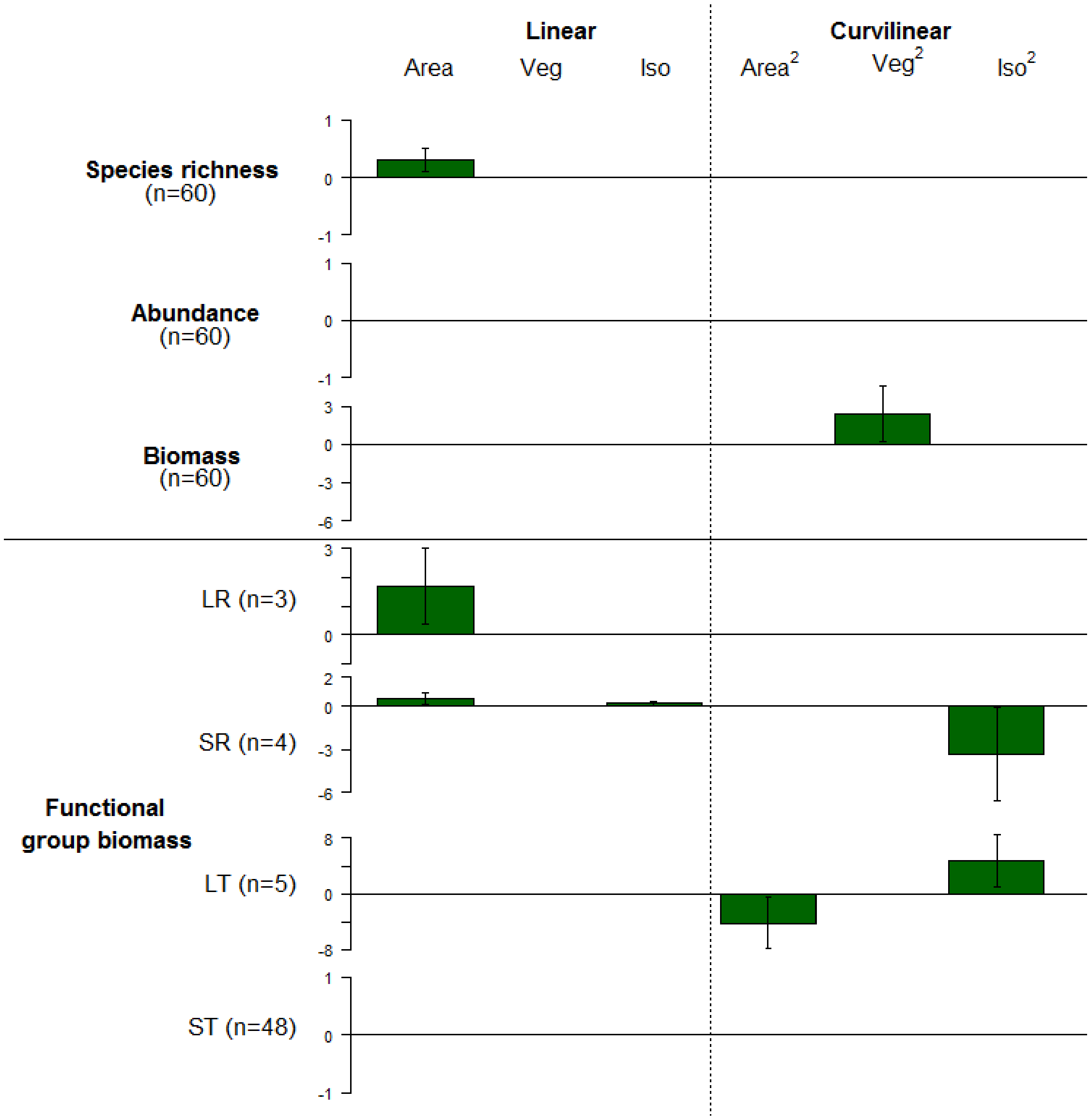

Figure 5.7. Plot of effect sizes (regression slope values) of explanatory variables (x axis) against all seven response variables (y axis). Effect sizes are plotted only for variables included in best models according to AICc model ranking and where confidence intervals do not overlap zero. For linear predictors, positive effect sizes indicate positive relationships between the predictor and response variables, negative effect sizes indicate negative relationships. For curvilinear predictors, a positive effect size indicates a convex relationship (i.e. multiplicatively increasing gradient), whilst a negative effect size indicates a concave relationship (i.e. multiplicatively decreasing gradient) between the response and predictor variable. Errors bars show 95% confidence intervals. Numbers in

brackets indicate the maximum number of species in the analysis. Abbreviations as follows: LR = large rollers, SR = small rollers, LT = large tunnellers, ST = small tunnellers.

*Table 5.3. Table of best models (Δ_i < 2) for all response variables. K= the number of parameter estimates in the model, AICc= model fit measure corrected for sample size, Δ_i= the difference between that model's AIC_c value and that of the best model, ω_i= the Akaike weight, giving the model's relative strength compared to other best models, LL= Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C)= Marginal (M) and conditional (C) R^2-values. *Abundance data were fitted using a negative-binomial distribution, for which there is currently no way of calculating R^2 values, so R^2 values are not shown. Biom= biomass, LR= large roller, SR= small roller, LT= large tunneller and ST= small tunneller.*

Response variable	**Model**	**K**	**AICc**	**Δi**	**ωi**	**LL**	**R^2 (M; C)**
Species richness							
	Area	3	113.55	0	0.21	-53.7	0.18; 0.40
	Area+Iso	4	114.93	1.37	0.1	-53.3	0.20; 0.40
	Area+Veg	4	115.13	1.57	0.09	-53.4	0.19; 0.41
	$Area^2$	4	115.37	1.82	0.08	-53.5	0.18; 0.40
Abundance							
	Area	4	1023.8	0	0.12	-507.7	NA*
	$Area^2$	5	1023.9	0.15	0.11	-506.7	NA*
	1	3	1024	0.24	0.1	-508.9	NA*
	$Area^2$+Veg^2	7	1024.5	0.72	0.08	-504.8	NA*
	$Area^2$+Iso	6	1024.6	0.77	0.08	-505.9	NA*
	$Area^2$+Veg^2 + Iso	8	1024.8	1.03	0.07	-503.8	NA*
	$Area^2$+Veg	6	1025.1	1.34	0.06	-506.2	NA*
	Area+Veg	5	1025.5	1.67	0.05	-507.5	NA*
Biomass							

	Area^2+Iso^2	7	112.13	0	0.58	-48.6	0.21; 0.62
	Area^2+Veg^2	7	112.76	0.63	0.42	-48.9	0.16; 0.61
LR biom							
	Area	3	21.21	0	0.29	-7.5	0.31; 0.31
	Area^2	4	23.08	1.87	0.12	-7.4	0.50; 0.50
SR biom							
	Area+Iso^2	5	83.07	0	0.13	-36.3	0.12; 0.12
	Area+Veg + Iso^2	6	83.21	0.14	0.12	-35.2	0.13; 0.13
	Area^2+Iso^2	6	83.55	0.48	0.1	-35.4	0.14; 0.14
	Area^2+Veg+Iso^2	7	84.15	1.08	0.07	-34.6	0.14; 0.14
	Area+Iso	4	84.35	1.28	0.07	-38	0.08; 0.08
	Area+Veg^2+Iso	6	84.47	1.41	0.06	-35.9	0.12; 0.12
	Area+Veg^2+Iso^2	7	84.83	1.76	0.05	-34.9	0.13; 0.13
LT biom							
	Area^2+Iso^2	6	145.2	0	0.28	-66.3	0.35; 0.48
	Iso^2	4	147.1	1.94	0.11	-69.4	0.22; 0.47
ST biom							
	1	2	31.95	0	0.17	-13.9	0; 0
	Veg	3	32.3	0.35	0.14	-13.1	0.03; 0.03
	Veg+Iso	4	33.54	1.59	0.08	-12.6	0.04; 0.04
	Veg^2	4	33.7	1.75	0.07	-12.7	0.03; 0.03
	Area	3	33.73	1.78	0.07	-13.8	0.00; 0.00
	Iso	3	33.88	1.93	0.07	-13.8	0.00; 0.00

5.4.4 Turnover of dung beetle species assemblages among sites (Hypothesis 4)

Analyses including all forest sites revealed highly significant turnover in species assemblages in relation to forest quality ($R^2 = 0.65$, $p < 0.001$), thus sites with more similar forest quality supported more similar species assemblages. Vector fitting showed a marginally non-significant difference in species assemblages between fragments and continuous forest sites ($R^2 = 0.16$, $p = 0.063$). This was because species assemblages in some of the larger, higher quality fragments were similar to those in continuous forest sites, although the majority of forest fragments supported distinct assemblages of dung beetles compared with those of continuous forest sites (Figure 5.8). These patterns may be linked to the similarity of forest quality in some of the larger, better-quality fragments to that in continuous forest sites (Figure 5.1). This similarity of species assemblages in large, high quality fragments to those in continuous forest contrasts contrasted with the analyses of total species richness, abundance and biomass, where even the ‘best’ fragments showed at least 30% reductions in total species richness, abundance and biomass compared to continuous forest sites (Figure 5.8). Inspection of species associations revealed that all of the large roller species were associated with large, high quality sites (species names in pink, Figure 5.8). However, for large tunnellers, one of the five species appeared strongly associated with poor quality, small sites (species name in green, Figure 5.8). These observations support the previous findings that rollers are more vulnerable to extinction following fragmentation than are tunnellers.

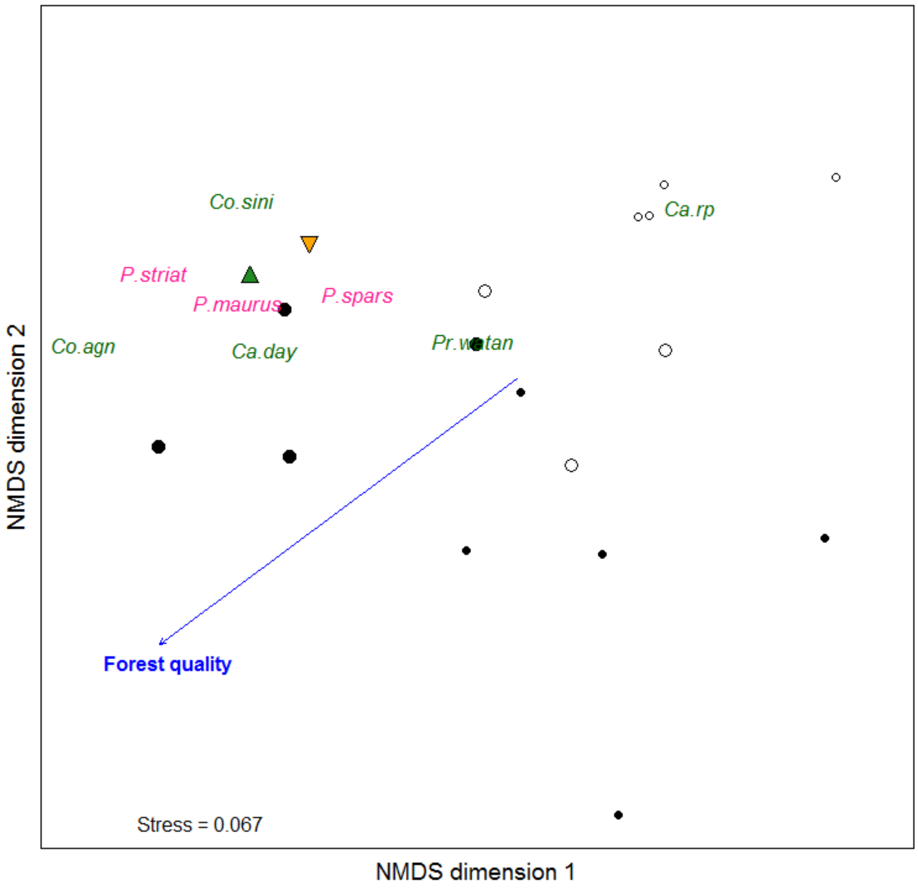

Figure 5.8. NMDS plot (Bray-Curtis method) comparing dung beetle species assemblages in forest fragments and continuous forest. Each data point represents a site and points that are closer together support more similar species assemblages. NMDS ordination was fitted for all species recorded at least twice at a site (n = 2 individuals) and at ≥2 sites, and based on Wisconsin double standardised abundance values (where species are standardised by their maximum value, then by sites and by site totals). Environmental vector correlations are plotted as blue arrows and are only plotted for significant variables (p < 0.05 based on Monte Carlo permutations). The longer the arrow, the stronger the correlation, but arrow length is scaled to fit the plot window meaning that arrow length cannot be compared across plots. To aid interpretation, sites larger than the mean log10 fragment size (1.95 on log10 scale) are plotted as large circles and those smaller than the mean as small circles, and sites with forest quality higher than the mean quality score are plotted as solid circles and those with forest quality lower than the mean as hollow circles. The two continuous forest sites are plotted as triangles, with

green the unlogged and yellow the twice-logged site. The scores of key functional species have been plotted, with large tunnellers in green font and large rollers in pink font. In this analysis, the stress value for the NMDS ordination was 0.067, indicating a very reliable configuration of sites (Zuur et al. 2007).

In the analysis of forest fragments, there was marked turnover in species assemblages among sites (Figure 5.9). Vector fitting revealed that changes in forest quality ($R^2 = 0.79$, $p < 0.001$), and to a lesser degree area ($R^2 = 0.43$, $p < 0.05$), but not isolation ($R^2 = 0.23$, $p = 0.18$) were correlated with turnover in species assemblages. The importance of forest quality, in particular, for explaining turnover in species assemblages contrasts with analyses of dung beetle species richness, abundance and biomass where fragment area was the most important variable, suggesting that effects of forest quality and area may affect different aspects of diversity. Nonetheless, the turnover of tunneller and roller species among fragments was consistent with preceding analyses (Figure 5.6), with larger rollers strongly associated with larger, better quality fragments, and large tunnellers more widely distributed across sites regardless of fragment area or forest quality (Figure 5.9).

Mantel tests revealed that similarity in species assemblages was significantly correlated with the geographic proximity of sites (Mantel r = 0.44, $p < 0.001$), showing that sites that were closer together tended to support more similar species assemblages. Partial Mantel tests showed that after accounting for spatial autocorrelation, species composition was significantly correlated with forest quality (Mantel r = 0.24, $p < 0.05$) and isolation (Mantel r = 0.27, $p < 0.05$) but not area (Mantel r = 0.05, $p = 0.34$).These Mantel test results support the NMDS analyses, showing that forest quality explained the most variation in turnover of species assemblages among sites. However, the significant effect of area on turnover from the NMDS analyses was not apparent in the partial Mantel test, and the non-significant relationship of isolation from the NMDS analyses was significant in the partial Mantel test. The relationship with isolation was probably masked in the NMDS analyses by spatial autocorrelation, given that sites that are close together spatially will also be similar distances from continuous forest (Mantel test of geographic distance versus fragment isolation matrices; Mantel r = 0.44, p < 0.001). However, the loss of the significant relationship between fragment area and species turnover in the partial Mantel tests is unlikely to be the result of fragment area being confounded by spatial autocorrelation (Mantel test of fragment area versus geographic distance; Mantel r = 0.07, p = 0.31). Instead this may be the result of species abundances being non-normally distributed, something that NMDS is able to cope with but for which the effectiveness of Mantel tests has yet to be tested (Borcard & Legendre 2012). Overall, forest quality was more important in explaining turnover in species composition among sites than was fragment area or isolation.

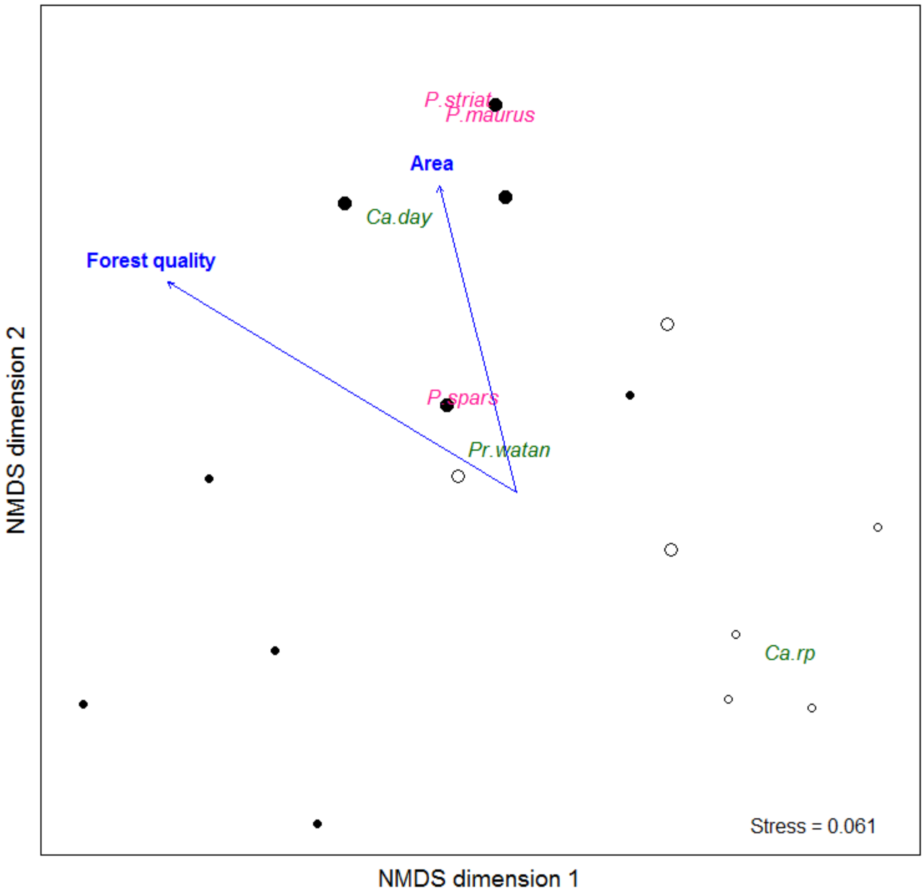

Figure 5.9. NMDS plot (Bray-Curtis method) comparing dung beetle species assemblages in forest fragments (excluding continuous forest sites). Each data point represents a site and points that are closer together support more similar species assemblages. NMDS ordination was fitted for all species recorded at least twice at a site (n = 2 individuals) and at ≥2 sites, and based on Wisconsin double standardised abundance values (where species are standardised by their maximum value, then by sites and by site totals). Environmental vector correlations are plotted as blue arrows and are only plotted for significant variables ($p < 0.05$ based on Monte Carlo permutations). The longer the arrow, the stronger the correlation, but arrow length is scaled to fit the plot window meaning that arrow length cannot be compared across plots. To aid interpretation, sites larger than the mean log10 fragment size (1.95 on log10 scale) are plotted as large circles and those smaller than the mean as small circles, and sites with forest quality higher than the mean quality score are plotted as solid circles and those with forest quality lower than the mean as hollow circles. The scores of key functional species have been plotted, with large

tunnellers in green font and large rollers in pink. The stress value for this NMDS ordination was 0.061, indicating a very robust site configuration (Zuur et al. 2007).

5.5 Discussion

5.5.1 Differences in dung beetle assemblages between continuous forest and fragments

There was little difference in dung beetle species richness, abundance or biomass between undisturbed primary forest and twice-logged forest. Despite sampling only one pristine and one twice-logged continuous forest site, the relatively small differences between these sites reported here concurs with previous work (Edwards et al. 2011b; Slade et al. 2011). These small differences are probably because twice-logged continuous forest in Sabah still supports the majority of large mammal species found in pristine forest (Ancrenaz et al. 2010; Clements et al. 2010), and because forest quality in the twice-logged site still exceeded that in the majority of fragments (Figure 5.1). Thus, it seems that fragmentation had a much larger effect than commercial selective logging on dung beetle assemblages. A substantial reduction in dung beetle species richness, abundance and biomass occurred following fragmentation, with pristine and twice-logged continuous forest sites both having over twice the number of species as forest fragments, and over three times the abundance and biomass of all species, rollers and tunnellers. There was an especially large difference in large roller biomass, which was eight times higher in continuous forest sites than in fragments.

Previous studies comparing dung beetle assemblages in continuous forest and fragments show little consistency in reported findings. For example, the reduction in species richness in fragments compared to continuous forest in previous studies varies from 0-60% and the decline in abundance from 40-70% (Klein 1989; Estrada & Coates-Estrada 2002; Feer & Hingrat 2005). This suggests that the 60% decline in species richness and 70% decline in abundance recorded in this study are comparatively large, especially as the previous studies compared continuous forest to fragments smaller than 80 ha, as opposed to 5-3,500 ha in this study. One explanation for these differences is the greater length of time since fragmentation in this study, resulting in more time for species to go extinct and reduced extinction ‘debt’ (Tilman et al. 1994; Gibson et al. 2013). In this study, fragmentation occurred at least 15 years before sampling, and probably longer, whereas fragments sampled by Klein (1989) and Feer & Hingrat (2005) were formed only 2-6 years prior to sampling. Given that it can take 15 years for fragments smaller than 100 ha to lose half of all species (Gibson et al. 2013), it highly unlikely that the full relaxation period had elapsed in the previous studies. Whilst there may still be a residual extinction debt in the fragments in this study, the greater time since fragmentation means that the assemblages sampled are likely to be closer to community relaxation than in other studies. Conversely, Estrada & Coates-Estrada (2002) conducted their study in sites fragmented over 25 years ago and so differences to this study may more likely be linked to ecological differences between the two study localities.

A major ecological difference between Southeast Asia and the Neotropics is in the large mammal faunas. The continuous forest sampled in this study supports large herds of Asian elephants (*Elephas maximus borneensis*), and other large herbivores such as Banteng (*Bos javanicus lowi*), that are subject to very low hunting pressure (Ancrenaz et al. 2005), leading to abundant dung resources in these sites. By contrast, there are fewer large mammalian herbivores in Neotropical rain forests (Cristoffer & Peres 2003), and there is also greater hunting pressure (Nichols et al. 2009). Elephants and Banteng are absent from the forest fragments sampled in this study (Timmins et al. 2008; Alfred et al. 2010), suggesting a greater decline in dung resource availability following fragmentation in this study than would be expected in the Neotropics, which may in turn explain the much greater decline in dung beetle diversity and abundance reported here.

In contrast to the large declines in species richness and biomass, turnover in species assemblages between continuous forest and fragments was more variable. Larger, higher quality fragments supported similar assemblages to continuous forest sites, but smaller, lower quality sites supported distinct species assemblages. Therefore, the larger, higher quality fragments supported some species characteristic of continuous forest sites, albeit at much lower abundances. Forest quality was the best predictor of turnover in species assemblages and so the similarity of species assemblages in better quality fragments and continuous forest sites probably results from environmental filters, such as soil and vegetation type, that are known to influence dung beetle distributions (Doube 1983; Davis et al. 2001). These filters can also explain turnover in species assemblages among forest fragments, which are discussed below.

5.5.2 Differences in dung beetle assemblages among forest fragments

Differences in dung beetle assemblages among fragments were less marked than those between continuous forest and fragments. Nonetheless, decreasing fragment area resulted in further declines in dung beetle species richness, although abundance and biomass were not related to fragment area. The decrease in dung beetle species richness with fragment area is widely supported by studies on a large range of taxa in oil palm landscapes (Eltz et al. 2003; Benedick et al. 2006; Struebig et al. 2008; Edwards et al. 2010; Hill et al. 2011), and other systems (e.g. Laurance et al. 2002; Nichols et al. 2007). Indeed, the slope coefficients of $\log_{10}$ species richness against $\log_{10}$ area from this study, as well as the R^2 value (coefficient = 0.30; R^2: Marginal = 0.18, Conditional = 0.40) were within the range of values reported in other studies (e.g. coefficient = 0.048-0.81 (Hill et al. 2011), $R^2 = 0.30$ (Nichols et al. 2007)). The theory of island biogeography and metapopulation dynamics explain the decline in species richness with fragment area, although isolation distance was less important in this study (MacArthur & Wilson 1967; Hanski & Ovaskainen 2000). This greater impact of fragment area than isolation on species richness fits with previous dung beetle studies (Nichols et al. 2007), suggesting that selective extinction is more important than selective colonisation in determining dung beetle species richness (Hill et al. 2011). This extinction is often considered to be stochastic if accompanied by declines in abundance (Klein 1989; Struebig et al. 2008), but abundance and biomass did not decline with decreasing fragment area in this study suggesting that extinctions may have been deterministic. Commonly proposed deterministic drivers of selective dung beetle extinctions include their patchy occurrence in space and time, their often restricted habitat preferences, and their dependence on mammal species and dung resources that are susceptible to fragmentation (Davis et al. 2001; Feer & Hingrat 2005). It is possible that these factors disproportionately affected the larger number of forest-specialist dung beetle species, but not the few generalist, disturbance-tolerant species in the community. This hypothesis could also explain the turnover in species assemblages reported in this study.

Turnover in species assemblages among fragments was better explained by forest quality than either area or isolation. Sites of better forest quality supported species assemblages more similar to those found in continuous forest sites (Figure 5.8). This turnover may be the result of forest-dependent species becoming extinct in sites of lower forest quality (and smaller size), and being replaced by more disturbance-tolerant and generalist species. This explanation is supported by the similarity of species assemblages in the smallest, lowest quality sites to the assemblage of a sample collected in an oil palm plantation (Appendix 3 figure A3.2). Oil palm and Eucalyptus plantations tend to be dominated by populations of widespread, disturbance-tolerant species (Gardner et al. 2007; Chapter 3/Senior et al. 2012; Edwards et al. 2013), that are often strong dispersers capable of increasing in abundance in fragments following the decline of more specialised competitors (Larsen et al. 2008). This effect of forest quality was not observed in continuous forest sites, suggesting that fragmentation effects, such as human encroachment and edge effects (Tabarelli et al. 2004), further reduced forest quality in fragments beyond the impacts of two selective logging rotations. Forested areas allocated for conversion to oil palm are typically logged prior to conversion (Swarna Nantha & Tisdell 2008), and so the timing of fragmentation just after logging is likely to have exacerbated declines in forest quality by combining the adverse impacts of logging and edge effects. Partial Mantel tests showed that forest quality remained an important predictor of species turnover after accounting for spatial autocorrelation of study sites and differences present prior to fragmentation. Thus, despite rarely being considered in studies of fragmentation, forest quality may be a significant driver of species compositional changes following fragmentation.

In contrast to turnover and species richness results, abundance and biomass of dung beetles were not affected by changes in area, quality or isolation. This resilience may be linked to the hyper-abundance of some mammal species, such as Bearded pigs (*Sus barbatus*) and Sambar deer (*Rusa unicolor*), in even very small forest fragments. These species are thought to persist in fragments by supplementing their diets with oil palm fruit from neighbouring plantations (Ickes 2001; Danielsen et al. 2009) and may be contributing to high dung availability in small fragments. However, large reductions in dung beetle abundance, biomass and species richness following fragmentation suggests that the occurrence of some mammal species within fragments does not compensate for the loss of large herbivores and other mammal species dependent on continuous forest (e.g. Damuth 1981).

Overall, fragment area was more important than forest quality or isolation for explaining changes in species richness among fragments. This finding is unlikely to be the result of fragment area showing greater variation and having more explanatory power in analyses than either forest quality or isolation, because variation in these variables was of a similar magnitude (see section 5.3.1). Furthermore, this study shows that isolation and forest quality still explained key changes in species turnover and large tunneller biomass respectively, suggesting that conservation efforts addressing fragment area, isolation and quality could yield different conservation benefits.

5.5.3 Conservation management implications

Compared to continuous forest, fragments supported significantly fewer species and individuals of dung beetle species, including fewer functionally important rollers and tunnellers. Consequently for dung beetle diversity and functioning, protecting forest fragments is no substitute for protecting continuous forest, even when continuous forest has been twice-logged. This implies that conservation efforts should be directed towards the protection of continuous forest sites, supporting suggestions that land sparing is better than land sharing for biodiversity conservation in oil palm landscapes

(Edwards et al. 2010; Phalan et al. 2011). Oil palm concessions often replace continuous, albeit highly degraded, forest, which means that HCV assessments for new oil palm plantings have to identify areas of HCV in continuous forest, that subsequently tend to be protected as isolated HCV areas within the concession area. Best practice encourages the use of buffer areas around HCV areas to maximise their protection, but this chapter shows that even very large fragments are unable to support the same species richness and abundance as continuous forest. Therefore, isolated HCV areas may be highly unlikely to maintain HCVs over time, and the effectiveness of connecting forest fragments to areas of continuous forest, for example by using corridors or riparian buffers (Beier & Noss 2008), should be examined. Designing landscapes in this way will require coordination among companies to link up conservation areas across concessions (Edwards & Laurance 2012).

Connecting HCV fragments to continuous forest may not be possible in all contexts because oil palm managers often have limited land and resources available for conservation (Meijaard & Sheil 2012). Therefore, advice is also needed on how to maximise the conservation benefit from HCV fragments in existing plantations and in new concessions. Among fragments, area was more important than either forest quality or isolation for maintaining species richness, evenness, and roller biomass. However, sites of higher forest quality supported species assemblages similar to those found in continuous forest. Therefore, for existing HCV areas, if it is not possible to connect areas to continuous forest, the best strategy for biodiversity conservation may be to improve forest quality in existing HCVs. Such management actions might increase the similarity of species assemblages in these sites to those in continuous forest, helping to protect forest-dependent species threatened by habitat loss and fragmentation. This assumes that these forest-dependent species still persist in or are able to recolonize these improved HCV areas.

Findings from this study suggest that the best strategy for promoting the effectiveness of HCV areas in new concessions is to maximise their size and maintain or enhance their forest quality. This study suggests that fragments larger than 100 ha can still support functionally important rollers (and tunnellers), as well as up to 50% of the species richness of continuous forest sites. Oil palm managers are often unwilling to give up extra land for conservation because of the loss of crop yield, but the protection of HCV areas of 100-500 ha should be a realistic target in large concessions (>15,000 hectares, Ruysschaert et al. 2011). Furthermore, the smallest 5-10 ha fragments sampled in this study supported just 20% of the species found in continuous forest, no large rollers, and species assemblages more similar to oil palm plantations than continuous forest (Figure 5.9). This suggests that protecting fewer, large fragments is likely to protect more forest-dependent and functionally important species than protecting more small fragments of equivalent total area.

5.5.4 Possible impacts on ecosystem functioning

Compared with continuous forest, forest fragments supported a greatly reduced biomass and abundance of tunnellers and rollers, particularly larger-bodied species. However, following fragmentation rollers and tunnellers responded differently to further declines in fragment area. Rollers showed large abundance and biomass declines in relation to fragment area, but large roller species did not markedly differ from small roller species in their responses. By contrast, tunneller abundance and biomass were not sensitive to decreasing fragment area, but did decline with increasing isolation distance. Thus, rollers were more adversely affected by decreasing fragment size and were almost entirely absent in fragments smaller than 40 ha, whereas tunnellers persisted in even the smallest fragments, although less well in more isolated fragments.

The sensitivity of rollers, and especially large species, to fragmentation corresponds with other findings showing that rollers are also absent in oil palm plantations (Edwards et al. 2013). Their decline in small fragments may be linked to altered microclimate and soil structure in smaller fragments, with increased soil surface temperatures and soil compaction potentially reducing both the ability of rollers to bury brood balls and also the survival of larvae in the soil (Edwards et al. 2013). These changes may not affect tunnellers to the same extent because they are stronger burrowers than rollers and their larvae develop deeper in the soil (Hanski & Cambefort 1991; Edwards et al. 2013). Instead, large tunneller populations are probably maintained in small fragments by the high availability of Bearded pig (*Sus barbatus*) and Sambar deer (*Rusa unicolor*) dung in these sites.

Large tunnellers are disproportionately important for dung removal and hence decomposition (Larsen et al. 2005b; Slade et al. 2007b), whereas rollers are less important for dung burial (Slade et al. 2007b), but are important for secondary seed dispersal (Andresen & Feer 2005). Consequently, the different responses of these two functional groups to fragmentation could have implications for dung removal and secondary seed dispersal following fragmentation. The findings from this study suggest that both dung burial and seed dispersal will be significantly reduced in fragments compared to continuous forest, but among fragments dung burial is predicted to remain constant in different sized fragments whereas secondary seed dispersal by rollers is likely to decrease with fragment size. Furthermore, there may be no secondary seed dispersal in the smallest fragments. This could have consequences for seedling recruitment in these fragments (Shepherd & Chapman 1998; Andresen 2002).

5.5.5 Conclusion

This chapter showed that forest fragmentation resulted in large declines in dung beetle species richness, abundance and biomass, and that declining fragment area caused further declines in species richness and roller biomass. Fragment forest quality and isolation had less impact, but differences in forest quality were strongly correlated with turnover in species assemblages among sites. The effects of fragmentation on dung beetle communities are likely to be linked to availability of dung resources, and the extinction of key mammal species following fragmentation. Maximising the size and quality of HCV areas within plantations may help to conserve dung beetle assemblages that are most similar to continuous forest and which support functionally important species of large rollers and tunnellers. These results imply that dung beetle ecosystem functions may respond idiosyncratically to fragmentation, with dung burial being maintained in small fragments, but secondary seed dispersal decreasing with decreasing fragment area. Experiments that directly measure dung burial and secondary seed dispersal are needed to test these predictions, and are considered in the next Chapter.

Chapter 6 - Ecosystem functioning in fragmented rainforest

6.1 Abstract

Oil palm companies certified by the Roundtable on Sustainable Palm Oil aim to reduce biodiversity losses by protecting High Conservation Value (HCV) forest, but it is not known whether these forest fragments can maintain ecosystem functions. I studied 18 forest sites (16 fragments, range 5-3,529 ha, and 2 continuous forest sites) in Sabah, Malaysia and assessed the impacts of fragmentation on ecosystem functions performed by dung beetles: dung removal, seed burial (by tunnellers), and seed dispersal (by rollers). There were only minor differences in dung removal, seed burial and seed dispersal between undisturbed and twice-logged continuous forest sites, but these ecosystem functions were at least 50% lower in forest fragments. This decline was largest for secondary seed dispersal with only 4/16 forest fragments having any seeds rolled at all, whereas 13/16 fragments had some dung removed or seeds buried. Among fragments, functions varied little in response to changing fragment area, forest quality or isolation, although dung removal, seed burial and secondary seed dispersal were highest in larger fragments. These ecosystem functions are likely to have key roles in maintaining the viability of plant species populations and so should be considered in HCV management plans. Continuous forest sites maintained far higher rates of these ecosystem functions than did fragments, even when heavily degraded (twice-logged), and degraded continuous forest should be a high priority for conservation. However, if only fragments can be maintained, then they need to be at least 100 ha in size to support key dung beetle functions.

6.2 Introduction

The detrimental impacts of deforestation and forest fragmentation on species richness and abundance are now well documented (Nichols et al. 2007; Gibson et al. 2011; Bregman et al. 2014). However, ecosystems consist of more than just static collections of species and individuals. They are dynamic systems reliant on interactions between species and the transfer of resources and energy (Morris 2010). For example, processes such as seed dispersal and decomposition result from individual species consuming resources, growing, reproducing and transferring energy (Reiss et al. 2009). These ecosystem processes are vital for the maintenance of the abiotic and biotic conditions essential for longer term species persistence (Millennium Ecosystem Assessment 2005; Hooper et al. 2012), but species extinctions can lead to declines in key ecosystem processes (Hooper et al. 2012). Therefore, it is vital to understand how deforestation and forest fragmentation influence ecosystem functioning.

Sustainability initiatives such as the Roundtable on Sustainable Palm Oil (RSPO) aim to mitigate the negative environmental impacts of deforestation and forest fragmentation by protecting HCV areas within plantations. However, methods for conserving forest areas with High Conservation Values (HCVs) do not explicitly consider ecosystem functioning, except in cases where it provides crucial ecosystem services in critical situations, such as flood and erosion prevention (HCV 4, Brown et al. 2013a). This subset of ecosystem services overlooks the important supporting and regulating services/processes that maintain abiotic and biotic conditions essential for species persistence, which could influence the maintenance of HCVs over time (Millennium Ecosystem Assessment 2005; Hooper et al. 2012). HCV assessors cannot be expected to comprehensively measure ecosystem functions during brief HCV assessments (Meijaard & Sheil 2012, Chapter 2), and so research is needed to quantify how the size and quality of HCV areas affects the maintenance of ecosystem functions. This research can be used by HCV assessors to inform management recommendations that ensure HCVs are maintained over time.

HCV areas tend to be isolated forest fragments within oil palm plantations (Edwards et al. 2010, Chapter 4). Differences in forest fragment area, forest quality and isolation can alter ecosystem functions either through impacts on species that mediate the functions (Larsen et al. 2005a), or through changes in abiotic conditions that directly affect functions. Whilst changes in abiotic conditions could directly impact ecosystem functions such as leaf litter decomposition, reliant on chemical decomposition (Meentemeyer 1978), previous studies have shown little change in leaf litter decomposition rates following selective logging or habitat fragmentation (Vasconcelos & Laurance 2005; Barlow et al. 2007). However, abiotic changes can have strong indirect effects on ecosystem functions by altering the abundance and behaviour of functionally important species (e.g. Doube 1990). For example, disturbed riverine and logged forest habitats show increased canopy openness and reduced heterogeneity of canopy habitats that support different assemblages of ants and dung beetles that are better able to tolerate these more exposed microhabitats (Davis et al. 1998; Klimes et al. 2012). Vegetation structure and abiotic conditions can be highly altered in forest fragments in response to edge effects (Laurance et al. 2002; Ewers & Didham 2007; Ewers et al. 2007) and human disturbances, such as logging, that increase canopy openness and so increase temperature and decrease humidity below the canopy (Hamer et al. 2003; Laurance et al. 2011; O'Brien et al. 2013). Therefore, these abiotic changes in response to fragmentation and logging could alter provision of ecosystem functions.

In addition to impacts on microclimate and vegetation structure, fragmentation affects species richness and abundance by reducing habitat availability and changing the structure of remaining habitat patches (i.e. number/shape of patches, distance between patches) (Fahrig 2003; Ewers & Didham 2006; Hanski et al. 2013). Habitat loss leads to local species extinctions in line with Species-Area Relationships (MacArthur & Wilson 1967), and altered patch network structure can change extinction and colonisation dynamics and reduce the viability of species' populations (Hanski et al. 2013). How these changes in biodiversity affect ecosystem functions will depend on the response of functionally important taxa to changes in fragment area, forest quality and isolation. Studies of functionally important dung beetles, birds, bees, ants and termites have reported decreasing species richness and abundance with declining fragment area (Chapter 5, Klein 1989; Laurance et al. 2002; de Souza & Brown 2009; Hill et al. 2011; Bregman et al. 2014). However, effects of these species declines on ecosystem functions such as pollination, dung and litter decomposition can only be inferred in the absence of direct measurements of the functions (Reiss et al. 2009). Slade et al (2011) reported reduced dung and seed removal following high-intensity commercial selective logging, but measurements of the response of multiple ecosystem functions to disturbance and fragmentation gradients are lacking (Loreau et al. 2001; Peh & Lewis 2012).

Dung beetles have critical roles in nutrient cycling and secondary seed dispersal, suppression of mammalian parasites and bioturbation (the mixing of soil and dung particles) (Nichols et al. 2008), making them an excellent taxon for measuring multiple ecosystem functions. Nutrient cycling and secondary seed dispersal influence soil fertility, plant productivity, seedling survival and plant composition and so are likely to be particularly important for overall ecosystem functioning (Nichols et al. 2008). Dung beetles separate into different functional groups in relation to their nesting behaviour, with tunnellers burying dung directly under the dung pile, rollers moving dung horizontally away from the dung pile and dwellers using dung *in situ* in the dung pile (Hanski & Cambefort 1991). These functional groups contribute to different ecosystem functions, with tunnellers being important for dung burial (nutrient cycling) and rollers for secondary seed dispersal (Estrada & Coates-Estrada 1991; Andresen & Feer 2005; Larsen et al. 2005a; Slade et al. 2007b). Dwellers contribute little to dung or seed removal (Slade et al. 2007b). In roller and tunneller groups larger species are especially important for these functions (Slade et al. 2007b; Dangles et al. 2012). Tunnellers' importance for dung burial is likely to be because they are the most speciose and abundant functional group (~85% of total dung beetle biomass and species richness in continuous forest), and because the group contains some disproportionately efficient larger species (e.g. *Catharsius sp.*, Andresen & Feer 2005; Slade et al.

2007). Rollers remove fewer seeds in total than tunnellers, but by moving seeds horizontally away from the dung pile where seed density is high, rollers may reduce density-dependent seedling mortality and, by burying seeds at shallow depths, rollers may promote seedling germination (Andresen & Feer 2005; Nichols et al. 2008). Reducing density-dependent seed and seedling mortality is crucial for seedling recruitment and the maintenance of seedling diversity (Bagchi et al. 2014). However, secondary seed dispersal by rollers has been largely overlooked in previous studies recording just the proportion of seeds removed from a site without separating those moved by rollers and tunnellers (Andresen & Feer 2005; Slade et al. 2007b, 2011). These separate measurements can also improve understanding of how different species' responses to fragmentation can impact different ecosystem functions, given that rollers decline more in abundance that tunnellers following fragmentation (Chapter 5). To address this knowledge gap, seed burial (by tunnellers) and secondary seed dispersal (by rollers) are measured separately in this chapter.

In Chapter 5, I showed there was little difference in large tunneller and roller biomass between twice-logged and pristine forest, but that biomass of both groups was significantly lower in forest fragments. These results suggest that there will be little difference in dung removal, seed burial or secondary seed dispersal between undisturbed and twice-logged continuous forest but that these ecosystems functions may be reduced in forest fragments compared to continuous forest sites. Results from Chapter 5 showed that among forest fragments, tunneller biomass showed little further decline with decreasing area, implying that dung removal and seed burial may still be maintained in even the smallest fragments. By contrast, roller biomass declined with decreasing fragment area suggesting that horizontal seed dispersal is likely to decline with decreasing fragment size. Previous studies have reported declines in seed dispersal and dung removal following forest fragmentation, but most research has been focussed in the Afro- and Neo-tropics in the context of small-scale, low-intensity agriculture or cattle pasture (Andresen 2003; Chapman et al. 2003). Oil palm agriculture is one of the most dominant crops in tropical landscapes, especially in Southeast Asia (Wilcove & Koh 2010), and so research is needed to assess how ecosystem functions are affected in oil palm dominated landscapes. This research can inform the management of HCV areas in oil palm plantations, and more widely help to evaluate whether forest fragments in intensive agricultural landscapes can maintain key ecosystem functions.

I measured rates of dung removal, seed burial and horizontal seed dispersal in 16 forest fragments, one heavily disturbed (twice-logged) continuous forest site and one unlogged continuous forest site in Sabah, Malaysia. This allowed me to assess differences in dung removal, seed burial and horizontal seed dispersal between unlogged and twice-logged continuous forest sites (Hypothesis 1), between continuous forest sites and forest fragments (Hypothesis 2), and among forest fragments in relation to fragment area, forest quality and isolation (Hypothesis 3). These hypotheses were as follows:

Hypothesis 1. There is no difference in dung removal, seed burial or secondary seed dispersal between twice-logged and unlogged continuous forest sites.

Hypothesis 2. Ecosystem functions (dung removed, seed burial and secondary seed dispersal) are lower in forest fragments than in continuous forest sites.

Hypothesis 3. Among forest fragments, dung removal and seed burial does not change in relation to fragment area, forest quality and isolation. Secondary seed dispersal declines with decreasing fragment area, but does not change in relation to forest quality or isolation.

6.3 Methods

6.3.1 Study sites

Dung removal, seed burial and horizontal seed dispersal were measured in two continuous forest sites and 16 forest fragments in eastern Sabah, Malaysia (5 °N, 117 °E, Chapter 4). The study took place during the ‘drier’ season between July and September 2013 (see Chapter 4 for detailed climatic information). The two continuous forest sites were in undisturbed, primary forest (Danum Valley Conservation Area) and in twice-logged forest (Ulu-Segama Malua Forest Reserve). Ulu-Segama Malua Forest Reserve was first logged between 1976 and 1991 (~120 m^3 ha^{-1} of timber removed), and then again between 2001 and 2007 (~35 m^3 ha^{-1} of timber removed) resulting in very highly degraded forest (Chapter 4; Edwards et al. 2011; Reynolds et al. 2011). The forest fragments varied in size from 5 to 3,529 ha, and so included larger fragments than in many Neotropical studies (e.g. Laurance et al. 2002a). Fragments were located between 0.2 and 46.7 km from continuous forest and had been isolated within oil palm plantations for at least 19 years at the time of sampling. The fragments varied in their history of disturbance and forest management, with at least 11 of the fragments having been selectively logged prior to fragmentation (Chapter 4). Eight fragments were managed by the Sabah Forestry Department (38-3,529 ha) and eight fragments by PPB (Wilmar International) oil palm plantations (5-120 ha). I quantified forest quality at each sampling station by recording ground cover, canopy cover, vegetation cover (above 2m), leaf litter depth, tree density, girth, identity (Dipterocarpaceae or not) and point of inversion, sapling density and girth (see Chapter 4 for more details). Principal Components Analysis (PCA) was used to combine these vegetation variables into an independent measure of forest quality for each forest site, and the first principal component (PC1) was extracted as a measure of forest quality. PC1 explained 33% of variation in vegetation variables and was characterised by a high density of large, tall Dipterocarps, a high canopy cover and deep leaf litter (Chapter 4 Table 4.2). PC1 characterised clear differences in forest quality among sites, identifying forest in undisturbed continuous forest as of highest quality (Chapter 5 Figure 5.1). Fragment areas were taken from Sabah Forestry Department and PPB plantations statistics, and isolation distances calculated in ArcMap as the distance to the closest continuous forest (defined as non-mangrove forest >10,000 ha). There were no significant correlations among fragment area, forest quality and isolation (Chapter 5 Figure 5.2).

6.3.2 Dung removal

At all 18 sites dung removal was measured at sampling stations placed at 100 m intervals along transects of 0.3-1 km in length (1 transect per site, 3-10 stations per transect depending on fragment size and shape, 143 stations in total, 123 in fragments, 20 in continuous sites). Between 8 and 11 am, 630 g 'treatment' piles of fresh cow dung were placed at each sampling station, and two 630 g 'control' dung piles were placed at the first and second stations along transects. After 24 hours, all dung piles were collected and weighed to calculate wet masses (g). Control dung piles were placed inside cages of 1 mm wire mesh that excluded all dung beetles, but allowed water loss by evaporation (Chapter 4). The percentage of dung removed from the treatment pile at each station was calculated relative to the mean of the two control piles.

6.3.3 Seed burial and horizontal seed dispersal

Seed burial and horizontal seed dispersal were measured at the same sampling stations where dung removal was studied. In each of the treatment dung piles I placed 300 aluminium beads (0.5 cm diameter) as seed mimics. After 24 hours, I recorded the percentage of beads that: 1) remained unburied, 2) had been dispersed horizontally by rollers, and 3) were buried under the dung pile by tunnellers. See Chapter 4 for full methodological details.

6.3.4 Analysis

6.3.4.i Differences in ecosystem functions between unlogged continuous forest, twice-logged continuous forest and forest fragments (Hypothesis 1 & 2)

To examine differences in dung removal, seed burial and horizontal seed dispersal (response variables) between unlogged continuous forest, twice-logged continuous forest and forest fragments I used Generalised Linear Mixed Models (GLMMs). Data from all 143 sampling stations across the two continuous forest sites (20 stations) and 16 fragments (123 stations) were analysed, with forest type ("unlogged continuous", "twice-logged continuous" or "fragment") as a categorical fixed effect and site as a random effect. Fitting site as a random effect accounted for the unbalanced number of sampling stations at each site and prevented pseudoreplication. GLMMs use pseudo Generalised-Least Squares methods for parameter estimation and so provide less biased estimates than linear models for unbalanced data, they can also account for non-normal data distributions (Bolker et al. 2009). Including site as a random effect meant that analyses were conducted at the site level, but using the variation between sampling stations to inform model fitting. Models were fitted with R package "lme4" using the function '(g)lmer'. Using AIC_c values, models containing 'forest type' were compared to models containing just the random effect of 'site' ('null model'), to test whether differences between forest types exceeded those within sites and so assess variation within sites. Means and confidence intervals of the three response variables were extracted for unlogged continuous forest, twice-logged continuous forest and fragment sites. Differences between the three habitat types were considered significant if confidence intervals did not overlap, and if the 'null model' had a higher AIC_c value than the model containing forest type. This was repeated for each of the three response variables (dung removal, seed burial and seed dispersal).

Parametric assumptions of data were tested prior to final analyses and appropriate error distributions chosen to ensure assumptions were met (Negative-binomial distribution for dung removal and seed burial, Poisson distribution for horizontal seed dispersal). Outlying points were detected by calculating Cook's distances, to identify points with large residuals and high leverage in the model. Data points with Cook's distance values greater than 4/N (i.e. 4/143 = 0.026) were excluded from analyses (Bollen & Jackman 1990), and so for dung removal and seed burial models all three sampling stations from one outlying site (site 18: 5 ha fragment) were removed. There is currently no method for calculating R^2 values for models with negative-binomial distributions, but for the horizontal dispersal model fitted with a poisson distribution I present marginal (fixed effects only) and conditional (fixed and random effects (sampling station)) R^2 values of each model (*sensu* Nakagawa & Schielzeth 2013). The conditional R^2 value allows for variation within sites to be quantified, relative to the variation explained by forest type.

6.3.4.ii Effects of fragment area, forest quality, and isolation on ecosystem functions (Hypothesis 3)

GLMMs were also used to examine differences in dung removal, seed burial and horizontal seed dispersal (response variables) among 16 fragments in relation to changes in fragment area, forest quality and isolation. Continuous forest sites were excluded from these analyses because they cannot be given area or isolation values. Data from all 123 sampling stations across the 16 forest fragment sites were analysed. Fragment area, forest quality and isolation were fitted as fixed effects and site was fitted as a random effect. Therefore, as for analyses of differences between continuous forest and fragments, analyses were effectively conducted at the site level but using the variation between sampling stations to inform model fitting. I tested for assumptions and outliers as described above (Section 6.3.4.i). The same outlying site was removed and the same error distributions were fitted as described in section 6.3.4.i.

For each of the three response variables, models were constructed with all possible combinations of fragment area, forest quality and isolation as well as two-way interactions and second-order polynomials (to test for curvilinear relationships or possible thresholds). I excluded three-way interactions from models to avoid over-fitting. A ‘null model’ was also included containing just the random effect of site, to test the overall goodness of fit of the models and to test whether differences among sites exceeded those within sites. These models were then ranked according to their AIC_c values to compare the relative importance of forest fragment area, forest quality and isolation for explaining differences in dung removal, seed burial and horizontal seed dispersal. The best model was defined as that with the lowest AIC_c value, and the best model set as any models with AIC_c values within 2 units of the best model (Bolker et al. 2009). Coefficients and 95% confidence intervals were then extracted from the single best model, or averaged across the set of best models. A significant relationship was assumed if 95% confidence intervals did not overlap zero. Conditional and marginal R^2 values were calculated.

6.4 Results

6.4.1.i Differences in ecosystem functions between unlogged continuous forest, twice-logged continuous forest and forest fragments (Hypothesis 1 & 2)

There were no significant differences in dung removal, seed burial or seed dispersal between unlogged and twice-logged continuous forest sites, although seed dispersal was slightly higher in unlogged forest and approached significance (Figure 6.2, Table 6.1). By contrast, dung removal and seed dispersal, but not seed burial, were significantly higher in both unlogged and twice-logged continuous forest sites than in forest fragments (Figure 6.1, Figure 6.2). Therefore, differences between continuous forest sites and fragments generally exceeded those between unlogged and twice-logged continuous forest sites.

The percentage of dung removed was on average 75% lower in forest fragments than in either unlogged or twice-logged continuous forest (Figure 6.1, Table 6.1). The highest percentage of dung removed in any fragment was 33% (site 14), whilst the lowest in continuous forest was 74% (site 2: twice-logged continuous forest). The percentage of seeds rolled was significantly lower in fragments than in both unlogged and twice-logged continuous forest, with over 90% fewer seeds rolled horizontally in fragments than in the continuous forest sites (Figure 6.2, Table 6.1). The percentage of seeds buried was not significantly different between fragments and continuous sites, probably because of large variation within sites (Figure 6.2, Table 6.1), but was on average 34% and 64% lower in fragments than in unlogged and twice-logged forest, respectively (Figure 6.2, Table 6.1).

Table 6.1. Table comparing means and 95% confidence intervals of dung removal, seed burial and seeds rolled in unlogged continuous forest, twice-logged continuous forest and fragments. Non-overlapping confidence intervals indicate a significant difference. The means and confidence intervals presented are back-transformed to the original variable scales from the log link functions used in the GLMMs explaining the asymmetrical 95% CIs shown here.

Response variable	**Estimate (and 95% CIs)**		
	Unlogged	**Twice-logged**	**Fragments**
Dung removed	85.1(59.0,122.8)	73.8 (49.8,109.4)	17.0 (13.5,21.5)
Seeds buried	24.4 (2.08,290.0)	44.3 (3.8,528.5)	4.8 (2.5,9.3)
Seeds rolled	1.5 (0.9,2.5)	0.3 (0.1,0.9)	0.02 (0.004,0.07)

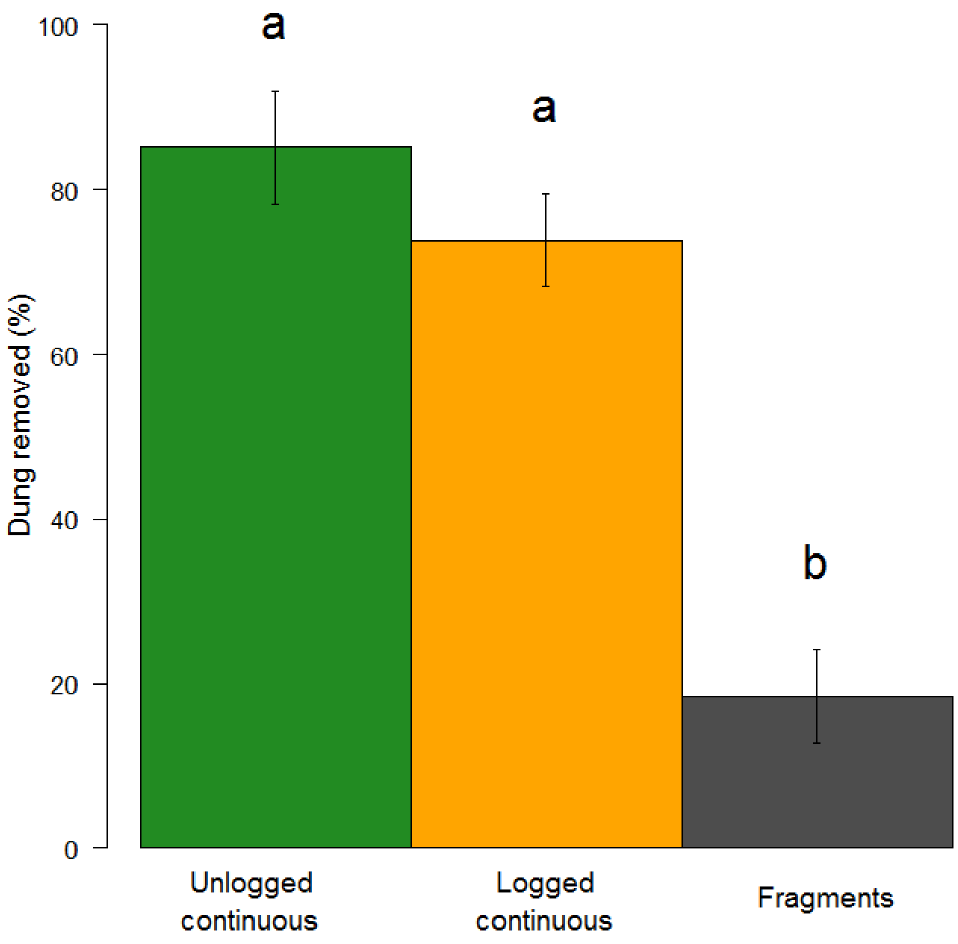

Figure 6.1. A comparison of dung removal in unlogged continuous forest (n = 1 site, 10 stations), twice-logged continuous forest (n = 1 site, 10 stations) and fragments (n =16 sites, 123 stations). Values plotted are mean values per sampling station, i.e. on average 85% of dung was removed at each sampling station in unlogged continuous forest. Letters indicate significant differences between sites, based on GLMMs. Error bars show standard errors.

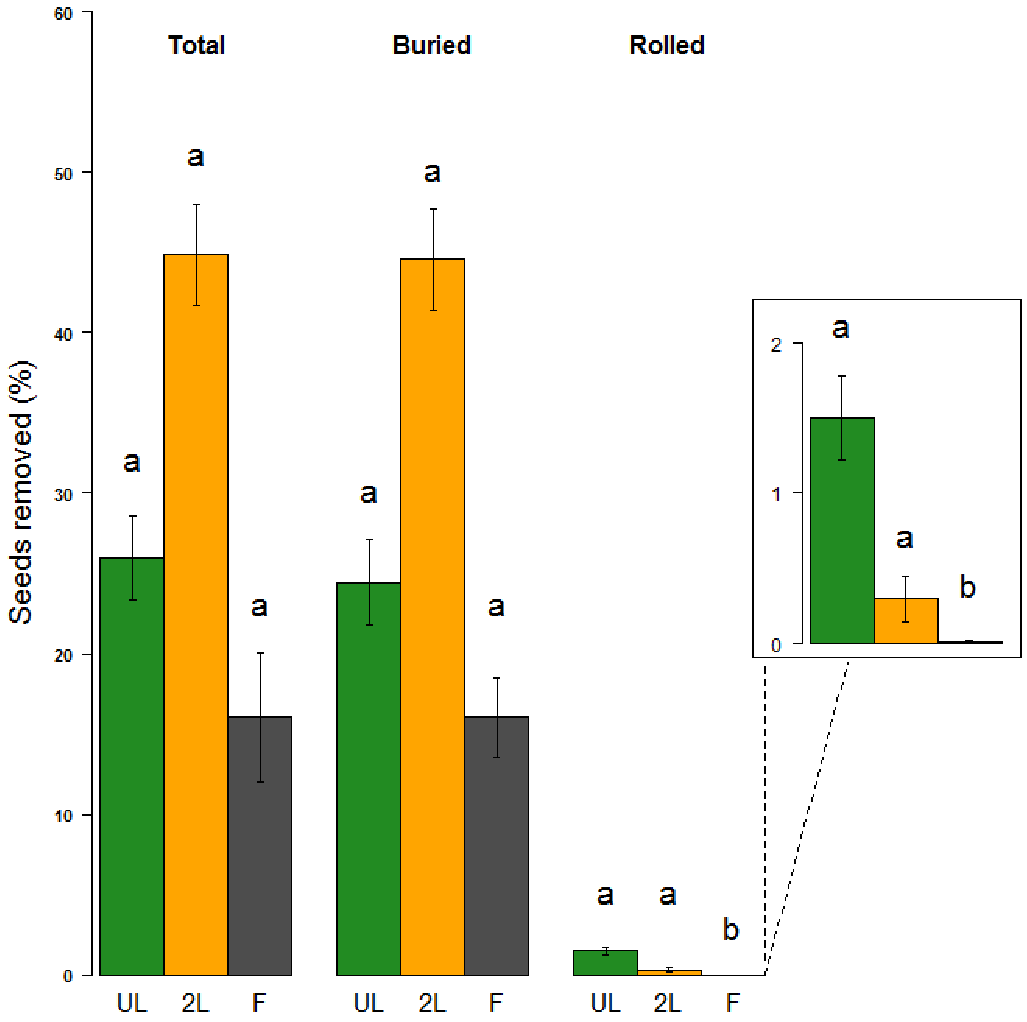

Figure 6.2. A comparison of the percentage of seeds removed in total, buried and rolled in unlogged continuous forest (n = 1 site), twice-logged continuous forest (n = 1 site) and fragments (n =16 sites). Values plotted are mean values per sampling station, i.e. on average 26% of seeds were removed in total at each sampling station in unlogged continuous forest. The inset shows a close up of the percentage of seeds rolled. Different letters above bars indicate significant differences between forest types, according to GLMMs. UL = unlogged continuous forest, 2L = twice-logged continuous forest and F = fragments. Error bars show standard errors.

For dung removal and horizontal seed dispersal, models containing ‘forest type’ as a fixed effect as well as ‘site’ as a random effect, had lower AIC_c values than models containing just ‘site’ ($\Delta_i > 2.84$), showing that forest type explained more variation in the data set than did within site variation for these functions (Table 6.2). Conversely, for seed burial the model containing just ‘site’ had a lower AIC_c value than the model containing ‘forest type’, indicating that there was more variation in seed burial within sites than between forest types (Table 6.2), and probably explaining the absence of a significant difference in seed burial between forest types.

*Table 6.2. Table of models comparing ecosystem functions between unlogged continuous forest, twice-logged continuous forest and forest fragments. For each response variable two models are presented, one including forest type and site as random effect ('Type') and one just containing the random effect of site ('1'). K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C): Marginal (M) and conditional (C) estimated R^2-vaues, based on Nakagawa & Schielzeth (2013). *Data were fitted using a negative-binomial distribution to account for overdispersion. There is currently no way of calculating R^2 values for this distribution, and so R^2 values are not shown for these models. These models also excluded one site (site 18) as it was an outlier.*

Response variable	Model	K	AICc	Δi	ωi	LL	R^2 (M,C)
Dung removal*							
	Type	5	1085.2	0	0.81	-537.4	-
	1	3	1088.0	2.84	0.19	-540.9	-
Seed burial*							
	1	3	928.8	0	0.64	-461.3	-
	Type	5	929.9	1.14	0.36	-459.7	-
Seed dispersal							
	Type	4	33.91	0	1	-12.8	0.30,0.30
	1	2	48.58	14.67	0	-22.3	0,0.50

6.4.1.ii Effects of fragment area, forest quality, and isolation on ecosystem functions (Hypothesis 3)

Differences in dung removal, seed burial and horizontal seed dispersal between continuous forest and fragments generally exceeded differences among fragments. For example, when outlying site 18 was excluded dung removal and horizontal seed dispersal were more than 50% lower in the 'best' fragments (Site 14 for dung removal, Site 9 for seed dispersal) compared with continuous forest sites (Figure 6.3). Among forest fragments there was no significant decline in horizontal seed dispersal in relation to fragment area, quality or isolation. Very few seeds were dispersed horizontally in fragments, although there was no horizontal dispersal in any fragments smaller than 120 ha. Dung removal significantly declined with increasing isolation of fragments (Figure 6.3, slope estimate: -0.34, 95% CIs -0.57, -0.11), and was significantly positively correlated with the quadratic of forest quality (Figure 6.3, slope estimate: 3.92, 95% CIs 0.15, 7.68), and significantly negatively correlated with the quadratic of area (Figure 6.3, slope estimate: -9.20, 95% CIs -13.56, -4.85). This meant that dung removal increased in medium sized fragments but decreased in small and large fragments (Figure 6.3), and this relationship was significant even when fragment area was the only explanatory variable. Dung removal increased with forest quality but more steeply in better quality sites, and also declined with increasing isolation distance. However, these relationships were only significant in models also containing area, indicating relatively weak relationships between dung removal and both forest quality and isolation. This showed that, among fragments, area had a stronger effect on dung removal than isolation and forest quality, but differences among fragments were far smaller than those between continuous forest and fragments.

Differences in seed burial across all sites were smaller than differences in dung removal. Seed burial was not significantly lower in fragments than in continuous forest, although seed burial in twice-logged continuous forest was higher than in all fragments (except for outlying site 18), and seed burial in unlogged continuous forest was higher than in 12/15 fragments (excluding site 18). In analyses of fragments, seed burial was significantly negatively related to the quadratic of area (Figure 6.3, seed burial: slope estimate: -9.20, 95% CIs -16.33,-2.06) and significantly positively related to the quadratic of forest quality (Figure 6.3, seed burial: slope estimate: 7.01, 95% CIs 1.50, 12.53). The relationship of seed burial with isolation (linear and quadratic) neared significance with confidence intervals only just overlapping zero, suggesting a possible decline in seed burial with increasing isolation, and a steeper decline in less isolated sites. As with dung removal, seed burial was highest in intermediate-sized fragments and lowest in the smallest and largest fragments. Seed burial increased with increasing vegetation quality, and more steeply in better quality fragments. However, the relationships of seed burial with area and forest quality were only significant in models also containing isolation distance, indicating relatively weak relationships and little overall difference in seed burial among fragments.

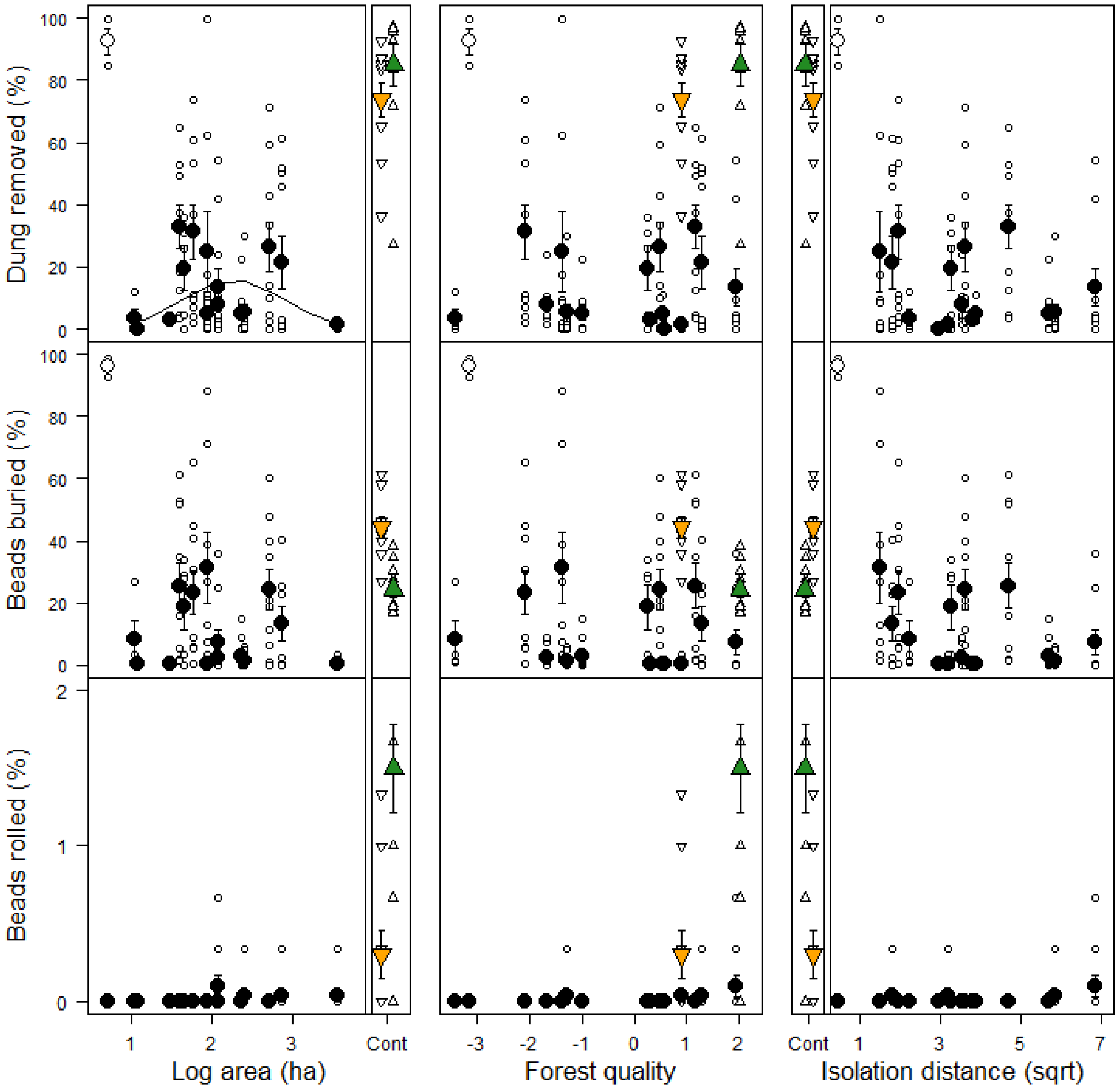

Figure 6.3. A comparison of dung removal, seed burial and seed dispersal in relation to log10 fragment area, forest quality and isolation distance (sqrt). Large and coloured symbols show means and standard error for each site, hollow symbols are values for each sampling station. Green and upward pointing triangles represent undisturbed continuous forest sites and stations; orange and downward pointing triangles represent twice-logged continuous forest sites and stations; and black and hollow circles represent fragment sites and stations. In plots of dung removal and seed burial the hollow circle is site 18 that was excluded from these models as it was an outlier.

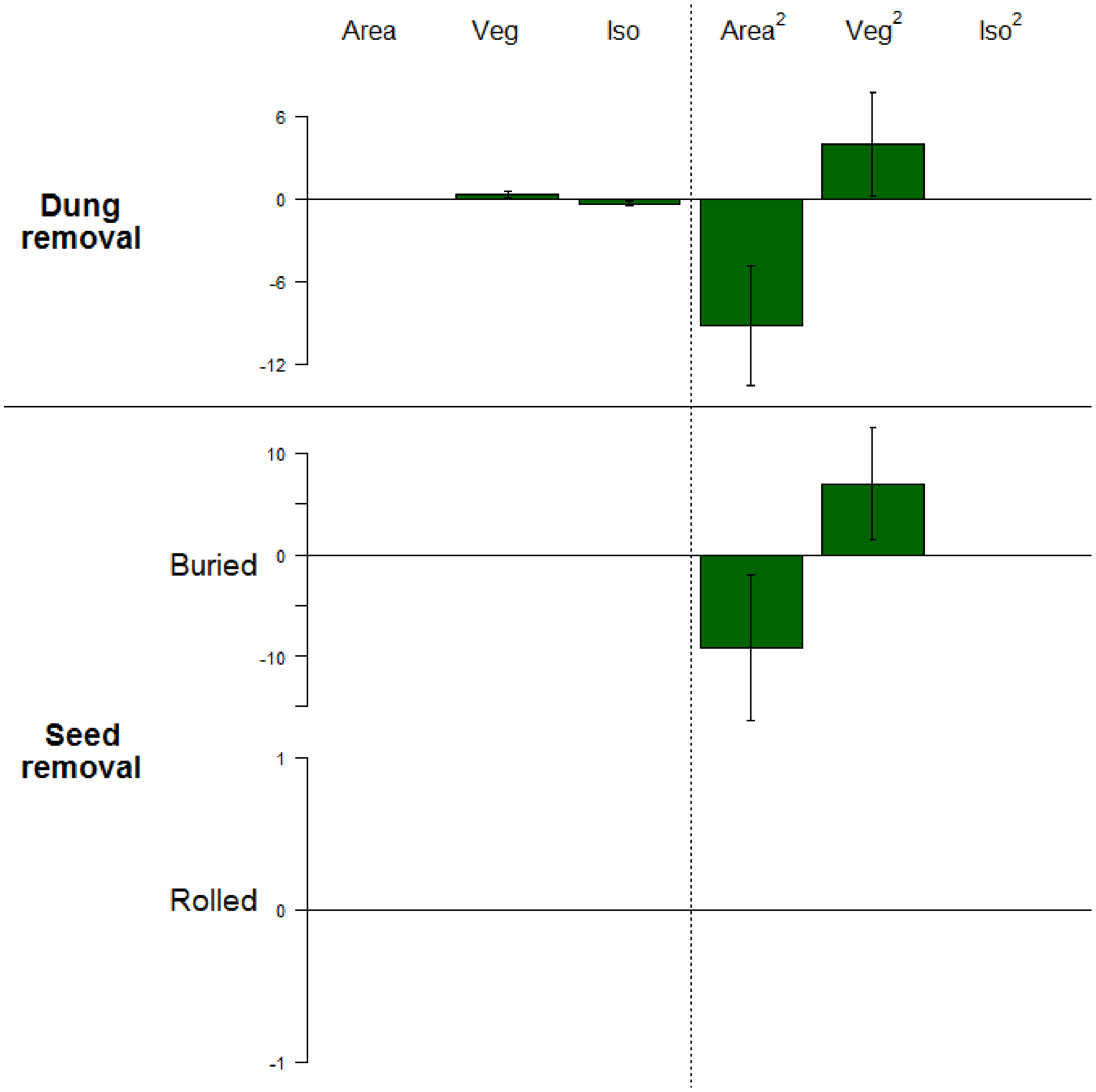

Figure 6.4. Plot of effect sizes (regression slope values) of explanatory variables (x axis) against response variables (y axis). Effect sizes are plotted only for variables included in best models according to AICc model ranking and where confidence intervals do not overlap zero. For linear predictors, positive effect sizes indicate positive relationships between the predictor and response variables, negative effect sizes indicate negative relationships. For curvilinear predictors, a positive effect size indicates a convex relationship, whilst a negative effect size indicates a concave relationship between the response and predictor variable. Errors bars show 95% confidence intervals. Veg = vegetation quality and Iso = isolation distance. There were no significant interactions.

Fragment area, isolation and forest quality were in the best model sets for all ecosystem functions (Figure 6.4, Table 6.3). Dung removal and seed burial increased significantly with area and forest quality, whilst isolation distance was only significantly related to dung removal, suggesting that area and forest quality were more important variables than isolation. However, for seed burial and horizontal seed dispersal the ‘null model’ containing just ‘site’ as a random effect was either the best (seed burial) or second best (horizontal seed dispersal) model (Table 6.3), showing that within fragment variation exceeded variation between fragments for these functions. Inspection of Figure 6.3 also shows substantial within fragment variation in dung removal, suggesting that other factors beyond fragment area, forest quality and isolation may also be important predictors of the three dung beetle functions measured in this study. Overall, following large declines in dung beetle functions from continuous forest to fragments, there was little difference in dung removal, seed burial and horizontal seed dispersal among fragments, although sites ≥120 ha supported both dung removal and some very low rates of horizontal dispersal.

*Table 6.3. Table of best models ($\Delta_i < 2$) explaining differences in ecosystem functions among forest fragments. K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C): Marginal (M) and conditional (C) estimated R^2-values, based on Nakagawa & Schielzeth (2013). *Models excluded outlying site 18 and fitted with a negative-binomial distribution to account for overdispersion. There is no current way of calculating R^2 values for this distribution.*

Response variable	Model	K	AICc	Δi	ωi	LL	R^2 (M,C)
Dung removal*							
	Area^2+Veg^2+Iso	8	850.6	0	0.36	-416.6	-
	Area^2+Veg+Iso	7	851.1	0.6	0.26	-418.1	-
	Area^2+Iso	6	851.4	0.9	0.23	-419.4	-
	Area^2+Veg^2+Iso^2	9	852.2	1.66	0.16	-416.3	-
Seed burial*							
	1	3	729.5	0	0.27	-361.7	-
	Iso^2	5	729.9	0.4	0.22	-359.7	-
	Iso	4	730.5	1	0.16	-361.1	-
	Area^2+Iso	6	731.1	1.61	0.12	-359.2	-
	Area^2+Veg^2+Iso	8	731.2	1.65	0.12	-356.9	-
	Veg	4	731.5	1.94	0.1	-361.6	-
Seeds rolled							
	Veg	3	17.0	0	0.18	-5.4	0.34,0.34
	1	2	17.1	0.08	0.17	-6.5	0,0
	Iso	3	17.6	0.6	0.13	-5.7	0.17,0.17
	Area	3	18.6	1.62	0.08	-6.2	0.06,0.06
	Area+Iso	4	18.7	1.67	0.08	-5.2	0.44,0.44
	Veg+Iso	4	18.7	1.69	0.08	-5.2	0.29,0.29
	Veg^2	4	18.7	1.72	0.08	-5.2	0.21,0.21
	Iso^2	4	19.0	1.92	0.07	-5.3	0.15,0.15
	Area+Veg	4	19.0	1.93	0.07	-5.3	0.40,0.40
	Area+Iso^2	5	19.0	1.94	0.07	-4.2	0.62,0.62

6.5 Discussion

6.5.1 Impacts of fragmentation on dung beetle functions

There was no significant difference in dung removal, seed burial or seed dispersal between unlogged and twice-logged continuous forest sites, supporting the prediction of hypothesis 1 that dung beetle functions would vary little between these sites (Hypothesis 1). There have been no previous studies specifically assessing the impact of two rotations of selective logging on dung beetle functions, although Slade et al (2011a) showed that dung removal and seed burial declined after high-intensity, but not low-intensity, selective logging in Sabah, Malaysia. The high-intensity logged sites used by Slade et al. (2011) were in the same forest management area as the twice-logged site used in this study, but were sampled prior to the second logging rotation. This suggests that the twice-logged forest site in this study was more degraded than the high-intensity sites sampled by Slade et al. (2011), yet contrary to their findings, shows that dung beetle functions can be maintained in highly degraded forest. I only sampled at one twice-logged and one unlogged continuous forest site and so it is possible that differences in dung beetle functions would emerge with greater replication. Nonetheless, these findings indicate a resilience of dung beetle functions to forest degradation and these high rates of functioning in degraded forest may help to promote forest regeneration in degraded forest sites, given that dung and seed burial can increase plant growth and seedling establishment (Andresen 2001; Bang et al. 2005).

In contrast to the negligible impacts of selective logging, forest fragmentation led to large declines in all dung beetle functions. Dung removal, seed burial and seed dispersal were all at least 50% lower in forest fragments than in continuous forest, supporting hypothesis 2. Declining dung removal and seed burial are consistent with Neotropical and Afrotropical studies (Klein 1989; Andresen 2003; Chapman et al. 2003), although fragments in this study were much larger (<3,529 ha) than those in the previous studies (<100 ha) suggesting that the impacts of fragmentation may be stronger than previously thought. Horizontal seed dispersal has not yet been measured separately to seed burial and so its decline in fragments is a novel finding that may have implications for plant recruitment. In unlogged forest, the percentage of seeds dispersed horizontally (~1-2%) was low compared to the number buried (~30%) showing that these horizontal dispersal events are relatively rare even in undisturbed sites. However, the ratio of seeds dispersed horizontally to those buried declined markedly in fragments compared to continuous forest sites with a relatively minor, and non-significant, decline in seed burial and a significant, almost total, decline in seed dispersal in fragments, suggesting that the decline of seed dispersal was not an artefact of insufficient sampling. Secondary seed dispersal by rollers and tunnellers lead to distinct seed dispersal distributions and so could have different impacts on seed fate and seedling germination (Andresen & Feer 2005; Lawson et al. 2012). Therefore, the different responses of seed burial and seed dispersal to fragmentation reported in this chapter indicate the importance of measuring these functions separately.

There was little difference in dung beetle functions among fragments of different size, forest quality and isolation distance. Horizontal seed dispersal was not affected by changes in area, quality or isolation, but dung removal and seed burial were apparently slightly higher in intermediate-sized, less isolated and better quality fragments. The weak effect of fragment area on dung removal contrasts to large declines with declining fragment area reported previously (Klein 1989; Andresen 2003). However, the fragments sampled in this study were much larger (up to 3,529 hectares) than those considered in the previous studies of ≤100 hectares. An equivalent comparison using the smallest fragments sampled in this study reveals a similar trend with very low rates of dung removal in fragments ≤40 hectares. Furthermore, no seed dispersal was recorded in fragments smaller than 100 hectares in this study, suggesting that smaller fragments support very low rates of dung beetle ecosystem functions. Low rates of horizontal seed dispersal were recorded in fragments larger than 100 hectares, but whether this seed dispersal is maintained over time will depend on residual extinction debt in these sites that could drive species extinctions for decades after fragment isolation (Turner et al. 1996; Wearn et al. 2012; Gibson et al. 2013). The large declines in ecosystem functioning in small fragments reported here have been shown elsewhere (Klein 1989; Andresen 2003), but this study also shows that fragments much larger than 100 hectares support greatly reduced rates of dung beetle ecosystem functions compared to continuous forest, showing that even large fragments are no substitute for continuous forest. Overall, there was little variation in dung beetle functions in relation to fragment area, forest quality or isolation, but seed dispersal and seed burial showed large within site variation which suggests that other factors may be important predictors of these functions.

6.5.2 Within site variation in dung beetle functions

Among forest fragments, dung removal, seed burial and seed dispersal were characterised by large within site variation (Figure 6.3), which generally exceeded variation among fragments (Table 6.3). This within site variation also appeared to be greater in fragments than in continuous forest sites. For example, within four of the fragments sampled (sites 5, 10, 12 and 14) the percentage of seeds buried per sampling station varied hugely from <1% to >60%, in contrast to variation from 17-38% among unlogged continuous forest sampling stations and 27-61% among twice-logged forest sampling stations. This suggests that localised abiotic and biotic factors may be important predictors of dung beetle functions, especially in forest fragments. It is possible that the microclimate at individual sampling stations influences bait detectability. For example, dung piles may dry out and lose attractiveness faster in more open, hotter and drier locations (Spector & Ayzama 2003; Larsen & Forsyth 2005). Open sites such as these were probably more common in fragments than in continuous forest sites, given that fragments had lower canopy cover and higher temperatures than continuous forest (Chapter 4). This could explain the variation in dung beetle functions in fragments. Higher temperatures in fragments could also lead to soil desiccation and compaction, which has been shown to reduce dung beetle abundances (Doube 1983) and could explain the reduction of rollers and seed dispersal in fragments (Edwards et al. 2013). Alternatively, the within site variation in functions could be the result of patchier dung beetle distributions in fragments. For example, reduced dung availability in fragments may mean that dung beetles have to disperse further to find dung, leading to patchier beetle distributions and more sporadic discovery of dung piles. If this were the case then species occurring in forest fragments would be expected to be species with good dispersal abilities. However, little is known about the dispersal ability of dung beetle species in Borneo and so research is required to assess the movement of different dung beetle species within fragmented landscapes and consequences of this for ecosystem functioning.

6.5.3 Altered functional requirements in forest fragments

The ultimate cause of both reduced dung beetle species richness and biomass, and reduced ecosystem functions following forest fragmentation may be due to reduced dung availability in fragments. Asian elephants (*Elephas maximus borneensis*), and other large herbivores such as Banteng (*Bos javanicus lowi*) found in continuous forest were absent in the forest fragments sampled in this study (Timmins et al. 2008; Alfred et al. 2010). These species produce the largest dung deposits and are likely to provide the majority of dung resources in natural forest, meaning that the availability of dung resources is probably greatly reduced in forest fragments. Cattle are occasionally kept in 7-15 year old oil palm plantations (Corley & Tinker 2008), but were not kept in plantations surrounding the fragments in this study and so unlike studies of fragments in cattle pasture matrices there was no supplement of cattle dung to substitute for the loss of native mammal dung (Amézquita & Favila 2010). Reduced dung availability can lead to reduced dung beetle biomass, especially of functionally important large-bodied species (Lumaret et al. 1992; Nichols et al. 2009), which could in turn explain the reduction in dung removal and seed burial in fragments. This means that the decline in dung removal in fragments may have occurred because there is less dung to decompose in forest fragments (Gregory & Gaston 2000). If this is the case, then declines in dung removal may not necessarily lead to an overall decline in nutrient cycling or loss of nutrients from forest fragments. For example, if there is a decline in herbivore dung availability in fragments and mammals are the dominant herbivores, then the amount of herbivory may also have declined and so leaf litter production and leaf litter decomposition may have increased. In this hypothetical example, the reduction in dung decomposition may be compensated for by increased leaf litter decomposition meaning that nutrients remain within the ‘closed-loop’ of the fragment ecosystem. Further research is needed to quantify potential shifts in different nutrient cycling components to assess whether other saprotrophic taxa are able to compensate for declines in dung removal.

There may be a reduced requirement for dung removal in forest fragments compared to continuous forest, but the same is unlikely to be true for secondary seed dispersal by dung beetles. Fragmentation can alter plant species composition and abundance (Benitez-Malvido & Martinez-Ramos 2003), but assuming that remaining species are reproductively active, one would expect the requirement for seed dispersal to be maintained in fragments. Secondary seed dispersal will remain a vital process to enhance the reproductive success and promote seedling establishment of animal-dispersed plant species in forest fragments (Vander Wall & Longland 2004). However, secondary seed dispersal by dung beetles is a by-product of dung removal, and so it is ultimately controlled by the availability of dung and not the availability of seeds. Therefore, a decline in dung availability in fragments could lead to reduced secondary seed dispersal even if seed production remains constant.

6.5.4 Plant composition and the viability of HCV fragments

Climax canopy tree composition in Southeast Asian forests is dominated by species of the Dipterocarpaceae family that are primarily gravity dispersed (Kettle 2012). However, in Bornean lowland rain forests Dipterocarps only account for ~22% of all trees, and up to 34% of plant species are animal dispersed (Sakai et al. 1999; Slik et al. 2003). Gibbons and other frugivores regularly consume and defecate seeds up to 2 cm in length from a range of plant species (McConkey 2009), and recruitment of these animal-dispersed species in fragments could be directly affected by reduced seed dispersal and seed burial. Declining seed burial may alter plant composition by increasing seed and seedling mortality through density-dependent mortality and seed predation (Andresen 2001; Terborgh et al. 2001; Bagchi et al. 2014). Rollers move fewer seeds in total than tunnellers, but these movements can reduce density-dependent seedling mortality and seed predation by moving seeds away from the dung where density is highest, and by burying them at shallower depths than tunnellers that are better suited to seedling germination and establishment (Andresen & Feer 2005; Nichols et al. 2008). Seed predation is often elevated in forest fragments (Terborgh et al. 2001; Andresen 2003), suggesting that secondary seed dispersal will be important for seedling recruitment in Southeast Asian forest fragments.

This chapter shows that wherever possible, HCV areas in plantations should protect continuous forest to maximise dung beetle ecosystem functions. This tallies with recommendations on how to minimise species extinctions following fragmentation (Pimm & Brooks 2013). Best practice in HCV identification and management indicates that buffers should be established around HCV areas to try and minimise encroachment and edge effects (Brown et al. 2013). However, this chapter shows that large fragments of 500-3,000 hectares do not support the same rate of dung beetle functions as logged or unlogged continuous forest, suggesting that even large buffer zones may be insufficient to ensure the maintenance of HCVs over time. Furthermore, given that many HCV areas consist of logged forest (section 6.3.1), and seed dispersal and decomposition can directly affect plant recruitment, reductions in these functions could inhibit forest regeneration in fragments, especially in the smallest fragments where no seed dispersal was recorded. This could hinder efforts by oil palm companies to enhance HCVs over time, and suggests that forest management interventions, such as enrichment planting, may be required to retain natural regeneration and species composition over time. Such management could also improve dung beetle functions given that dung removal and seed burial were higher in better quality sites.

Enrichment planting and climber cutting could increase recruitment of canopy tree species, canopy cover and vertical vegetation complexity in less disturbed sites (Chapter 4). However, the fragments with highest forest quality in this study had lower rates of dung removal than continuous forest sites, suggesting that improvements in forest quality in fragments will never restore rates of this function to the levels found in continuous forest sites (Figure 6.3). Furthermore, whilst studies have shown that dung beetles and other invertebrates can quickly re-colonise areas of rehabilitated forest contiguous with less disturbed forest areas (Edwards et al. 2012a; Barnes et al. 2014), this has not been demonstrated in fragmented habitats and would only be feasible if functionally important species still persist in fragments prior to rehabilitation or can recolonize after rehabilitation. Research is needed in this respect to assess the dispersal abilities of functionally important dung beetle species.

6.5.5 Conclusion

Secondary seed dispersal and dung removal by dung beetles were greatly reduced in forest fragments compared to continuous forest. Horizontal seed dispersal was most adversely affected and was only recorded in 4/16 forest fragments whereas dung removal and seed burial were maintained in the smallest forest fragments, albeit at reduced rates compared to continuous forest. Continuous forest, even when twice-logged, is irreplaceable for the maintenance of dung beetle ecosystem functions and so oil palm managers and HCV assessors should focus on protecting unlogged and degraded continuous forest wherever possible. If only fragments can be protected then their size should be maximised to maintain some horizontal seed dispersal and dung removal. This chapter investigated how dung beetle ecosystem functions responded to forest fragmentation, and Chapter 5 revealed major changes in dung beetle species richness and roller and tunneller biomass in response to fragmentation. Analyses are needed to link changes in dung beetle species richness and functional group biomass to changes in ecosystem functions, and are considered in Chapter 7. This can help us understand mechanisms underpinning changes in function, and hence to better predict changes in function in response to future land-use changes.

Chapter 7 - Relating species richness to ecosystem function in fragmented tropical landscapes: the importance of functionally dominant species

7.1 Abstract

Biodiversity declines have been linked to changes in ecosystem functioning based on highly-controlled experiments, but there is little evidence for how species losses affect ecosystem functioning in natural ecosystems. I analysed the relationship between dung beetle biomass and species richness and three ecosystem functions (dung removal, seed burial and seed dispersal). I used data collected from 16 forest fragments and two continuous forest sites, which provided a natural gradient of species richness and biomass in response to habitat fragmentation and degradation. Biomass was a more important predictor of dung removal and seed burial functions than was species richness. A single genus of large tunnellers (*Catharsius spp*.) was responsible for 77% of dung removal in forest fragments, compared to ~33% in continuous forest, demonstrating the importance of disturbance-tolerant species for maintaining ecosystem functioning in degraded landscapes. However, dung removal rates in fragments were highly variable compared with continuous forest where the combination of high species richness and high biomass led to consistently high rates of dung removal. Species richness of rollers was also the best predictor of seed dispersal in fragments, showing that high dung beetle species richness is needed for multiple dung beetle functions. Maximising the size of forest fragments in oil palm plantations could increase dung beetle species richness and biomass and improve the stability of dung beetle functions in these agricultural landscapes.

7.2 Introduction

Biodiversity underpins the functioning of ecosystems and the provision of ecosystem services (Millennium Ecosystem Assessment 2005; Hooper et al. 2012). However, anthropogenic loss, fragmentation and degradation of natural habitats are causing global declines in biodiversity and widespread species extinctions (Pimm et al. 1995; Green et al. 2005; Kissinger et al. 2012). These biodiversity losses are altering ecosystem functioning and the delivery of ecosystem services, such as decomposition and pollination, required for stable ecosystems and provision of natural resources (Cardinale et al. 2012; Hooper et al. 2012). Consequently, it is crucial to understand how biodiversity contributes to ecosystem functioning in order to predict changes in function resulting from habitat degradation and fragmentation.

Initial theoretical research into the biodiversity and ecosystem functioning (BEF) relationship proposed a positive linear relationship between species richness and ecosystem functioning (Schulze & Mooney 1994). Several decades of research have subsequently shown that this strict linear relationship is too simplistic for most taxa and ecosystem functions , but that there is strong evidence for a positive relationship between the number of species and the rate of ecosystem functioning (Loreau et al. 2001; Hooper et al. 2012). Key mechanisms that have been proposed to support this positive relationship are the ‘complementarity effect’ and the ‘selection effect’ (Loreau & Hector 2001). ‘Complementarity’ suggests that niche partitioning and facilitation among species leads to more efficient resource use and functioning when more species are present, and broadly supports a linear positive relationship whereby each additional species increases ecosystem functioning. Complementarity can occur spatially or temporally and includes the buffering role that different species play in providing ecosystem functions under different environmental conditions (e.g. Brittain et al. 2013). The ‘selection effect’ argues that certain species tend to be functionally dominant and that increasing species richness merely increases the probability of these functionally dominant species being present. The selection effect supports a saturating relationship between species richness and function whereby only the addition of functionally dominant species leads to any substantial increase in function (Naeem et al. 2009). In reality, the relative importance of these two mechanisms varies depending on the scale of study, ecosystem function and study taxon, but both mechanisms have important roles in ecosystem functioning (Hooper et al. 2005), and consideration of these mechanisms helps in understanding the contribution of species richness and composition to ecosystem functioning.

The ‘selection effect’ is derived from the fact that individual species vary greatly in their contribution to different ecosystem functions. For example, research from tropical forests in Mexico and Malaysia showed that just 13% of tree and dung beetle species provided 90% of carbon storage and 50% of dung removal, respectively (Balvanera et al. 2005; Slade et al. 2007a). This functional dominance generally occurs when species have key functional traits or when they are highly abundant (Bengtsson 1998; Jaillard et al. 2014). All ecosystems, including highly diverse tropical ecosystems are characterised by uneven species abundances, whereby some species are far more common than others (Fisher et al. 1943b), and studies in marine and terrestrial systems have shown that the most common species can be functionally dominant in terms of productivity, bioturbation and carbon storage (Solan et al. 2004; Gaston 2010). Key functional traits vary depending on the taxon and function considered, but body size is a universally important functional trait because large-bodied species consume more resources and are more functionally efficient (White et al. 2007). For example, larger plants contribute more to primary productivity and larger dung beetles bury more dung (Doube 1990; Huston 1997a; Larsen et al. 2005b). Many BEF experiments are carried out in controlled conditions where species biomass or abundance is held constant and species richness is varied, and yet biomass compensation often outweighs any impacts of species richness on functioning in the field (Reiss et al. 2009). Therefore, given the potential importance of species traits and biomass in determining rates of ecosystem functioning (Bengtsson 1998), more studies are needed that directly compare the effects of species richness and biomass on ecosystem functions, especially under natural levels of diversity in the field.

Forest fragmentation can provide natural gradients of species richness, because species richness declines with decreasing fragment size in line with Species-Area Relationships (MacArthur & Wilson 1967). However, species extinctions following fragmentation are typically non-random (Hill et al. 2011) and so they can lead to non-random impacts on ecosystem functioning (Petchey & Gaston 2002). In cases when ‘response traits’ to fragmentation are also ‘functional effect traits’ (Chapter 5; Lavorel & Garnier 2002) then the loss of species with these traits will lead to changes in functioning in response to habitat fragmentation. For example, large-bodied frugivorous birds are vital for long-distance seed dispersal but are vulnerable to extinction following fragmentation (Moran et al. 2009). Alternatively, if functional traits are not response traits then functioning may be maintained in fragments. This can occur if functionally important species are resilient to fragmentation or if other disturbance tolerant species can compensate for the loss of functionally important species found only in undisturbed forest (Schwartz et al. 2000; Smith & Knapp 2003). For example, invasive black rats (*Rattus rattus*) and colonist silvereyes (*Zosterops lateralis*) were able to pollinate three native plant species following the loss of endemic pollinators in New Zealand (Pattemore & Wilcove 2012). Furthermore, Schleuning et al. (2011) showed that leaf litter decomposition increased following fragmentation whilst antbird predation decreased in response to respective increases and declines in isopod and antbird abundance in fragments compared to continuous forest. These idiosyncratic effects of species loss and fragmentation on ecosystem function highlight the importance of measuring species responses to fragmentation and their functional contributions. There is an urgent need for more studies in fragmented natural ecosystems.

Expansion of oil palm agriculture over the last 40 years has caused widespread forest loss and fragmentation in Southeast Asia and increasingly in Africa and the Neotropics (Butler et al. 2009; Garcia-Ulloa et al. 2012). Research is needed to assess the impacts of tropical forest fragmentation on functionally important species and their ecosystem functions. Dung beetles are an excellent study group for addressing this question, because they have key functional roles in tropical forests, contributing to dung removal and secondary seed dispersal (Nichols et al. 2008), and they exhibit different interspecific responses to forest fragmentation (Chapter 5; Larsen et al. 2005).

In Chapter 5, I showed that dung beetle species richness and biomass declined following fragmentation, and that species richness declined further with declining fragment area, whilst biomass showed no further declines beyond those of fragmentation *per se*. However, biomass responses to fragment area varied depending on functional group, with large tunneller biomass (species important for dung removal and seed burial) showing no decline with fragment area but roller biomass (species important for seed dispersal) declining with fragment area. Reflecting these patterns, dung removal and seed burial varied little in response to fragment area whereas seed dispersal declined weakly with fragment area, suggesting that biomass of functionally important rollers and tunnellers determined responses of these ecosystem functions, rather than declines in species richness. I test this hypothesis in this chapter. However, the resilience of large tunneller biomass and dung removal to declining fragment area, in spite of declining species richness, suggests that large tunnellers may become increasingly more important for dung removal in fragments compared with continuous forest sites, where other species may contribute to dung removal in these highly species diverse sites. I showed in Chapter 4 that large tunneller biomass was dominated by two species from a single genus, *Catharsius spp.*. Therefore, to test the relative importance of large tunnellers for dung removal in continuous forest and fragment sites I used exclusion treatments to compare dung removal across 18 study sites when *Catharsius spp.* were present and absent. By doing this, I was also able to assess whether a single, disturbance-tolerant species (*Catharsius renaudpauliani*) can maintain functioning following the loss of other species in response to fragmentation, and compare the importance of *Catharsius spp.* relative to other functional groups for dung removal. This chapter tests the following hypotheses:

Hypothesis 1. Biomass is a more important predictor of dung removal, seed burial and seed dispersal than species richness.

Hypothesis 2. Dung beetle biomass and dung removal is dominated by *Catharsius spp.* across all sites, and excluding *Catharsius spp.* leads to large reductions in dung removal.

Hypothesis 3. *Catharsius spp.* are responsible for a greater proportion of dung removal in fragments than in continuous forest sites. Dung removal is supplemented by high biomass of species other than *Catharsius spp.* in continuous forest sites.

7.3 Methods

Dung beetles and their ecosystem functions (dung removal (with and without *Catharsius spp.*), seed burial and seed dispersal) were sampled in an unlogged continuous forest site (site 1), a twice-logged continuous forest site (site 2) and 16 forest fragments (sites 3-18; 5-3,529 ha) in Sabah, Malaysia between April and September 2012 and 2013 (Chapter 4). All forest fragments were isolated within oil palm plantations, and were situated between 0.2 and 46.7 km from continuous forest. There was considerable variation in forest quality among sites (Chapter 4) which broadly increased with fragment area, and was highest in continuous forest sites. Dung beetles and ecosystem functions were sampled in different years, but at the same sampling stations, which were spaced at 100 m intervals along transects of 0.3-1 km (1 transect per site). Dung beetles were sampled using human dung-baited pitfall traps and ecosystem functions were measured using fresh cattle dung. Previous analyses revealed little difference in species assemblages between dung types or years (Chapter 4), supporting the robustness of this experimental design.

Beetles collected during dung-baited pitfall trapping were identified to species level in Sabah using an optical microscope. Species richness and biomass were calculated for each sampling station as the number and dry mass of species, respectively. It was not possible to obtain accurate dry mass (g) estimates of biomass for all species collected from sampling stations in the field and so biomass for each sampling station was estimated based on extrapolation of a regression of body length against dry mass for 10 species. The body lengths of all sampled species were measured and their dry mass estimated based from the regression (Chapter 4). Dung removal (with and without *Catharsius spp.)* was measured as the change in dung wet mass over 24 hours, after accounting for mass changes due to evaporation. It was not logistically possible to obtain sufficient cattle dung to record dung removed with and without *Catharsius spp.* on the same day, and so measurements at the same sampling stations were taken on different days. *Catharsius spp.* were excluded using a 60 x 60 cm grid of 12 mm wire mesh placed under the dung pile that allowed all species except for *Catharsius spp.* to remove dung (see Chapter 4). Seed burial and seed dispersal were measured using aluminium beads placed inside the dung pile as seed mimics. After 24 hours, beads that had been moved by rollers (seed dispersal), left unburied or buried by tunnellers (seed burial) were counted. For full methodological details see Chapter 4.

7.3.1 Comparing the impacts of biomass and species richness on dung removal, seed burial and seed dispersal (Hypothesis 1)

Three analyses were carried out to compare the impacts of biomass and species richness on: 1) dung removal, 2) seed burial and 3) seed dispersal. Species richness and biomass estimates used in each of these analyses represented the number and biomass of species involved in each of the functions, i.e. because all species contribute to dung removal, this analysis used biomass and species richness of all species. However, seed burial and seed dispersal are functions of tunnellers and rollers respectively and so these analyses used biomass and species richness of tunnellers and rollers respectively. For all three functions, data from all 143 sampling stations across unlogged continuous forest (10 stations), twice-logged continuous forest (10 stations) and forest fragments (123 stations) were analysed in Generalised Linear Mixed Models (GLMMs) with ‘site’ fitted as a random effect. Fitting this random effect accounted for non-independent sampling stations within each site and for the unequal number of sampling stations across sites.

To compare the importance of biomass and species richness, five GLMMs were fitted for each of the three ecosystem functions, examining: 1) a ‘null’ model containing just the random effect ‘site’, 2) biomass, 3) species richness, 4) species richness and biomass, and 5) the full model including the interaction between species richness and biomass. The interaction was included to assess whether complementarity or facilitation between species led to a non-linear increase in function compared to the additive model of species richness and biomass. The ‘null’ model was included to test whether within site differences exceeded those between sites. These five models were then ranked using AIC_c values and coefficients and 95% confidence intervals were extracted from the best model(s). The best model was that with the lowest AIC_c value and best models were those within 2 AIC_c values of the single best model. Relationships between each function (response variable) and biomass, species richness or their interaction (explanatory variables) were defined as significant if the explanatory variable was present in the best model set and if 95% CIs did not overlap zero. Prior to analyses, biomass values were logged (base 10) to ensure normality, and then species richness and log10 biomass were standardised (mean subtracted and then divided by the standard deviation) to allow direct comparison of the slope of the relationship between biomass, species richness and function. Dung removal models were fitted using a binomial error distribution, but seed burial and dispersal data were highly overdispersed and so were fitted using a negative-binomial error distribution.

7.3.2 Comparing the importance of *Catharsius spp*. for dung removal in unlogged continuous forest, twice-logged continuous forest and forest fragments (Hypotheses 2-3)

To assess the importance of *Catharsius* spp. for dung removal in different forest types, GLMMs were used to compare the percentage of dung removed with and without *Catharsius* spp. in unlogged continuous forest (10 stations), twice-logged continuous forest (10 stations) and forest fragments (123 stations). The following two models were compared using AIC_c values: 1) a ‘null’ model containing just ‘site’ fitted as a random effect and, 2) a model containing the interaction between ‘forest type’ and the ‘presence of *Catharsius* spp.’ as well as ‘site’ as a random effect. ‘Forest type’ and ‘presence of *Catharsius* spp.’ were both categorical variables with three (unlogged continuous, twice-logged continuous and fragment) and two levels (with and without *Catharsius* spp.) respectively meaning that the interaction had six levels. The ‘null’ model was included to assess whether within site variation in dung removal exceeded differences between forest types. Means and 95% CIs were extracted for dung removal with and without *Catharsius* spp. in each of the three forest types. Differences between the three habitat types and *Catharsius* treatments were considered significant if confidence intervals did not overlap, and if the ‘null model’ had a higher AIC_c value than the alternative model. Dung removal data were overdispersed and so were fitted using a negative-binomial error distribution. This analysis was conducted only for dung removal, and not for seed burial or seed dispersal because these functions were not expected to be dependent on *Catharsius* spp. presence/absence.

The above analysis compared the absolute percentage of dung removed with and without *Catharsius* spp., but I also wanted to compare the relative contribution of *Catharsius* spp. to dung removal in the three forest types. Therefore, the relative percentage of dung removed was calculated as:

$$\frac{100\ \times\ (\%\, DR\ w/\ Catharsius\ spp_i - \%\, DR\ w/o\ Catharsius\ spp_i)}{\%\, DR\ w/\ Catharsius\ spp_i}$$

Equation 7.1. Equation for calculating the relative proportion of dung removed (DR) by Catharsius *spp. at each sampling station after 24 hours* $(_i)$.

The aim of this analysis was to assess the contribution of *Catharsius* spp to dung removal and so stations where little dung removal occurred (<10%) were excluded from analyses. This meant that data from 81 stations and three fragment sites (sites 11, 15 and 16) were excluded from analyses, and the final analysis was carried out using data from 62 sampling stations at 15 study sites (42 stations from fragments, 10 from twice-logged continuous forest, and 10 from unlogged continuous forest). GLMMs were fitted to compare the relative percentage of dung removed by *Catharsius* spp. (Equation 7.1) in the three forest types. A 'null' model with 'site' as a random effect and a second model containing 'forest type' and the random effect were again compared using AIC$_c$ values and means and 95% CIs were extracted. For this analysis, the response variable was fitted using a negative-binomial error distribution to account for overdispersion. Sensitivity analyses were conducted where stations were excluded from analyses when <5% and <20% of dung was removed and these analyses produced the same qualitative differences between forest types as in the analysis using the 10% threshold (Appendix 4, Table A4.1).

7.3.3 Assessing the contribution of non-*Catharsius spp*. to dung removal (Hypothesis 3)

The final analysis in this chapter sought to examine which other dung beetle functional groups were also important contributors to dung removal, after accounting for the dominant role of *Catharsius* spp. To assess this I analysed dung removal without *Catharsius* spp. in relation to the biomass of non-*Catharsius* large tunnellers (n = 3 species >10 mm in length, 20% of biomass in continuous forest, 7% in fragments), small tunneller biomass (n = 54 species < 10 mm in length, 15% of biomass in continuous forest, 43% in fragments), large roller biomass (n = 3 species > 10 mm, 16% of biomass in continuous forest, 5% in fragments) and small roller biomass (n = 4 species < 10 mm in length, 2% of biomass across all sites). Using data from all 143 sampling stations, 15 GLMMs were fitted with the percentage of dung removal (w/o *Catharsius* spp) as the response variable and all possible combinations of the four functional beetle groups (large and small tunnellers and rollers) as fixed, continuous, explanatory variables. 'Site' was included as a random effect in all 15 models and in a 16th model, the 'null' model, without any of the fixed effects. The 16 models were then ranked using AIC$_c$ values and slope estimates and 95% CIs extracted from the best model set. Slopes and 95% CIs were model-averaged if the best model set contained more than one model. All 16 models were fitted with binomial error distributions and the biomass of each functional group was logged (base 10) to ensure normality and then standardised (mean subtracted and then divided by the standard deviation) prior to analyses to allow direct comparison of slope coefficients. The analysis was also repeated without continuous forest sites (using data from 123 sampling stations across 16 fragments) to assess whether the potential role of these important functional groups differed in continuous forest versus fragments.

7.4 Results

Dung-baited pitfall trapping recorded large variation in species richness and biomass across the 18 study sites. Average biomass in fragments was about 2 g per sampling station (range: 0.1-11 g per sampling station) compared to 7 g per sampling station in the two continuous forest sites (range: 3-11 g per sampling station) and on average 8 species were sampled from each sampling station in fragments (range: 2-20 species), compared to 20 species in continuous forest (range: 13-23 species; Table 7.1). Across all sites, small tunnellers made up ~80% of species and individuals, but large tunnellers were dominant in terms of biomass, with the five large tunneller species comprising on average 50% of biomass, and the two *Catharsius* spp. making up on average 44% of all biomass (Table 7.1). This dominance of large tunnellers and *Catharsius* spp. was even higher when sites with very low biomass were excluded (excluding stations with <1 g beetle biomass, n = 5 fragment sites), with *Catharsius* spp. making up 60% and other large tunnellers 2% of biomass in the remaining 11 fragments, and 48% and 19% of biomass, respectively, in the two continuous forest sites. There was also large variation in dung removal, seed burial and seed dispersal across study sites. For example, ~20% of dung was removed from fragment sampling stations (range: 0-100% dung removed per sampling stations) compared to 80% dung removal in continuous forest (range: 30-100% dung removal per sampling stations). All three functions were higher in continuous forest than in fragments and tended to show greater within site variation in fragments than in continuous forest (Table 7.1).

Table 7.1. Summary table showing mean species richness, guild biomass (% of total) and rates of ecosystem functions (%) in unlogged continuous

forest (UL), twice-logged continuous forest (2L) and forest fragments. LT = large tunnellers.

Forest type		**UL**	**2L**	**Fragments**
Species richness		19.4	19	7.8
Biomass	***Catharsius* spp.**	52.9	42.5	43.3
	Other LT	19.5	19.6	6.6
	Large rollers	10.9	22.3	5.2
	Small rollers	0.8	2.0	2.4
	Small tunnellers	15.9	13.5	42.5
Function	**Dung removal**	85.1	73.8	17.0
	Seed burial	24.4	44.3	4.8
	Seed dispersal	1.5	0.3	0.02

7.4.1 Comparing the impacts of biomass and species richness on dung removal, seed burial and seed dispersal (Hypothesis 1)

Biomass was a better predictor of dung removal and seed burial than species richness, but roller species richness was a better predictor of seed dispersal than roller biomass. On average, <5% of dung was removed and <10% of seeds were buried at sampling stations with beetle biomass of ≤1 g, and dung and seed burial at these sampling stations never exceeded 20% (Figure 7.1). Conversely, dung removal and seed burial varied from 0-100% among sampling stations with fewer than 10 species, suggesting that dung removal and seed burial were sometimes high at species-poor sampling stations. However, dung removal and seed burial at stations with high biomass (>1 g) was more variable than at stations with high species richness (>15 species), suggesting that high species richness provides more stable rates of dung removal and seed burial than high biomass. Dung removal and seed burial were positively correlated with total biomass and tunneller biomass, respectively (Figure 7.1, dung removal, slope estimate: 1.68, 95% CIs 0.83, 2.52; seed burial, slope estimate: 0.63, 95% CIs 0.41, 0.86). Species richness was not included in the best model for seed burial (Table 7.2), but it was for dung removal. There was no significant relationship between species richness and dung removal when the relationship with biomass had been accounted for (slope estimate: -0.14, 95% CIs -1.03, 0.74), but there was a significant positive interaction between species richness and biomass (slope estimate: 0.86, 95% CIs 0.10,1.62) indicating that stations with high species richness and high biomass had the highest rates of dung removal.

Virtually no seeds were dispersed horizontally at sampling stations where biomass was <1 g or where fewer than three roller species occurred (Figure 7.1). However, as with dung removal and seed burial, there was less variation in seed dispersal at stations with high roller species richness (≥5 species) than at stations with high roller biomass (≥1 g), with many stations with high biomass having no seed dispersal whilst all stations with high species richness had some seeds dispersed. Seed dispersal was positively correlated with roller species richness (slope estimate: 0.72, 95% CIs 0.39, 1.07). Roller biomass was present in the best model set for seed dispersal, but was not significantly related to seed dispersal (slope estimate: -0.93, 95% CIs -1.90, 0.04). However, seed dispersal was only recorded at 18 sampling stations, suggesting that these results may be less robust than those for dung removal and seed dispersal. Thus I conclude that seed dispersal is a relatively rare dung beetle function in this study system.

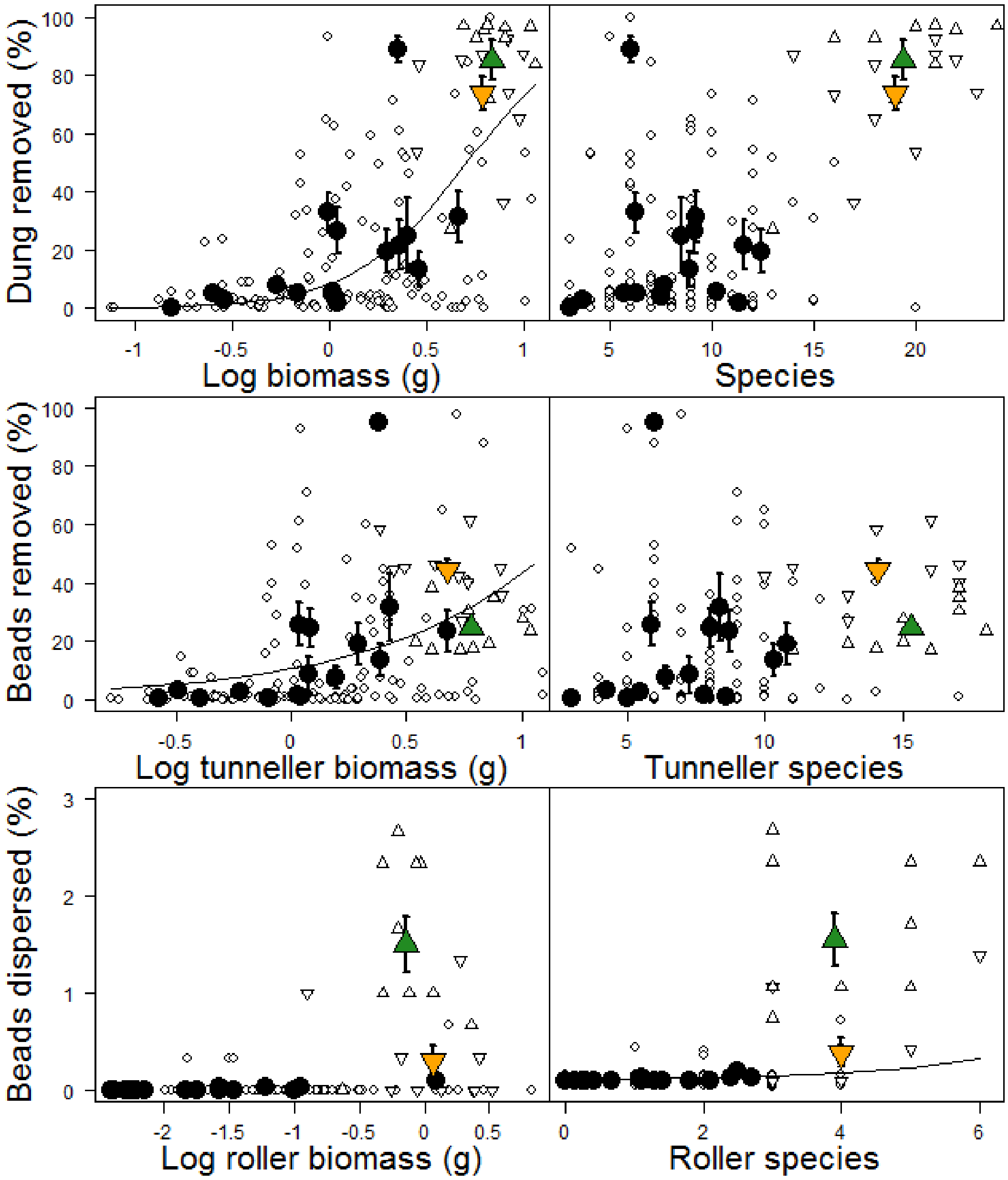

Figure 7.1. Plot showing the relationships of species richness (right column) and biomass (left column) with dung removal (top row), seed burial (middle row) and seed dispersal (bottom row). Upward pointing triangles and green fill represent unlogged continuous forest stations and sites, downward pointing triangles and orange fill represent twice-logged continuous forest stations and sites and circles and black fill represent fragment stations and sites. Error bars show standard error. Best fit lines are taken from GLMMs fitted to station data and are only plotted for significant relationships of variables present in the best model set for each function. Plotted biomass values are log10 transformed. Site means are plotted to show general trends.

The relative importance of biomass and species richness varied depending on the ecosystem function, with biomass being more important than species richness for dung removal and seed burial but roller species richness being most important for seed dispersal. However, both species richness and biomass appeared in the best models for dung removal and seed dispersal suggesting that both have important roles in determining rates of dung beetle functions (Table 7.2). For all three functions, there appeared to be considerable within site variation (Figure 7.1), but the ‘null’ model had the highest AIC_c value for all functions (Table 7.2) showing that within site variation always explained less variation than species richness and biomass.

*Table 7.2. Table of all fitted models comparing the effects of species richness and biomass on dung removal, seed burial and seed dispersal. Best models are shown in bold font. K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C): Marginal (M) and conditional (C) estimated R^2-vaues, based on Nakagawa & Schielzeth (2013). *Models fitted with a negative-binomial distribution to account for overdispersion. There is no current way of calculating R^2 values for this distribution. Bio = biomass, Sp = species richness.*

Function	Model	K	AICc	Δi	ωi	LL	R^2 (M,C
Dung removal							
	Bio*Sp	**5**	**112.7**	**0**	**0.7**	**-51.1**	**0.48,0.48**
	Bio+Sp	4	115.3	2.6	0.2	-53.5	0.51,0.51
	Biomass	3	116.7	4.0	0.1	-55.3	0.44,0.51
	Species	3	124.7	11.9	0.0	-59.2	0.24,0.41
	1	2	132.2	19.5	0.0	-64.1	0,0.47
Seed burial							
	Biomass*	**4**	**116.2**	**0**	**0.6**	**-54.0**	**-,-**
	Bio+Sp*	5	118.4	2.1	0.2	-54.0	-,-
	Bio*Sp*	6	119.9	3.7	0.1	-53.7	-,-
	Species*	4	120.5	4.3	0.1	-56.1	-,-
	1*	3	122.1	5.9	0.0	-57.9	-,-
Seed dispersal							
	Species*	**4**	**79.3**	**0**	**0.4**	**-35.5**	**-,-**
	Bio+Sp*	**5**	**80.1**	**0.8**	**0.3**	**-34.8**	**-,-**
	Bio*Sp*	6	81.4	2.2	0.1	-34.4	-,-
	Biomass*	4	82.7	3.4	0.1	-37.2	-,-
	1*	3	83.8	4.5	0.0	-38.8	-,-

7.4.2 Comparing the importance of *Catharsius spp*. for dung removal in unlogged continuous forest, twice-logged continuous forest and forest fragments (Hypotheses 2-3)

Exclusion of *Catharsius* spp. resulted in >50% reduction in dung removal across all sites, demonstrating the importance of this genus for dung removal. However, the impact of excluding *Catharsius* spp. varied depending on the forest type (Table 7.3; Figure 7.2). In continuous forest sites (twice-logged and unlogged; sites 1 and 2) excluding *Catharsius* spp. did not cause a significant reduction in dung removal, in contrast to forest fragments where there was a significant reduction in dung removal when *Catharsius* spp. were absent. Despite there being no significant effect of *Catharsius* spp. exclusion in continuous forest sites, dung removal was still on average 25% lower in continuous forest in the absence of *Catharsius* spp. and *Catharsius* spp. removed more dung in absolute terms in continuous forest than in fragments (average dung removal, continuous forest: 163 g; fragments: 73 g). Within-site variation in dung removal explained far less variation than was explained by differences between either forest type or the presence of *Catharsius* spp. (Table 7.4).

Table 7.3. Table comparing means and 95% confidence intervals of dung removal with or without Catharsius *spp. in unlogged continuous forest (UL), twice-logged continuous forest (2L) and fragments. Non-overlapping confidence intervals indicate a significant difference. The means and confidence intervals presented are back-transformed to the original variable scales from the log link functions used in the GLMMs explaining the asymmetrical 95% CIs shown here.*

Dung removed	**Estimate (and 95% CIs)**		
	UL	**2L**	**Fragments**
***Catharsius* spp**	85.2 (64.1,113.1)	74.1 (54.4,100)	17.0 (14.2,20.4)
No *Catharsius* spp	51.3 (35.6,74.0)	56.0 (39.5,79.5)	5.8 (4.2,7.8)

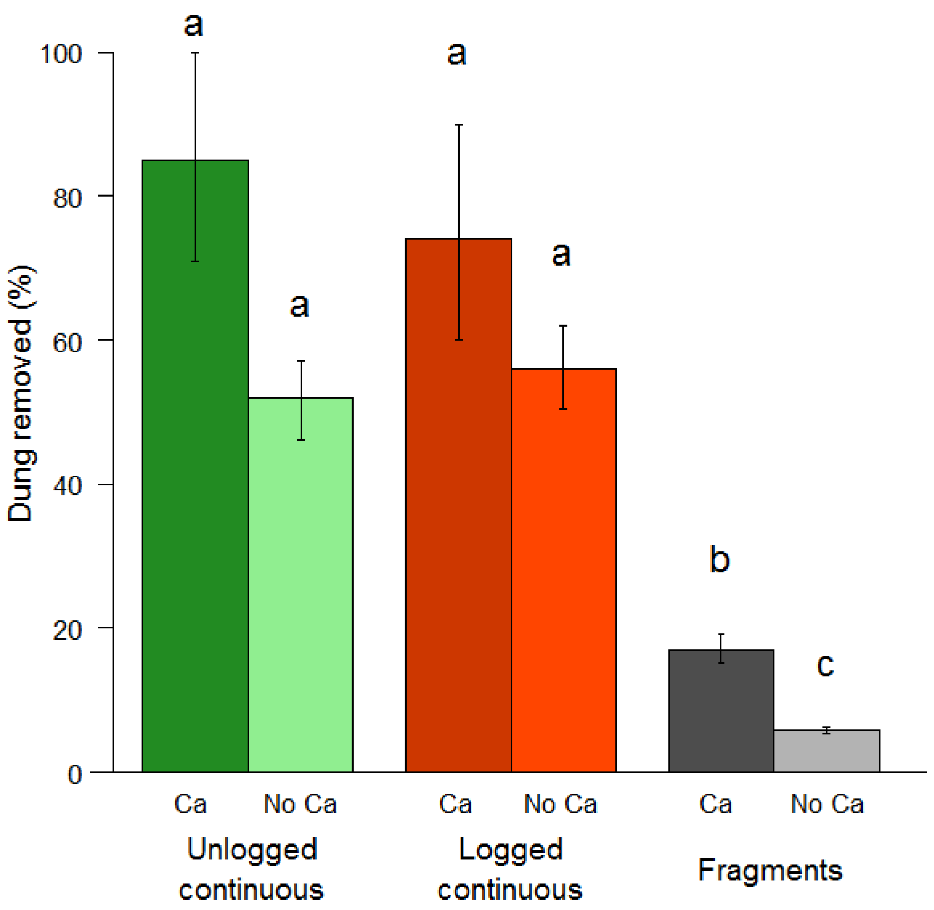

Figure 7.2. Plot comparing dung removal with (darker bars) and without Catharsius *spp. (lighter bars) in unlogged continuous forest, twice-logged continuous forest and forest fragments. Means and standard errors are plotted and are calculated for all 143 sampling stations. Letters indicate significant differences between bars based on whether 95% CIs from GLMMs are overlapping.*

Exclusion of *Catharsius* spp. led to greater, but non-significant declines in absolute dung removal in continuous forest than in forest fragments, but analyses of relative dung removal revealed that *Catharsius* spp. were responsible for relatively more dung removal in fragments than in either unlogged or twice-logged continuous forest. Restricting analysis to sampling stations where >10% of dung was removed showed that *Catharsius* spp. were responsible for 77% (95% CIs 70.8, 83.4) of dung removal in fragments compared to 24% (95% CIs 17.9, 32.6) and 42% (95% CIs 33.1, 52.3) of dung removal in twice-logged and unlogged continuous forest sites (Figure 7.3). *Catharsius* spp. also contributed significantly less to dung removal in twice-logged continuous forest than in unlogged continuous forest. The ‘null’ model had an AIC_c value of just 0.5 higher than the model containing forest type, showing that there was also large within-site variation in dung removal by *Catharsius* spp., but this explained less variation in the data than differences between forest types (Table 7.4). Therefore, dung removal in forest fragments was predominantly by *Catharsius* spp., whilst other species contributed to dung removal in continuous forest sites. However, large within-site variation in dung removal by *Catharsius* spp. suggested that reliance on this genus for dung removal can lead to high local variation in dung removal at sites. Furthermore, non *Catharsius* species contributed more to dung removal in twice-logged continuous forest than in unlogged continuous forest, suggesting that other species may help to maintain dung removal following disturbance in continuous forest sites.

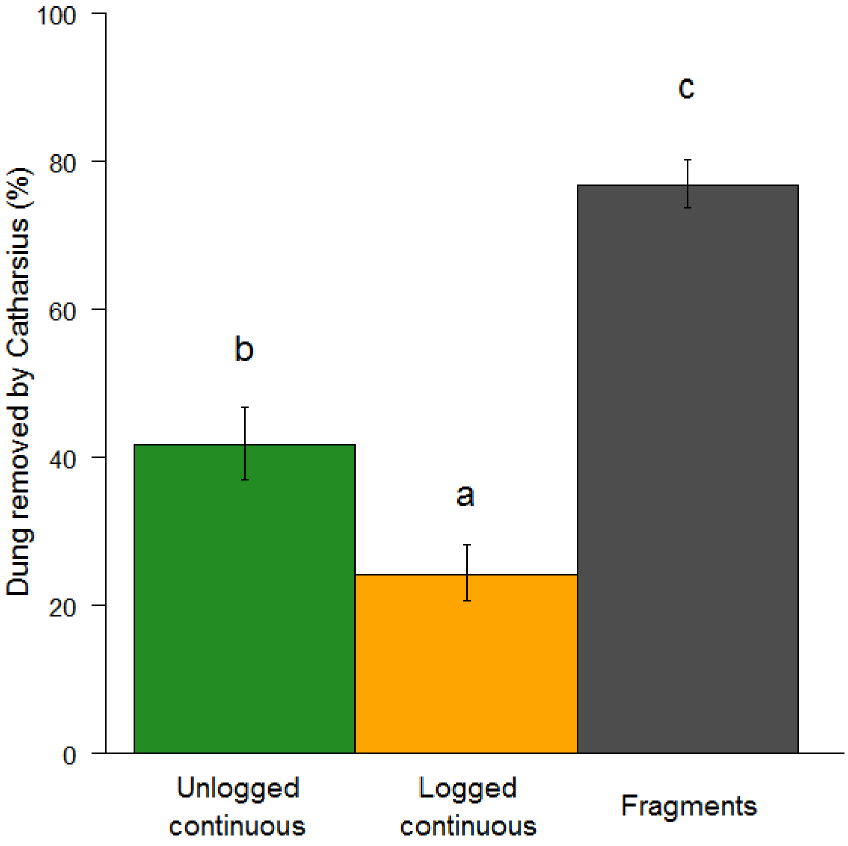

Figure 7.3. Barplot comparing the relative percentage of dung removed by Catharsius *spp. in unlogged continuous forest, twice-logged continuous forest and forest fragments. Means and standard errors are plotting and are calculated based only on sampling stations where >10% dung was removed. Letters indicate significant differences between bars based on whether 95% CIs from GLMMs are overlapping.*

7.4.3 Assessing the contribution of non-*Catharsius spp*. to dung removal (Hypothesis 3)

In continuous forest sites, 67% of dung that was removed was removed by species other than *Catharsius* spp., whilst in forest fragments only 23% of dung was not removed by *Catharsius* spp. *(*Figure 7.2*)*. In analyses of all sites, dung removal in the absence of *Catharsius* spp. showed a strong positive correlation with the biomass of other large tunnellers (Figure 7.4, slope estimate: 1.72, 95% CIs 0.74, 2.70) and a weaker positive relationship with small roller biomass (slope estimate: 0.92, 95% CIs 0.18, 1.65). Biomass of small tunnellers and large rollers were also included in the best model set, but neither variable was significantly correlated with dung removal in the absence of *Catharsius* spp. *(*Table 7.4*)*. Therefore, across all sites it was mainly other large tunneller species and to a lesser extent small roller species that provided most dung removal when *Catharsius* spp. were not present.

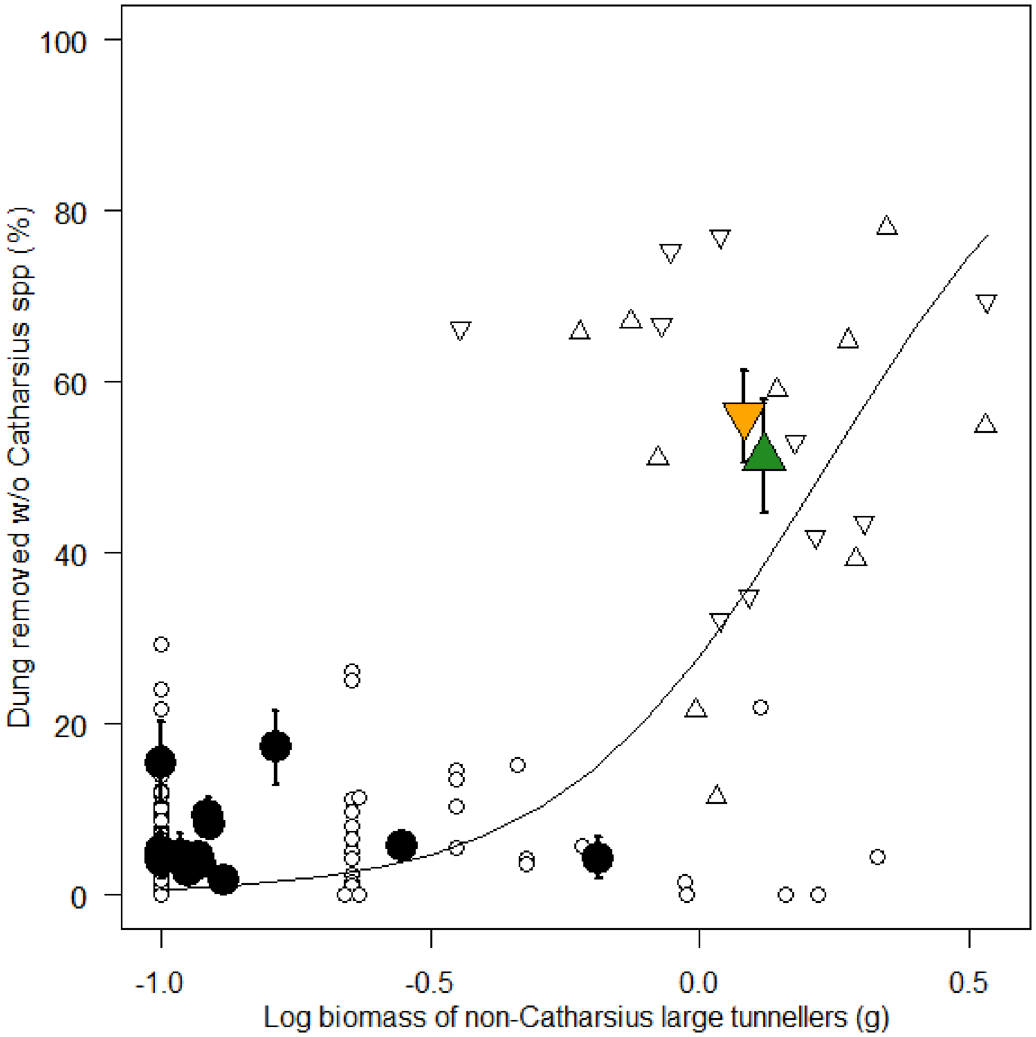

*Figure 7.4. Plot showing the relationship between the biomass of non-*Catharsius *large tunnellers and dung removal when* Catharsius spp. *are excluded. Plot shows that non-Catharsius large tunnellers are able to provide high dung removal rates in the absence of* Catharsius *spp., but only in continuous forest sites. Upward pointing triangles and green fill represent unlogged continuous forest stations and sites, downward pointing triangles and orange fill represent twice-logged continuous forest stations and sites and circles and black fill represent fragment stations and sites. Best fit line is taken from a GLMM fitted to data from stations, with site as a random effect. Site means are plotted to show general trends. Error bars show standard error and biomass values are log10 transformed.*

However, analysis of just the 16 fragment sites revealed that other large tunneller species and small rollers had little contribution to dung removal in the absence of *Catharsius spp.*, implying the effect evident in Figure 7.4 was primarily due to continuous forest sites. In the analysis of fragments, the 'null' model best explained variation in dung removal, indicating that dung removal was highly spatially variable within individual fragment sites when no *Catharsius spp*. were present (Table 7.4). This finding is intuitive given that large tunneller biomass in fragments was dominated by *Catharsius spp.* and that the three non-Catharsius large tunneller species were largely confined to continuous forest sites (Figure 7.5). Furthermore, *Catharsius spp.* biomass in fragments was increasingly dominated by the disturbance-tolerant species *Catharsius renaudpauliani* as fragment size decreased, because *Catharsius dayacus* declined in abundance with fragment size. This shows that large tunneller biomass, and dung removal, in fragments was essentially dominated by one species (Figure 7.5).

Therefore, these analyses revealed evidence of redundancy in dung removal in continuous forest sites, with other species of large tunneller and small rollers able to contribute to dung removal in the absence of *Catharsius spp*. However, in fragments dung removal appeared almost wholly reliant on *Catharsius spp.*, particularly *C. renaudpauliani*, with only weak evidence that small tunnellers contributed to dung removal and so dung removal was highly variable in fragments in the absence of *Catharsius spp*.

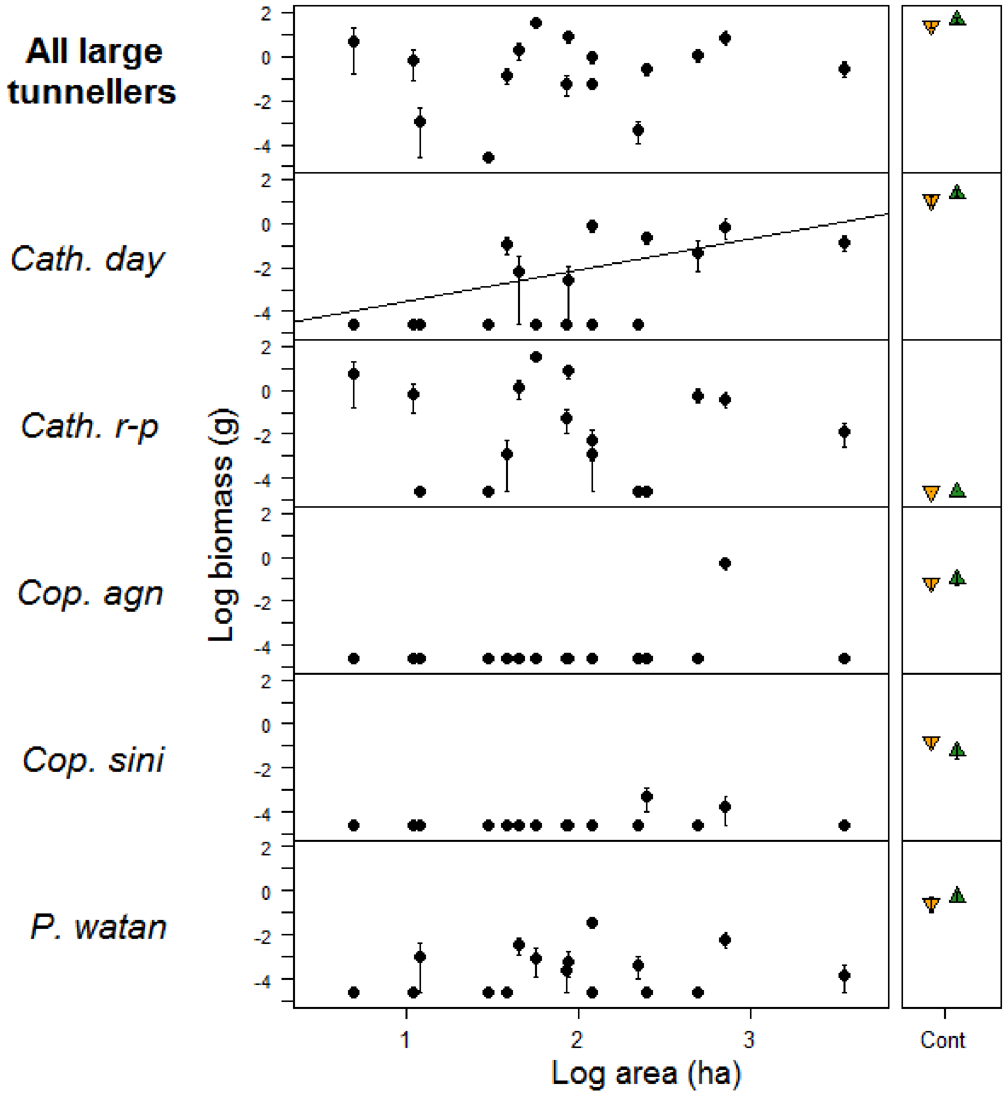

Figure 7.5. Scatterplots showing log10 biomass of all large tunnellers and that of the five large tunneller species in relation to log10 area. Green triangles represent unlogged continuous forest, orange triangles twice-logged continuous forest and black circles forest fragments. Error bars show standard error. The best fit line is plotted for the only significant relationship of Catharsius dayacus *biomass against area based on a linear model containing the 16 fragment sites. Abbreviations as follows: Cath. = Catharsius, day = dayacus, r-p = renaudpauliani, Cop. = Copris, agn = agnus, sini = sinicus, P = Proagaderus and watan = watanabei.*

Table 7.4. Table of fitted models for three separate analyses: 1) comparing dung removal in different forest types with and without Catharsius spp (‘**Catharsius exclusion**’), *2) comparing dung removal in different forest types by* Catharsius spp *only (‘**Catharsius only**’), and 3) comparing contributions of different dung beetle guilds to dung removal in the absence of* Catharsius spp. *(‘**No Catharsius**’). For the first two analyses two models are presented, the ‘global’ model (see section 7.3.2 for detail) and null model. For the final analysis, best models are shown for an analysis containing all 18 study sites and an analysis of just forest fragments (16 sites). For these analyses, only the best models (Δ_i <2) are presented for the sake of brevity. Best model(s) are shown in bold font. K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters. *Models fitted with a negative-binomial distribution to account for overdispersion. There is no current way of calculating R^2 values for this distribution.*

	Model	K	AICc	Δi	ωi	LL
1) Catharsius exclusion						
	Forest type**Catharsius****	**8**	**237.2**	**0**	**1.0**	**-110.3**
	1*	3	251.8	14.6	0.0	-122.9
2) Catharsius only						
	Forest type*	**5**	**110.9**	**0**	**0.56**	**-49.9**
	1*	**3**	**111.4**	**0.5**	**0.44**	**-52.5**
3) No Catharsius						
All sites						
	OLT+SR*	**4**	**48.0**	**0**	**0.5**	**-19.8**
	OLT+ST+SR*	**5**	**49.5**	**1.5**	**0.3**	**-19.5**
	OLT+LR+SR*	**5**	**49.9**	**2.0**	**0.2**	**-19.8**
Fragments						
	1*	**3**	**54.0**	**0**	**0.7**	**-23.9**
	ST*	**4**	**55.9**	**2.0**	**0.3**	**-23.8**

7.5 Discussion

7.5.1 The biodiversity-ecosystem function relationship

Dung beetle biomass was a better predictor of dung removal than species richness, and tunneller biomass a better predictor of seed burial than tunneller species richness. This meant that some sampling stations with very low species richness could support extremely high rates of dung removal and seed burial, because of the biomass of a few highly abundant species. These findings broadly support hypothesis 1, and strongly support previous suggestions that biomass compensation may be a crucial and overlooked component of the BEF relationship (Bengtsson 1998; Reiss et al. 2009). Most controlled experiments assessing the BEF relationship keep biomass constant across diversity treatments (Bengtsson 1998), but my findings suggest that increased biomass can compensate for declining species richness in real ecosystems. Therefore, the ‘selection effect’ appeared to be a key driver of dung beetle functions in this system, whereby a small number of functionally dominant species were able to maintain high rates of dung removal at some sampling stations with low species richness (Figure 7.1). However, the best model for dung removal also contained a significant positive interaction between biomass and species richness, showing evidence of ‘complementarity’ and challenging hypothesis 1. This result was probably driven by the fact that dung removal at sampling stations with high beetle biomass was highly variable, with no dung removal at some stations and almost complete removal at others, whereas the stations with high biomass and high species richness had consistently high dung removal. Therefore, dung removal was consistently higher when there was a high biomass of more species, suggesting that higher species richness increased the stability of dung removal. Possible mechanisms for this species richness effect could include higher detection of dung piles when more species are present, or facilitation between nocturnal and diurnal species, as suggested by Slade et al. (2007), whereby diurnal species spread out dung leading to more efficient removal by nocturnal species.

Contrary to dung removal and seed burial results, seed dispersal findings did not support hypothesis 1, and seed dispersal rates were more closely correlated with roller species richness than roller biomass. This identifies some idiosyncrasy in species contributions to functioning, depending on the function considered. The relationship of seed dispersal with roller species richness may be related to community assembly. Smaller roller species were more resistant to fragmentation than larger species, occurring in most forest fragments whilst large rollers were absent from smaller fragments (Chapter 5). Therefore, the species found at sampling stations with few roller species are likely to have been small rollers rather than large rollers, and these small species are less functionally important than the larger species (Slade et al. 2007a). This could explain why seed dispersal was only recorded at stations with ≥3 roller species, when large rollers were more likely to be present. The further increase in seed dispersal as roller species richness increased from 3-5 species (Figure 7.1) could be explained by the fact that the three large roller species in this study system exhibit stratified diel activity, with two diurnal and one nocturnal species. This means that functionally important large roller species are active throughout the 24 hour diel period, which may explain higher rates of seed dispersal when all species are present (Slade et al. 2007a). This temporal niche complementarity may be more important for seed dispersal than dung removal and seed burial, because the most functionally important large tunneller species for these functions are all nocturnal (Slade et al. 2007a; Edwards et al. 2013). This highlights the need for high functional diversity with both roller and tunneller functional groups if seed dispersal is to be maintained along with dung removal and seed burial. However, seed dispersal was a rare function in undisturbed continuous forest accounting for ~2% seeds moved and was not recorded in the majority of fragments, so these analyses had limited statistical power. Further sampling could help clarify the importance of this secondary seed dispersal for plant recruitment, given the rarity of the function. There was also considerable within-site variation in seed dispersal, roller biomass and roller species richness, that may have been reduced with further sampling effort.

7.5.2 Interspecific differences in dung beetle functional contributions

Catharsius spp. were responsible for ~ 50% of dung removal across all sites, and ~77% in forest fragments, strongly supporting hypothesis 2 which predicted that this genus was disproportionately important for dung removal. *Catharsius* spp. are the largest dung beetle species in this study system and so their functional importance fits with numerous studies documenting the importance of large dung beetles for dung removal (Doube 1990; Larsen et al. 2005b; Slade et al. 2007a). Studies on plant productivity and marine nutrient fluxes have also identified a dominant role of larger individuals for these functions (Huston 1997b; Norkko et al. 2013), showing that higher metabolic rates and energy demands of large species are crucial determinants of species' functional contributions (Reiss et al. 2009). The functional dominance of a few species of large tunneller aligns strongly with the finding that biomass rather than species richness best explained dung removal, given that large tunnellers were the majority of dung beetle biomass.

A key finding of this study was that *Catharsius* spp. contributed more to biomass and dung removal in fragments than in continuous forest sites, suggesting that biomass compensation can help to bolster ecosystem functioning following disturbance in natural ecosystems. Functional contributions in both undisturbed and twice-logged continuous forest sites were much more evenly distributed across species than in forest fragments, with *Catharsius* spp. contributing only ~33% of dung removal in continuous forest. This could be indicative of higher competition for dung resources in continuous forest sites, given that species richness was highest in these sites and included other large-bodied, highly competitive species. Large-bodied rollers and tunnellers are strong competitors, able to quickly remove dung resources compared with many smaller species (Doube 1990). These large-bodied species were present at high abundances in continuous forest sites and were largely absent from most forest fragments and it is likely that they were able to compete with *Catharsius* spp., so preventing this genus from being competitively and functionally dominant in continuous forest. Conversely, because *Catharsius* spp. were among the only large-bodied species to persist in forest fragments it is likely that their functional dominance extended from their ability to outcompete most other smaller species in these sites. The *Catharsius* genus consists of two morphologically and functionally similar species that appear to have different disturbance tolerances, with the disturbance-intolerant *C. dayacus* that dominates in continuous forest and the disturbance-tolerant *C. renaudpauliani* that appears to replace *C. dayacus* in forest fragments (Figure 7.5). It is unclear why *C. renaudpauliani* thrives in fragments when *C. dayacus* and all other large species decline following fragmentation, but its resilience to fragmentation means that this species is almost individually responsible for maintaining dung removal in fragments.

7.5.3 Resilience of ecosystem functioning following disturbance

Catharsius spp. were responsible for ~77% of dung removal in forest fragments, suggesting that species in this genus were able to compensate for the loss of other large-bodied and functionally important species following fragmentation. This result shows that single, disturbance tolerant species can play key roles in maintaining ecosystem functioning following species losses. Theoretical and experimental research has highlighted the potential importance of dominant and common species for the maintenance of ecosystem functioning following species loss (Smith & Knapp 2003; Gaston 2010), but this is one of the first examples from a real-world disturbance gradient in highly diverse ecosystem. Peters et al. (2009) showed that a disturbance-tolerant army ant species (*Dorylus molestus*) was able to compensate for the loss of a disturbance-intolerant species (*Dorylus wilverthi*) following fragmentation of an African rainforest. However, that compensation was a replacement of one dominant species in continuous forest with another dominant species in fragmented forest. In this study dung removal was reliant on multiple species and dung beetle guilds in continuous forest and compensation by *Catharsius renaudpauliani* was unable to fully compensate for loss of these other species. Therefore, my findings highlight the need for high diversity to maintain stable rates of ecosystem function following disturbance. Much previous evidence for this has been from controlled experiments in low-diversity grassland ecosystems (e.g. Tilman et al. 2006). This study reveals that diversity is also crucial for maintaining consistent rates of ecosystem functioning under natural conditions in high-diversity tropical ecosystems. Further research into whether diversity is more important to ecosystem functioning in more diverse and less even tropical ecosystems (e.g. Wright 2002), than in temperate communities is required, especially given the rapid current biodiversity losses in the tropics (Phalan et al. 2013).

7.5.4 Conclusion

Biomass was generally a better predictor of dung beetle ecosystem functions than species richness. However, high species richness may led to more stable provision of dung removal, seed burial and seed dispersal functions by increasing the chance of species assemblages containing a greater number of functionally important, large-bodied species. In continuous forest sites, species contributions to dung removal were more even than in forest fragments, but were still reliant on a suite of large tunnellers. In forest fragments dung removal was heavily reliant on *Catharsius* spp. for providing 77% of dung removal at dung piles that they located. However, the discovery of dung piles by *Catharsius* spp. was highly variable leading to less stable dung removal in forest fragments. This shows that disturbance tolerant, large-bodied species can be crucial for ecosystem functioning following forest fragmentation, but that dung beetle ecosystem functions are more stable when species richness is high.

Chapter 8 - General discussion

8.1 Summary of thesis findings

This thesis assessed biodiversity and ecosystem functioning in tropical landscapes dominated by oil palm plantations, using dung beetles as a focal taxon. It discussed conservation strategies used in oil palm landscapes and compared the impacts of selective logging and forest fragmentation on the maintenance of ecosystem functioning. Here I review the key findings from each Chapter, discuss further work and the wider implications of my results for ecosystem functioning and conservation within managed tropical landscapes.

Chapter 2 summarised how the High Conservation Value (HCV) approach can contribute to conserving biodiversity in managed tropical landscapes. The HCV approach is widely used in voluntary sustainability standards for oil palm and soya production, and it can contribute to biodiversity conservation in these systems. The Chapter discussed how a lack of a robust scientific evidence base may be hindering the effectiveness of the HCV approach for conservation. Strategies for improving the evidence base are considered, with an emphasis on the need for relevant academic research combined with a strong appreciation of practical challenges faced by HCV assessors. I recommend better knowledge exchange between scientists and HCV users based on multi-stakeholder meetings and the construction of databases of easily-accessible information in order to improve the effectiveness of the HCV approach.

Chapter 3 re-analysed data from 6 published studies on 487 bird, ant and beetle species to assess how the conversion of logged tropical forest to oil palm plantations affects species based on their feeding guild, body size, local population size and geographic range. Large bodied, abundant forest species and species from higher trophic levels declined most in abundance following conversion to oil palm plantations. The most abundant species in oil palm plantations were small bodied, lower trophic level species that had low abundances in forest, and were often hyper-abundant in plantations.

The proportion of omnivorous species in oil palm plantations also increased compared to logged forest. These results revealed consistent responses of different taxa to the reduced resource heterogeneity in oil palm plantations. I recommended increasing the structural complexity and habitat heterogeneity of plantations, in order to increase functional and species diversity within plantations.

Chapter 4 described the unlogged continuous forest site, twice-logged continuous forest site and 16 forest fragments sampled for dung beetles and their ecosystem functions in this thesis. It described the development of robust protocols for dung beetle sampling and quantification of dung removal, seed burial and seed dispersal functions. Dung beetle sampling over two days was sufficient to compare assemblages across sites as shown by low rates of new species accumulation at the end of sampling. Data revealed little inter-annual variation in species assemblages or in relation to bait type, supporting subsequent analyses in Chapter 7 comparing samples of dung beetle composition and measurements of their ecosystem functions from different years and using different dung baits.

Chapter 5 assessed dung beetle species richness, abundance, biomass and species composition in unlogged continuous forest, twice-logged continuous forest and forest fragments of different size, isolation and forest quality. High intensity selective logging of continuous forest had no significant impact on any aspect of dung beetle diversity. However, species richness, abundance and biomass were significantly lower in forest fragments than in continuous forest sites, and this decline was greatest for functionally important large rollers and tunnellers. Differences among fragments were relatively small, but species richness and roller biomass declined with decreasing fragment size whereas tunneller biomass showed no significant change with fragment size. Turnover patterns in species assemblages among sites were best explained by changes in forest quality. I concluded that larger, higher quality fragments can be of conservation value for dung beetles, because they support similar species assemblages to continuous forest sites and support functionally important rollers and tunnellers.

Chapter 6 investigated the impacts of selective logging, forest fragmentation and changes in fragment area, quality and isolation on dung removal, seed burial and seed dispersal by dung beetles. Heavily logged continuous forest supported similar rates of these ecosystem functions to unlogged continuous forest, but dung removal, seed burial and seed dispersal in forest fragments was >50% lower than in continuous forest sites. Among forest fragments there was little further change in dung beetle functions, but seed dispersal was not recorded in fragments smaller than 100 ha, whereas dung removal and seed burial were still maintained in the smallest fragments. These results showed that even heavily disturbed continuous forest can maintain dung beetle ecosystem functions and that these areas should be a conservation priority. By contrast, forest fragments supported greatly reduced rates of dung beetle ecosystem functions, and I concluded that fragments needed to be at least 100 ha to support dung removal and secondary seed dispersal functions.

Chapter 7 compared the importance of dung beetle biomass and species richness for dung removal, seed burial and seed dispersal. It also assessed the role of functionally dominant *Catharsius* spp. for dung removal following forest fragmentation. Biomass was a better predictor of dung removal and seed burial than species richness, because these functions were largely dependent on large-bodied *Catharsius* spp. This single genus was responsible for 77% of dung removal in forest fragments, compared to ~33% in continuous forest sites, but reliance on this single genus led to highly variable dung removal and seed burial among forest fragments. In contrast, high species richness and high biomass in continuous forest sites led to consistently high rates of these functions. Across study sites, species richness was a better predictor of changes in seed dispersal. These findings illustrate the importance of disturbance-tolerant species for ecosystem functioning following fragmentation, but reveal that high species richness is needed to maintain consistently high rates of ecosystem functioning.

8.2 Impacts of selective logging, fragmentation and oil palm expansion on biodiversity

In this thesis, I examined the impacts of three types of land-use change on biodiversity and ecosystem functioning: selective logging, fragmentation and conversion of forest to oil palm. Chapters 5-7 compared dung beetle diversity and functioning in unlogged and logged continuous forest with forest fragments of different size, forest quality and isolation. Chapter 3 quantified the impacts of converting logged forest to oil palm plantations on birds, ants and beetles in relation to their species traits. Here I synthesise the relative impacts of these different disturbances and consider possible ecological mechanisms for these impacts.

Chapters 5 and 6 showed that forest fragmentation was far more detrimental to dung beetle diversity and functioning than selective logging. The relatively small impacts of selective logging on tropical forest species has been shown previously for a range of vertebrate, invertebrate and plant taxa, suggesting that this is a conserved pattern (Berry et al. 2010; Edwards et al. 2011b), even when timber extraction rates are very high. A meta-analysis by Nichols et al. (2007) also showed that fragmentation was more detrimental to dung beetle communities than selective logging. In Chapter 5, I suggested that this detrimental effect of fragmentation could be linked to reduced mammal abundance in fragments compared to continuous forest, and the loss of large herbivores in fragments. There is limited research on the impacts of fragmentation on mammal communities, especially in Southeast Asian oil palm-dominated landscapes, and less research still that directly links dung beetle assemblages to mammal assemblages (Nichols et al. 2009; Culot et al. 2013). Such studies should be a research priority.

Dung beetle assemblages are known to respond to changes in vegetation structure and habitat quality (Davis et al. 1998, 2001), and logging has been shown to cause changes in dung beetle community composition (Edwards et al. 2013). This thesis revealed that compositional changes in response to selective logging, even when logging was high intensity (Chapter 4), are smaller than those caused by fragmentation. Importantly, it also showed that selective logging led to little change in the biomass of functionally important rollers and tunnellers, supporting the finding that logging has little impact on functional diversity (Edwards et al. 2013). This result could partly be explained by the fact that the twice-logged continuous forest site sampled in this study was still of higher forest quality than the majority of fragments. Many of the fragments were formed from forest that had also been heavily logged, but it is likely that fragmentation caused further changes to forest quality that were more detrimental than high intensity selective logging. It is well documented that forest fragmentation interacts synergistically with other types of disturbance, such as logging and fire (Barlow et al. 2006; Laurance & Useche 2009). Furthermore, edge effects such as elevated tree mortality and wind disturbance have been shown to penetrate as far as 400 m into forest fragments (Laurance et al. 2002). Therefore, it is highly likely that these synergistic disturbances further reduced forest quality in the fragments sampled in this thesis, which consequently altered dung beetle assemblages.

Reduced forest quality as a result of disturbances, such as logging and edge effects, often leads to reduced habitat complexity and altered vegetation structure (Okuda et al. 2003), and these changes can be even more extreme following conversion of forest to oil palm plantations (Foster et al. 2011; Luskin & Potts 2011). This habitat simplification might explain the loss of some forest specialist species following fragmentation and oil palm conversion, given that high structural diversity is crucial for high animal diversity in tropical forests (Novotny et al. 2006). In Chapter 3 I discussed how structural diversity is lost following the conversion of forest to oil palm which can lead to declines of the most species-rich and specialist groups. I also showed that disturbance tolerant omnivores, that may be rare in forest, can thrive in structurally simple oil palm plantations. These structural patterns led to consistent turnover in assemblages of birds, ants and beetles following conversion of forest to oil palm, and could also explain turnover in dung beetle assemblages following fragmentation. In fact, dung beetle species assemblages in small, low quality fragments were very similar to those sampled in oil palm plantations (Chapter 5).

Furthermore, better quality and larger fragments supported species assemblages more similar to continuous forest sites. Therefore, it seems highly likely that simplification of habitat structure leads to the loss of a higher number of more niche specialised species and an increase in the abundance of a few generalist species following either forest fragmentation or forest conversion. In fragments, species turnover of beetles was coupled with a strong negative effect of declining fragment area on species richness, driven by increased rates of extinction in small fragments.

Forest fragment area and forest quality were the most important determinants of dung beetle diversity, but less isolated fragments had higher large tunneller biomass and dung removal. I showed in Chapter 7 that dung removal in fragments was almost entirely dependent on *Catharsius renaudpauliani*. This species also persists in oil palm plantations (Edwards et al. 2013) so it is unlikely that effects of isolation are a result of its limited dispersal through the oil palm matrix. Instead, apparent effects of isolation may instead be linked to mammal dispersal and dung resources in the matrix and fragments. Many mammal species use forest fragments, and are more abundant in areas that are closer to continuous forest (Azhar et al. 2014). In particular, more generalist mammals such as Bearded pigs (*Sus barbatus*) and Sambar deer (*Rusa unicolor*), can be more abundant in oil palm landscapes than in forest, feeding on oil palm fruit in plantations by night and resting in adjacent forested areas during the day (Ickes 2001; Danielsen et al. 2009). Therefore, dung availability in less isolated fragments could be increased by the presence of generalist mammals in fragments, and the supplementary spill-over of more forest-dependent species. Assuming beetles are not dispersal limited and that their population sizes respond rapidly to increased resources, high dung availability may lead to high rates of dung removal in these sites. This effect in less isolated sites is also supported by the extremely high dung removal and seed burial rates in site 18 that was the least isolated fragment, being only 0.2 km from continuous forest, and ≥2 km closer to continuous forest than any other fragment (Chapter 6). This site was included in the study primarily to maximise variation in areas of fragments studied, rather than any consideration of isolation distance. More studies are needed in less isolated fragments and in the oil palm matrix to assess spill-over of dung beetles or mammals over these shorter distances from continuous forest. Such research could test whether this spill-over can maintain higher dung removal and seed burial in less isolated fragments and also in the matrix, where dung burial could improve soil fertility and potentially improve palm oil yield. It would be interesting to assess whether *Catharsius renaudpauliani* also plays a dominant role in dung removal in oil palm plantations, as it does in fragments (Chapter 7). This research would build on findings from Chapter 3 and Chapter 7 to assess the role of numerically dominant, disturbance-tolerant species for maintaining ecosystem functioning in plantations.

8.3 Maintaining ecosystem functioning following land-use change

A key finding from my thesis was the reliance of dung removal in forest fragments on *Catharsius renaudpauliani* (a large tunneller species), and the fact that this resulted in highly variable dung removal in fragments compared to continuous forest (Chapter 7). High species richness combined with high biomass in continuous forest sites led to consistently high rates of dung removal, and high roller species richness was also important for high rates of secondary seed dispersal. Firstly, this finding illustrates the importance of high species richness for increasing the stability of ecosystem functioning, and for the provision of multiple ecosystem functions. Secondly, the key role of *Catharsius renaudpauliani* illustrated the importance of functional compensation by disturbance-tolerant species in maintaining ecosystem functioning following habitat disturbance. Both functional compensation and the role of biodiversity in stabilising ecosystem functioning are crucial to understanding the maintenance of ecosystem functioning following disturbance and biodiversity losses. However, evidence for these processes from diverse, natural ecosystems is scarce making the findings in Chapter 7 novel and important (Gonzalez & Loreau 2009; de Mazancourt et al. 2013).

The concept of compensatory dynamics is long established in ecology, and Crowell defined the term ‘ecological release’ in 1962 to describe the increase in abundance of weakly competitive bird species on the Bermudas when more competitive species were absent (Crowell 1962). Competing species often evolve variable and asynchronous strategies to be able to co-exist and this means that different species will be more abundant under different abiotic conditions (Gonzalez & Loreau 2009). From an ecosystem functioning perspective, these divergent strategies to avoid interspecific competition may result in the maintenance of functions under different abiotic conditions, for example, following disturbances (Gonzalez & Loreau 2009). It is plausible that ecological release explains the importance of *Catharsius renaudpauliani* for dung removal in forest fragments, because this species was not recorded in continuous forest sites and appears to be disturbance-tolerant. *Catharsius renaudpauliani* may be outcompeted in relatively undisturbed continuous forest sites but appears to be adapted to more open habitats, possibly including forest gaps. However, *Catharsius renaudpauliani* did not fully compensate for the loss of other functionally important species in this study following fragmentation, and dung removal rates were highly variable in fragments (Chapter 7). This variability could either be because fewer dung resources in fragments led to a reduced requirement for dung removal, or because reliance on this single species led to reduced resource use efficiency.

Niche divergence or expansion typically leads to reduced resource use efficiency by species, because traits required to adapt to one abiotic condition may alter other aspects of behaviour (Gonzalez & Loreau 2009). For example, if *Catharsius renaudpauliani* is a gap species then it may also be highly dispersive in order to find patchily distributed gap habitats, which could lead to more stochastic discovery of these gap habitats and dung resources therein. This behaviour could explain the highly variable rates of dung removal in forest fragments, and may lead to slower rates of dung burial. Slower dung burial could increase nitrogen volatilisation and reduce nitrogen mineralisation in the soil if dung remains on the soil surface for longer in fragments (Nichols et al. 2008). Reduced nitrogen mineralisation could be exacerbated in forest fragments because the fragments in this study were hotter and drier than continuous forest sites which would increase nitrogen volatilisation (Chapter 4; Nichols et al. 2008).

Reduced resource use efficiency of single species is a prevailing argument behind the importance of diversity for stable ecosystem functioning, particularly across space and time (Loreau & Hector 2001; Gonzalez & Loreau 2009), and has led to a focus on ‘response diversity’ for maintaining ecosystem functioning following disturbance (Mori et al. 2013). Advocates of response diversity argue that it enables species communities to maintain functioning following disturbance, and that more research is needed on how functions are maintained following realistic species losses in response to disturbance (Mori et al. 2013). My findings show that there is a degree of response diversity within the dung beetles assemblages in this study system, because *Catharsius renaudpauliani* was able to partially compensate for the loss of other species following forest fragmentation. However, forest fragments did not have the full response diversity of continuous forest sites needed to provide consistently high rates of dung removal. By contrast, highly degraded twice-logged continuous forest still retained substantial response diversity and was able to maintain high rates of ecosystem functioning.

Previous studies have shown declines in the temporal stability of parasitism and pollination in response to declining diversity (Balvanera et al. 2005; Tylianakis et al. 2006), whereas research on antbird foraging and army ant swarming showed that single disturbance-tolerant species can partially compensate for species losses following fragmentation (Peters et al. 2009; Touchton & Smith 2011). My findings suggest that single species cannot always compensate for species losses following fragmentation and that a greater focus is needed on research addressing the issue of maintaining response and functional diversity in fragmented landscapes. This topic would benefit from further research that specifically investigated the spatial and temporal variability of ecosystem functions in tropical agriculture landscapes.

8.4 Wider applicability of findings

This thesis primarily used dung beetles as a focal taxon to study impacts of fragmentation on biodiversity and ecosystem functioning, but many of the findings provide important indicators of wider taxonomic and functional impacts. Dung beetles have been proposed as ecological indicator species, because they can be cheaply sampled and accurately represent patterns of other taxonomic groups and habitat patterns (Spector 2006; Gardner et al. 2008). The congruent responses of dung beetles with other species groups probably results from their habitat specialisation and relatively small range sizes (Davis et al. 2001; Spector & Ayzama 2003; Spector 2006). This means that dung beetles show diverse responses to environmental change and disturbance, including subtle disturbances from canopy loss to major impacts from habitat conversion (Davis et al. 1998; Nichols et al. 2008), and can be used to monitor the impacts of disturbance for management purposes (Spector 2006). I have already discussed the findings from Chapter 3 which revealed consistent ecological responses of three divergent taxa to the conversion of forest to oil palm, and here I discuss the wider applicability of findings from Chapters 5-7 based on analyses of dung beetle diversity and functions.

In Chapter 5 I showed that forest fragment size was generally a better predictor of dung beetle diversity than habitat quality or isolation. This supports findings from other studies of dung beetles as well as studies on other taxa such as plants, birds, butterflies and mammals (Hill & Curran 2003; Benedick et al. 2006; Michalski & Peres 2007; Nichols et al. 2007; Bregman et al. 2014). These findings suggest that Species-Area Relationships and extinction dynamics are consistently important drivers of species responses to fragmentation. However, forest quality was also crucial for explaining turnover in species assemblages among fragments. Forest quality is commonly overlooked in fragmentation studies (Nichols et al. 2007; Bregman et al. 2014) and my findings show that its inclusion is vital for understanding the ecological impacts of tropical forest fragmentation. Dung beetle functions were generally less affected by fragment characteristics than was species diversity (Chapter 6), although seed dispersal was not recorded in fragments smaller than 100 ha. In fact, fragmentation itself had the greatest impact on functioning, and even large fragments (500-3,529 ha) had far lower rates of dung removal, seed burial and seed dispersal than continuous logged forest sites. There has been relatively little research into the impacts of fragmentation on ecosystem functioning, although one study in Kenyan forest fragments revealed idiosyncratic responses of different ecosystem functions to fragmentation (Schleuning et al. 2011). However, the largest forest block in that study was 9,500 ha and so fragmentation effects cannot be directly compared to this study, and it is clear that further research is needed to assess ecosystem functioning in fragmented landscapes.

Findings from Chapter 7 on the importance of disturbance-tolerant species for ecosystem functioning provides real-world support for previous experimental research from species-poor grassland systems (Smith & Knapp 2003; Jaillard et al. 2014). The necessity for high species richness to maintain stable dung beetle functions (Chapter 7), provides evidence from a high diversity tropical forest system to support extensive studies on the role of diversity in maintaining plant productivity in low diversity grassland systems and experimental species manipulations (Tilman et al. 2006; de Mazancourt et al. 2013). The role of species richness for dung removal and plant productivity suggests that common mechanisms may be important for a range of different ecosystem functions. Plant productivity and dung removal are distinct functions, but it appears that both can be maximised through interspecific competition and niche partitioning of various resources. For example, plant productivity through species' partitioned use of resources such as light, nitrogen, phosphorus and micronutrients, and dung removal by niche partitioning of species in relation to dung type, soil structure, soil type and forest quality (Doube 1983, 1990; Davis et al. 1998). Species' morphological and behavioural adaptations for exploiting these resource gradients can explain how species respond and provide ecosystem functions following disturbance. Therefore, a clear knowledge of species' responses to disturbance is crucial for understanding the provision of different ecosystem functions, and the maintenance of multi-functionality following land-use change (Maestre et al. 2012; Pasari et al. 2013).

8.5 Conservation in managed tropical landscapes

Chapters 5 and 6 showed that continuous forest, even after high-intensity selective logging, had far greater conservation value for dung beetles and their functions than large forest fragments (up to 3,529 ha). I conclude that conserving degraded continuous forest should be a higher priority, not just because it can support a large number of species found in unlogged continuous forest (Berry et al. 2010; Edwards et al. 2011b; Woodcock et al. 2011), but also because it appears to be functionally similar to unlogged continuous forest. Protection of continuous forest in oil palm landscapes has been promoted, for example through 'biobanking' (Edwards et al. 2010; Edwards & Laurance 2012). The idea of 'biobanking' stems from the land-sparing conservation strategy and allows oil palm companies to clear small forest patches in their concessions if an area of equivalent land area is protected elsewhere as part of a larger forest reserve (Edwards & Laurance 2012). This landscape-level conservation does not fit the current certification requirements of the Roundtable on Sustainable Palm Oil (RSPO) which, through the use of the High Conservation Value approach, focuses on conservation measures within individual oil palm concessions. In Chapter 2, I briefly discussed the difficulty of landscape-level conservation under the current HCV approach. For example, landscape-scale conservation measures such as forest corridors would typically span multiple oil palm concessions and so can only be effective if all of these concessions are RSPO-certified and the companies agree to coordinate conservation efforts. Such strategies can be even more challenging if plantations are owned by small-holders who rarely have the resources to commit to conservation (Chapter 3). These practical barriers to implementation mean that national level conservation planning and landscape-scale HCV assessment may be essential for effective conservation in oil palm, and other tropical agricultural landscapes (Edwards & Laurance 2012). It is imperative that scientists working in these systems increase efforts to communicate their findings with HCV assessors and government policy makers in order to move towards landscape-level conservation measures in tropical agricultural landscapes.

In the immediate term, conservation strategies in plantations will continue to focus on the protection of isolated natural forest fragments for reducing biodiversity losses. Therefore, it is vital that these fragments provide maximum conservation benefit. Chapters 5 and 6 showed that the fragments sampled in my study varied in their conservation value in relation to their size, and to a lesser extent in relation to their forest quality and degree of isolation. Larger fragments supported higher dung beetle species richness and higher abundance of functionally important large tunnellers and rollers. Furthermore, larger and better quality fragments supported species assemblages more similar to those found in continuous forest sites. Therefore, I conclude that fragments should be at least 100 ha in size to maintain some level of dung beetle diversity, dung removal and seed dispersal. This recommendation is broadly supported by research from the Amazon which showed that fragments larger than 100 ha were able to support some large mammal species 30 years after isolation (Michalski & Peres 2007). However, there is a lack of evidence on the conservation value of larger forest fragments, because most large-scale fragmentation studies only consider fragments up to 100 ha in size (Laurance et al. 2002; Ewers et al. 2011). Extinction debt and synergistic disturbances could lead to further biodiversity losses in large fragments centuries after isolation (Turner et al. 1996; Laurance & Useche 2009; Wearn et al. 2012), and even if forest fragments can maintain current diversity, they may not be able to preserve species under climate change if species are required to shift their distributions (Brodie et al. 2012). Therefore, continued research is needed into whether tropical forest fragments can increase habitat connectivity and help species disperse or shift their distributions through agricultural landscapes.

8.6 Conclusions

Species assemblages in oil palm plantations are dominated by small-bodied species from lower trophic levels that are rare or absent in closed-canopy rainforest. Heavily-logged continuous tropical forest supports greater diversity of dung beetles and much higher rates of ecosystem functioning than forest fragments. Large and better-quality fragments support species assemblages more similar to continuous forest and support some dung beetle functions. Dung removal in forest fragments is dependent on a few large-bodied, disturbance-tolerant dung beetle species that partially compensate for the loss of other species, but this dependence leads to highly variable rates of dung removal in fragments.

Appendix 1

A1.1 Glossary of key terms

HCV National Interpretation (NI): documents designed to give country-specific detail to broad HCV definitions. Typically developed by members of national environmental and social NGOs. They may provide some specific recommendations, e.g. what defines a *significant* population of key species, or the size required to qualify for HCV 2. HCV NIs are not endorsed by the HCV Resource Network or peer reviewed. Not all countries have NIs and of those that do, the quality is highly variable.

Peer review of HCV assessments: During public consultation of HCV assessments, anyone can request a peer review if they deem the assessment insufficient or inaccurate; e.g. insufficient community or expert consultation or inadequate management plans. The peer review can be done by members of the HCV Resource Network Technical Panel, which consists of HCV international experts on HCV, such as members of environmental and social NGOs. Peer reviews can also be done by third parties. The review examines whether the HCV assessment was carried out in line with HCV 'best practice' (Brown et al. 2013). Whoever requests the peer review must cover the cost.

Significant values: "those recognised as being either unique, or outstanding relative to other examples in the same region, because of their size, number, frequency, quality, density or socio-economic importance, on the basis of existing priority frameworks, data or maps, or through field studies and consultations undertaken during the HCV assessments (Brown et al. 2013)."

The HCV approach/concept: the broad concept designed to protect critical environmental and social values using six high conservation values.

The HCV (assessment) process: the activity of identifying HCVs, and suggesting management and monitoring plans for a proposed development area.

A1.2. Requirements for certification, beyond an HCV assessment.

Legality. The first step in any certification process is to comply with local and international laws, such as environmental protection laws.

Environmental and Social Impact Assessments. Legally required in many countries. May be combined with HCV assessment, but tend to be more limited in scope.

Secure tenure, customary rights and consent. Ensures the company have rights to the land. Any development should not affect local communities without their free, prior and informed consent (FPIC).

Certification scheme requirements. The requirements typically include those listed above, as well as additional requirements. For example, the RTRS rules that new soy plantings cannot replace any native forest.

Appendix 2

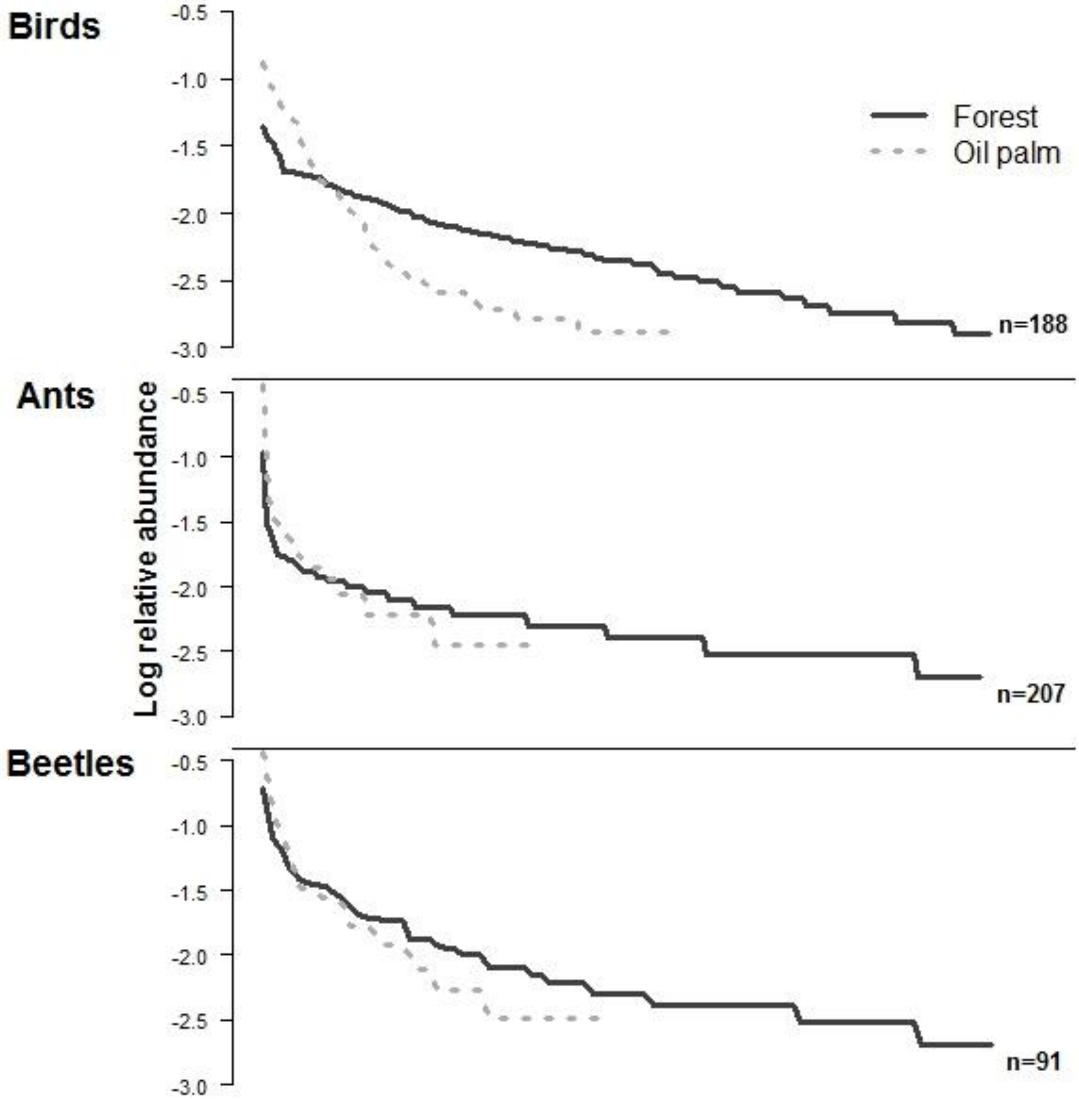

Figure A2.1. Rank abundance curves for birds, ants, and beetles in forest (dark grey lines) and oil palm (light grey lines) habitats. Values plotted are log relative abundances of each species/genera across all studies. X-axes labels are suppressed to aid interpretation, but total number of ranks in each taxa is listed on each panel.

Appendix 3

*Table A3.1. Table of models comparing all response variables between continuous forest and forest fragments. For each response variable two models are presented, one including forest type (and site as random effect) and one just containing the random effect (site). K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C): Marginal (M) and conditional (C) estimated R^2-vaues, based on Nakagawa & Schielzeth (2013). *Abundance data were fitted using a negative-binomial distribution to account for overdispersion. There is currently no way of calculating R^2 values for this distribution, and so R^2 values are not shown for these models. R: roller, T: tunneller, S: small and L: large.*

Response variables	Model	K	AICc	Δi	ωi	LL	R^2 (M;C)
Species richness							
	Type	3	713.1	0	0.99	-353	0.35;0.60
	1	2	722.8	9.7	0.01	-359	0;0.60
Abundance*							
	Type	4	1246.8	0	0.97	-619	NA
	1	3	1253.8	7	0.03	-624	NA
Biomass							
	Type	4	118.7	0	0.93	-55	0.28;0.68
	1	3	124.0	5.3	0.07	-59	0;0.67
Simpsons							
	1	3	148.1	0	0.54	-71	0;0.48
	Type	4	148.4	0.3	0.46	-70	0.06;0.48
Alpha							
	Type	4	617.3	0	0.98	-304	0.19;0.34
	1	3	625.0	7.7	0.02	-309	0;0.32
Biomass R							
	Type	3	83.3	0	0.89	-39	0.18,0.41
	1	2	87.5	4.24	0.11	-42	0;0.48
Biomass T							
	Type	3	146.2	0	0.92	-70	0.22,0.57
	1	2	151.0	4.76	0.08	-73	0,0.58
Biomass LR							
	Type	3	31.5	0	1	-13	0.28;0.28
	1	2	47.8	16.3	0	-22	0;0.50

Biomass SR							
	Type	3	81.2	0	0.67	-37	0.07;0.25
	1	2	82.6	1.4	0.33	-39	0;0.28
Biomass LT							
	Type	3	178.8	0	0.86	-86	0.21;0.62
	1	2	182.5	3.7	0.14	-89	0;0.62
Biomass ST							
	Type	3	41.0	0	0.88	-17	0.05;0.05
	1	2	45.0	4.1	0.12	-20	0;0.01
Abundance R							
	Type	3	63.8	0	0.86	-29	0.10,0.21
	1	2	67.4	3.64	0.14	-32	0,0.27
Abundance T*							
	Type	4	1193.0	0	0.94	-592	NA
	1	3	1198.7	5.68	0.06	-596	NA
Abundance LR							
	Type	3	34.4	0	1	-14	0.25;0.25
	1	2	48.6	14.2	0	-22	0;0.45
Abundance SR							
	Type	3	70.4	0	0.75	-32	0.07;0.18
	1	2	72.6	2.2	0.25	-34	0;0.21
Abundance LT							
	Type	3	56.2	0	0.95	-25	0.10;0.13
	1	2	62.2	6	0.05	-29	0;0.19
Abundance ST							
	1	2	15.1	0	0.5	-6	0;0
	Type	3	15.2	0	0.5	-4	0.02;0.02
Sp. rich. (forest sp.)							
	Type	3	124.8	0	1	-59	0.38;0.58
	1	2	136.7	11.9	0	-66	0;0.60
Abund. (forest sp.)*							
	Type	4	1238.0	0	0.97	-615	NA
	1	3	1245.1	7.1	0.03	-619	NA
Biomass (forest sp.)							
	Type	3	28.2	0	0.98	-11	0.07;0.07
	1	2	35.9	7.8	0.02	-16	0;0.04

Table A3.2. Table of coefficients (means) and confidence intervals of functional group abundances in continuous forest and fragments. Values are not in the original abundance scale, see Chapter 5 table 5.1 for details of links or transformations.

Variable	Mean (Cont, Frag)	Confidence intervals (Cont; Frag)
Roller abundance	0.29, -0.76	(-0.35,0.93); (-1.09,-0.42)
Tunneller abundance	4.48, 3.19	(3.72,5.23): (2.92,3.46)
Large roller abundance	0.01, -2.71	(-0.43,0.44); (-3.43,-1.99)
Small roller abundance	0.07, -0.80	(-0.61,0.75); (-1.14,-0.48)
Large tunneller abundance	0.18, -0.87	(-0.30,0.67); (-1.17,-0.58)
Small tunneller abundance	0.57, 0.30	(0.24,0.90); (0.15,0.45)

Table A3.3. Total number of individuals of each species caught at each site, separated by guild, with sites ranked from largest to smallest (left to right). Abbreviations as follows: Ca. = Catharsius, C. = Copris, Inda. = Indachorius, M. = Microcopris, Micronth. = Micronthophagus, Oc. = Ochicanthon, O. = Onthophagus, P. = Paragymnopleurus, Pr. = Proagaderus, S. = Sisyphus, 1 = Danum Valley Conservation Area, 2 = Ulu-Segama Malua Forest Reserve, 3 = Lungmanis VJR, 4 = Ulu Sapa Payau VJR, 5 = Sungai Sapi C VJR, 6 = Materis VJR, 7 = Keruak VJR, 8 = 'Watercatchment' HCV area, 9 = Labuk Road VJR, 10 = 'Sabahsar' HCV area, 11 = 'Rekasar' HCV area, 12 = 'Yongpeng' HCV area, 13 = Sungai Sapi A VJR, 14 = Pin Supu forest, 15 = Meranti' HCV area, '16 = 'Jatu' HCV area, 17 = 'Lunpadas' HCV area, and 18 = 'Delilah' HCV area.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Large tunnellers																		
Ca. dayacus	73	54	8	16	5	10	-	-	17	1	-	-	1	7	-	-	-	-
Ca. renaudpauliani	-	-	3	14	17	-	-	1	2	41	4	98	12	1	-	-	7	13
C. agnus	31	25	-	61	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. sinicus	21	33	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Pr. watanabei	60	45	1	8	-	0	2	18	-	2	1	3	3	-	-	1	-	-
Small tunnellers																		
C. ramosiceps	8	6	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-
M. doriae	9	6	-	71	-	-	1	-	-	-	-	-	-	-	-	-	-	-
M. hidakai	6	2	14	-	-	-	-	-	-	4	-	10	1	-	-	-	-	1
O. pastillatus	-	1	-	1	6	-	-	-	38	-	-	-	-	-	-	-	-	-
O. (Inda.) sp 1	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
O. (Inda.) aff.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-

semidanumensis																		
O. (Inda.) aff. paramasaoi	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
O. (Inda.) aff. Pseudoworoae	-	-	-	-	2	-	-	-	-	-	-	-	2	-	1	-	-	-
O. (Micronth.) sp 4	1	-	8	-	4	5	1	-	-	-	-	-	16	-	-	-	-	-
O. sp aff cf batillifer	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
O. sp aff deliensis	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. angustatus	3	3	-	2	3	-	-	-	1	-	-	-	-	43	-	-	-	-
O. aphodioides	3	5	1	-	10	3	-	-	-	-	-	-	-	-	-	-	-	-
O. sp aff aphodioides	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
O. arayai	1	4	2	-	-	5	-	-	-	11	-	7	-	2	-	-	2	2
O. borneensis	15	23	13	9	3	2	1	-	59	-	-	-	-	-	-	-	-	-
O. agg. cervicapra	530	345	15	34	5	2	10	45	-	95	9	186	52	-	-	-	53	2
O. cf batillifer	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
O. cf quasijohkii	-	-	-	32	13	-	-	-	2	-	-	-	1	1	-	-	-	-
O. cf rutilans	-	-	-	-	-	1	1	-	-	10	-	-	-	-	-	-	-	2
O. deflexicollis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. dux	6	-	-	5	-	-	-	-	-	-	6	-	-	8	1	-	-	-
O. fuji	-	12	2	25	-	2	-	-	-	1	2	-	2	3	-	3	-	-
O. hidakai	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
O. incises	9	14	3	-	11	31	19	1	-	2	-	11	2	1	-	-	2	-
O. laevis laevis	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

O. mulleri	15	-	7	-	-	3	-	5	27	10	-	49	5	4	-	-	9	-
O. agg. obscurior	26	133	5	12	10	122	14	6	-	91	4	68	46	8	1	-	12	4
O. agg. ochromerus	7	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. agg. pacificus	2	2	-	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-
O. pavidus	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
O. rorarius	1	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. rudis	8	19	5	-	1	1	-	-	-	1	-	2	1	-	-	-	-	-
O. rugicollis	11	31	22	-	-	51	12	-	-	25	1	42	-	-	-	2	52	1
O. sarawacus	2	1	-	42	-	-	-	-	97	-	-	-	-	3	-	-	-	-
O. agg. semiaureus	10	2	125	-	10	50	30	46	9	44	119	54	17	147	33	12	3	-
O. semicupreus	2	2	13	1	1	2	-	14	8	39	10	70	6	-	1	2	4	6
O. sp aff borneensis	5	-	-	4	2	-	-	-	-	-	-	-	-	1	-	-	-	-
O. taeniatus	-	-	1	1	2	2	-	-	-	-	-	-	1	-	-	-	-	-
O. vulpes	52	35	32	31	95	11	1	30	-	-	8	-	95	8	2	-	-	-
O. waterstradti	30	-	2	6	10	4	1	-	-	-	-	-	7	2	-	-	-	-
O. sp A	-	-	-	-	3	-	-	3	1	-	-	-	-	-	-	-	-	-
O. sp B	-	-	-	-	1	-	-	1	-	-	-	1	-	-	-	-	1	-
O. sp C	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-
O. sp D	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
O. aff sp D	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
O. sp M	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Large rollers																		
P. maurus	10	28	2	-	-	-	1	-	113	-	-	-	-	2	-	-	-	-

P. sparsus	66	106	12	-	1	3	1	5	1	-	-	-	-	-	-	-	-	-
P. striatus	9	17	-	4	-	-	-	-	14	-	-	-	-	-	-	-	-	-
Small rollers																		
S. thoracicus	103	252	41	10	3	71	50	22	11	1	2	10	9	1	-	-	2	1
Oc. danum	3	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Oc. dytiscoides	7	-	-	-	-	73	10	-	-	-	-	-	-	-	-	-	-	-
Oc. masumotoi	4	7	15	17	41	5	-	28	11	-	16	-	85	2	2	-	-	-
Dwellers																		
Oniticellus tessellatus	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Total	1095	1225	352	421	262	463	155	227	417	378	183	615	365	246	41	20	149	32

Table A3.4. Summary data of species richness, abundance and biomass at each forest site. Means and standard deviations per sampling station at each site are shown. Biomass values are all in grams (g) and are presented for all species and by functional group. Site numbers are as defined in legend of Table A5.3.

Site	**Species richness**		**Abundance**		**Biomass**		**Large roller biomass**		**Small roller biomass**		**Large tunneller biomass**		**Small tunneller biomass**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	19.4	3.1	115.5	62.0	7.2	2.4	0.79	0.5	0.06	0.1	5.23	2.2	1.15	0.8
2	19	2.9	122.5	52.7	6.7	2.5	1.48	1.0	0.13	0.1	4.14	2.0	0.90	0.3
3	11.3	2.5	35.2	12.4	1.3	0.7	0.12	0.1	0.03	0.0	0.57	0.6	0.57	0.3
4	11.6	4.5	42.1	20.9	3.3	2.3	0.06	0.1	0.02	0.0	2.33	2.1	0.87	0.6
5	9.1	2.7	26.2	13.5	1.4	0.9	0.01	0.0	0.03	0.0	1.05	0.9	0.33	0.2
6	10.2	1.9	46.3	18.8	1.2	0.5	0.02	0.0	0.09	0.1	0.55	0.4	0.50	0.3
7	5.7	1.4	15.5	6.1	0.3	0.1	0.02	0.1	0.03	0.0	0.03	0.1	0.21	0.1
8	7.6	2.4	22.7	9.3	0.6	0.3	0.04	0.1	0.03	0.0	0.27	0.2	0.28	0.1
9	8.9	1.5	41.7	20.1	3.7	2.8	1.95	1.9	0.01	0.0	0.98	0.8	0.73	0.3
10	8.5	1.3	47.3	18.2	3.0	1.9	0	0	0	0	2.47	1.9	0.56	0.3
11	6.3	1.8	26.1	12.0	0.9	0.7	0	0	0.02	0.0	0.28	0.4	0.55	0.4
12	9.2	2.3	61.5	24.9	5.4	3.1	0	0	0.01	0.0	4.58	3.0	0.77	0.4
13	12.4	2.7	73	15.9	2.2	1.0	0	0	0.12	0.1	1.29	1.1	0.76	0.1
14	6.2	1.8	24.6	4.0	1.1	0.4	0.03	0.1	0	0	0.41	0.4	0.62	0.1
15	3.7	1.2	13.7	8.0	0.3	0.2	0	0	0	0	0	0	0.33	0.2
16	3	0	6.7	4.6	0.2	0.1	0	0	0	0	0.04	0.1	0.13	0.1
17	7.5	3	37.3	15.5	1.3	0.9	0	0	0	0	0.81	1	0.51	0.3
18	5	2	10.7	6.0	2.1	2.7	0	0	0	0	2.01	2.7	0.06	0.0

Table A3.5. Table of best models ($\Delta i < 2$) of abundance by body size and functional group. K: the number of parameter estimates in the model, AICc: a measure of model fit corrected for sample size, Δ_i: the difference between that model's AIC_c value and that of the best model, ω_i: the Akaike weight, representing the model's relative strength compared to other best models, LL: Log-likelihood, the overall model fit with no adjustment for the number of parameters, and R^2 (M; C): Marginal (M) and conditional (C) estimated R^2-vaues, based on Nakagawa & Schielzeth (2013).

Response variable	**(by body size and functional group)**	**K**	**AICc**	**Δi**	**ωi**	**LL**	**R^2 (M; C)**
Large roller abundance							
	Area	3	23.37	0	0.25	-8.6	0.29; 0.29
	Area + Veg	4	24.35	0.98	0.15	-8.0	0.41; 0.41
	Area + Iso	4	25.2	1.84	0.1	-8.4	0.34; 0.34
	Area^2	4	25.34	1.97	0.09	-8.5	0.41; 0.41
Small roller abundance							
	Area + Iso^2	5	58.9	0	0.11	-24.2	0.25; 0.25
	Area + Veg + Iso^2	6	59.01	0.11	0.1	-23.1	0.23; 0.23
	Area + Veg^2 + Iso	6	59.36	0.46	0.08	-23.3	0.22; 0.22
	Area + Veg + Iso	5	59.39	0.49	0.08	-24.4	0.17; 0.17
	Area^2 + Iso^2	6	59.64	0.75	0.07	-23.5	0.33; 0.33
	Area + Iso	4	59.66	0.77	0.07	-25.7	0.16; 0.18
	Area^2 + Veg + Iso^2	7	60.56	1.67	0.05	-22.8	0.28; 0.28
	Area + Veg^2 + Iso^2	7	60.77	1.88	0.04	-22.9	0.24; 0.24
Large tunneller abundance							
	Iso	3	46.54	0	0.16	-20.2	0.14; 0.14
	Area^2 + Iso	5	47.14	0.6	0.12	-18.3	0.16; 0.16
	Area^2 + Iso^2	6	47.2	0.66	0.12	-17.2	0.16; 0.16
	Iso^2	4	47.61	1.07	0.1	-19.6	0.11; 0.11
	Area^2 + Veg^2 + Iso	7	48.17	1.62	0.07	-16.6	0.19; 0.19
	Area + Iso	4	48.37	1.83	0.07	-20.0	0.14; 0.14
Small tunneller abundance							
	1	2	12.25	0	0.3	-4.1	0; 0
	Iso	3	14.12	1.87	0.12	-4.0	0; 0

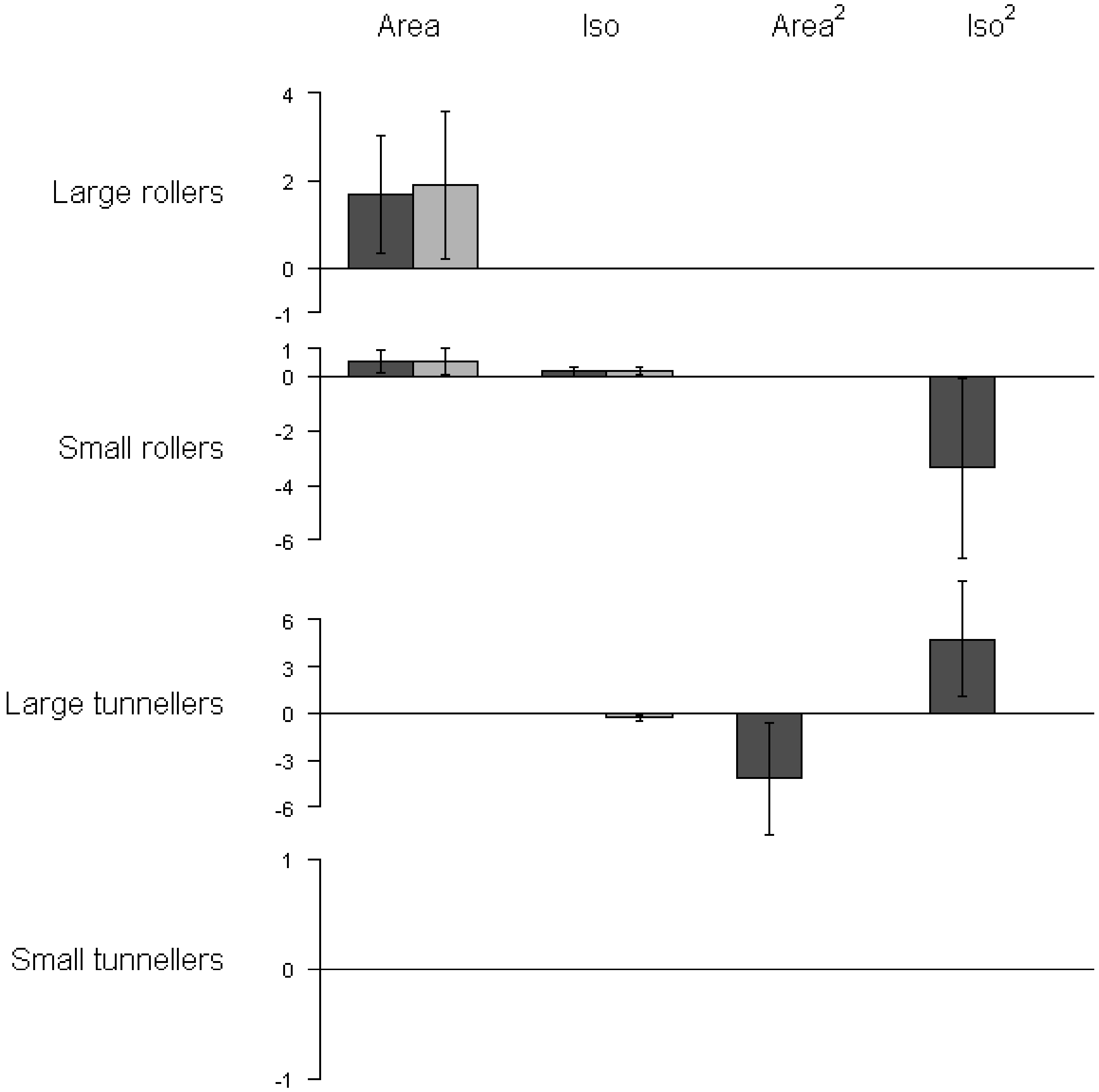

Figure A3.1. A comparison of effect sizes from abundance and biomass models by body size and functional group. Effect sizes are regression slope values of explanatory variables (x axis) against response variables (y axis). Effect sizes are plotted only for variables included in best models according to AICc model ranking and where confidence intervals do not overlap zero. For linear predictors, positive effect sizes indicate positive relationships between the predictor and response variables, negative effect sizes indicate negative relationships. For curvilinear predictors, a positive effect size indicates a convex relationship, whilst a negative effect size indicates a concave relationship between the response and predictor variable. Errors bars show 95% confidence intervals. Numbers in brackets indicate the maximum number of species in the analysis.

Abbreviations as follows: Iso = isolation distance. Dark grey bars show effect sizes for biomass and light grey for abundance.

Table A3.6. Comparison of analyses of turnover in species assemblages, with different dissimilarity indices and species subsets. I present results for analyses of all sites and only fragments. Species subsets are as follows: all species occurring at least twice AND at ≥2 sites (n = 46 species), on species occurring at least five times AND at at ≥2 sites (n = 38 species), and on species occurring at least twice AND at at ≥5 sites (n = 22 species). Dissimilarity indices are Morisita Horn (MH), Bray-Curtis (BC) and Chao-Jaccard (CJ). Stress values are taken from Non-metric Multi Dimensional Scaling analysis, and significant variables and R^2 *values estimated using vector fitting.*

N species	Analysis	Index	Stress	Significant variables	MNS variables	R^2: Veg	R^2: Area	R^2: Iso	R^2: Type
46	Fragments	MH	0.06	Veg, Area	-	0.78	0.50	0.29	NA
46	Fragments	BC	0.06	Veg, Area	-	0.79	0.43	0.23	NA
46	Fragments	CJ	0.07	Veg	Area	0.77	0.33	0.21	NA
46	All sites	MH	0.07	Veg	Type	0.75	NA	NA	0.15
46	All sites	BC	0.07	Veg	Type	0.68	NA	NA	0.16
46	All sites	CJ	0.06	Veg	Type	0.63	NA	NA	0.15
38	Fragments	MH	0.06	Veg	-	0.79	0.29	0.28	NA
38	Fragments	BC	0.05	Veg, Area	-	0.81	0.38	0.29	NA
38	Fragments	CJ	0.06	Veg	Area	0.79	0.36	0.32	NA
38	All sites	MH	0.05	Veg	Type	0.78	NA	NA	0.15
38	All sites	BC	0.04	Veg	Type	0.67	NA	NA	0.16
38	All sites	CJ	0.04	Veg	Type	0.72	NA	NA	0.16
22	Fragments	MH	0.07	Veg	Area	0.85	0.33	0.32	NA
22	Fragments	BC	0.07	Veg	Area, Iso	0.81	0.35	0.33	NA
22	Fragments	CJ	0.06	Veg	Area	0.79	0.32	0.22	NA
22	All sites	MH	0.07	Veg	-	0.71	NA	NA	0.14
22	All sites	BC	0.06	Veg	Type	0.68	NA	NA	0.13
22	All sites	CJ	0.06	Veg	-	0.63	NA	NA	0.08

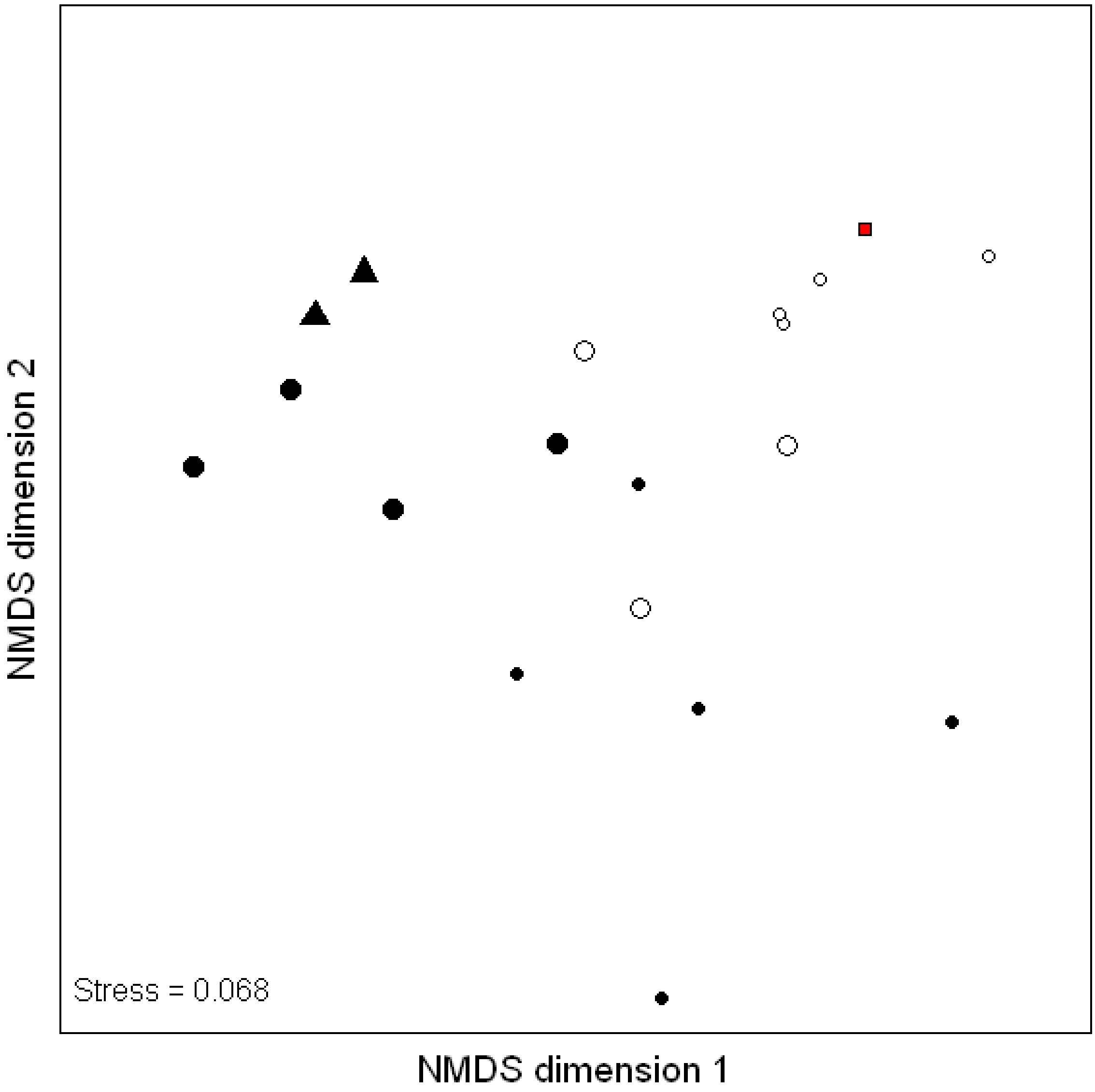

Figure A3.2. A comparison of dung beetle species assemblages in all forest sites and an oil palm plantation. In the plot points (sites) that are closer together support more similar species assemblages. NMDS plot (Bray-Curtis method) fitted for all species recorded at least twice (n = 2 individuals) and in at least 2 stations within a site. NMDS ordination was based on Wisconsin double standardised abundance values. To aid interpretation, sites larger than the mean fragment size are plotted as large circles and those smaller than the mean as small circles, and sites with vegetation quality higher than the mean quality score of all sites are plotted as black circles and those with vegetation quality lower than the mean as hollow circles. The two continuous forest sites are plotted as large, black triangles, and the oil palm site as a small red square.

Appendix 4

Table A4.1. Comparison of the percentage of dung removed by Catharsius spp. in fragments, twice-logged continuous forest and unlogged continuous forest. Values shown are 95% confidence intervals for analyses excluding stations where < 5% of dung was removed (n = 77 stations), <10% of dung was removed (n = 62 stations) and <20% of dung was removed (n = 53 stations). 2L = twice-logged continuous forest, UL = unlogged continuous forest.

Site	**5%**	**10%**	**20%**
Fragments	59.8, 74.4	70.8, 83.5	72.3, 86.7
2L	15.6, 37.3	17.9, 32.6	17.9, 32.6
UL	29.9, 57.9	33.1, 52.3	33.1, 52.3

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