DUNG BEETLE ASSEMBLAGES ON TROPICAL LANDBRIDGE ISLANDS

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SUMMARY

Understanding and predicting the effects of tropical forest fragmentation on biodiversity and ecosystem functioning is extremely important for conservation planning. This thesis provides one of the first comprehensive studies on a group of ecologically important invertebrates – dung beetles, on forested landbridge islands in Lake Kenyir, Peninsular Malaysia. I show patterns of changes in dung beetle assemblages on islands of varying sizes and in their key ecological function. I also examined the dynamics and underlying drivers of dung beetle distribution on the small islands, and discuss the conservation value of small forest fragments based on these results.

Chapter 1 gives a general overview of our current understanding of forest fragmentation in the tropics and dung beetle ecology. In Chapter 2, I examined the overall effects of forest fragmentation on dung beetle assemblages. I found that below island area of 35.8 ha, species richness and community composition were driven by a small island effect (SIE), rather than by a direct relationship with area. Likely as a result of SIE, no significant nested pattern was found among the dung beetle assemblages on islands. Dung beetle species with low baseline density and inability to forage on forest edge were found to be rarer among sites hence likely more prone to local extinction. These results highlight the stochastic nature of dung beetle communities on small islands, and the need for better understanding of minimum fragment size, capable of retaining functional ecological communities, for effective conservation management.

In Chapter 3, I show that the foraging height of the little studied arboreal dung beetles (represented by *Onthophagus* sp. 7), were present in higher numbers at 5 m from the forest floor relative to at 15 m in the foliage on smaller islands, indicating a possible downward shift in their vertical stratification in response to forest fragmentation. This expands our current understanding of effects of forest fragmentation to a three-dimensional paradigm.

In Chapter 4, I specifically determined the population dynamics on the small islands. Results from the replicated dung supplementation experiment did not support the food limitation hypothesis. On the other hand, results from the *Paragymnopleurus maurus* translocation experiment indicate that dispersal limitation is likely an important driver of species presence on small islands. The results of the dispersal limitation experiment were confounded by the presence of invasive ant species, which highlights the need for extensive planning before utilizing assisted colonization as a conservation tool. These results highlight the potential of landbridge islands as experimental ground to test ecological theories, and highlight possible hope for the "functional" rehabilitation of small forest fragments.

Chapter 5 moves from species and community ecology to ecosystem function, and reports that dung burial rate generally decreased in small islands, with dung beetle abundance being the strongest correlate. I compare results with previous studies and suggest that, whether dung beetle diversity or abundance plays a more important role in dung burial may depend on the site and community composition. In this chapter, I also compare different sampling methods and show that human dung is the most effective bait for dung beetle diversity surveys. In Chapter 6, I provide an overview of the results and give overarching discussion and recommendations for future studies.

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CHAPTER 1

General introduction

Forest fragmentation in the Tropics

Anthropogenic forest loss, fragmentation and degradation are prevalent and accelerating throughout the tropics (Achard *et al.* 2002, Wright 2005, Sodhi *et al.* 2007). These threats are of greater concern in SE Asia because the region is covered by biodiversity hotspots (Achard *et al.* 2002, Sodhi *et al.* 2004), with the highest number of endemic bird and mammal species in the tropics (Sodhi *et al.* 2009), and currently suffering the highest rate of habitat loss (Sodhi *et al.* 2010). Forest loss and disturbance often involves conversion of the continuous forest to isolated fragments set in a matrix of non-forest habitat types (e.g. agricultural areas). Although there have been numerous studies on the detrimental effects forest fragmentation on the forest dwelling biotas across the tropics (see reviews by Saunders *et al.* 1991, Turner 1996), such knowledge is still relatively poor in SE Asia (Laurance & Bierregaard 1997, Sodhi *et al.* 2007). Among the small number of studies determining the effects of forest fragmentation on biological communities in SE Asia, the focus has thus far been on amphibians (Bickford *et al.* 2010), birds (Pattanavibool *et al.* 2004, Castelletta *et al.* 2005), and mammals (Lynam & Billick 1999, Laidlaw 2000). Few studies have been done on the invertebrates in forest fragments in SE Asia (Koh *et al.* 2002), although they are a numerically dominant group across the terrestrial habitats that play important roles in ecosystem functioning (Samways 1993). Invertebrates can also generally be good indictors of ecological changes (Kremen *et al.* 1993).

The species-area relationship (SAR) (Arrhenius 1921) and the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson 1967) have been the most important theoretical bases for the research on forest fragmentation (Rosenzweig 1995). When applied to habitat islands embedded in various type of matrix, however, the permeability of the matrix to different taxa must be taken into consideration (Laurance 2008, Koh & Ghazoul 2010). Forested landbridge archipelagos created by damming have the advantage of a uniform water matrix between fragments, and may serve as useful model systems of the study of effects of forest fragmentation on floral and faunal communities (Diamond 2001).

According to the classic SAR, species richness declines with fragment area with an approximately linear relationship on a log scale (Gleason 1922). Lomolino and Weiser (2001) argued, however, that there is an upper limit for area below which species richness varies independently of area – also called the small island effect (SIE). Their explanation for the SIE is that, factors associated with larger islands, such as more diverse habitat types, higher populations sizes which lead to lower extinction risks, may disappear when island size is below a certain limit, and stochastic events have stronger effects than area (Lomolino 2000, Lomolino & Weiser 2001). Although the existence of SIE and the methodological approach to identifying it are debated (Triantis *et al.* 2006, Burns *et al.* 2009), with accelerating anthropogenic habitat fragmentation, it is important to understand the role of fragment size in determining the number of species when fragments are small, which are becoming ubiquitous in many of the remaining tropical lowland forests (Turner & Corlett 1996).

Dung beetle ecology

Dung beetles belong to three subfamilies of Scarabaeidae (Coleoptera): the Scarabaeinae, Aphodiinae and Geotrupinae, and are characterized by their use of dung, and in some cases other organic debris, at both adult and larval stages (Hanski & Cambefort 1991). Although some species of other beetle families also use dung at the adult or larval stage, these are not considered true dung beetles (Hanski 1991). Worldwide there are more than 5,000 dung beetle species, with the highest diversity in the tropics (Hanski & Cambefort 1991). The majority of them fall in the subfamily Scarabaeinae (Hanski 1991), which is the dominant group in tropical regions while Aphodiinae and Geotrupinae tend to be more important in the temperate regions (Halffter & Matthews 1966). It is estimated that there are in total between 1,000 and 2,000 species of dung beetles in SE Asia (Hanski & Krikken 1991). Due to the region’s complex geological history with diverse faunal origins and shifting paleoclimates, similarities in dung beetle faunas are relatively low among the islands of this archipelago, thus resulting in high endemism (Hanski & Krikken 1991). Majority of the known dung beetle species in SE Asia belong to a single genus *Onthophagus* that includes small (< 13 mm) and mostly diurnal species (Hanski & Krikken 1991).

Dung beetles can be divided broadly into four main guilds: the rollers, tunnellers, dwellers and kleptoparasites. The rollers (telocoprid nesters) separate a piece of dung from the dung pad to form it into a ball, and roll it away anywhere between 5 cm to 18 m from the dung pad, where the dung ball is buried (Hanski & Cambefort 1991). The tunnellers (paracoprid nesters) remove dung vertically from the source by making a tunnel either directly beneath or to the side of the dung pad in the soil, through which bits of dung are buried. Unlike rollers and tunnellers, the dwellers (endocoprid nesters) remain in the dung pad to both feed and breed and do not relocate the dung. There is a fourth guild, the kleptoparasites, which do not dig or provision their own nest, but steal the dung of other species, both rollers and tunnellers (Hanski & Cambefort 1991).

The majority of dung beetles feed on dung (coprophagous), mostly that of mammals, although many species feed on carrion (necrophagous), some rotting fruit (saprophagous), and other decomposing materials (Hanski & Cambefort 1991, Larsen *et al.* 2006). Many SE Asian species are copro-necrophagous – utilizing both dung and carrion (Hanski & Cambefort 1991). Food location in dung beetles is primarily through olfaction, by either cruising flights or perching on low vegetation (Hanski & Cambefort 1991). Vision is poorly developed but light is used for orientation and a general stimulus (Hanski & Cambefort 1991). Studies have also found that some dung beetles can utilize polarized moonlight for navigation (Dacke *et al.* 2003, Dacke *et al.* 2004). Most species remain very close to the soil, often within a few centimeters (Hanski & Cambefort 1991), although some specialized species are found 5 m or higher from the ground, to forage for dung of arboreal mammals (Davis *et al.* 1997). It has been suggested that the arboreal dung beetles move closer to the forest floor in disturbed forests compared to the primary forest, possibly as a result of changes in the canopy cover and food resources (Davis & Sutton 1998).

Fecundity in dung beetles varies among species but is generally low, with the female able to lay 2 – 70 eggs in her lifetime for most species (Hanski & Cambefort 1991). Many species of dung beetles exhibit parental care, which improves the survivorship of progeny (Halffter & Matthews 1966). Field and laboratory observations indicate that some dung beetles can survive for three or more years (Edwards 1988). However, detailed biological and population ecological information is lacking in SE Asia (Hanski & Krikken 1991).

Ecological functions of dung beetles

Dung consumption and relocation by dung beetles make them key players in a series of ecological functions, including nutrient recycling, soil aeration, secondary seed dispersal and parasite control (Nichols *et al.* 2008). By burying freshly deposited animal dung into the soil, dung beetles prevent the loss of nitrogen in the dung through ammonia (NH_3) volatilization, and promote the conversion of it into labile forms available for uptake by plants (Losey & Vaughan 2006). This is done not only by the physical relocation of dung below the soil surface, but also by altering the microorganism fauna in the dung through the feeding and nesting activities by dung beetles (Yokoyama *et al.* 1991). Tunnels made by the dung beetles during dung burial also help to move large amount of soil to the surface, and increase the soil aeration and permeability (Mittal 1993). Seed dispersal by frugivorous animals is an important mechanism in the tropics (Howe & Smallwood 1982). However there are a number of post-primary seed dispersal risk factors, that affect the seed fates of seeds embedded in animal droppings, including predators, pathogens, and unsuitable sites for germination (Chambers & MacMahon 1994). Dung beetles do not utilize the seeds in dung but may bury them together with dung into the soil, vertically below the dung pad (by tunnellers) or horizontally away from the dung pad (by rollers) (Andresen & Feer 2005). These processes typically reduce seed predation and pathogens (Estrada & Coates-Estrada 1991, Andresen & Levey 2004), relocate seeds to favorable microclimates for germination (Andresen & Levey 2004), and decrease post-dispersal clumping (Andresen 2001, Andresen & Feer 2005). Also, the feeding and nesting behaviors of dung beetles serve to suppress the abundance of dung-breeding flies and dung-dispersed nematodes and protozoa (see review by Nichols *et al.* 2008). In summary, dung beetles play important roles in maintaining the integrity of natural ecosystems especially by facilitating nutrient recycling and secondary seed dispersal. By increasing soil fertility, increasing crop productivity and suppressing parasites, dung beetles also provide ecosystem services that are intimately linked to human health and economy.

Dung beetles as study taxon for fragmentation research

Dung beetles have strong habitat specificity, with distinct groups of species found to be associated with forest, edge and pasture habitats (Halffter & Favila 1993). They have also been shown to be sensitive to tropical forest modification and fragmentation, resulting in decline in both species diversity and abundance (Halffter & Arellano 2002, Davis *et al.* 2004, Davis & Philips 2005, Nichols *et al.* 2007). Because of the dependence of dung beetles on mammal dung, decrease in the abundance mammals was shown to negatively affect the dung beetle communities (Estrada *et al.* 1999, Andresen & Laurance 2007, Nichols *et al.* 2009). Surveys of dung beetles are cost-effective and easily standardized, making them an excellent indicator taxon (Gardner *et al.* 2008).

There have been an increasing number of ecological studies looking at the effects of tropical forest fragmentation, in particular, on dung beetles assemblages (see review by Nichols *et al.* 2007). Overall, dung beetle species richness was found to increase with the fragment area in most studies, and in approximately half of the studies, decrease with fragment isolation (Nichols *et al.* 2007). Similarly, dung beetle abundance was positively correlated with fragment area in most cases, and negatively, but weakly, correlated with isolation distance (Nichols *et al.* 2007). Dung beetle community composition was also affected by fragmentation in several studies, with assemblages in smaller fragments with lower community similarity to the intact forest (Klein 1989, Andresen 2003). In one study based on landbridge islands in Lake Guri, Venezeula, Larsen *et al.* (2005) found that the large-bodied dung beetles were more prone to extinction on isolated islands.

The decline or loss of dung beetles, and changes in their community composition, may have significant consequences in the maintenance of the ecosystem functions provided by dung beetles outlined above. However, empirical data from forest fragments on the level of reduction in the dung burial – the key function of dung beetles, are scarce (Andresen 2003, Larsen *et al.* 2005). Even fewer data are available on the links between changes in dung beetle diversity and abundance, and consequences in dung burial (Larsen *et al.* 2005, Slade *et al.* 2007). In SE Asia, the only known studies on the ecosystem functioning of dung beetles are by Slade *et al.* (2007) and Lee *et al.* (2009). Using exclusion experiments under field conditions, Slade *et al.* (2007) showed that dung burial was positively affected by the number of functional guilds present at dung. Lee *et al.* (2009) carried out the first ecological study on dung beetles in Peninsular Malaysia and Singapore, where they showed that dung burial was reduced in more disturbed forests compared with old-growth forests.

No study has systematically examined the impacts of tropical forest fragmentation on dung beetle assemblages in SE Asia. My thesis aims to provide relatively comprehensive empirical data on the patterns of changes in the dung beetle assemblages on forested landbridge islands of varying sizes, and in their key ecological function – dung burial. Furthermore, I examine dynamics and underlying drivers of dung beetle distribution on the small islands, and discuss the conservation value of small forest fragments based on these results. I also take advantage of landbridge islands as natural experimental ground, and demonstrate the feasibility of, and draw insights from controlled and replicated ecological experiments at whole island scale.

Specifically, this thesis aims to answer the following research questions:

1) How do fragment size, isolation, and other geographical and environmental variables of the islands, such as the amount of edge and the basal area of woody species, affect the dung beetle species richness?
2) Is there a small island effect among the islands, and if so, what is the upper limit in island size for the effect of area in determining species richness to diminish relative to other factors?
3) How does forest fragmentation affect the community composition of dung beetles on the islands?
4) What species traits of dung beetles are associated with their rarity on the islands hence possibly their local extinction proneness?
5) How does forest fragmentation affect the foraging height of arboreal dung beetles with decreasing fragment area?
6) Are the dung beetles on the small islands food or dispersal limited?

7) How does forest fragmentation affect dung burial by dung beetles and which attribute of the dung beetle community (species richness, abundance, body mass and functional guilds) is the best predictor for dung burial rate?

I hope that my research will provide insights into the ecology and conservation of this important taxonomic group.

CHAPTER 2

Dung beetle assemblages on tropical landbridge islands: small island effect and vulnerable species

ABSTRACT

There have been few studies on the effects of tropical forest fragmentation on biological communities, especially the invertebrates, in SE Asia. In this chapter, I examine the determinants of species richness at large and small islands. Furthermore, I investigate the traits of dung beetle species that are related to their vulnerability to local extinction following forest fragmentation. Our regression tree analysis revealed an area threshold at 35.8 ha indicating a small island effect. Tree basal area was the most important predictor of species richness in small islands (< 35.8 ha). The small island effect was also manifested in patterns of dung beetle community composition where communities on small islands (< 35.8 ha) departed from the mainland and larger island composition, and were highly variable with no significant nested pattern among all sites. The communities exhibited a low degree of spatial autocorrelation, suggesting that dispersal limitation may play a part in structuring dung beetle assemblages. Species with lower baseline density and inability to forage on forest edge were found to be rarer among sites hence likely more prone to local extinction. I highlight the stochastic nature of dung beetle community composition on small islands and argue that this will result in reduced ecosystem functionality.

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INTRODUCTION

Anthropogenic habitat loss and associated fragmentation is the leading cause of terrestrial biodiversity loss (Brooks *et al.*, 2002; Reed, 2004; Brook *et al.*, 2008). Numerous studies have determined the effects of forest fragments on biotic communities embedded in a matrix of man-made landscape, e.g. agricultural land, plantations or even urban areas (Fahrig, 2003; Bickford *et al.*, 2010). The Equilibrium Theory of Island Biogeography (ETIB) has been the theoretic basis for habitat fragmentation studies where patches are treated as islands (Rosenzweig, 1995). However, unlike real islands, terrestrial habitat patches are not surrounded by a uniform matrix (e.g., water) but by mosaic habitats with variable degrees of hostility and permeability for different taxa (Ricketts, 2001; Revilla *et al.*, 2004). As a result, patterns in these studies cannot be extrapolated unless the effect of the matrix is taken into consideration (Prugh *et al.*, 2008; Umetsu *et al.*, 2008; Koh & Ghazoul, 2010). On the other hand, forested landbridge archipelagos created by hydro-electric reservoirs may be the closest representation to the real island biogeography setting providing unique opportunities for the study of the effects of anthropogenic forest fragmentation on biodiversity (Diamond, 2001).

The species–area curve has been frequently used to explain the decrease in species richness in habitat fragments. The typical observed pattern is a species area relationship (SAR) (Arrhenius, 1921; Gleason, 1922) based on the log-log model ($\log S = c + z \log A$, where c is the intercept and z the slope). Due to ubiquitous support, SAR has been referred to as one of nature's most general patterns (Lomolino, 2000). Despite its universal recognition, a potentially important feature of the SAR – the small island effect (SIE) – has been largely overlooked by ecologists and biogeographers (Lomolino, 2000; Lomolino & Weiser, 2001). SIE pertains to the pattern where below a certain area, species richness may vary independently of island area. Higher richness in larger area may have to do with factors that correlate with larger size, such as greater habitat heterogeneity and higher population levels, thus lower extinction risks. These effects may disappear on small islands where population sizes are generally low, suggesting that stochastic events may play more significant roles than area. In some cases certain habitat conditions such as those pertaining to soil maturity and moisture can only occur on islands above a certain size, posing a natural threshold on the species diversity an island may support (Niering, 1963). Based on a meta-analysis across diverse taxa and archipelagos, Lomolino & Weiser (2001) found support for SIEs in 73% of the 102 cases using breakpoint regressions. The upper limit of SIE varies among different taxa and types of archipelagos with a median value of around 40 ha (Lomolino & Weiser, 2001). However, there are still debates over the existence of the SIE (Burns *et al.*, 2009) and the appropriate methodological approach in identifying it (Triantis *et al.*, 2006). With increasingly rapid anthropogenic habitat fragmentation, it is important to understand how this potential area threshold varies to improve conservation management strategies.

Dung beetles are key bioindicators and are important for ecosystem functioning. Most species utilize mammalian dung for food and breeding although some feed on other types of decomposing materials: carrion, rotting fruits or fungi. They have been shown to be sensitive to tropical forest modification and fragmentation (Halffter & Arellano, 2002; Davis *et al.*, 2004; Davis & Philips, 2005; Nichols *et* *al.*, 2007), changes in mammalian communities (Estrada *et al.*, 1999; Andresen & Laurance, 2007; Nichols *et al.*, 2009), and provide a cost-effective indicator group for tropical forest disturbances (Davis *et al.*, 2001; Gardner *et al.*, 2008). Recent results from dung beetle studies in fragmented tropical forests show that species richness is positively correlated with area (Klein, 1989; Andresen, 2003; Feer & Hingrat, 2005) and negatively correlated with isolation (Estrada *et al.*, 1999). However few studies examined the community shift of dung beetles in tropical forest fragments (Larsen *et al.*, 2005). Even fewer studies have looked at how geographical and environmental characters, together with species traits influence dung beetle community structure in forest fragments (Larsen *et al.*, 2008). Both decreases in dung beetle diversity and changes in their community structure have negative consequences to ecosystem functioning, including dung burial and nutrient recycling (Stokstad, 2004; Horgan, 2005; Slade *et al.*, 2007; Yamada *et al.*, 2007), secondary seed dispersal (Feer, 1999; Andresen, 2001, 2003; Bang *et al.*, 2005) and biological control (Bornemissza, 1970; Fincher, 1973; Gronvold *et al.*, 1992; Nichols *et al.*, 2008).

Here, by examining dung beetle assemblages in 24 landbridge islands and three mainland control sites in the tropical forests of Peninsular Malaysia I ask the following questions: (1) Is there support for SIE in the study archipelago? (2) What are the determinants of species richness on the islands? (3) Do patterns in community composition support the existence of SIE? I hypothesize that on small islands, idiosyncratic processes not only render species richness independent of area but also cause community composition to be more variable (Levin, 1992; Leibold *et al.*, 2004). (4) What traits of dung beetles are correlated with species' rarity hence proneness to local extinction in forest fragments? I hope that my results will be relevant for the management of biodiversity in Southeast Asian forest fragments, a region experiencing the highest deforestation in the tropics (Sodhi *et al.*, 2010).

MATERIALS AND METHODS

Study site

This research was conducted in Lake Kenyir, a hydroelectric reservoir in the state of Terengganu, northeastern Peninsular Malaysia (5°00´ N, 102°48´ E; 145 m a.s.l.) formed by the damming of the upper tributaries of the Terengganu River in 1986. The dam flooded 36,900 ha within the 260,000 ha catchment area of dense hilly forest. Over 340 land bridge islands were formed from former hilltops, ranging in size from less than one ha to over 1,000 ha. Most of them have steep banks and narrow littoral zones. Forests on the islands and surrounding mainland were selectively logged before the creation of the dam. The vegetation type in the area is tropical humid forests and consists mainly of lowland and mid-elevation dipterocarp forests. The region generally experiences heavy rain due to the northeast monsoon from November to March and a hot and dry season from May to October, with annual precipitation varying between 2,700 mm to 4,000 mm (Furtado *et al.*, 1977).

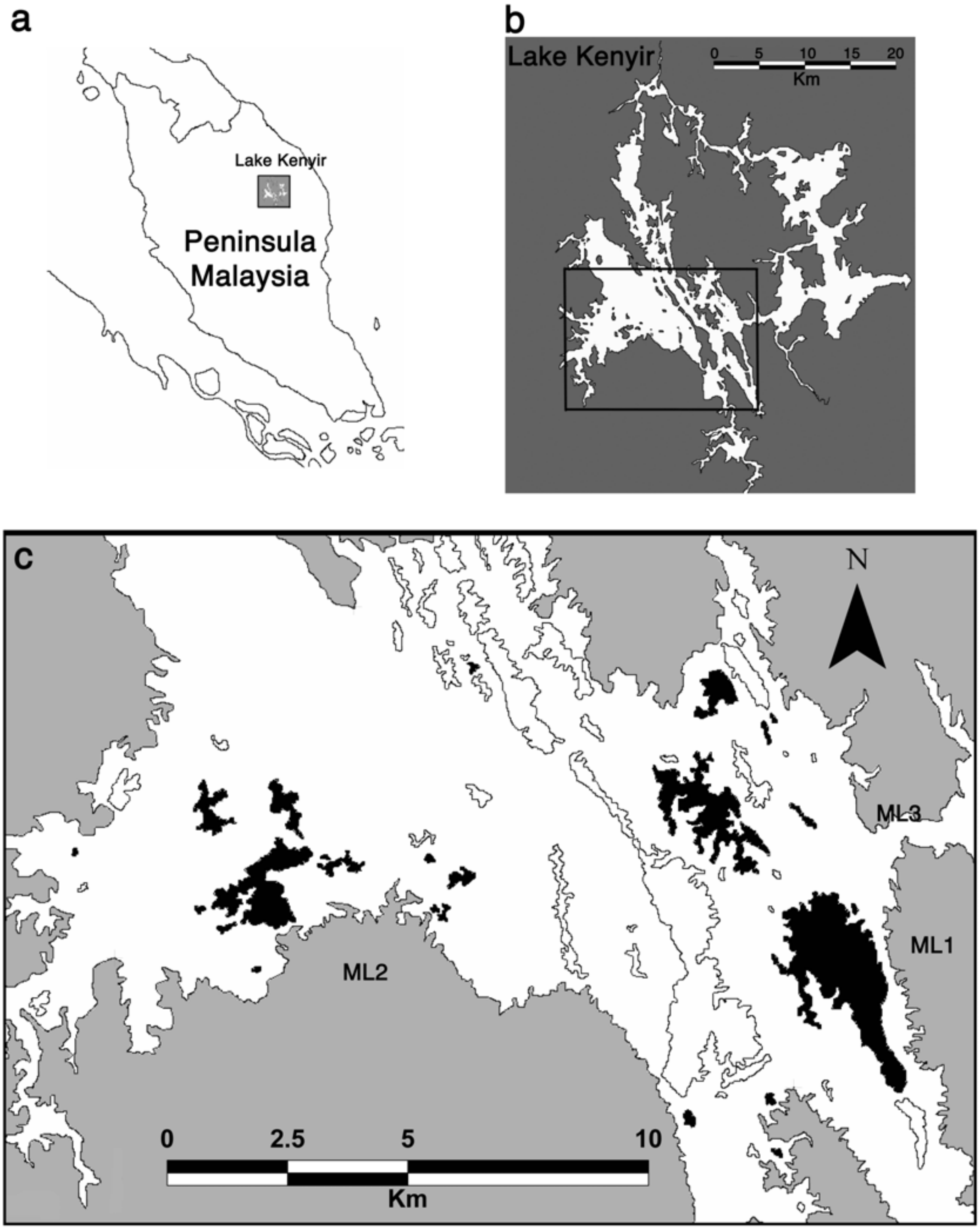


Figure 2-1. Map of Lake Kenyir with relative position within Peninsular Malaysia (a & b). The 24 islands included in this chapter are highlighted in black, and three mainland sites (ML) are labeled (c).

Dung beetle sampling

Twenty-four islands ranging in size from less than one ha to 383.3 ha were selected for this study together with three mainland forest patches as baseline references (Fig. 2-1; also see Appendix A). Fieldwork was conducted between Jun 2008 and Oct 2009. Each island/mainland site was surveyed at least twice (Appendix A). Coprophagous (feces-feeding) dung beetles were sampled using pitfall traps (200 ml plastic cups) buried in the ground and filled with approximately 50 ml salt water and a small amount of detergent to reduce surface tension (Larsen & Forsyth, 2005). Approximately 15 – 20 g human dung was suspended above each trap, in plastic mesh, with a rain cover above. Human dung has been shown to be able to attract a great diversity of dung beetles species in rain forests, including those that feed on carrion and other resources (Howden & Nealis, 1975; Hanski, 1983), and is more effective than herbivorous dung (Doube & Wardhough, 1991). Traps were spaced to a minimum 50 m interval to achieve trap independence (Larsen & Forsyth, 2005) and left open for 48 hrs before the beetles were collected. For islands below 5 ha, three to five traps were set up during each sampling round. For larger islands and mainland two to six sampling locations were systematically chosen depending on forest area and at each location three traps were set up during each sampling round (Appendix A).

Species traits

In total, six ecologically relevant species traits were obtained: body size, diet breadth, diel activity, guild, baseline density, and edge tolerance. Body size has been shown to be collinear with other meaningful traits, such as body mass and wing loading (Larsen *et al.*, 2008) hence can be used as a surrogate for mass and flight ability related traits. The product of elytra width and body length measured from the anterior margin of the pronotum to the pygidium was used as a measure of body size. The mean of body size was taken from between 1 and 30 individuals for each species. To quantify diet breadth, we also baited the coprophagous species with carrion and decaying fruits. These food sources besides dung may be important for dung beetles in rain forests in Southeast Asia (Hanski & Cambefort, 1991). Pitfall traps baited with fish (n = 24) and partially fermented banana (n = 24) were set up in the mainland forests (also see Chapter 5). Due to the difference in sampling effort of dung and carrion traps we used only presence-absence data for diet breadth, e.g. 1 (only dung diet) and 2 (both dung and carrion). The diel classification of the nocturnal and/or rare species and all guild classifications are based on literature (Hanski & Cambefort, 1991; Davis, 1999; Slade *et al.*, 2007). The diel activities of four species are unknown. The majority of the Southeast Asian dung beetles are diurnal species (Hanski & Cambefort, 1991) and a small number of daytime traps were used to confirm this for the common species. Baseline densities are defined as the average number of individuals per trap in three mainland forests. To measure the edge tolerance of dung beetles a total of 12 human dung baited pitfall traps (to be consistent with the main collection method) and one flight interception trap were set up on the forest edges of the mainland forests and beetles caught in these edge traps are considered edge tolerant, i.e. non-forest specific.

Geographical and environmental variables

To examine potential factors affecting dung beetle assemblages we measured four geographical variables: island area, isolation (distance from the nearest landmass

> 100 ha), edge index, geographical coordinates (UTM system) and three environmental variables: basal area of woody species, leaf litter depth, and soil pH. Isolation was measured as the distance from the nearest large landmass (islands > 100 ha or mainland) because these have high dung beetle species diversity and abundance (Appendix A) and can be sources of immigration for the small islands located nearby. Edge index is essentially a circularity index, calculated as the ratio between the perimeter of an island and that of a circle of the same area as a measure of the relative amount of forest edge (Meyer & Kalko, 2008). Basal area was estimated using the angle count method (Variable Radius Plot sampling) at each dung beetle trapping point. This method provides a quick and unbiased estimation for tree basal area in wide zone by estimating the dbh (diameter at breast height) of the trees weighted by their distances from the counting point (Schreuder, 1993). In short, each tree of X cm dbh adds 1 m^2/ha to the total basal area if it is within a radius X/2 m of the counting point, where X is any number and only the dbh : distance (2 cm : 1m) ratio need to be measured. This was done simply by holding a ruler at 0.6 m in front of the surveyor's eye while scanning the surrounding forest. All trees with dbh subtending the angle formed by the surveyor's eye and a 1.2 cm mark on the ruler would exceed the 2 cm : 1 m ratio and were counted. Leaf litter depth was measured with a ruler and soil pH with the Kelway® Soil Tester each at three points within 5 m from each dung beetle trapping point.

Statistical analyses

All statistical analyses were conducted in Program R (R Development Core Team, 2009) with specified packages unless otherwise noted. Two arboreal specialists, *Onthophagus deliensis* and *Onthophagus* sp. 7, were excluded from all analyses (except for the species sampling adequacy analysis) because they forage mostly above 5 m from the forest floor (Davis *et al.*, 1997) and pitfall traps on the ground will not accurately represent their populations (Davis & Sutton, 1998) (Tregidgo *et al.*, in press).

Species sampling adequacy

Sampling adequacy for all sites were evaluated based on randomized (100 x) sample based species accumulation curves and the bootstrap estimator for the total species richness in EstimateS (Version 8.0, R. K. Colwell, http://viceroy.eeb.uconn.edu/estimates). Bootstrapping provides a robust way to estimate the total species number (Magurran 2004).

Regression tree for island species richness and dung beetle local rarity

I used regression tree analysis to evaluate the effects of geographical and environmental variables on species richness in a hierarchical manner. Regression tree analysis uses dichotomous keys to recursively partition the data into mutually exclusive subsets that are increasingly homogeneous with respect to the defined groups, providing a tree-like model (McCune & Grace, 2002). As a nonparametric method, regression tree is robust to many data issues such as nonlinear relations and missing values providing a useful tool to analyze complex ecological data (De'ath & Fabricius, 2000). It is therefore powerful in detecting any potential threshold in the effect of area on species richness. I assume that if a SIE exists, its upper limit will be the splitting factor at the top node in the tree, which represents the predictor that explains the largest deviance in the data, and subsequently area should be a predictor for islands above the threshold size but not for those below the threshold size. Mainland forests were not included in the regression analyses because of the difficulty in assigning areas to these forests. I used the $\log_{10}$-transformed species richness on 24 islands as the response variable and four potential predictors, including three geographical variables of area, isolation, edge index, and one environmental variable of basal area. These were used to grow an overlarge tree with a minimum splitting group of size two and cost complexity measure of 0.0001. This was subsequently pruned to the optimum tree size (i.e., a tree size that minimizes the cost-complexity measure by snipping off the least important splits and hence reducing data overfitting and is within 1 SE of the minimum-error tree) through 10-fold cross-validations. I then regressed the log-species richness against the predicted values by this tree to generate an R-squared measure of model fit. I used the package *rpart*.

To test the robustness of my regression model I used a random forest, which combines the predictions of many independent models for a more-accurate classification (Breiman, 2001). I used the package *randomForest* (Liaw & Wiener, 2002) to generate 1000 trees and examined the relative importance of the candidate traits in predicting the species richness based on the overall accuracy of these models.

I also used the regression tree approach to identify the key traits of dung beetle species associated with their local rarity, measured as the proportion of sites where a species was not detected. I adopted a similar set of criteria as before in generating an optimum tree with rarity as the response and six traits (body size, diet breadth, diel activity, guild, baseline density, and edge tolerance) as predictors.

Generalized linear models

To cross-examine the effects of the geographical and environmental variables on dung beetle species richness in a heuristic manner, I employed an information-theoretic approach (Burnham & Anderson, 2002). A set of *a priori* generalized linear models with Gaussian error structure were assembled using all combinations of candidate predictors potentially important for dung beetle species richness: area, isolation, edge index and basal area. The global model included all the predictors and the null model included none of the predictors. Species richness, area, isolation and edge index were $\log_{10}$-transformed to account for non-normality and to achieve equal variances in model residuals. The same model set was first evaluated for all islands (n = 24) and then for islands with sizes equal to and below the upper limit of SIE. I compared and ranked models using Akaike's information criterion corrected for small sample size (AIC_c). ΔAIC_c denotes the difference in AIC_c from the model with the minimum AIC_c and models with $\Delta AIC_c \leq 2$ are considered to have substantial support. AIC_c weights ($wAIC_c$) provided relative weight of any particular model, which varied from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson, 2002). Model fit was assessed using percentage deviance explained (%DE).

SAR curves

To provide comparison with conventional approach to SIE, three regression models were fitted to the $\log_{10}$-species richness and $\log_{10}$-area data for 24 islands surveyed – the simple linear regression, hockey stick regression and piecewise linear regression. The simple linear regression model represents the classic log-log model of SAR, implemented using the lm() function. If a SIE exists, it should be represented by a breakpoint in the linear relationship and the latter two regression models tested this. The hockey stick regression consists of two segments, a flat line (slope equals zero) joined by a non-zero-slope regression line at the break point (Lomolino & Weiser, 2001). This was implemented using the thresholddose081117() function developed by Lutz & Lutz (2009). The piecewise regression consists of two linear regression lines joined together at the break point (Gentile & Argano, 2005; equation 3), and was implemented using the piecewise.linear() function in the package *SiZer*. The significance of the break points was evaluated by their 95% confidence intervals (CI) in the latter two regressions. I compared model parsimony using AIC_c (Burnham & Anderson, 2002).

NMDS

The variation in dung beetle community composition among the 24 islands and three mainland sites was visualized using non-metric multidimensional scaling (NMDS) in the package *vegan*. The input community matrix was based on the average catch per trap standardized by Wisconsin double standardization, where species are first standardized by maxima and then sites by site totals. The Bray–Curtis dissimilarity measure was used and a stable solution was reached after maximum 20 random starts.

Nestedness

Species assemblages in an island system often display a nested pattern where the species composition of small assemblages is a nested subset of larger assemblages. However, there has been substantial controversy in the literature over the best methods to define and quantify nestedness (Brualdi & Sanderson, 1999; Ulrich & Gotelli, 2007). A recently devised metric, Nested NODF calculates nestedness independently among sites and species, and has been shown to be independent of matrix shape and size (Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009). We adopted this metrics to examine the nestedness of the metacommunity in Lake Kenyir using the package *vegan*. We used the null model algorithm *r2* (Wright *et al.*, 1998) that simulates the original species frequencies and generated 1000 null models to test for the significance of the effect size.

Abundance spectra

The dung beetle community compositions and probable reorganizations of species abundances in Lake Kenyir were visualized using abundance spectra, which use ordered species lists ranked by species' abundance in the mainland forests representing pre-fragmentation systems (Mac Nally, 2007).

Partial Mantel's test

To test for spatial autocorrelation in dung beetle community composition among all 27 sites, we conducted a partial Mantel's test using the package *vegan* on three distance matrices: the community dissimilarity matrix (Bray–Curtis distance), the geographical distance matrix and the environmental dissimilarity matrix (Bray–

Curtis distance). The environmental variables used are basal area of woody species, leaf litter depth and soil pH. The partial Mantel's test examines the residual variability in species composition that is spatially structured, after removing the effects of the environmental variables (Legendre & Legendre, 1998). Standardized Mantel statistics was calculated using Pearson's product-moment correlation. The significance was assessed with 10000 permutations of the rows and columns in the community dissimilarity matrix.

RESULTS

General sampling results

Across all 27 sites, I collected 49 dung beetle species representing 11 genera totaling 7121 individuals from pitfall traps baited with human dung (Appendices A&B). Among the islands, dung beetle abundance significantly decreased with island area (Spearman's $\rho = 0.66$, $P < 0.001$). The bootstrap estimator showed that sampling at all sites reached more than 70% of the total species richness (Appendix A). Traps baited with fish caught 151 individuals belonging to 18 coprophagous species. However traps baited with banana did not catch any coprophagous dung beetles. Therefore the diet breadth of all species was either 1 (dung only), or 2 (dung and carrion) (Appendix B).

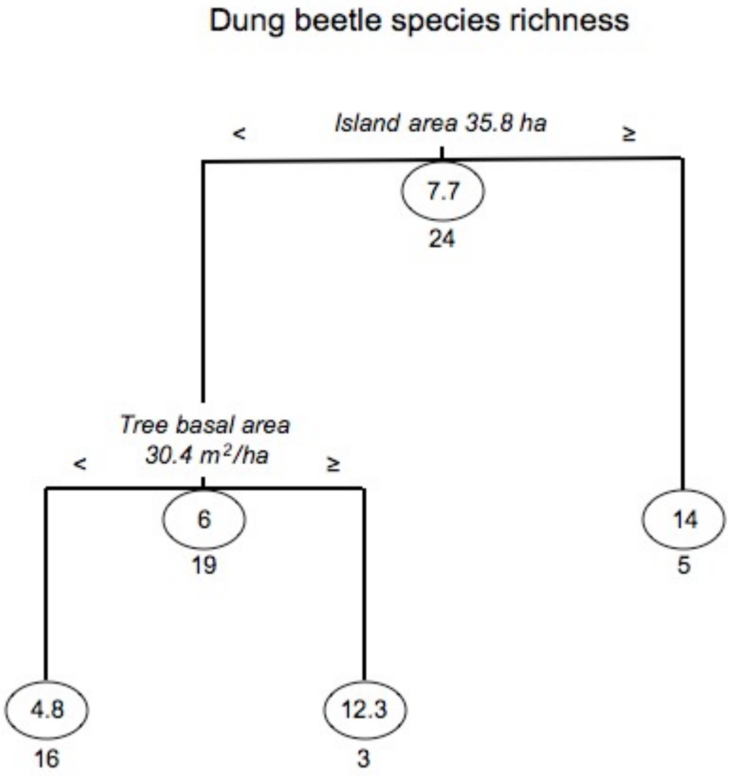


Figure 2-2. Optimum regression tree for predicting dung beetle species richness on 24 islands of Lake Kenyir. Values in ovals represent mean species richness; numbers represent the number of islands at each node. Variables tested were island area, isolation, edge index and tree basal area. See methods for details on these variables.

Regression tree for island species richness supported a breakpoint in area

Only island area and basal area of trees were selected in the optimal tree model and they explained 76% of the variation in the data (Fig. 2-2). An island size of 35.8 ha was the splitting factor at the first node, representing a potential SIE threshold (i.e., a breakpoint). According to this model, five islands above this size have a mean species richness of 14 (first terminal node from the right; Fig. 2-2). For islands below this size threshold, species richness is best explained by tree basal area. Sixteen islands with mean basal area less than 30.4 m^2/ha have on average 4.8 species (first terminal node from the left; Fig. 2-2), whereas three islands with basal area above 30.4 m^2/ha have on average 12.3 species (second terminal node from the left; Fig. 2-2). The variable importance ranking generated by the random forest also showed that island area was the most important predictor according to the percentage increase in the mean square errors (68.4%) followed by basal area (21.3%).

Generalized linear models for dung beetle species richness

I tested generalized linear models on species richness for the all islands (n = 24) and for islands below the 35.8 ha breakpoint suggested by the regression tree analysis (n = 19). For all islands area was most important in determining species richness; basal area and isolation were also present in the top three models (Table 2-1). Together these three predictors explained 38.6% of the total deviance in the data (fourth ranked model). For islands below 35.8 ha area, the top ranked model has only basal area as the predictor, explaining 14.9% of the deviance, which supports the regression tree result (Fig. 2-2). Two other factors, distance and edge were also included in the competing models, explaining 14.3% and 7.7% of the deviance respectively as single predictors. This suggests relatively important roles of isolation and island edge in explaining species richness on these small islands. Island area did not appear in any top ranked models. The null model closely followed the two best approximating models and all other top ranked models ($\Delta AIC_c < 2$) explained 7.7 – 26% of the deviance in the data, suggesting an increased stochasticity on islands below 35.8 ha.

Table 2-1. Best approximating generalized linear models of species richness for all islands (n = 24) and for islands ≤ 35.8 ha (n = 19). Global model: log(richness) ~ log(area) + log(distance) + basal + log(edge index) with Gaussian error structure. Area: island area. Distance: distance from the nearest large landmass (> 100 ha). Basal: basal area estimate for woody species. Edge: edge index (ratio between perimeter of island and perimeter of a circle with the same area, to assess the influence of edge). *K* = number of model parameters, AIC_c = Akaike's information criterion corrected for small sample size, ΔAIC_c = difference between AIC_c of the top-ranked and current model, $wAIC_c$ = AIC_c weight, %DE = percentage deviance explained by the model.

Model description	***K***	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**%DE**
All islands (n = 24)					
~ area + basal	4	7.654	0	0.265	36.0
~ area	3	7.858	0.205	0.239	27.2
~ area + distance	4	8.605	0.952	0.165	33.5
~ area + basal + distance	5	9.923	2.269	0.085	38.6
Islands <= 35.8 ha (n = 19)					
~ basal	3	6.077	0	0.171	14.9
~ distance	3	6.203	0.126	0.161	14.3
~ 1	2	6.307	0.230	0.153	0
~ basal + edge	4	6.65	0.573	0.129	26.1
~ edge	3	7.619	1.542	0.079	7.7
~ basal + distance	4	7.983	1.906	0.066	20.8

Non-significant breakpoint in Species Area Relationship (SAR)

The hockey stick and piecewise linear regression estimated a breakpoint at 21.6 ha (upper and lower 95% CI 0 and 383.2 ha) and 32.4 ha (upper and lower 95% CI 1.5 and 129.7 ha) respectively (Fig. 2-3). Given the large range of the CI's with the lower limits close to zero, neither of the breakpoint estimates is considered significant in an ecologically meaningful sense. Based on model AIC_c, the simple linear model (slope $z = 0.19$) was still the most parsimonious model although both breakpoint regression models have marginally higher R squared values (Fig. 2-3).

Dung beetle community composition

While mainland forests and large islands resembled each other in dung beetle community composition, most islands below 35.8 ha differed largely from the mainland communities as well as from each other forming a 'dust cloud' around the centre of the ordination chart (Fig. 2-4; NMDS stress = 22.8). The two small islands located near the center of the NMDS chart are geographically very close to mainland 2 (Appendix A; Island 11 and 19, which were connected by narrow landbridge when water level of the lake was extremely low). An orderly area-related nested pattern was not found among the dung beetle metacommunity (NODF = 58.3, $P = 0.64$). Using the abundance spectra, those species occurrences that departed from a perfectly nested pattern can be visualized as isolated points on the lower right of the panel (Fig. 2-5). The changes in species relative abundance from the mainland sites to the small islands were also shown in this figure. Partial Mantel test showed a marginally significant but low degree of spatial autocorrelation in dung beetle community composition among sites ($P < 0.05$, $r = 0.12$) after accounting for other environmental variables.

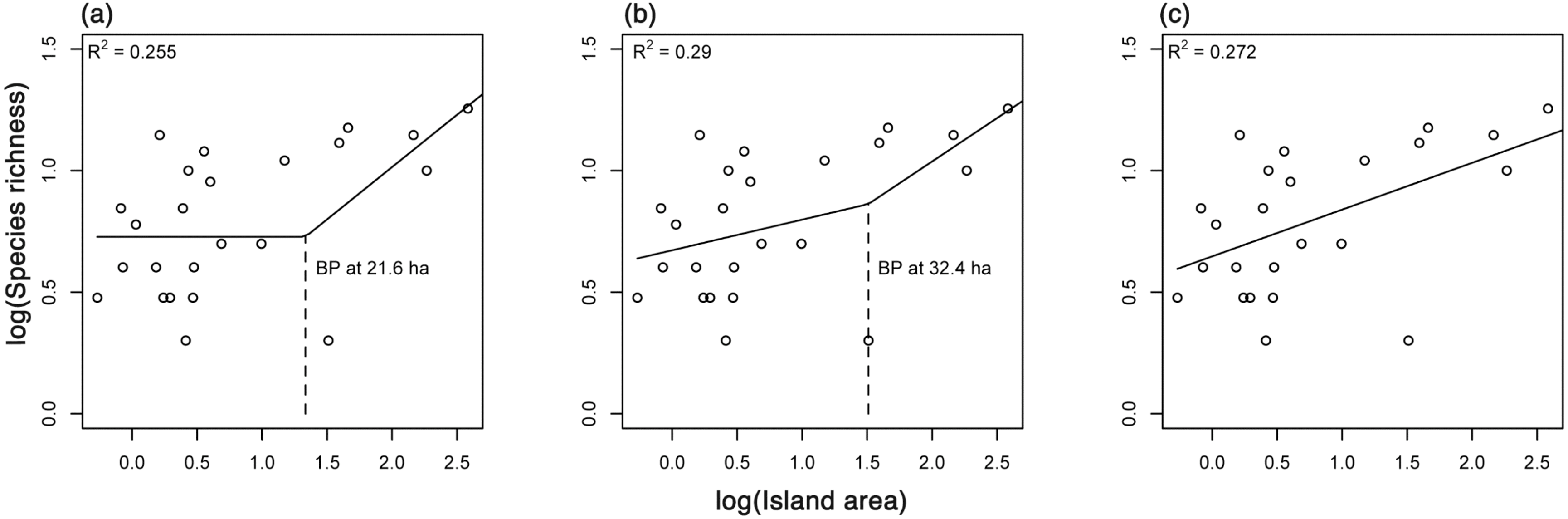


Figure 2-3. Modeling species-area relationship across 24 islands with three regression models. Most parsimonious model was simple linear model (c): $K = 3$, $\text{AIC}_c = -62.2$, $\Delta\text{AIC}_c = 0$, $w\text{AIC}_c = 0.822$; second ranked model was Hockey stick regression (a): $K = 4$, $\text{AIC}_c = -58.5$, $\Delta\text{AIC}_c = 3.61$, $w\text{AIC}_c = 0.135$; third ranked model was piecewise linear regression (b): $K = 5$, $\text{AIC}_c = -56.2$, $\Delta\text{AIC}_c = 5.90$, $w\text{AIC}_c = 0.043$. Breakpoints (BP) and R squared values are shown on the plots. K = number of model parameters, AIC_c = Akaike's information criterion corrected for small sample size, ΔAIC_c = difference between AIC_c of the top-ranked and current model, $w\text{AIC}_c$ = AIC_c weight.

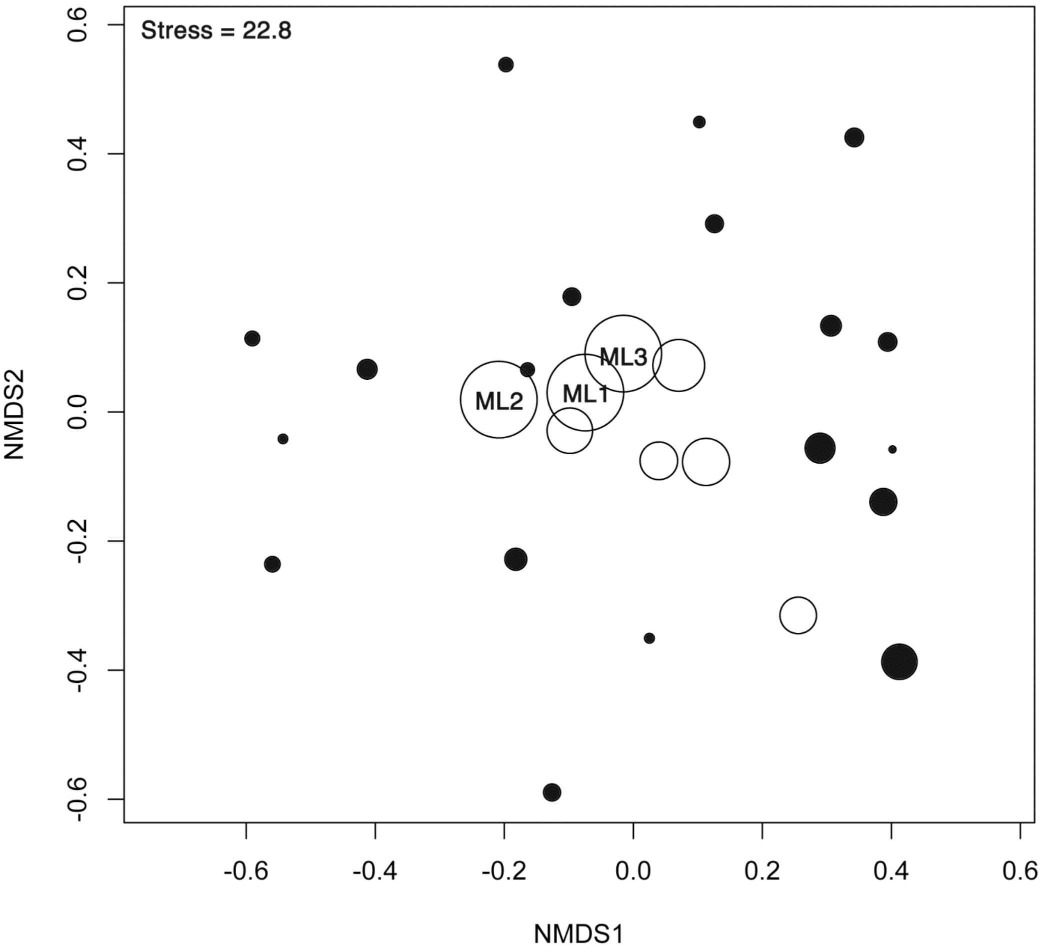


Figure 2-4. Non-metric Multidimensional Scaling (NMDS) for all 27 island and mainland sites. Size of the circles represents the size of the site rescaled for visualization. Largest circles are mainland sites (ML). Dark circles represent islands below 35.8 ha, the SIE threshold estimated from the regression tree analysis.

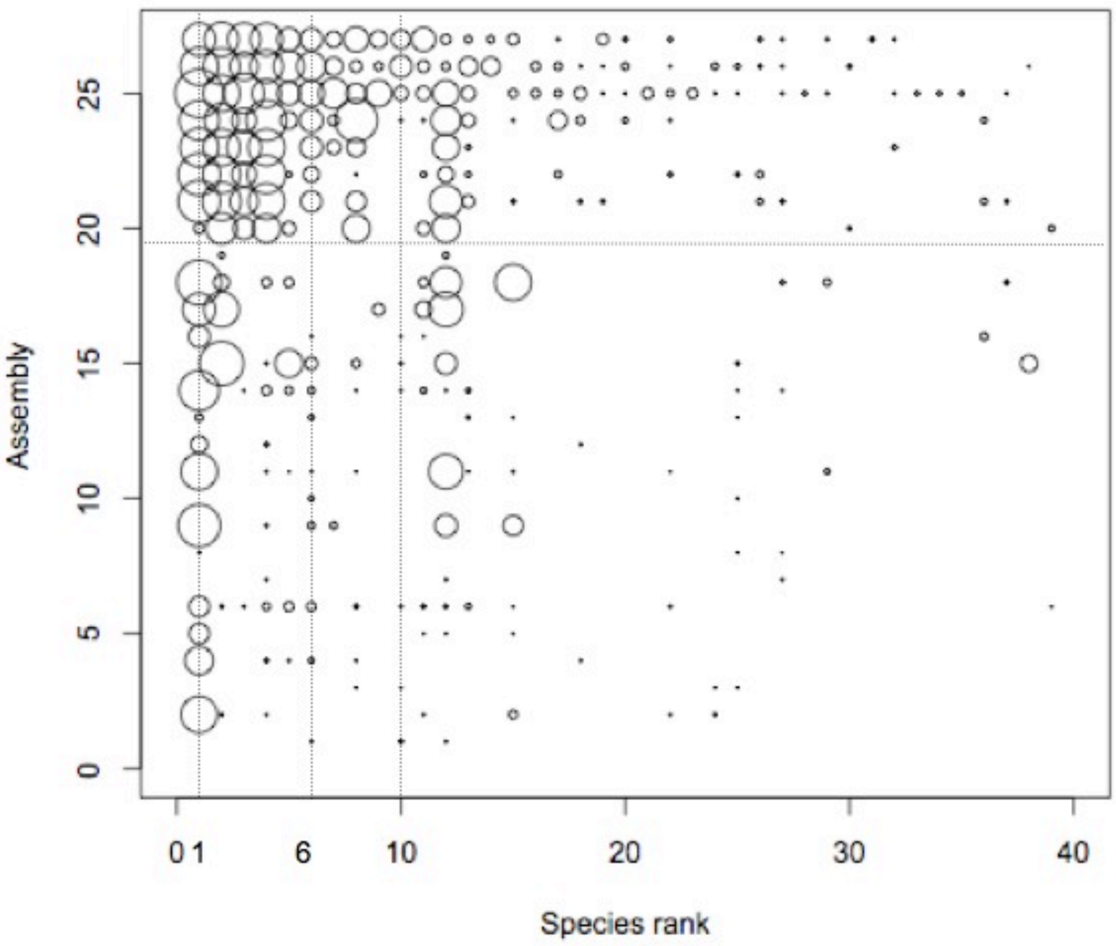


Figure 2-5. Abundance spectrum of all 27 sites. Top three rows are mainland sites followed by islands in descending order of area. The horizontal dotted line delimit the 35.8 ha threshold. X-axis are species ranked by their baseline abundance. Species highlighted by vertical dotted lines are rank 1: *Paragymnopleurus maurus*, rank 6: *Copris doriae* and rank 10: *Catharsius molossus*. Size of the circle represents the local abundance of the species rescaled for visualization.

Regression tree for dung beetle local rarity

The optimum tree identified three traits important in affecting species local rarity: baseline density, edge tolerance and diet breadth (Fig. 2-6), explaining 81.4% of the variance in the data. The results from the random forest confirmed the reliability of this tree model. In particular, the most important traits ranked by the percentage increase in mean square errors are as follows: baseline density (46.0%), edge tolerance (11.5%) and diet breadth (5.6%). According to the optimum tree model, the mean proportion of islands in Lake Kenyir where a species was absent varies between 37.7% and 94.0%. For instance, 20 out of 47 species that are naturally uncommon (with < 0.035 individuals per trap in mainland forests) are estimated to be absent on 94.0% of the islands (the first terminal node from the right; Fig. 2-6). Conversely six species that are most common (with ≥ 0.374 individuals per trap in mainland forests), able to forage on the forest edge and feed on both dung and carrion have the highest occurrences among islands (absent from 37.7% of the islands; the first terminal node from the left; Fig. 2-6).

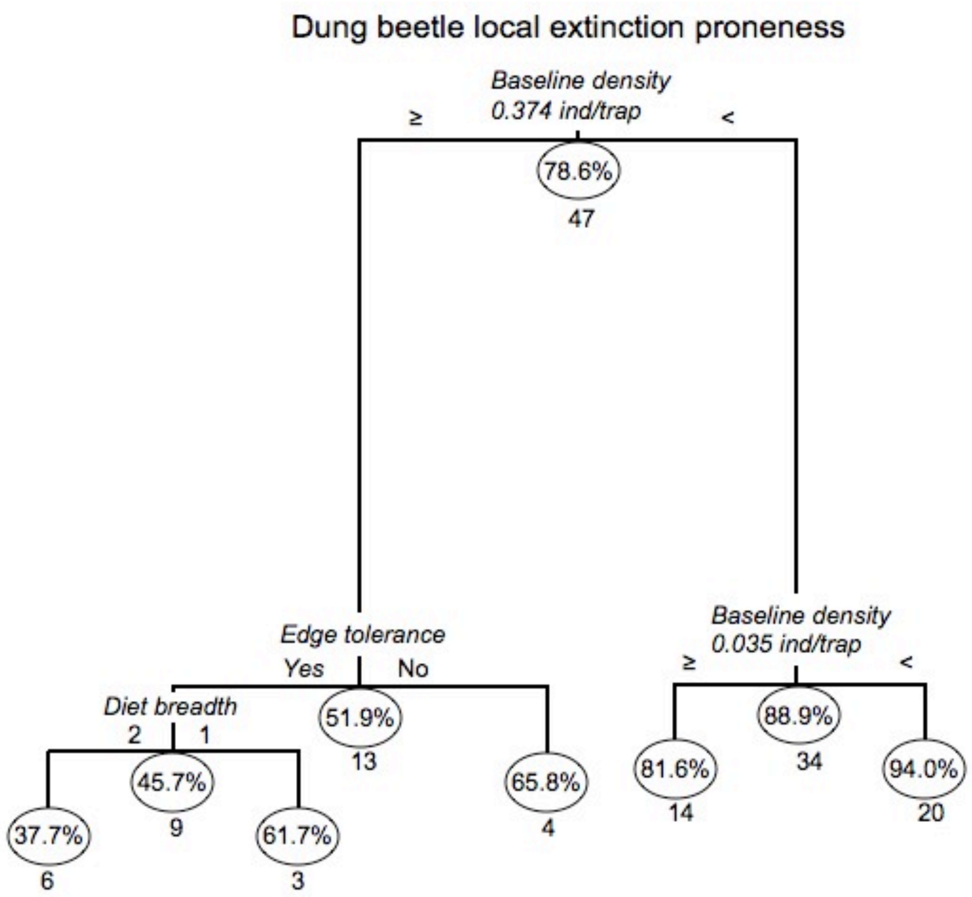


Figure 2-6. Optimum regression tree for predicting dung beetle local extinction proneness. Percent in ovals represents local extinction proneness; numbers represent the number of species at each node. Species traits tested were baseline density (as in mainland forests), edge tolerance, diet breadth, diel activity, body size and guild. See methods for details on the species traits.

DISCUSSION

Overall, my results show that for islands below 35.8 ha at Lake Kenyir, species richness and community composition were driven by a small island effect, rather than by a direct relationship with area. This was supported by the regression tree analysis and generalized linear models. In comparison, the breakpoints in the SAR estimated by conventional regressions did not have enough statistical support (Fig. 2-3). The regression tree analysis and generalized linear models were more heuristic as they took into consideration the effects of other geographical and environmental variables on island species richness. Regression tree analysis also did not assume an overall linear relationship between the predictors and the response, therefore was a more flexible and powerful tool for investigating ecological relationships (De'ath & Fabricius, 2000). The breakpoint linear regressions did not appear to be well supported likely due to the small sample size of large islands (only five islands above 35.8 ha were available). Although the hockey stick and piecewise regression models explained more variation in the data they had an additional one and two parameters, respectively (Fig. 2-3), which made them less parsimonious. For these reasons, I interpret my results according to the regression tree analysis and generalized linear models.

Our estimated upper limit of SIE is at 35.8 ha, lower than the 100 ha estimated by Lomolino & Weiser (2001) using a Scarab beetle data set from the Florida Keys, a marine, and thus more isolated, archipelago. Although I note that the method they used has received some criticism (Burns, 2009), Lomolino & Weiser (2001) suggested that the upper limits of SIEs should be higher for biotas of more isolated archipelagos than those of lakes and rivers, because the former typically have infrequent immigration as well as lower extinction rates. Compared to other fragmentation studies (Fig. 3 in Lomolino & Weiser, 2001) I sampled a notably higher proportion of islands that fell within the range of SIE, which enabled me to gain more insights to this understudied ecological pattern. The overall slope of SAR ($z = 0.19$) was much lower than that of true oceanic archipelagos ($z = 0.35$) and close to that of continental habitat islands ($z = 0.22$) (MacArthur & Wilson, 1967), which implies that such lake archipelagos may be more appropriate model systems in understanding the real world habitat fragmentation (Laurance, 2008; Koh & Ghazoul, 2010).

The observed ecological patterns are likely caused by multiple underlying mechanisms that operate at different scales (Levin, 1992; Leibold *et al.*, 2004). In Lake Kenyir, area was the primary underlying driver of species richness across the entire range of island sizes understudy (0.5 – 383.3 ha). However, its role in determining species richness diminished in comparison with other geographical and environmental characteristics on small islands. I show that below 35.8 ha, area becomes unimportant and tree basal area has the strongest positive effect on species richness; isolation and the relative amount of forest edge are also important. This pattern is consistent with the explanation in that below the upper limit of SIE species richness is largely related to the inter-island differences in habitat and resource availability characteristics (Lomolino & Weiser, 2001). The topography of Lake Kenyir is irregular and the position of an island and its exposure to different climatic conditions or other environmental forces are potentially relevant but difficult to quantify. I are also unable to assess the availability of mammalian dung on these small islands because most of the mammals are non-resident and visit opportunistically. Sights and signs of the Asian elephant (*Elephas maximus*), wild boar (*Sus scrofa*) and primates have been recorded on most of these islands (L. Qie pers. obs.) but these mammals can cross water barriers. The types of food resource on an island can influence the type and visitation rate of mammals, for which I are unable to give an unbiased measure. These and other stochastic events may jointly influence the dung beetle diversity on small islands and contribute to the observed large amount of unexplained deviance in the generalized linear models (Table 2-1).

The community composition on islands below 35.8 ha noticeably departed from that of the mainland sites and larger islands, but instead of forming a separate cluster they radiated from the original community in all directions in the NMDS graph (Fig. 2-4). This confirmed my prediction that if idiosyncratic island characteristics override area effects, the resulting community composition would be more variable. A significant nested pattern was missing in this archipelago. The nested NODF metric has been shown to be relatively sensitive to rare species on poor islands (Santos *et al.*, 2010). A number of such incidences were observed where on some small and poor islands there were still ‘surprise’ species (Fig. 2-5). Furthermore, highly variable community composition on small islands has also been observed in birds (Terborgh *et al.*, 1997; Lees & Peres, 2006). I argue that SIE not only manifests itself in terms of species richness, but also in terms of community composition.

I used dung beetle species local rarity to estimate their local extinction proneness. Because sampling effort on these islands was adequate, the probability of pseudoabsences confounding my results is low. My regression tree model on the local rarity of 47 dung beetle species show that common species and species that are able to forage at the forest edge have higher occurrences and hence are less prone to extinction. This is consistent with the conclusion of Larsen *et al.* (2008) in a similar system in Venezuela. However, body size is not as important in explaining rarity as opposed to their finding, where large-bodied dung beetles were more prone to extinction. In particular, two of the most widespread species, *Paragymnopleurus maurus* and *Copris doriae* (rank 1 and 6 in Fig. 2-5), are also among the larger species (Appendix B), and the largest species, *Catharsius molossus*, was present in some of the most depauperate islands (rank 10 in Fig. 2-5). I also show that species that feed on both dung and carrion have higher occurrences on islands hence are more resilient to local extinction (Fig. 2-6). This is not surprising because mammalian dung is likely an ephemeral resource especially on most of the small islands that lack resident mammals. Species that can utilize other decomposing materials such as carrion will improve their chances of persistence.

An interesting finding in my study is the spatial autocorrelation of the community composition among the study sites. There may be two reasons for this pattern. First, the landscape consisted of numerous mountain ridges oriented from northwest to southeast, which were partially submerged after the area was flooded (Fig. 2-1). These may have acted as terrestrial barriers to dung beetle dispersals before the hydroelectric dam was built, causing species distribution to be more dissimilar along the longitudinal gradient. Therefore, the observed spatial autocorrelation may partially reflect the historical regional distribution of dung beetles. However, the lack of pre-fragmentation data prevented me from verifying this hypothesis. Second and more importantly, this spatial autocorrelation suggests dispersal limitation of dung beetles after the former hilltops became islands. Dung beetles living in the rain forest foraging close to the forest floor may not be adapted to navigate outside the forest or across large expanse of open water (Stokstad, 2004). Exceptions may be the canopy specialists (Davis *et al.*, 1997; Davis & Sutton, 1998), which are excluded from my data analyses here. Experimental evidence showed that variation in flight ability of tropical forest birds correlated strongly with the species distributions on lake islands in Panama (Moore *et al.*, 2008). Dispersal was also shown to be a key in structuring ground beetles communities on lake islands in Northern Poland (Zalewski & Ulrich, 2006). Unfortunately, the relative flight abilities of different dung beetle species are poorly known. It is suggested that there are two forage-flight patterns in dung beetles: large bodied dung beetles tend to fly rapidly and continuously for long distance while small species perch on leaves and fly occasionally for short distances (Larsen *et al.*, 2008). The question here is, however, not only whether the dung beetles can, but also whether they will fly across open water between the islands. Dung beetles are shown to be able to use polarized light for navigation (Dacke *et al.*, 2003; Dacke *et al.*, 2004). It is possible therefore that they can use the polarized light from the water surface to avoid water and hence limiting their dispersal.

In addition, less isolated islands were found to harbour more species in my study (Table 2-1), which provides indirect evidence for differences in the dispersal ability among dung beetle species. Hence, source-sink dynamics may exist between neighboring sites for species that do cross the water barrier, and this may explain why some rare species are found on some of the poor islands. Many common species were also found in much lower densities on the smaller islands (rank 2 to 11 in Fig. 2-5) with some having notable temporal fluctuations (Chapter 4), hence I postulate that some of these populations are in fact being maintained by immigrations from mainland or large islands located nearby. If this is the case, the source-sink dynamics may have depressed the SIE threshold than expected when all islands had closed populations. Furthermore, these islands have been isolated for 24 years and the faunal relaxation on some islands may still be ongoing. Although it is still uncertain how long the process of relaxation will take and it may vary among taxa, the species richness decay of tropical forest birds was estimated to have an approximate 50-year half-life (Brooks *et al.*, 1999). It is possible that my study merely captured a snapshot of the dung beetle communities in this lake archipelago and given time, many extant species of dung beetles on the islands may go extinct, resulting in a different species-area relationship altogether (Triantis *et al.*, 2010).

In conclusion, my study shed light on the small island effects on dung beetle richness and communities. Along with my understanding of correlates of local rarity, I showed that common species and those able to forage on forest edge have a higher chance of survival on small islands. Species richness and community composition on islands below 35.8 ha in area clearly exhibited increased variability. Dung beetle assemblage on any such island is probably a random selection from the pool of resilient species, thus representing a community greatly shifted from the intact one on mainland sites. This compositional shift also affects the functional role of the dung beetle group, which results in decreased level of ecosystem functioning, such as dung removal and secondary seed dispersal (Slade *et al.*, 2007; Nichols *et al.*, 2008; Chapter 5). Because these small islands are more susceptible to stochastic events, their communities can be drastically altered over time and species already in low abundance (Appendix A) likely will face elevated risk of local extinction. Therefore, to fully understand the importance of community dynamics in small fragments, more long-term monitoring programs are urgently needed, e.g. those at Barro Colorado Island, Panama (Robinson, 1999) and the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon (Ferraz *et al.*, 2007). Such projects should also address long-term fragmentation effects on functionally important groups, such as dung beetles. My results also add to the ongoing debate on the conservation values of small habitat fragments. I highlight the need to understand minimum fragment size, capable of retaining predictable and functional ecological communities, for effective conservation management and maintenance of tropical forest ecosystem stability.

CHAPTER 3

Vertical stratification responses of arboreal dung beetles to tropical forest fragmentation

ABSTRACT

Little is known about how arboreal arthropods respond to forest disturbance. In this chapter, I assessed how rain forest fragmentation affected the vertical stratification of arboreal specialist dung beetles on landbridge islands of different sizes in Lake Kenyir. The arboreal dung beetle species (*Onthophagus* sp. 7) were found in higher numbers at 5 m compared to 15 m from the forest floor on smaller islands, suggesting a downward shift in its foraging possibly in response to fragmentation. Biotic and abiotic factors associated with forest fragmentation likely affected the dung beetles foraging height were discussed. I highlight the need to consider three dimensions of forest ecology in future forest fragmentation studies.

This chapter is based on a study designed by L. Qie, J. Barlow and N. S. Sodhi, as an undergraduate research opportunity for D. J. Tregidgo. Data collection was conducted by L. Qie and D. J. Tregidgo. L. Qie and J. Barlow analysed the data and a modified version of this chapter was prepared for publication by D. J. Tregidgo.

Tregidgo, D. J. Qie, L., Barlow, J. Sodhi, N. S. & Lim. L.-H. S., 2010. Vertical Stratification Responses of an Arboreal Dung Beetle Species to Tropical Forest Fragmentation. *Biotropica,* 42, 521-525.

INTRODUCTION

Erwin (1983) described tropical forest canopies as “The last biotic frontier”, referring in particular to our poor understanding regarding the great richness of arthropods they support. The greatest threat to the planet’s biodiversity is thought to come from habitat loss and fragmentation, which are occurring at rates that lack historical precedent in tropical rainforests (Laurance & Bierregaard 1997), an ecosystem that encompasses approximately half of the Earth’s biodiversity (Dirzo & Raven 2003). Despite this, almost nothing is known about the response of arboreal arthropods to forest disturbance (Davis & Sutton 1998). This study investigates how the vertical distribution of arboreal dung beetle species is affected by habitat fragmentation on an archipelago of forested islands in Peninsular Malaysia.

Dung beetles are a useful taxon to study disturbance such as fragmentation because they are excellent bioindicators of habitat quality and environmental change (Spector 2006, Gardner *et al.* 2008). They also play important roles in such fundamental ecological processes as decomposition, nutrient recycling, soil aeration, secondary seed dispersal and vertebrate parasite suppression (Nichols *et al*. 2008). Knowledge of species responses to disturbance is increasing, yet fragmentation studies rarely consider species-level responses, which Didham *et al*. (1998) suggest to be the key to understanding the mechanisms behind fragmentation-induced community change. Developing an evidence-based understanding of these changes is valuable for predicting and preventing further biodiversity loss (Gardner *et al.* 2009).

To the best of my knowledge, this is the first study to investigate (1) arboreal dung beetles in Peninsular Malaysia and (2) how habitat fragmentation affects the vertical stratification of dung beetles. A previous study in Malaysian Borneo by Davis and

Sutton (1998) reported that canopy loss led to arboreal dung beetles foraging at ground level. They caught dung beetles that exist almost solely in the canopy of primary forest (Davis *et al*. 1997) in significantly greater numbers in ground pitfalls of logged forest. Consequently, based on their study, I hypothesize that arboreal dung beetles would be found at lower heights in more disturbed habitats, such as small fragments. I tested this hypothesis by examining how decreasing forest area, forest structural changes and edge effects alter the vertical stratification of arboreal dung beetles.

MATERIALS AND METHODS

Arboreal dung beetle sampling

Field work was conducted between 1-12 August 2008 at Lake Kenyir (see Chapter 2 for site description). I set 135 baited pitfall traps overall, with traps arranged along vertical transects at three levels: ground level, 5 m and 15 m. Vertical transects were set on three small islands (1-3 ha), three large islands (146-383 ha) and three mainland sites (22,830–434,300 ha of continuous forest) (Appendix A; the island of 1 ha was not included in the table). In order to aid distinguishing between fragment area effects and edge effects (Didham *et al.* 1998) vertical transects on large islands and mainland sites were set at the “edge” (within 20m of the lakeshore) and in the “core” (approximately 50m from the lakeshore) of the forests. Due to their small size, all vertical transects on the small islands were classed as “edge”, and as a consequence they had only half the vertical transects (three per island) of large islands and mainland sites (six per island or site).

Ground pitfall traps and arboreal traps of the same basic design each consisted of a 230 cm^3 plastic cup containing approximately 100 cm^3 of killing solution (detergent and salt water), a rain cover, and a polyester mesh containing bait (15-20 g human faeces) suspended above the cup. Human faeces have been found to attract a greater abundance and richness of dung beetles (Howden & Nealis 1975, Hanski 1983). A landing platform was included on arboreal traps as some species land in the vicinity of dung and walk towards it (Scheffler 2002 and L. Qie pers. obs.). Each trap was left for 96 hours before the beetles were collected.

Statistical analysis

I employed an information-theoretic approach (Burnham & Anderson 2002) to examine how forest fragmentation, together with basal area and edge effect, may have influenced the vertical stratification of the most widespread species of canopy dung beetles, *Onthophagus* sp. 7. The count data at 5 and 15 m were bound together into a two-vector response variable, which was modelled using generalized linear mixed models (GLMMs) with a quasibinomial error structure. Five fixed effects (forest area, basal area, forest edge, possible interactions between forest area and basal area, and between basal area and forest edge) were included in the global model, with all combinations of these as other candidate models. Forest area was $\log_{10}$-transformed to account for non-normality. Site was treated as a random effect to account for the spatial autocorrelation among samples at the same sites. Initial examination of the models revealed an outlier in the data with nine beetles caught at 15 m and two at 5 m - a proportion that contributed to a deviance value of 45.7 out of the total deviance 147.7. A dummy variable was introduced for this single trap point on Island 2 M3EDGE (equals 1 at this trap point and 0 elsewhere) in order to exclude the outlier influence without simply deleting it from the data (Langford & Toby 1998). Models were checked for the homogeneity of their residuals. I compared and ranked models using Akaike's information criterion for overdispersed count data corrected for small sample size ($QAIC_c$) following Burnham & Anderson (2002). $QAIC_c$ weights ($wQAIC_c$) provided relative weight of any particular model, which varied from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson 2002). Model fit was assessed using percentage deviance explained (%DE). All Statistical analyses were undertaken in the R software environment (R Development Core Team 2009).

RESULTS

Three dung beetle species were caught in arboreal traps at 15m: *Onthophagus deliensis*, an unnamed species, *Onthophagus* sp. 7, and *Caccobius unicornis* (a kleptoparasite). I believe that both *Onthophagus* species are arboreal specialists rather than sub-canopy foragers using a non-selective perching strategy reported in the neotropics (Louzada 1998). Relatively few species have been observed displaying perching behaviour in Southeast Asia (Hanski & Krikken 1991, Davis 1999). Furthermore, both species possess morphological adaptations for canopy foraging such as an elongate curved hind metatarsus used to grip the dung ball that they clutch while falling from to the canopy to the ground (Davis *et al*. 1997). I restricted my analyses to *Onthophagus* sp. 7 because it was the most abundant and the only widespread species caught in arboreal traps, making up 90.6 percent of individuals caught in arboreal traps, and 56.3 percent of those caught altogether. Although

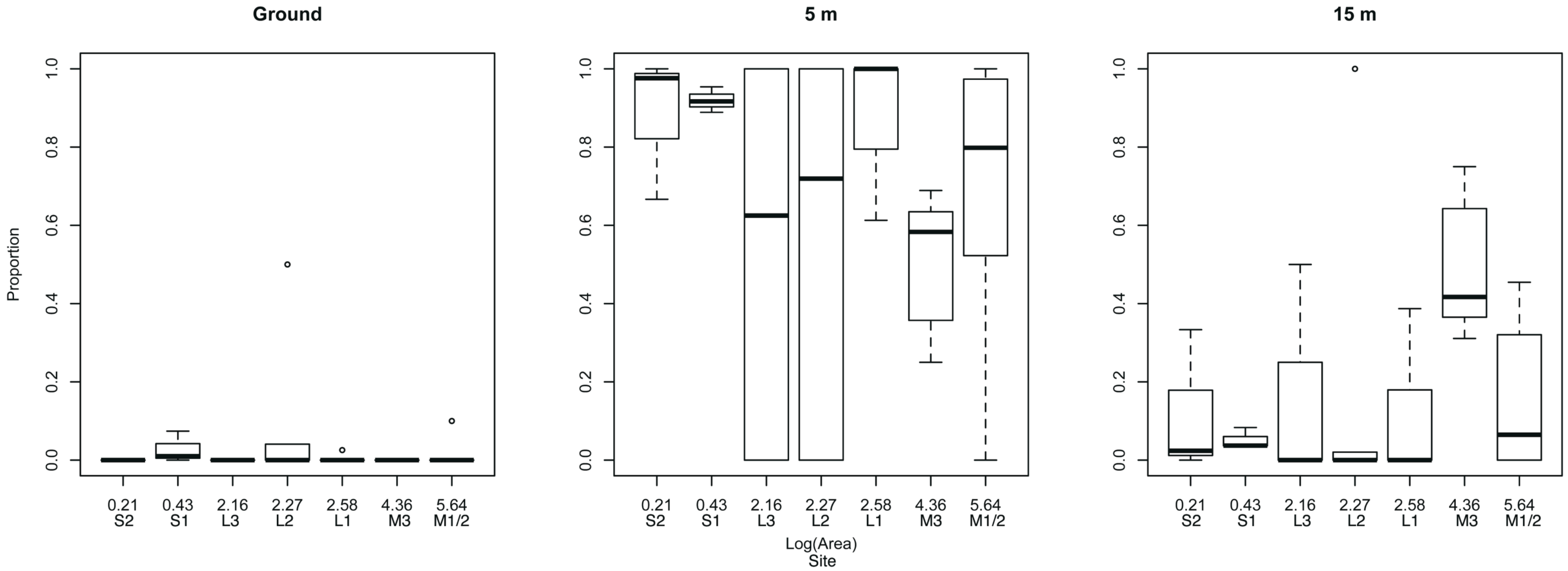


Figure 3-1. Boxplots showing the relative abundance of *Onthophagus* sp. 7 in traps on the ground and at 5 m and 15 m from the ground. The horizontal lines show the median values. The bottom and top of the box show the 25th and 75th percentiles.The vertical dashed lines show either the maximum value or 1.5 times the interquartile range of the data, whichever is the smaller. Points more than 1.5 times the interquartile range above the third quartile and points more than 1.5 times the interquartile range below the first quartile are defined as outliers and plotted individually. The outlier in the 15 m graph was the edge vertical transect M3EDGE on Island 2. The X axis was not drawn to scale.

Table 3-1. Six best approximating Generalized linear mixed-effects models and summary statistics for *Onthophagus* sp. 7 caught at 15 m versus 5 m (n = 42). All models used a quasibinomial error structure and included site as a random effect. Other predictor variables were forest area (Area), basal area (Basal), forest edge (Edge), the interaction between forest area and basal area (Area:Basal), the interaction between basal area and forest edge (Basal:Edge). An additional dummy variable M3EDGE entered all models to account for the effect of an outlier (see text). K = number of model parameters, *LL* = minimum negative log-likelihood, QAIC_c = Akaike's information criterion for overdispersed count data corrected for small sample size, ΔQAIC_c = difference between QAIC_c of the top-ranked and current model, $w\text{QAIC}_c$ = QAIC_c weight, %DE = percentage deviance explained by the model. β_0 and β_1 = parameter estimates, SE = standard error.

Model description	***K***	***LL***	**QAIC_c**	**ΔQAIC_c**	**$w\text{QAIC}_c$**	**%DE**	**β_0**	**SE**	**β_1**	**SE**
~ 1	4	-50.95	48.83	0.00	0.364	31.0				
~ Area	5	-48.43	49.70	0.87	0.235	34.4	0.4447	0.00020		
~ Basal	5	-50.55	51.24	2.41	0.109	31.6	0.0158	0.00002		
~ Edge	5	-50.95	51.55	2.72	0.093	31.0	-0.0193	0.00017		
~ Area + Basal	6	-47.84	52.16	3.34	0.069	35.2	0.4465	0.00017	0.0179	0.00002
~ Area + Edge	6	-48.43	52.59	3.77	0.055	34.4	0.4440	0.00017	-0.0069	0.00017

another species (*O. deliensis*) was caught in considerable numbers in arboreal traps, it was present only on the mainland sites (264 individuals spread across all three), and Island 19, which is the island closest to the mainland (9 individuals). Additionally, as *Onthophagus* sp. 7 was nearly absent in the ground traps (1.9% of the species' total abundance) I restricted my analyses to those caught at 5 m and 15 m. I did not catch a single dung beetle on the smallest island that traps were set on (1 ha, not included in Appendix A). Because I am interested in the abundance ratio between dung beetles at different vertical levels in the forest and total absence does not provide any information in this context this island was omitted from analyses.

The count data of *Onthophagus* sp. 7 and proportions of counts between 15 m and 5 m showed considerable variation (Fig. 3-1) that could not be accounted for by the explanatory variables, and the global model (all variables and interactions) explained less than 37 percent of the null deviance (Table 3-1). After accounting for the outlier at M3EDGE none of the fixed effects entered the top-ranked model in the model set. However this null model ($w\mathrm{QAIC}_c = 36.4\%$) was closely followed by the single variable forest area model ($w\mathrm{QAIC}_c = 23.5\%$, $\Delta\mathrm{QAIC}_c = 0.87$) suggesting a substantial support for the positive effect of forest area on the proportion of *Onthophagus* sp. 7 at 15 m to 5 m (estimate = 0.45, SE = 0.0002). The importance of basal area and forest edge were represented by the third- and fourth-ranked single variable models ($\Delta\mathrm{QAIC}_c = 2.41$ and 2.72 respectively) and should not be overlooked. The third-ranked model suggests that basal area increased the proportion of *Onthophagus* sp. 7 at 15 m albeit with a small effect size (estimate = 0.016, SE = 0.00002). According to the fourth-ranked model, edge may have led to a small decrease in the proportion of *Onthophagus* sp. 7 at 15 m (estimate = -0.019, SE = 0.0002). The fifth- and sixth-ranked models comprised of forest area acting together with either basal area or forest edge but had less empirical support ($\Delta\mathrm{QAIC}_c > 3$). Models with multiple factors and interaction terms had considerably less support from the data hence were not presented in Table 3-1.

DISCUSSION

This study supports the hypothesis that arboreal dung beetles move closer to the ground in more fragmented habitats (smaller islands). However by sampling at three vertical heights simultaneously I have shown that arboreal dung beetles were still less abundant at ground level, even in fragments. Additionally, there is limited support to suggest some arboreal specialists (*O. deliensis*) may be extirpated in fragmented landscapes (it was only caught on the mainland and the closest island to the mainland), but the inference is weakened by small sample sizes. There are a number of possible explanations for the positive fragment area-elevation relationship observed in this study. The vertical distribution of arthropods is generally determined by (1) abiotic factors; (2) resource availability; (3) forest physiognomy and tree architecture; and/or (4) arthropod behaviour *per se* (Basset *et al*. 2003). I discuss the results with a focus on abiotic factors (insolation) and resource (dung) availability.

Insolation within tropical rainforests increases with elevation, and Vulinec *et al.* (2007) suggest that the resultant high temperatures in the upper canopy may limit dung beetles due to physiological constraints. Davis & Sutton (1998) proposed that changes in light and temperature may be responsible for ground-level foraging of arboreal dung beetles in disturbed habitats. They discuss Walter's (1984) "canopy effect" (similar to "edge effects"), whereby he likened a guild of arboreal dung beetles to savannah dung beetles, suggesting that a similarity in microclimatic conditions in their habitats had permitted savannah beetles to establish in the canopy. Davis & Sutton (1998) suggest a reverse of this hypothesis, that greater insolation in edge and disturbed sites create similar microclimatic conditions to those normally only found at greater elevations in pristine forest, at lower elevations in disturbed forest. Similarly, it is possible that the edge effects associated with fragmentation may cause such "canopy conditions" to occur at lower elevations. My data lend limited support for this hypothesis, although edge *per se* was less likely a causal factor than fragmentation itself (Table 3-1).

This study supports Davis & Sutton's (1998) conclusions that forest disturbance causes arboreal dung beetles to forage at lower elevations, and also adds to their findings by showing that such drops in elevation occur not just from the canopy to the ground, but also within the canopy (Table 3-1; Fig. 3-1). The data also shows that even in fragments, their optimal range remains around 5 m rather than the ground itself. Arboreal trapping, as opposed to just ground trapping in Davis & Sutton's (1998) study, permits us to make such observations. Using only data from ground traps, their conclusions were based on an assumption derived from previous observations, that arboreal dung beetles in ground traps means there are less above ground. Another drawback of only setting ground traps is that they may attract dung beetles to the ground that normally forage in the understory.

Scheffler (2002) states that the vertical distribution of dung beetles is likely to be mainly determined by dung availability. Mammalian declines can dramatically reduce dung beetle abundance due to their strong dependence on mammal dung (Nichols *et al.* 2009). As it has been suggested that arboreal dung beetles feed specifically on the dung of primates (Davis *et al.* 1997, Vulinec *et al.* 2007), and Harcourt and Doherty (2005) state that fragmentation clearly threatens primate survival, I can speculate that primate populations and biomass are important factors in explaining the findings of this study. Although I did not collect data on primate abundance in this study, they were observed on all islands and mainland sites, but I cannot be sure if they are residents or visitors. As more dung is found lower in the vertical forest profile, a decrease in primates and therefore their dung, could cause arboreal dung beetles to move down in order to fulfil their nutritional needs.

The functional role of arboreal dung beetles is very poorly understood, but it is possible that the loss of some species, or their reduced abundance in fragments could have a significant negative impact on the ecological services that they provide. A considerable proportion of frugivore mass in rainforests is made up by primates, who eat huge quantities of fruit and act as important primary seed dispersers via defecation (Primack & Corlett 2005). Dung beetles are important secondary seed dispersers and can significantly increase a seed's chance of germination and recruitment (Andresen 2002, 2003; Feer & Forget 2002). As much primate dung gets caught in canopy vegetation and never reaches the forest floor (Davis *et al*. 1997), arboreal dung beetles play an important role in removing this dung (and the seeds it contains) from the canopy, and falling to the ground with it (Gill 1991). Hence arboreal dung beetles increase the chance that seeds reach the ground, decrease their risk of predation, and consequently increase a seed's chance of germination and recruitment. The potential importance of this role is supported by the very high abundance of arboreal dung beetles sampled in this study, with arboreal traps catching 62.1 percent of individuals (two-thirds of traps were arboreal).

This study suggests that fragmentation can have important effects on the vertical stratification on the dung beetle community. It supports previous observations that some arboreal dung beetle species seem to be able to cope with forest disturbance by moving closer to the forest floor. The absence of one arboreal species from most fragments suggests that some specialist arboreal species will not have the versatility to cope with such a change. It is clear that focusing only on two-dimensions of forest ecology, as most ecological studies do, only gives a small part of the bigger picture, and that more consideration of the canopy is necessary in future studies.

CHAPTER 4

Small islands as experimental grounds: dung supplementation and dung beetle translocation experiments

ABSTRACT

In this chapter I examine two competing hypotheses for the distribution of dung beetles. The food limitation and dispersal limitation hypotheses were examined using dung supplementation and dung beetle translocation experiments on small islands of Lake Kenyir. With dung supplementation experiment, I hypothesized that if food was limiting on the small islands, the additional dung supply on the experimental islands would have a positive effect on the dung beetle abundance compared to the control islands. With the dispersal limitation hypothesis, I hypothesized that if dispersal was the main limiting factor, not food, then if a species previously not recorded on the island was translocated onto the island, it should survive. Results from dung supplementation experiments on eight islands, with another eight islands as control, did not support the food limitation hypothesis. However the dung beetle translocation experiment on two islands partially supported the dispersal limitation hypothesis. Translocated dung beetles (*Paragymnopleurus maurus*) survived until the last survey 51 days after release on one islands, while the translocated population crashed immediately on the other island, most probably due to the predation of the invasive ant *Anoplolepis gracilipes*. I conclude that dispersal limitation is likely more important than food limitation for the dung beetle distribution on small islands of Lake Kenyir, with predation being a confounder.

INTRODUCTION

Resource limitation is one of the central rules in ecology because individuals or populations are ultimately limited by food supply (White 1978). Food limitation is potentially of special importance for communities in habitat fragments or islands given their isolated nature, and possibly poor habitat quality – emigration is difficult as food resources become limiting. There has been evidence that the insectivorous Eastern Yellow Robin (*Eopsaltria australis*) experienced relative food shortage in small forest fragments surrounded by a matrix of agricultural land in Australia, resulting in lower reproductive performance (Zanette *et al.* 2000). For dung beetles, theoretically, the most important resource is mammalian dung, although some dung beetles are able to utilize carrion and other rotten bio-matter (Hanski & Cambefort 1991). However, dung availability on small islands is likely limited but this is difficult to quantify in-situ, because the majority of mammals are not permanent residents and capable of moving between islands. Furthermore, dung is rapidly depleted by biotic and abiotic processes. Thus the direct assessment of food limitation for dung beetles on islands is difficult, and an alternative to measuring food availability is to experimentally manipulate food supply through supplementation to test if the resource is limited.

There have been a considerable number of food supplementation experiments under field conditions on terrestrial vertebrates, and Boutin (1990) reviewed 138 such studies. Collectively, these case studies show that food supplementation increased the population densities but did not change the population dynamics and, in particular, food addition did not prevent major declines in fluctuating populations (Boutin 1990). However, there has been a lack of well replicated food supplementation experiments in tropical environments (Boutin 1990), and a general lack of studies that target invertebrates.

To determine whether dung beetle populations on the small islands of Lake Kenyir are limited by food availability, I experimentally added cattle dung onto eight islands at approximately regular intervals. These islands (treatment), together with eight control islands were surveyed over time to monitor their dung beetle populations. I hypothesized that if dung beetle populations on small islands were limited by food, dung supplementation would have a positive effect on dung beetle abundances on the treatment islands as compared to the control islands.

However, food limitation is only one variable affecting dung beetle presence and abundance on islands. Dispersal limitation is another potentially important factor affecting the natural communities in habitat fragments or islands. Even volant animal groups, such as birds have shown some extreme dispersal limitation across forested islands in central Panama, and that species persistence may have been differentially mediated by their respective dispersal abilities (Moore *et al.* 2008). My previous study on dung beetles on the islands of Lake Kenyir also found that isolation and possibly, the geographical location, may have played a role in structuring the island communities (Chapter 2). This suggests that dung beetle communities on the islands were likely to be dispersal limited.

To test for dispersal limitation, as a competing hypothesis to food limitation, in dung beetle communities on the small islands of Lake Kenyir, I also adopted an experimental approach. If dispersal limitation is significant and food not limited, then if a species previously not recorded on an island were to reach it, it should survive. To this aim I translocate the most common and widespread roller species *Paragymnopleurus maurus* to two small and relatively isolated islands where *P. maurus* was not found during previous surveys, and use recapture analysis to monitor survivorship.

Island biotas and forest fragments are particularly vulnerable to invasive species (Simberloff 1995, Sakai *et al.* 2001). On the small islands of Lake Kenyir, the invasive ant species *Anoplolepis gracilipes* had high occurrence and appeared to be in much higher abundance than they are on the large islands and mainland forests (L. Qie, pers. obs.). Thought to be originally from Africa or Asia, *A. gracilipes* is now a tramp species that has spread to most parts of the world including Australia and islands in the Indian Ocean and Caribbean (Holway *et al.* 2003). It has been shown to have negative impact on native animals including the red land crabs in the Christmas Island (Abbott 2005) and other invertebrates on Bird Island, Seychelles (Hill *et al.* 2003). It is possible that the presence and abundance of this tramp ant species may affect the survival of translocated dung beetle *P. maurus* on the two small islands. Therefore to take into consideration this additional factor in the dung beetle translocation experiment, the ground-dwelling ant species was surveyed and compared between six island and mainland sites.

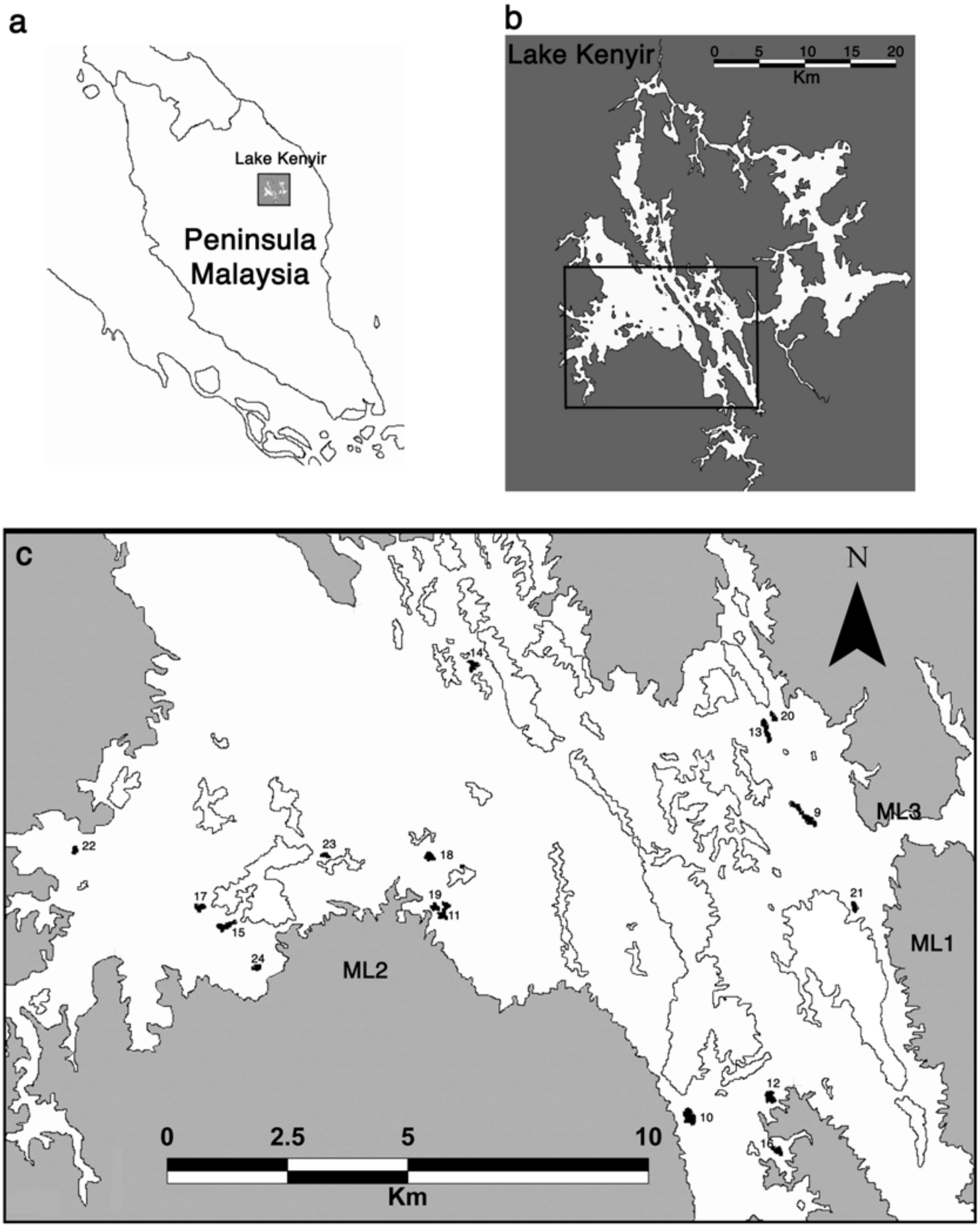


Figure 4-1. Map of Lake Kenyir with relative position within Peninsular Malaysia (a & b). The 16 small islands included in the dung supplementation experiment are highlighted in black (c), along with island codes. Island 22 and 24 were also recipient islands for the *Paragymnopleurus maurus* translocation experiment.

MATERIALS AND METHODS

Study site

See Chapter 2 for the description of sites in Lake Kenyir.

Dung supplementation experiment

Among the 24 islands under study in Chapter 2 I selected 16 small islands below 5 ha in size (Island 9 – 24, Appendix A, Fig. 4-1) for the dung supplementation experiment. These islands have been shown to fall within the small island effect (SIE) range (< 35.8 ha, see results in Chapter 2) hence environmental factors (such as food availability) other than island size are expected to have stronger influences on the dung beetle populations on these islands. Their small sizes also make experimental manipulations at whole island scale possible. Four to seven repeated dung beetle surveys were conducted on these islands between 16 June 2008 and 12 April 2009 to establish baseline diversity and abundance data (Appendix A). During each survey between three and five human dung baited pitfall traps were set up on each island. The trap setup was similar to the method described in Chapter 2, but traps were not filled with any solution, to prevent mortality, and small draining holes were made in the bottom of the cup with a piece of tissue paper placed in the cup to drain or absorb excess rain water, also providing cover for the dung beetles captured. Each trap was also covered by an inverted funnel to prevent beetles from escaping. Traps were checked after 48 hrs and dung beetles were identified, counted and released at the same location.

I started the dung supplementation experiments on 12 April 2009. To assign islands to treatment or control group, I first paired up those islands that have closely located neighbors because geographical location was shown to have an influence on dung beetle community composition (see result of partial Mantel’s test in Chapter 2). For the relatively isolated islands, those with similar dung beetle community composition (Fig. 2-4 in Chapter 2) were paired. In each island pair, one island was randomly drawn as treatment and the other control (Appendix A). Between 12 April 2009 and 1 September 2009 I placed 10 kg cattle dung in 0.5 – 1 kg piles onto the each of the eight treatment islands every 10 – 15 days. All cattle dung was collected from the same cow farm and frozen stored at -20°C for at least 24 hrs to kill the beetles within the dung before being transported to the islands. I surveyed all 16 islands approximately every month during this period, using human dung baited live traps as described above to monitor the dung beetle communities over time. All pitfall trapping surveys used human dung as bait because human dung has been shown to be more effective bait for dung beetles than cattle dung, attracting species including those captured using cattle dung as bait (Chapter 5). Dung supplementation, however, used cattle dung, because it is a uniform resource for the experiment, and represents the most abundant food source of dung beetles in the tropical forests – herbivorous dung (Hanski & Cambefort 1991). Large herbivores such as the Asian elephant (*Elephus maximus*) are present in my study site and visit the small islands (L. Qie, pers. obs.), so supplementation of cattle dung on the small islands simulates frequent large herbivore visits to the islands.

Paragymnopleurus maurus translocation experiment

Paragymnopleurus maurus was chosen for the translocation experiment because it is the most common species in the mainland forest, with the highest incidence among the islands (found in 18 out of 24 islands, Appendix A). I chose two relatively isolated islands, Islands 22 and 24 (Fig. 4-1), where *P. maurus* was not found, as the experimental islands. Between 14 and 15 May 2010, 534 live individuals of *P. maurus* were collected with human dung baited live pitfall traps in the mainland forest and marked with Sharpie® waterproof silver ink marker before being released onto Island 22. Beetles were stored in a cage for no more than 6 hrs before release. Beetles were released at 10 to 15 different locations and along the trail in between them on each island to minimize aggregation. Between 18 and 20 May 2010, 293 individuals were collected and released onto Island 24 in a similar manner. I allowed approximately 24 hrs after release before conducting the first round of post-translocation surveys on both islands (i.e., on Day 1). The second and third round of post-translocation surveys were conducted on Day 25 and 51 respectively. For each post-translocation survey, 15 human dung baited live traps as described above were set up on each island. I consider the detection probability of dung beetles maximized with the high trap density. To minimize the mortality of dung beetle captured, traps were left open for only 24 hrs and all beetles were released immediately after traps were checked.

Sampling of ground-dwelling ant species

To compare the species density of ground-dwelling ants on Islands 22, 24 and other islands of larger sizes with an objective to determine the status of the tramp species *Anoplolepis gracilipes*, I conducted quick assessments between June and July 2010 on five islands of varying sizes and Mainland 3, using protein and sugar-solution baits based on method adapted from Wielgoss *et al.* (2010). Two locations 50 m apart were chosen at each site where the leaf litter on the forest floor was cleared. At each location, I placed two baits of tuna (from canned tuna flakes in water, drained of excess fluid before use) and two cotton wool balls saturated with 70% sugar solution on the forest floor, at the four corners of a 15 x 15 cm square. All baits were approximately 2 cm^3 in size. Baits of the same type were placed diagonally across from each other. All baiting locations were monitored by the same person at 15 min intervals after baits were placed for 1 hour. The maximum abundance of all ant species occurring at the baits was recorded separately for each bait type. For abundant ant species their numbers were estimated to the nearest 50. Voucher specimens were collected for each species for identification.

Statistical analyses for the dung supplementation experiment

I first tested for temporal autocorrelation within the dung beetle abundance time series data of all 16 islands individually using the autocorrelation function, which computes the cross-correlation between two data series. Then I analyzed the temporal trends of the dung beetle count data by fitting a generalized additive mixed effects model (GAMM) with a negative binomial error structure. Individual islands were treated as a random effect. The only fixed effect considered in the model was time (measured in days since start of the first sampling, fitted with a smoother function). To examine the temporal trends of dung beetle abundance on individual islands, a generalized additive model (GAM) was used to model the dung beetle abundance against island and the smoother function of time.

To smooth out the periodic fluctuation in the time series and examine the overall treatment effect over time, I also generated a second dataset using the average trap counts of dung beetles over time periods each equal to half the fluctuation cycle, which was determined through inspecting the GAMM output (see results). A generalized linear mixed effects model (GLMM) was then fitted to this dataset using a quasipoisson error structure, due to overdispersal. The same two predictors, time (but without the smoother) and treatment, were included in the model as the fixed effects and island was included as a random effect.

Models were validated by inspecting residual distribution. I compared and ranked GLMMs using Akaike's information criterion for overdispersed count data corrected for small sample size ($QAIC_c$). $\Delta QAIC_c$ denotes the difference in $QAIC_c$ from the model with the minimum $QAIC_c$ and models with $\Delta QAIC_c \leq 2$ are considered to have substantial support. $QAIC_c$ weights ($wQAIC_c$) provide relative weight of any particular model, which varied from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson 2002). Model fit was assessed using percentage deviance explained (%DE).

All statistical analyses were conducted in R Program (R Development Core Team 2009) unless otherwise specified.

RESULTS

Temporal fluctuation in dung beetle abundance on 16 islands

The dung beetle communities on the majority of the 16 islands were depauperate, to the extent that the modal catch for individual traps was zero (Fig. 4-2). Spatial and temporal variation in dung beetle abundance was also high and, for example, the number of beetles per trap on Island 14 varied between 0 and 139 (mean = 12.9, SD = 26.5; Fig. 4-2). Between June 2008 and October 2009 dung beetle abundance on all 16 islands exhibited an overall declining trend (top ranked model in Table 4-1) but fluctuating at an approximate 100-day period (Fig. 4-3a). There was also considerable variation of dung beetle abundance among the islands (Fig. 4-3b). Based on the approximate 100-day fluctuation cycle, I generated the average number of dung beetles over each 50-day period for all 16 islands, and tested the effect of dung supplementation on dung beetle abundance over time using this dataset.

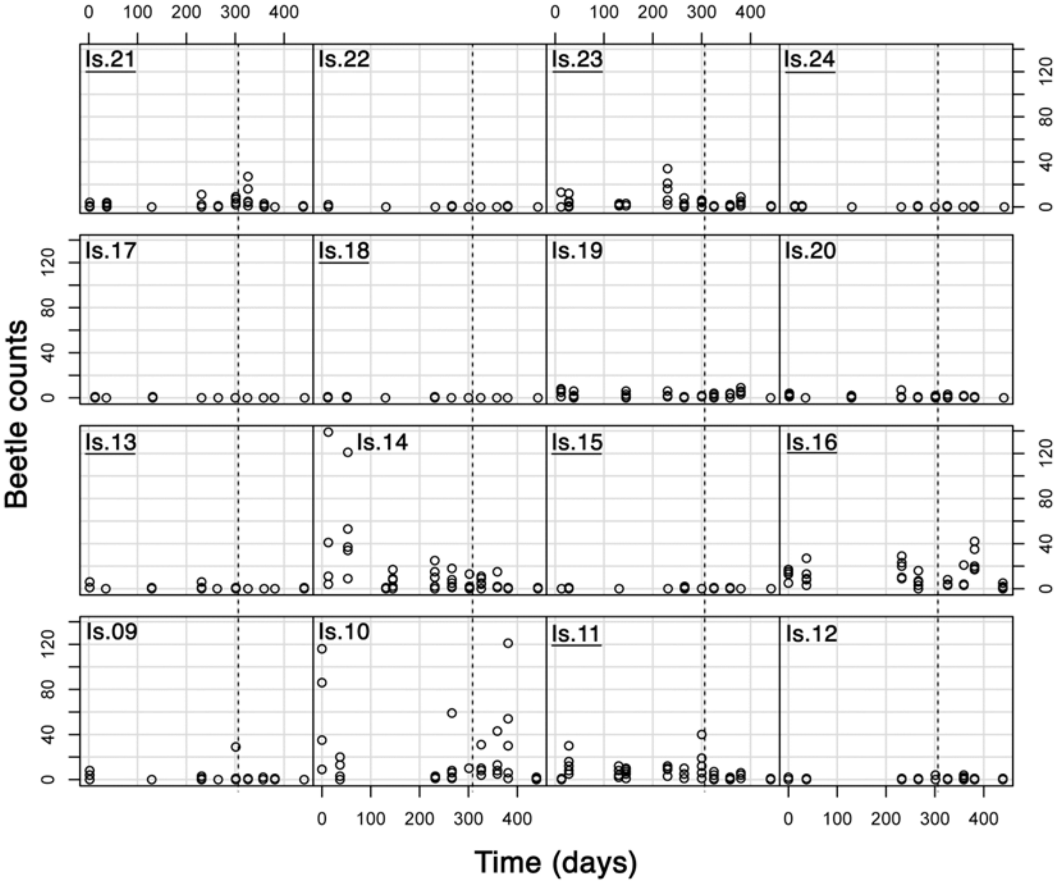
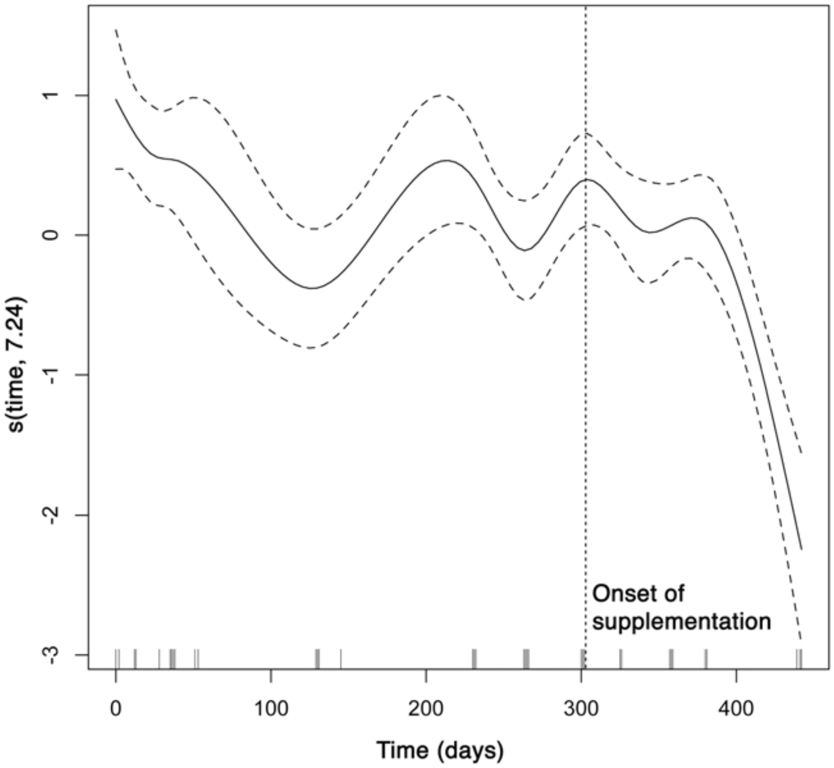


Figure 4-2. Combined dung beetle abundance on 16 small islands between 16 June 2008 and 1 September 2009. Dashed lines mark the onset of the cattle dung supplementation on eight of the islands (with island labels underlined) on 12 April 2009.

a



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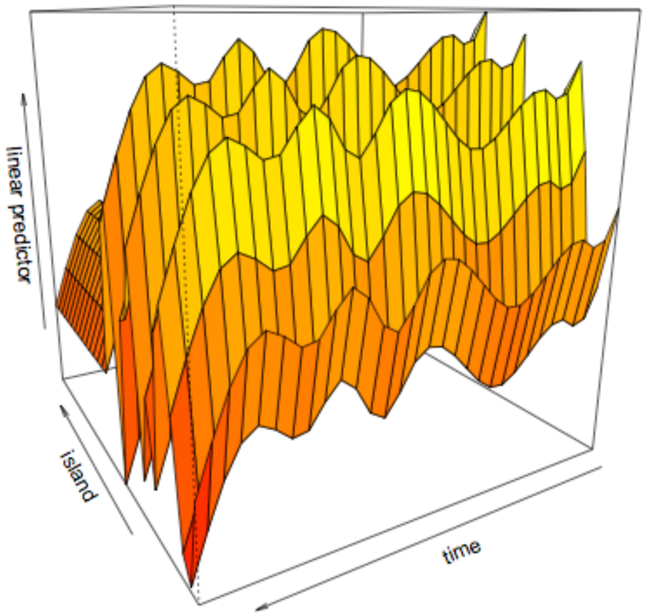

Figure 4-3. (a) Estimated smoothing curve for dung beetle abundance of all 16 islands. The y-axis shows the contribution of the smoother to the fitted values. The smoother used was a cubic spline function with effective degree of freedom = 7.24 (*P* < 0.001). The solid line is the smoother and the dotted lines 95% confidence bands. The vertical lines along the x-axis indicate the values of the observations. (b) Three-dimensional graph showing the fitted values (linear predictor) using the smoother function for individual islands. Period of fluctuation was visually estimated to be approximately 100 days.

Table 4-1. Ranking of GLMMs for testing the effect of time period, dung supplementation and their interaction on dung beetle abundances on 16 islands. All models used a quasipoisson error structure and included island as a random effect. Fixed effects tested are time period (in 50 days), dung supplementation and their interaction (period : supplementation). K, number of model parameters; LL, minimum negative log-likelihood; QAIC$_c$, Akaike's information criterion for overdispersed count data corrected for small sample size; ΔQAIC$_c$, difference between QAIC$_c$ of the top-ranked and current model; wQAIC$_c$, QAIC$_c$ weight; %DE, percentage deviance explained by the model; β0, β1 and β2, parameter estimates for period, supplementation and their interaction respectively; SE, standard error.

Model description	***K***	***LL***	**QAIC$_c$**	**ΔQAIC$_c$**	***w*QAIC$_c$**	**%DE**	**β_0**	**SE**	**β_1**	**SE**	**β_2**	**SE**
~ period	4	-174.2	115.5	0	0.630	21.1	-0.166	0.028				
~ period + supplementation	5	-173.65	117.4	1.86	0.249	21.4	-0.176	0.032	0.199	0.303		
~ period + supplementation + period : supplementation	6	-172.35	118.8	3.29	0.121	22.0	-0.172	0.031	2.288	2.116	-0.270	0.274
~ supplementation	4	-213.95	140.0	24.45	0	3.1			-0.583	0.315		
~ 1	3	-220.85	142.1	26.54	0	0						

Little evidence for effect of dung supplementation on dung beetle abundances

The best ranked GLMM contained only time period as the single predictor for dung beetle abundance, explaining 21.1% of the deviance in the data (Table 4-1). The model that included the interaction term between period and supplementation was ranked third and received considerably less support from the data ($\Delta QAIC_c = 3.29$). This shows that there is little evidence for the effect of dung supplementation on dung beetle abundances on the small islands over time. Furthermore, according to this model, the parameter estimate for this interaction term was negative, suggesting supplementation reduced abundances, contrary to the expectation that additional cattle dung would increase the dung beetle abundance.

Contrasting outcomes of P. maurus translocation to two islands

I recaptured five marked individuals of *P. maurus* (0.9% of 534 individuals released) on Day 1 after translocation to Island 22. All five individuals were found dead in the traps with the ant species *A. gracilipes* present in and around the traps. No individual of *P. maurus* was captured on Island 22 during the surveys on Day 25 and 51 (Fig. 4-4). On Island 24, however, 39 individuals of *P. maurus* (13.3% of 293 individuals released) were recaptured on Day 1 after translocation. This number dropped to 17 (5.8%) on Day 25 and returned to 41 (14%) on Day 51 (Fig. 4-4). All recaptured individuals on Island 24 were alive and released immediately.

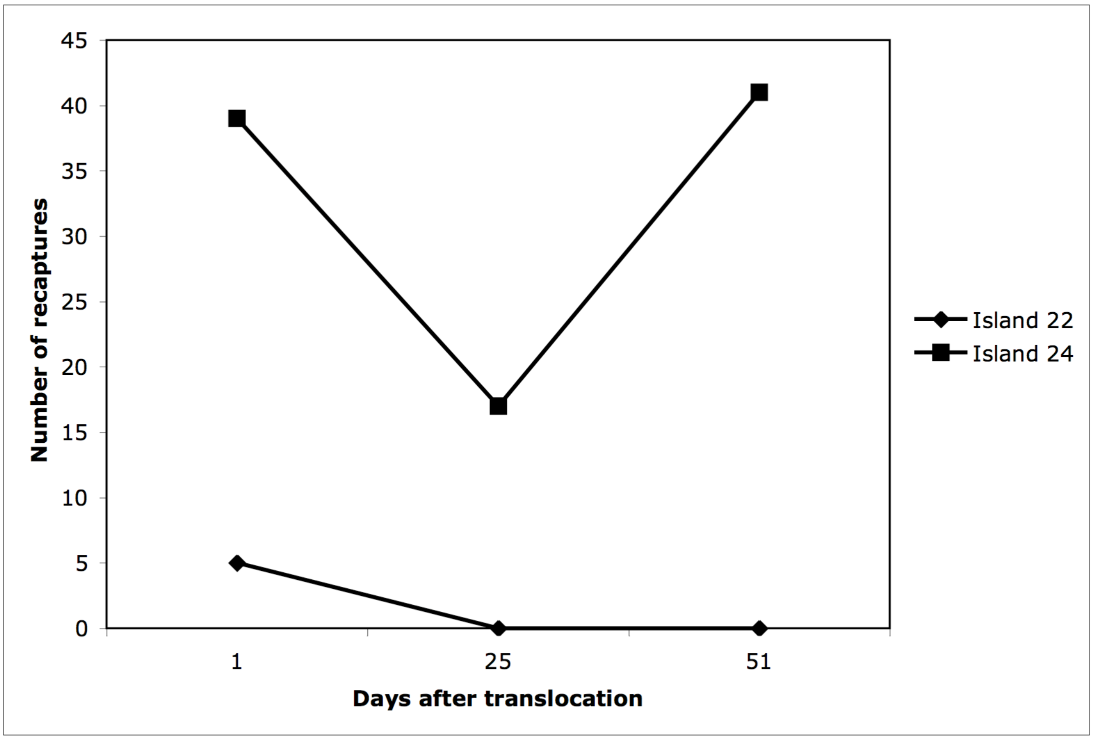

Figure 4-4. Number of *Paragymnopleurus maurus* detected after translocation to Islands 22 and 24.

Table 4-2. Ground-dwelling ant species present at sugar and tuna baits. Numbers of *Anoplolepis gracilipes* were estimated to the nearest 50.

Site	**Ground-dwelling ant morphospecies**	**Maximum worker recruitment of all species at sugar baits**	**Maximum worker recruitment of all species at tuna baits**	**% Presence of *Anoplolepis gracilipes* at both baits combined**
Mainland 3	4	25	8	0
Island 3	2	17	45	0
Island 4	3	7	10	0
Island 22	1	500	500	100
Island 23	2	205	255	87.0
Island 24	2	350	220	38.6

Hyper-abundance of A. gracilipes on Island 22

Rapid assessment on ground-dwelling ants revealed that there was a sharp increase in the abundance of *A. gracilipes* with decreasing island size (Table 4-2). *Anoplolepis gracilipes* was not found during the quick assessment on the mainland site or on the two larger islands, but was found to have the highest relative abundances on the small islands (Table 4-2). On Island 22 in particular, *A. gracilipes* was the only species of ground-dwelling ant found, and was in considerably higher density than other islands (Table 4-2). During the *P. maurus* translocation experiment on Island 22, *A. gracilipes* was observed foraging on the forest floor across all parts of the island, and was seen to attack the newly released individuals of *P. maurus*. On Island 24 however, *A. gracilipes* was found in much lower densities and comparable numbers with another ant species (Table 4-2). Foraging activities of *A. gracilipes* on the forest floor during the *P. maurus* translocation experiment on Island 24 were also observed but at considerably lower levels compared to Island 22.

DISCUSSION

To my best knowledge this dung supplementation study is the first replicated and controlled food supplementation experiment on an invertebrate group under field conditions. First and foremost I demonstrated the feasibility of ecological experiments at this scale using small islands in a lake archipelago. Using an information-theoretic approach the best model suggested that cattle dung supplementation did not have a positive effect on the dung beetle abundances on the eight treatment islands as compared to eight control islands over a six-month period. Data on the duration of development and life cycle of dung beetles are scarce, but the normal time lapse from egg to adult appears to be typically 30 – 50 days, and breeding of dung beetles in the tropics is likely year-round with no marked seasonal changes (Halffter & Matthews 1966). Although the supplementation experiment could not be continued for a longer period of time due to logistical constraints, I note that six months is long enough for new generations of dung beetles to emerge. Therefore if the dung beetle populations on the treatment islands had higher breeding success and/or lower adult mortality, as a result of additional food compared to the control islands, the effect would have been apparent over the six-month treatment period.

The dung beetle abundances on the small islands in Lake Kenyir exhibited considerable temporal fluctuations (Fig 3). It is not clear what could have caused the approximately 100-day fluctuating cycles, because the weather periods changed much more gradually at my sites during the dung supplementation study, consisting of two minor wet monsoon seasons in June – September 2008 and 2009, a major wet monsoon season in November 2008 – January 2009, and relatively drier months in between. The result may indicate intrinsic instability in dung beetle populations on small islands. In Chapter 2, I found that the community composition of dung beetles on these small islands appeared to be largely stochastic. It is hence likely that these populations were sensitive to mild changes in environmental conditions. This may have been reflected as changes in the level of their foraging activities that led to fluctuations in the observed abundances. Over the entire 17 months period during which the 16 small islands were regularly surveyed, the dung beetle abundances clearly showed decline (Fig 3; top ranked model in Table 4-1). Southeast Asia experienced a period of drought between January and March 2010. Whether the observed decline was related to the drought or some natural super-annual fluctuation in these populations remains unclear. Long-term studies are needed to monitor these populations in order to provide better understanding of the far-reaching effects of forest fragmentation on animal communities.

Although the food limitation hypothesis is not supported by the data, the dispersal limitation hypothesis may be partially supported although confounded by ant predation. Of the 293 *P. maurus* translocated onto Island 24, 41 individuals were recaptured after 51 days, at the same level as immediately upon release (39 individuals, Fig. 4-4). The detection probability of *P. maurus* upon release on Island 24 was 13.3% (39 out of 293). Although it is possible that the beetles were more active during the survey on Day 51, hence this survey had a higher detection probability; I believe a large proportion of the released population had survived up to Day 51. This means that the translocated population had been able to find food on the small island. *Paragymnopleurus maurus* was attracted to fish baits in a previous study (Chapter 2) and they may be able to survive by utilizing carrion apart from dung as a food source. To be more conclusive on the status of this translocated population, more follow-up surveys should be conducted.

In contrast, the translocated *P. maurus* population onto Island 22 crashed immediately after release (Fig. 4-4) and this was coincidental with the abnormal hyper abundance of the ant species *A. gracilipes* on this island (Table 4-2). Individuals of *P. maurus* were seen being attacked by *A. gracilipes* upon release; and the only five individuals recaptured were found dead in the live traps with *A. gracilipes* in and around the traps. These suggested that *A. gracilipes* was probably an important factor, contributing to the failure of the translocated individuals of *P. maurus* to survive on Island 22 soon after release. On Island 24, *A. gracilipes* was not the only ant species found and was not in hyper-abundance as it was on Island 22 (Table 4-2). This helps to explain why the translocated population *P. maurus* appeared to be surviving relatively well on Island 24, even though a smaller number of beetles were released (293 onto Island 24 as compared to 534 onto Island 22). *Anoplolepis gracilipes* is a tramp ant species that has been known to occur in hyper abundances in its introduced habitats (Abbott 2005) and was associated with the decline of many native animals, including invertebrates (Hill *et al.* 2003, Bos *et al.* 2008). It is possible that the diet *A. gracilipes* was more protein-limited and hence there is an increased need for predation on other animals as protein sources. *Anoplolepis gracilipes* was considerably more abundance and more numerically dominant over other ant species on small islands in Lake Kenyir, which suggests that these small islands are probably more susceptible to invasive species (Sakai *et al.* 2001). Island 24 should not be an isolated case. My finding highlights a third important factor in recolonization potential of dung beetles on small islands, other than food limitation and dispersal limitation: predation.

Global biodiversity is threatened due to the acceleration of anthropogenic habitat destruction and fragmentation. For example, many of Southeast Asia’s endemic species are threatened by the loss of more than 70% of their original habitat (Sodhi *et al.* 2010). Reintroduction and translocation as a species conservation tools are not a new idea (Griffith *et al.* 1989, Wolf *et al.* 1996), and are becoming a more common practice (Soorae 2008). Furthermore, climate change is predicted to increase the species extinction risk – with as much as 37% of species in regions representing some 20% of the earth’s terrestrial habitat possibly going extinct by 2050, on the basis of mid-range climate-warming scenarios (Thomas *et al.* 2004). Translocating animals to help them keep track of suitable habitat with climate change is also termed ‘assisted colonization’, and being increasingly discussed as a new addition to the conservation management toolbox (Sax *et al.* 2009, Schlaepfer *et al.* 2009, Willis *et al.* 2009). However, translocation or reintroduction efforts have been strongly biased for mammals (Fischer & Lindenmayer 2000) and there have been only a handful of case studies on translocation or reintroduction of insects. Among these are several species of weta (Orthoptera: Anostostomatidae) in New Zealand (Stringer & Chappell 2008, Watts *et al.* 2008), the field cricket (*Gryllus camprestris*) in the UK (Pearce-Kelly 2008), the Karner blue butterfly (*Lycaeides melissa samuelis*) in USA (Soorae 2008). Dung beetles are sensitive to habitat disturbances and perform important ecological functions (Nichols *et al.* 2008) such as dung burial (Slade *et al.* 2007), secondary seed dispersal (Andresen 2003) and biological control (Fincher 1973). Species richness and abundance of dung beetles are decreasing with forest modification and fragmentation throughout the tropics (Nichols *et al.* 2007) and they may soon need effective conservation measures. On the other hand, the loss of dung beetles will result in disruption of ecosystem services in disturbed habitats (Stokstad 2004). The translocation study of *P. maurus* provides preliminary data on the potential usefulness of small islands or forest fragments as dung beetle recolonization sites, and moreover, the feasibility of functional “rehabilitation” of such habitats.

CHAPTER 5

Linking biodiversity and ecosystem functioning of dung beetles on landbridge islands

ABSTRACT

Dung beetles are a functionally important group in the tropical forests. This study examined the impact of forest fragmentation on the primary ecological function of dung beetles, dung burial, on the landbridge islands of Lake Kenyir (Peninsular Malaysia). I found that dung beetle abundance was the most important predictor of dung burial, although other factors such as body mass and species richness, also positively correlated with dung burial. Among the four main functional groups of dung beetles at this site, the small diurnal tunnellers, appeared to be the most important for dung burial. I also compared the dung beetles communities sampled using human dung, cattle dung and fish, and discuss the implications of different used for dung beetle diversity surveys.

INTRODUCTION

The ecosystem consequences of reduced or altered biodiversity have been debated in ecology (Schwartz *et al.* 2000, Naeem 2002). In many cases, a few dominant species perform most important ecological roles and the level of ecosystem functioning usually saturates at relatively low species richness (Schwartz *et al.* 2000, Hooper *et al.* 2005). However, many uncommon species may have strong effects at the local scale (Berlow 1999) and may be critical to the ecosystem stability in the long term (Hobbs *et al.* 2007). Natural communities contain functional redundancy, in the sense that there are multiply species for the same ecological function, and fall in the same functional group. Therefore, it has been argued that the diversity of functional groups, more than that of species, is important in maintaining ecosystem functions (Kremen 2005).

Dung beetles, through their feeding and breeding activities primarily involving dung, perform a series of ecosystem functions, including nutrient cycling, soil aeration, secondary seed dispersal, and parasite control (Nichols *et al.* 2008). All of these are initiated with dung burial – the physical relocation of freshly deposited dung to beneath the soil surface. The efficiency of dung burial is especially high in the tropical forests, where newly deposited mammal feces are typically buried within hours (Larsen *et al.* 2005). However, dung beetles are sensitive to habitat disturbances and fragmentation in the tropics (Nichols *et al.* 2007), resulting in declines in species richness, abundance, and loss of important functional groups (Andresen 2003, Davis *et al.* 2004, Larsen *et al.* 2007).

Effects of changes in dung beetle species and functional group diversity have been previously studied by Larsen *et al.* (2005) and Slade *et al.* (2007). Larsen *et al.* (2005) showed that decreased species richness led to reduced dung burial rate on tropical landbridge islands in Venezuela, and that the large-bodied dung beetles, which were most extinction-prone, were also the most efficient group in dung burial. Using exclusion experiments, Slade *et al.* (2007) demonstrated the positive effect of functional group diversity on dung burial rate, and the disproportional importance of the large nocturnal tunnellers. Hence both studies pointed to the large-bodied dung beetles as being more important in ecosystem functioning.

Dung beetle communities were largely affected by island size in Lake Kenyir (Chapter 2), providing natural experimental ground for determining the relationship between biodiversity and ecosystem functioning. This study aimed to provide additional evidence on how changes in species richness, abundance and functional groups of dung beetles may impact dung burial on tropical landbridge islands of different sizes.

Cattle dung was used for the dung burial experiment as well as during my earlier dung beetle pitfall surveys at Lake Kenyir. I analysed the dung burial data against the diversity data from cattle dung sampling instead of human dung sampling for the consistency of dung type. However because the type of bait used can affect sampling efficiency, I also compared the dung beetle communities sampled using human dung, cattle dung and fish, to provide data on the diet preference of dung beetles. Human dung has been shown to be able to attract a great diversity of dung beetles species in rain forests, including those that feed on carrion and other resources (Howden &

Nealis 1975, Hanski 1983), and is more effective than herbivorous dung (Doube & Wardhaugh 1991). I also discuss the results in light of the most effective biodiversity survey methods for dung beetle monitoring programs.

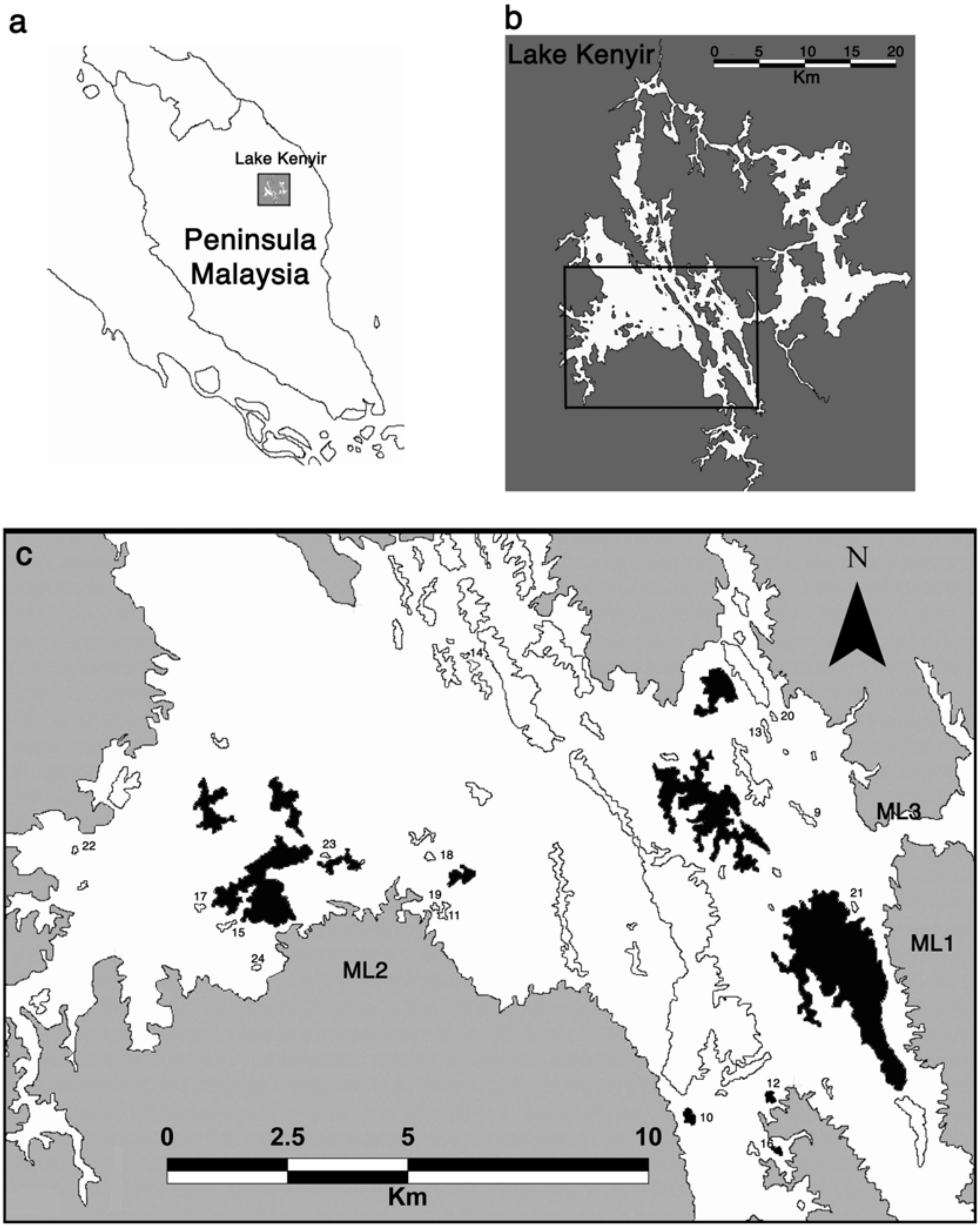

Figure 5-1. Map of Lake Kenyir with relative position within Peninsular Malaysia (a & b). The 11 islands for pitfall trapping using cattle dung are highlighted in black (c), along with three mainland control sites (ML1, ML2 and ML3).

MATERIALS AND METHODS

Study site

See Chapter 2 for the description of sites in Lake Kenyir.

Dung beetle sampling using cattle dung

Between 8 June and 13 August 2007, 11 islands ranging in size from 2.5 ha to 383.3 ha and three mainland forest patches (Fig. 5-1; Appendix A) were surveyed for dung beetles using cattle dung as bait. Two to six sampling plots at each island or mainland site were systematically chosen depending on forest area, and at each plot five traps were set up spaced to 30 m intervals. Trap design was the same as the human dung baited traps in Chapter 2, except that the bait was 15 – 20 g fresh cattle dung. Newly deposited cattle dung was collected from the nearby farms (before dung beetles at the farm entered the dung pads) and homogenized before use. Traps were left open for 48 hrs before the beetles were collected.

Dung beetle sampling using fish and banana

To investigate the diet preference of dung beetles, between 27 August and 1 September 2009, I set 24 pitfall traps baited with fish and 24 pitfall traps baited with banana in the mainland forest (Mainland 1), spaced to 50 m intervals. Trap design and collection method was the same as the cattle dung traps. Frozen fish were left under ambient temperature (25 – 29 ºC) for 15 hrs before use in the field. Banana were cut and left in a plastic box under ambient temperature for two days for fermentation before use. Amount of fish and banana bait for each trap was between 30 – 40 g.

Dung burial experiment

Dung burial experiment was conducted between 27 October and 3 November 2007 in the same sites where dung beetles were sampled using cattle dung baited pitfall traps, and cattle dung collected and homogenized in the same manner as above was used in the dung burial experiment. For each sampling plot, three of the five trapping points were randomly selected as dung burial experiment locations. At each location, the leaf litters on the forest floor were cleared and two cattle dung pads of 50 g, each on a piece of thin plastic coated paper, were placed side by side. One of the dung pads was enclosed in a polyester mesh bag with 2 mm mesh size to prevent dung burial. Rain covers were supported above the pads. Dung pads were collected after 24 hrs and oven dried to constant weight. To calculate the dung burial in 24 hrs, I subtracted the dry mass of the exposed dung pad from that of the bagged dung pad, and divided this mass loss by the dry mass of the bagged dung pad.

Statistical analyses

Species sampling adequacy

Sampling adequacy of dung beetles using cattle dung at each site and using fish at the mainland forest was evaluated based on randomized (100 x) sample based species accumulation curves and the bootstrap estimator for the total species richness in EstimateS (Version 8.0, R. K. Colwell, http://viceroy.eeb.uconn.edu/estimates). Bootstrapping provides a robust way to estimate the total species number (Magurran 2004).

Species rank abundance curves and functional groups

For dung beetle communities from human dung, cattle dung and fish respectively, rank abundance curves were generated based on the baseline density of all species (i.e., the mean number of beetles per trap at the mainland forests). Functional group classification was based on literature (Hanski & Cambefort 1991, Davis 1999, Slade *et al.* 2007) (Appendix B). Relative abundance of functional groups was examined based on the baseline densities.

Modeling dung burial and its predictors

Important factors affecting the dung burial rate may include the dung beetle abundance, total dung beetle body mass, species richness, functional group diversity, and abundance of specific functional groups. Because of the commonness of the large diurnal roller *Paragymnopleurus maurus*, the small diurnal roller *Sisyphus thoracicus*, and the small diurnal tunneller *Onthophagus babirussoides*, between two to four functional groups were present at most sites, lacking a gradient in functional group diversity among sites. Therefore instead of functional group diversity, this analysis considered the importance of specific functional groups: the small diurnal tunnellers (SDT), the large nocturnal tunnellers (LNT), the small diurnal rollers (SDR) and the large diurnal rollers (LDR). I did not include the kleptoparasite because it consists of only a single species, *Caccobius unicornis*, which utilizes dung balls made by other species (Davis & Huijbregts 2000), hence do not directly contribute to the dung burial. I modeled the percentage dung burial in 24 hrs against seven measures of the dung beetle community: beetle abundance, total body mass, species richness, abundance of the SDT, LNT, SDR and LDR. Because these variables are correlated with each other, I used seven single-predictor generalized linear models and a null model as control. The mean number of beetles per trap was used as the measure of abundance. A canopy specialist, *Onthophagus* sp. 7, was excluded from the modeling analysis because they forage mostly above 5 m from the forest floor (Davis *et al.* 1997) and pitfall traps on the ground will not accurately represent their populations (Davis & Sutton 1998, Tregidgo *et al.* 2010). The beetle body size measure (the product of the body length and elytra width) described in Chapter 2 was used as a surrogate for beetle body mass, because the beetle dry mass was found to vary greatly depending on the internal conditions of the individuals (e.g., some specimens appeared to be nearly 'hollow' and weighed considerably less than others of the same size, data not shown). The percentage dung burial was arcsine transformed to achieve normal distribution in model residuals. Models were compared and ranked using Akaike's information criterion corrected for small sample size (AIC_c). ΔAIC_c denotes the difference in AIC_c from the model with the minimum AIC_c and models with $\Delta AIC_c \leq 2$ are considered to have substantial support. AIC_c weights ($wAIC_c$) provide relative weight of any particular model, which varied from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson 2002). Model fit was assessed using percentage deviance explained (%DE). Models were implemented in R Program (R Development Core Team 2009).

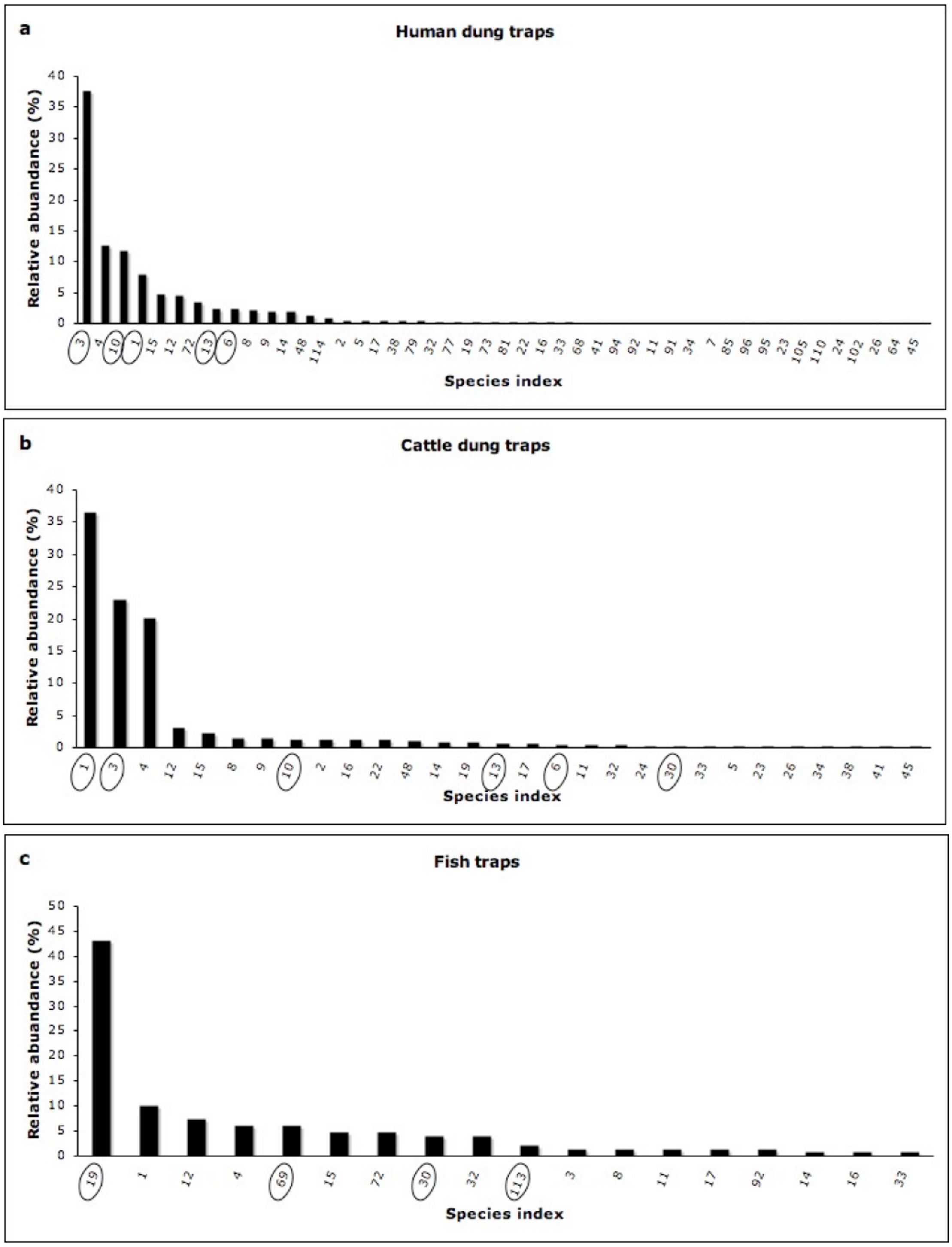

Figure 5-2. Rank abundance curves for dung beetle communities sampled using human dung (Chapter 2), cattle dung and fish. Relative abundance was based on number of beetles captured per trap in the mainland forests (baseline density). A number of species were highlighted (see text for details).

RESULTS

Dung beetles sampling

Across all 11 islands and three mainland forest patches I collected 29 dung beetles species totaling 1493 individuals from pitfall traps baited with cattle dung (Appendix A & B). Among the 11 islands, species richness decreased significantly with island area (Spearman's $\rho = 0.70$, $P = 0.02$). Although beetle abundance generally decreased with island area (Appendix A), this correlation was not significant (Spearman's $\rho = 0.41$, $P = 0.2$). The fish baited pitfall traps on the mainland forest collected 151 individuals representing 18 species. However the banana traps did not collect any coprophagous species. The bootstrap estimator showed that the sampling using cattle dung at all sites and the sampling using fish reached more than 80% of the total species richness (Appendix A; 90% for fish).

Dung beetle communities sampled by human dung, cattle dung and fish

Dung beetles species captured in cattle dung traps were a subset of those captured in human dung traps. Two individuals of *Hybosoridae phaeochroops* (#30, Fig. 5-2b) were collected using cattle dung as bait but not present in human dung traps. This species, known to feed primarily on carrion, belongs to the beetle family Hybosoridae and is not considered a true dung beetle species (Hanski 1991), hence is only included here for comparison. The abundance of dung beetles from human dung sampling was also significantly higher than that from cattle dung sampling (1.10 ± 2.42 as compared to 0.28 ± 0.65 individuals per trap, $P = 0.02$, paired T-test, one-tail). Among the 18 species found in fish traps, 15 were also found in the human dung traps, and 14 were also found in the cattle dung traps (Appendix B).

Relative abundance of most shared species between human dung and cattle dung sampling remained similar between both bait types (Fig. 5-2a&b). However, the most abundant species in human dung traps was *P. maurus* (37.7%, #3 in Fig. 5-2a), a large diurnal roller, which was the second most abundant species in fish traps (23%). On the other hand, the most abundant species in cattle dung traps was *O. babirussoides* (36.6%, #1 in Fig. 5-2b), a small diurnal tunneller, which was ranked fourth in human dung traps (7.8%). Other species that showed notable changes in their relative abundance between both dung types include two diurnal tunnellers, *O. rutilans* (#10), *O. aphodiodes* (#6), and *C. unicornis* (#13), a kleptoparasite (Fig. 5-2a&b).

Although a number of the common species in dung traps were also present in fish traps, the relative abundance ranks were considerably different (Fig. 5-2c). The most abundant species in fish traps was *O. semifex* (43.1%, #19 in Fig. 5-2c), a diurnal tunneller, known as a carrion specie (Krikken & Huijbregts 2008), which was also present in the dung traps but rare (Fig. 5-2a&b).

Dung burial rate best predicted by total dung beetle abundance

All six abundance components were shown to increase dung burial (Table 5-1). The best single-predictor model for dung burial rate was the total dung beetle abundance, explaining 35.8% of the total deviance in the data ($w\mathrm{AIC}_c$ = 0.21, Table 5-1; Fig. 5-3). The second ranked model was the total dung beetle mass (using size as surrogate), although without substantial support ($\Delta\mathrm{AIC}_c$ = 2.16). None of the four functional groups or the total species richness was considered plausible single-predictors for the dung burial rate (fourth to eighth ranked models, after the null model in Table 5-1). However among the three functional groups, the small diurnal tunnellers appeared to be more important than others, explaining 16.5% of the deviance in the data (Table 5-1). This is consistent with the best model because the small diurnal tunnellers were also the most numerically abundant group in the mainland forest (Fig. 5-4). The second most important functional group was the large diurnal rollers (fifth ranked model, Table 5-1), represented by a single common species *P. maurus* (#3 in Fig. 5-2b).

Table 5-1. Ranking of generalized linear models testing the effect of total beetle abundance, total beetle body mass, specie richness, and the abundance of small diurnal tunnellers (SDT), large nocturnal tunnellers (LNT), small diurnal rollers (SDR) and large diurnal rollers (LDR), respectively, on dung burial rate. Because of correlation among variables, only single-predictor models were tested, along with a null model. *K*, number of model parameters; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, difference between AIC_c of the top-ranked and current model; $wQAIC_c$, AIC_c weight; %DE, percentage deviance explained by the model; β_0, parameter estimates for the predictors; SE, standard error.

Model description	***K***	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**%DE**	**β_0**	**SE**
~ beetle abundance	3	-16.86	0	0.214	35.8	0.020	0.008
~ total mass	3	-14.71	2.16	0.073	25.0	3.7E-04	1.8E-04
~ 1	2	-13.98	2.89	0.051	0.0	-	-
~ SDT	3	-13.19	3.67	0.034	16.5	0.019	0.013
~ LDR	3	-12.81	4.05	0.028	14.2	0.042	0.030
~ SDR	3	-11.99	4.87	0.019	9.0	0.015	0.014
~ species richness	3	-11.3	5.57	0.013	4.4	0.004	0.006
~ LNT	3	-10.9	5.97	0.011	1.6	0.104	0.234

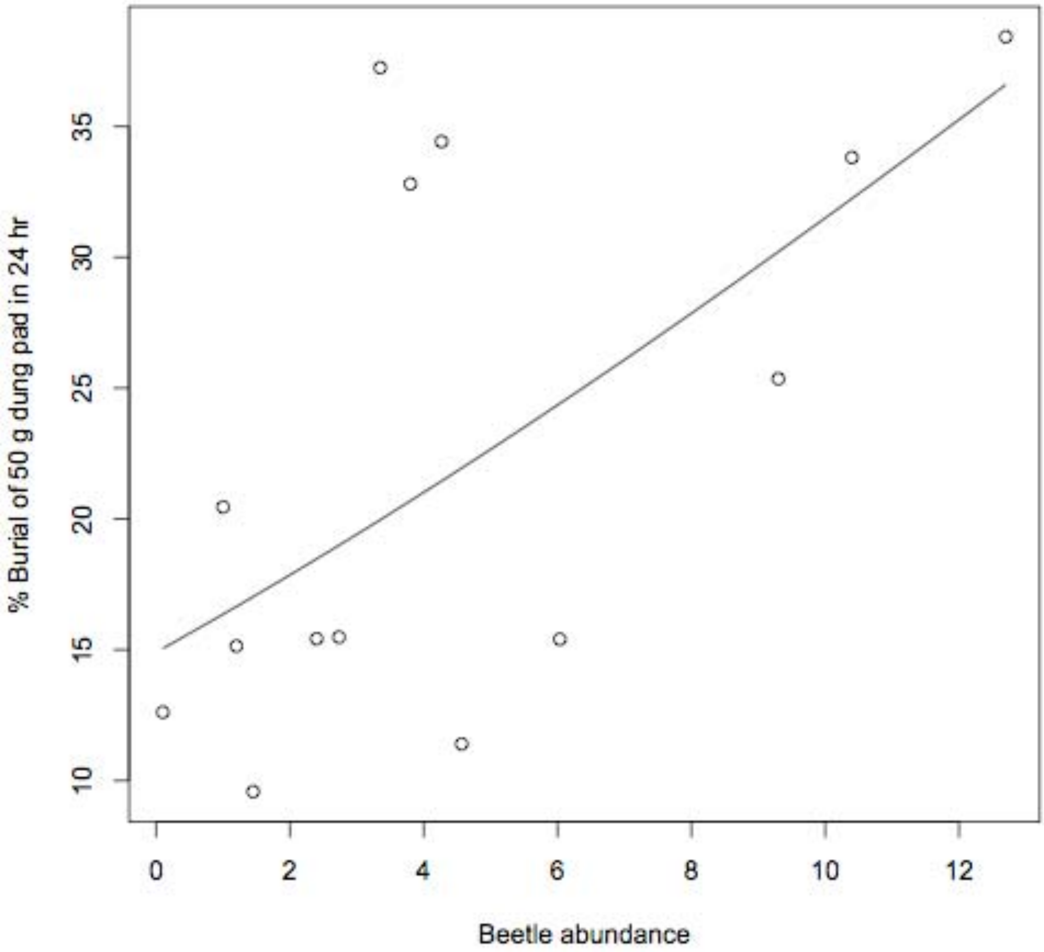

Figure 5-3. Percentage dung burial rate plotted against dung beetle abundance (number of beetles per trap) for 11 islands and three mainland control sites. Solid line were based one the prediction by the model with dung beetle abundance as single-predictor (best model; see Table 5-1). Because the percentage dung burial was arcsine transformed before used in the linear model, the back-transformed result showed a non-linear relationship.

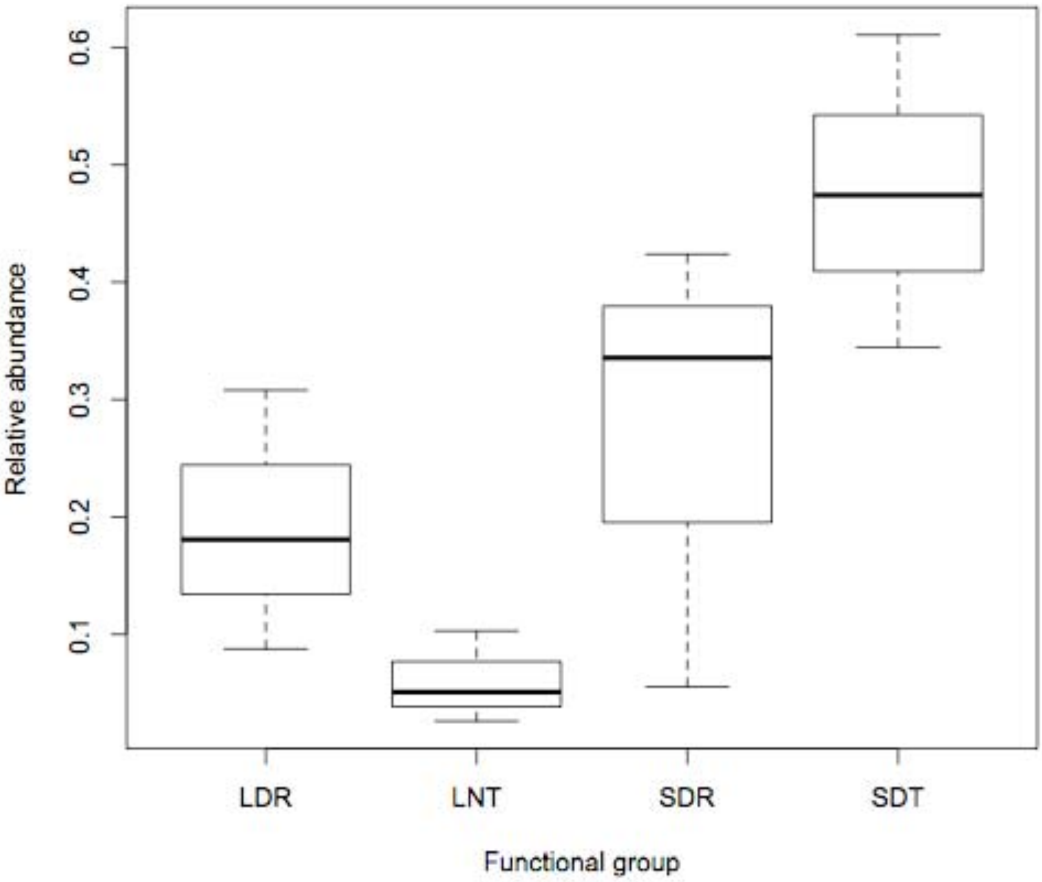

Figure 5-4. Relative abundance of the four functional groups tested in the models for their effect on dung burial: large diurnal rollers (LDR), large nocturnal tunnellers (LNT), small diurnal rollers (SDR) and small diurnal tunnellers (SDT). Data were based on the number of beetles per trap in the mainland forests (baseline density). The horizontal lines show the median values. The bottom and top of the box show the 25th and 75th percentiles. The vertical dashed lines show either the maximum value or 1.5 times the interquartile range of the data, whichever is the smaller.

DISCUSSION

My results showed that the best predictor for dung burial rate on the landbridge islands was beetle abundance, although other correlated factors, such as total body mass of dung beetles and species richness also had a positive effect on dung burial. The evidence on the importance of species richness on ecosystem functioning was not strong as hypothesized or shown (Larsen *et al.* 2005). My study suggested that in terms of dung burial, dung beetles simply “won by the numbers”. However, this does not contradict with the finding of Larsen *et al.* (2005), that the dung burial efficiency positively correlated with the body mass of the dung beetle species, which was based on the amount of dung buried by each individual. Intuitively a large dung beetle has higher energy requirement hence consumes larger amount of dung as compared to a small dung beetle. An interesting finding in my previous study was that, the large-bodied species were not necessarily more extinction prone on the islands of Lake Kenyir (Chapter 2), as was the case in the study by Larsen *et al.* (2005). Hence on the small islands in Lake Kenyir there was an overall lack of dung beetles – of any species. As a result the dung burial rate was low and about 5 g in 24 hrs (10% of a 50 g dung pad; Fig. 5-3) in the most depauperate island.

Among the four functional groups, the abundance of the small diurnal tunnellers appeared to be the most important in dung burial. This differed from the results in Slade *et al.* (Slade *et al.* 2007), where the large nocturnal tunnellers were the most efficient in dung burial. However, this is likely due to the fact that in my site the small diurnal tunnellers were the most abundant group (Fig. 5-4), majority of which belong to the specieous genus *Onthophagus* (Hanski & Krikken 1991). This is in line with the total beetle abundance being the best predictor for dung burial. Conversely, the large nocturnal tunneller group was the least abundant (Fig. 5-4), consisting of only three species in the cattle dung community (Appendix B), and the largest species in this group, *Catharsius molossus*, potentially most efficient in dung burial, was not common (#8 in Fig. 5-2b). In the study by Slade *et al.* (Slade *et al.* 2007) on the other hand, there were four species in the large nocturnal tunneller group with two *Catharsius* species, and one of them was found in abundance at the site. Therefore the answer for which dung beetle functional group is the most important may depend on the site in question, and specifically its community composition.

Comparing the sampling using human dung and cattle dung, the results showed that human dung was more effective bait for dung beetles, both in terms of species richness and abundance (Fig. 5-2). Human dung was shown to be able to attract a great diversity of dung beetles in South-east Asia (Hanski 1983) and elsewhere (Doube & Wardhaugh 1991, Larsen *et al.* 2006). Dung beetle communities typically consist of a large number of rare species (Hanski & Cambefort 1991). Results from this study confirmed this, and showed that it is especially the case in the human dung sampling (Fig. 5-2). This result may also suggest the broad diversity spectrum of dung beetle species captured using human dung as bait. Dung beetles are useful indicator taxa for habitat modifications and fragmentation (Nichols *et al.* 2007, Gardner *et al.* 2008). With dung beetles more and more often used in biodiversity monitoring programs, it is important to have a standard and effective sampling protocol for rapid biodiversity assessment. This protocol is currently being developed (The Scarabaeinae Research Network In preparation) and includes the pitfall trap design (similar to my study), trap spacing (100 m to maximize trap independence), bait type (20 g human dung), trapping period (3 × 24 hr with re-baiting every 24 hr).

My study showed that dung beetle abundance is important for maintaining its dung burial functions. Additionally, human dung is the most effective bait to attract rainforest dung beetles.

CHAPTER 6

General discussion

Based on a group of landbridge islands in a hydroelectric reservoir formed 24 years ago, this thesis looks at the effects of tropical forest fragmentation on dung beetle assemblages, at both ground level and in the canopy, and their ecological function. Several species traits were identified to be associated with species found on a greater number of islands hence likely more resilient to local extinction. This thesis also specifically determines the population dynamics on the small islands and tested, using experimental approach, at whole island scale, two competing hypotheses for dung beetle distribution: the food limitation and dispersal limitation hypotheses.

I found that species richness of dung beetles decreased with island area, although there was increased stochasticity among the small islands below 35.8 ha, i.e., the small island effect (SIE). Common species (species with higher density in the mainland forests) and those able to forage on the forest edge were likely the species more resilient to local extinction. The canopy dung beetles (represented by *Onthophagus* sp. 7) were present in higher numbers at 5 m from the forest floor relative to at 15 m in the foliage on smaller islands, indicating a downward shift in their vertical stratification in response to forest fragmentation. The primary ecological function of dung beetles – dung burial – decreased on the small islands, with dung beetle abundance being the strongest correlate of dung burial. Using dung supplementation and dung beetle translocation experiments, I show that, dispersal limitation, not food limitation, is the important driver of dung beetle distribution on the depauperate small islands, with predation by invasive ants also likely playing a role.

Effects of forest fragmentation on dung beetle assemblages

Knowledge on the effects of forest fragmentation on biological communities in SE Asia is relatively poor (see Chapter 1). My study is among the first comprehensive forest fragmentation studies on an important insect group in SE Asia – dung beetles. Using standardized surveys on dung beetles on a total of 24 forested landbridge islands together with three mainland control forests, I clearly show that forest fragmentation result in species loss (Turner 1996) (Chapter 2), and also a downward shift in the foraging height of the canopy specialists in small islands (Chapter 3). This expands our understanding of the forest fragmentation dynamics to a three-dimensional paradigm: animals in fragmented forests are not only suffering from reduced area, but also from reduced vertical habitat zone due to canopy deterioration, and along with it, compressed vertical stratification, increased competition, and altered biotic conditions in the third dimension (Davis & Sutton 1998). In the case of the canopy dung beetles, which possibly rely primarily on arboreal mammals, such as primates, for food sources, the cause and consequence may be relatively easily hypothesized. However more studies on primarily arboreal vertebrate and invertebrates are needed to develop more general patterns.

The community compositional changes from continuous forests to forest fragments have also been studied for various taxa (Lynam & Billick 1999) (Terborgh *et al.* 1997, Benedick *et al.* 2006). Most often community composition displays a nested pattern with decreasing fragment size, as a result of an orderly sequence of species extinctions. In my results, however, the dung beetle communities showed increased stochasticity in the small islands (< 35.8 ha), and did not follow a significant nested pattern. This observation is closely associated with the area threshold detected by heuristic statistical tools including the regression tree analysis and generalized linear models (Chapter 2). For islands below 35.8 ha in Lake Kenyir, both species richness and community composition were driven by a small island effect, rather than by a direct relationship with area. Thus my study provides new emprirical evidence for the small island effect (Lomolino & Weiser 2001), that has been debated in ecology (Triantis *et al.* 2006, Burns *et al.* 2009). More importantly, it highlights the importance of understanding the species distribution and their dynamics in small fragments. I found that common species and those able to forage on forest edge had a higher chance of survival on small islands; tree basal area was the most important predictor of species richness in small islands, with isolation (and even the geographical location) and amount of edge playing roles. However, a large portion of the variation remained unexplained both in species richness and community composition among the small islands. The dung beetle assemblages on small islands therefore, were likely rather random selection from the resilient species, and susceptible to stochastic environmental events. This implies that, the long-term population persistence and conservation value of small forest fragments need to be more carefully examined (Turner & Corlett 1996, Tscharntke *et al.* 2002).

Ecosystem consequences of tropical forest fragmentation

Understanding of the effects of forest fragmentation does not stop at the species and community level, but moves further to the ecosystem level effects. Although the link between biodiversity and ecosystem functioning has been investigated (Schwartz *et al.* 2000, Naeem 2002), direct evidences from field studies from forest fragments are scarce (Didham 1998, Andresen 2003), and such data have not been available from

SE Asia. This study therefore, provides the first dataset on the ecosystem consequences of forest fragmentation in SE Asia, using dung beetles and dung burial as the model system. This taxa – function association is particularly strong in the tropical forests, meaning that dung beetles are primarily responsible for dung burial. Although dung beetles seldom occur alone in animal droppings, and in the temperate systems, other groups such as termites and earthworm also incorporate dung into soil (Herrick & Lal 1996, Groffman 2004), they are certainly the most important taxa for dung burial in tropical forests (Nichols *et al.* 2008). Slade *et al.* (2007) conducted an elegant dung beetle exclusion experiment in Borneo and proved the importance of functional group diversity on dung burial. In Venezuela, on a group of landbridge islands similar to those in Lake Kenyir, Larsen *et al.* (2005) found that dung beetle species richness was positively correlated with the dung burial. My dung burial experiment however, shows that dung burial on the islands is best predicted by dung beetle abundance (Chapter 5). Collectively, these evidences from different forest sites in the tropics seem to suggest that, exactly which attribute of the dung beetle community is most important in dung burial may depend on the specific site and community composition. In any case, it is clear that forest fragmentation will have a detrimental effect on dung burial. The small islands with depauperate dung beetle communities in Lake Guri, Venezuela (Larsen *et al.* 2005) saw large accumulations of howler monkey (*Alouatta seniculus*) dung, indicating serious reduction in nutrient recycling and parasite control due to lack of dung burial (Klein 1989, Vulinec 2002). Although accumulation of unburied dung has not been observed in Lake Kenyir, my dung supplementation study shows that adding dung to the small islands will not increase the dung beetle population in a relatively short term. This suggests that it is possible for these islands to be in a situation where dung is abundant but dung beetles are lacking.

Underlying drivers for community composition on small islands

Therefore the underlying drivers of dung beetle distribution and ecosystem functioning on small islands have been of particular interest of this thesis. Results from multiple parts of this thesis collectively point to dispersal limitation as among the most important factors influencing the dung beetle assemblages on small islands. First, I found that species able to adapt to the forest edge occurred on greater number of small islands (Chapter 2). Edge adapted species are more likely to disperse to islands because, to cross the water barrier a species must be able to tolerate relatively high insolation and temperature, similar to the conditions near the forest edge, hence such species should have higher immigration rates onto small islands. Second, I found that isolation negatively affected the species richness on islands, and that geographical location explained the variation among community composition on islands to a mild degree (Chapter 2). These suggest that how many species and what species can be found on the islands may depend on the species' dispersal abilities. Third, and more interestingly, a translocated population of *P. maurus* onto Island 24 (0.5 ha) survived reasonably well up till my last survey, 51 days after release (Chapter 4). This result, together with that from the food supplementation experiment provided evidence on the importance of dispersal limitation in shaping the island communities. However, more such experimental data from more islands should be collected. Nonetheless, Larsen *et al.* (2005) reached similar conclusion in their study in Lake Guri using a different approach. By releasing dung beetles on the islands' shores and in open water, they found that dung beetles in general navigated poorly outside the forest, which means crossing the water barrier is challenging for most species. Therefore the relative dispersal ability across water may strongly and differentially influence the immigration rate of different dung beetle species onto islands, and in turn affect the population dynamics on islands. Future studies can include methods that give direct measures of the immigration and emigrations rates of dung beetles on islands, for example, mark and recapture experiments conducted on neighboring islands, although it requires large number of beetles to be released (Larsen 2006). Another possibility is to set up flight interception traps on the forest edge of the islands and have collection containers below the trap separate for beetles flying into and flying out from the forest.

“Functional” rehabilitation of fragmented habitats

The *P. maurus* translocation experiment also sheds light on future projects aiming for species conservation and ecosystem rehabilitation. For species that are threatened by habitat fragmentation or climate change due to poor dispersal abilities, assisted colonization may be a way to help these species establish new populations in new habitats, provided that the introduced area provides favorable habitats. On the other hand, for habitat fragments that have lost functionally important species due to low recolonization rate, it may be possible to reintroduce selected species that have difficulty arriving there by themselves. *Paragymnopleurus maurus* is a large diurnal roller, which was most common in the mainland forest and it commonly occurred on the islands in Lake Kenyir (Appendix A). It seems relatively resilient because it is edge tolerant and may feed on both dung and carrion, indicating its generalistic foraging behaviour (Appendix B). It is possible that *P. maurus* was present on Island 24 previously but went locally extinct because the island is relatively isolated from large landmass (Appendix A). The recapture density of translocated *P. maurus* was between 1.1 – 2.7 individuals/trap (17 – 41 individuals in 15 traps), which is comparable to the existent dung beetle capture densities on most other islands below 5 ha (Appendix A). Therefore the translocated population (293 individuals) is estimated to be near the natural population size that Island 24 may support. *Paragymnopleurus maurus* is relatively important for dung burial (Chapter 5) thus there may be hope for the "functional" rehabilitation of small islands. However for such conservation effort to be effective, long term monitoring and perhaps regular population augmentation are needed.

Landbridge islands formed by damming as experimental ground

I based my entire study in the group of forested landbridge islands formed by the building of a hydroelectric dam in 1986. These forested islands on large manmade lakes are a particularly valuable study system because they share the same age and similar historical flora and fauna composition. The islands are embedded in a uniform matrix – water, without the confouding effect of matrix type (Prugh *et al.* 2008, Umetsu *et al.* 2008), and usually have ideal control forest sites on the mainland. Diamond (2001) called it "unplanned natural experiment", and likened the resulting island communities to the numerous outcomes from shaking up a kaleidoscope, with general patterns but "fascinating differences of detail because of effects of chance". These islands thus provide unique opportunities to examine effects of fragmentation, fauna relaxation, and ecosystem consequences. The best examples of such studies include the Barro Colorado Island and other islands in Panama's Lake Ganun (Leigh *et al.* 1993, Robinson 1999, Meyer & Kalko 2008), and islands in Lake Guri in Venezuela (Terborgh *et al.* 1997, Terborgh *et al.* 2001, Feeley 2003, Larsen *et al.*

2005). Furthermore, we can use these natural experimental grounds in a more proactive way by conducting more experiments at whole island scale to test ecological theories as well as conservation measures. I have shown some interesting results from dung supplementation and dung beetles translocation experiments. What can also be done in the future is determine the threat of invasive species such as *A. gracilipes* on other groups including dung beetles, with controlled ant extermination experiments on islands where they have established large colonies.

As a caveat, applicability of results from studies based on the landbridge islands to forest fragments on land may be limited, because the matrix of habitat islands are less hostile, hence its permeability for different taxa need to be accounted for (Koh & Ghazoul 2010). Some of the studies in the thesis (such as Chapter 3 and 4) were limited by sample sizes due to high logistical requirement of the experiments, so caution should be exerted when interpreting these results in general senses.

In conclusion, this thesis is a useful collection of empirical evidences from Lake Kenyir, Peninsular Malaysia, on the consequences of tropical forest fragmentation on dung beetle assemblages and their ecosystem functioning. The study taxa and the study site are not only excellent model systems but also ecologically important on their own right. Hopefully this work contributes to the tropical forest ecology and conservation knowledge in SE Asia where natural forests are rapidly diminishing and conservation actions are urgently needed.

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Appendix A. Chronology of surveys and experiments, environmental variables, and summary of sampling results at all sites in Lake Kenyir. S_{obs} is the total No. of observed species. S_{obs}' is No. of species excluding two canopy specialists (see Chapter 2)

Study site	Area (ha)	Surveys Jun - Aug 2007 (cattle dung)	Dung burial experiment Oct - Nov 2007	Surveys Jun 2008 - Apr 2009 (human dung)	Arboreal dung beetle surveys Aug 2008	Surveys Apr 2009 - Oct 2009 (human dung)	Dung supplementation	Dung supplementation pairing	No. *P. maurus* released
Mainland 1	-	1	Yes	2	1	-	-	-	-
Mainland 2	-	1	Yes	2	1	-	-	-	-
Mainland 3	-	1	Yes	2	1	-	-	-	-
Island 1	383.3	1	Yes	2	1	-	-	-	-
Island 2	184.7	1	Yes	2	1	-	-	-	-
Island 3	146.1	1	Yes	2	1	-	-	-	-
Island 4	45.8	1	Yes	2	-	-	-	-	-
Island 5	39.2	1	Yes	2	-	-	-	-	-
Island 6	32.4	1	Yes	2	-	-	-	-	-
Island 7	14.9	1	Yes	2	-	-	-	-	-
Island 8	9.9	1	Yes	2	-	-	-	-	-
Island 9	4.9	-	-	5	-	4	Control	Island 21	-
Island 10	4.0	1	Yes	5	-	4	Control	Island 16	-
Island 11	3.6	-	-	7	-	4	Treatment	Island 19	-
Island 12	3.0	1	Yes	5	-	4	Control	Island 18	-
Island 13	2.9	-	-	6	-	4	Treatment	Island 20	-
Island 14	2.7	-	-	7	1	4	Control	Island 23	-
Island 15	2.6	-	-	6	-	4	Treatment	Island 17	-
Island 16	2.5	1	Yes	4	-	4	Treatment	Island 10	-
Island 17	2.0	-	-	6	-	4	Control	Island 15	-
Island 18	1.7	-	-	6	-	4	Treatment	Island 12	-
Island 19	1.6	-	-	6	1	4	Control	Island 11	-
Island 20	1.5	-	-	6	-	4	Control	Island 13	-
Island 21	1.1	-	-	6	-	4	Treatment	Island 9	-
Island 22	0.9	-	-	5	-	4	Control	Island 24	534
Island 23	0.8	-	-	7	-	4	Treatment	Island 14	-
Island 24	0.5	-	-	6	-	4	Treatment	Island 22	293
Total									

Appendix A. (continued)

								Cattle dung sampling					
Study site	**Edge index**	**Distance (m)**	**Basal (m^2/ha)**	**Litter (mm)**	**Soil pH**	**UTMx**	**UTMy**	**S_{obs}**	**% Bootstrap Mean**	**Total indiv.**	**Indiv./trap**	**% Dung burial (24 hrs)**	**Total beetle mass/trap (mm^2)[a]**
Mainland 1	-	-	34.2	46.3	6.2	249775.4	549135.6	14	88.2	181	6.0	15.4	271.2
Mainland 2	-	-	27.2	42.9	6.1	240044.4	548269.3	17	85.1	137	4.6	11.4	208.9
Mainland 3	-	-	30.3	67.4	6.5	249254.7	551763.3	21	86.3	381	12.7	38.4	689.5
Island 1	15.8	206	23.5	48.6	6.5	248306.7	548719.1	11	82.7	279	9.3	25.4	256.9
Island 2	22.2	425	26.8	28.4	6.2	245817.8	551450.1	5	96.7	128	4.3	34.4	102.8
Island 3	15.7	53	22.7	48.6	6.3	236434.3	549981.6	9	87.6	82	2.7	15.5	159.2
Island 4	8.3	400	26.9	50.0	6.5	246064.8	554233.1	6	91.5	67	3.4	37.2	132.5
Island 5	13.6	930	21.3	57.6	5.8	235327.1	551800.8	5	83.9	29	1.5	9.6	24.5
Island 6	9.7	209	21.0	59.6	6.3	237018.5	551790.6	2	80.6	2	0.1	12.6	2.1
Island 7	11.8	215	30.5	64.8	6.2	238070.6	550637.1	7	86.4	57	3.8	32.8	309.9
Island 8	8.2	651	20.7	59.9	5.8	240649.9	550325.6	2	85.1	12	1.2	15.1	21.5
Island 9	14.9	968	28.8	95.6	6.5	247714.0	551508.1	-	-	-	-	-	-
Island 10	9.4	226	8.8	38.9	6.0	245372.2	545041.2	5	88.2	104	10.4	33.8	197.3
Island 11	10.4	124	38.2	52.4	6.4	240211.7	549484.5	-	-	-	-	-	-
Island 12	9.6	56	30.2	74.1	6.5	247020.3	545584.6	2	94.8	24	2.4	15.4	254.1
Island 13	12.8	553	18.8	46.8	6.3	246976.3	553235.9	-	-	-	-	-	-
Island 14	10.3	203	17.4	71.6	5.9	240899.0	554598.7	-	-	-	-	-	-
Island 15	13.6	135	23.6	59.6	6.5	235644.5	549211.3	-	-	-	-	-	-
Island 16	10.5	156	20.6	64.6	6.6	247155.4	544503.0	1	100	10	1	20.5	113.6
Island 17	9.8	181	16.0	57.8	5.7	235161.0	549582.4	-	-	-	-	-	-
Island 18	13.2	708	18.9	61.9	6.5	239953.0	550671.8	-	-	-	-	-	-
Island 19	10.3	34	37.5	55.0	6.6	240056.8	549609.6	-	-	-	-	-	-
Island 20	10.6	322	20.3	47.8	4.9	247147.7	553522.3	-	-	-	-	-	-
Island 21	10.5	66	23.9	56.7	6.5	248832.0	549560.1	-	-	-	-	-	-
Island 22	14.7	322	18.0	68.8	6.0	232704.5	550057.5	-	-	-	-	-	-
Island 23	14.9	200	27.9	57.0	6.5	237810.3	550712.0	-	-	-	-	-	-
Island 24	20.2	506	25.8	38.6	5.8	236282.5	548380.3	-	-	-	-	-	-
Total								29		1493			

[a] The beetle body size measure (product of the body length and elytra width) was used as a surrogate for body mass (see Chapter 5).

Appendix A. (continued)

	Human dung sampling				
Study site	**S_{obs} human dung**	**% Bootstrap Mean**	**S_{obs}' human dung**	**Total indiv.**	**Indiv./trap**
Mainland 1	26	89.8	25	466	20.3
Mainland 2	29	89.8	27	641	24.7
Mainland 3	34	89.3	32	1274	55.4
Island 1	19	92.1	18	849	35.4
Island 2	11	95.2	10	430	22.6
Island 3	15	93.3	14	592	23.7
Island 4	16	87.1	15	381	27.2
Island 5	14	88.2	13	155	10.3
Island 6	2	81.0	2	4	0.3
Island 7	12	89.2	11	305	25.4
Island 8	6	93.6	5	101	10.1
Island 9	5	80.6	5	48	2.1
Island 10	10	91.9	9	381	19.1
Island 11	13	85.2	12	263	8.2
Island 12	5	80.5	4	11	0.5
Island 13	3	86.0	3	18	0.7
Island 14	11	82.6	10	632	18.1
Island 15	2	80.3	2	4	0.1
Island 16	8	86.7	7	233	12.3
Island 17	3	73.5	3	3	0.1
Island 18	3	73.5	3	3	0.1
Island 19	15	87.9	14	67	2.2
Island 20	4	78.7	4	30	1.1
Island 21	7	81.3	6	58	2.1
Island 22	4	73.5	4	4	0.2
Island 23	7	81.6	7	164	4.8
Island 24	3	77.9	3	4	0.1
Total	49		47	7121	

Appendix B. Dung beetle species of Lake Kenyir and their traits, abundance and occurrence. Trait data are mainly available for species sampled using human dung (Chapter 2). Diel activity (D: diurnal; N: nocturnal). Guild (D: dweller; K: kleptoparasite; R: roller; T: tunneller). Functional group is based on body size, diel activity and guild, defined only for species sampled using cattle dung (LDR: large diurnal roller; LNT: large nocturnal tunneller; SDD: small diurnal dweller; SDR: small diurnal roller; SDT: small diurnal tunneller; Chapter 5). Diet breadth is the number of food types a species was attracted to in pitfalls (1: only dung; 2: both dung and carrion; Chapter 2). Forest edge (Yes: able to forage on forest edge; No: unable to forage on forest edge; Chapter 2). Baseline density is the average number of individuals per trap in the mainland forests using human dung as bait. Occurrence is number of sites a species was found out of a total of 27 sites during human dung sampling.

Species	Body size (mm^2)	Human dung	Cattle dung	Fish	Diel activity	Guild	Functional group	Diet breadth	Forest edge	Baseline density	Occurrence
Caccobius unicornis Fabricius	4.0	Yes	Yes	-	D	K	-	1	Yes	0.79	14
Catharsius molossus Linnaeus	377.2	Yes	Yes	Yes	N	T	LNT	2	No	0.71	10
Copris agnus Sharp	117.8	Yes	-	Yes	N	T	-	2	No	1.10	6
Copris doriae Harold	73.2	Yes	Yes	Yes	N	T	LNT	2	Yes	1.47	17
Copris haroldi Lansberge	98.8	Yes	Yes	-	N	T	LNT	1	No	0.15	2
Copris ramosiceps Gillet	64.5	Yes	-	-	N	T	-	1	No	0.03	3
Copris sp. 1	99.2	Yes	-	-	N	T	-	1	Yes	0.10	1
Copris sp. 2	73	Yes	-	-	N	T	-	1	No	0	1
Liatongus femoratus Illiger	38.7	Yes	Yes	-	D	T	SDT	1	Yes	0.06	9
Ochicanthon peninsularis Krikken & Huijbregts	16.0	Yes	Yes	-	-	R	-	1	No	0.01	2
Ochicanthon sp. 1	16	Yes	-	-	-	R	-	1	No	0	1
Onthophagus angustatus Boucomont	32.3	Yes	Yes	-	D	T	SDT	1	Yes	0.17	11
Onthophagus aphodiodes Lansberge	7.7	Yes	Yes	-	D	T	SDT	1	Yes	0.74	4
Onthophagus babirussoides	21.0	Yes	Yes	Yes	D	T	SDT	2	Yes	2.57	18
Onthophagus congerro	28.7	Yes	Yes	Yes	D	T	SDT	2	No	0.10	4
Onthophagus deflexicollis Lansberge	16.7	Yes	-	-	D	T	-	1	No	0	1
Onthophagus deliensis Lansberge	9.6	Yes	-	-	-	-	-	-	-	-	-
Onthophagus laevis Harold	21.0	Yes	Yes	-	D	T	SDT	1	No	0.03	1
Onthophagus leusermontis	19.6	Yes	Yes	Yes	D	T	SDT	2	Yes	1.54	12
Onthophagus ochromerus Harold	31.3	Yes	-	-	D	T	-	1	No	0.12	4
Onthophagus pedator Sharp	32.9	Yes	-	-	D	T	-	1	No	0.00	2
Onthophagus penicillatus Harold	51.7	Yes	-	-	D	T	-	1	No	0.03	1

Appendix B. (continued)

Species	Body size (mm^2)	Human dung	Cattle dung	Fish	Diel activity	Guild	Functional group	Diet breadth	Forest edge	Baseline density	Occurrence
Onthophagus peninsulotagal	21.3	Yes	-	-	D	T	-	1	No	0.01	3
Onthophagus pseudotaeniatus	20.4	Yes	Yes	-	D	T	SDT	1	No	0.13	6
Onthophagus quasiobscurior	22.4	Yes	Yes	-	D	T	SDT	1	No	0.45	11
Onthophagus rectecornutus	28.81	Yes	-	-	D	T	-	1	Yes	0.01	1
Onthophagus rorarius Harold	46.7	Yes	Yes	-	D	T	SDT	1	Yes	0.63	13
Onthophagus rudis Sharp	15.4	Yes	Yes	Yes	D	T	SDT	2	Yes	0.04	8
Onthophagus rugicollis Harold	26.6	Yes	-	-	D	T	-	1	No	0.07	4
Onthophagus rutilans Sharp	44.2	Yes	Yes	-	D	T	SDT	1	No	3.82	10
Onthophagus semicupreus Krikken & Huijbregts	-	-	-	Yes	-	-	-	-	-	-	-
Onthophagus semifex Krikken & Huijbregts	46.9	Yes	Yes	Yes	D	T	SDT	2	Yes	0.09	8
Onthophagus sumaveiensis	17.7	Yes	-	Yes	D	T	-	1	No	0.03	1
Onthophagus vulpes Harold	28.5	Yes	Yes	Yes	D	T	SDT	2	No	0.14	5
Onthophagus sp. 1	6.7	Yes	-	-	D	T	-	1	No	0.08	1
Onthophagus sp. 2	6.7	Yes	Yes	Yes	D	T	SDT	2	Yes	0.03	4
Onthophagus sp. 3	16.7	Yes	-	-	N	T	-	1	No	0.03	1
Onthophagus sp. 4	26.7	Yes	Yes	-	D	T	SDT	1	No	0	3
Onthophagus sp. 5	16.1	Yes	Yes	Yes	D	T	SDT	2	Yes	0.62	19
Onthophagus sp. 6	13.8	Yes	-	-	D	T	-	1	No	0.01	1
Onthophagus sp. 7	9.7	Yes	-	-	-	-	-	-	-	-	-
Onthophagus sp. 8	20	Yes	-	-	D	T	-	1	No	0	1
Onthophagus sp. 9	13.8	Yes	Yes	-	D	T	SDT	1	No	0	1
Onthophagus sp. 10	-	-	-	Yes	-	-	-	-	-	-	-
Oniticellus tessellatus Harold	28.33	Yes	Yes	-	D	D	SDD[a]	1	No	0	1
Panelus sp. 1	3.3	Yes	Yes	-	-	R	-	1	Yes	0.03	2
Paragymnopleurus maurus Sharp	113.6	Yes	Yes	Yes	D	R	LDR	2	Yes	12.36	21
Paragymnopleurus striatus Sharp	178.5	Yes	-	-	N	R	-	1	No	0.30	2
Pleuraphodius sp.	1.8	Yes	-	-	-	D	-	1	No	0.03	1
Sisyphus thoracicus Sharp	17.8	Yes	Yes	Yes	D	R	SDR	2	Yes	4.13	14
Yvescambefortius sarawacus Gillet	68.0	Yes	Yes	Yes	D	T	SDT	2	No	0.05	4

[a] Excluded from dung burial analysis in Chapter 5 because dwellers do not contribute to dung burial.