SPECIES RICHNESS AND ECOSYSTEM FUNCTIONING OF SOUTHEAST ASIAN DUNG BEETLE FAUNA

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I think it pisses God off if you walk by the color purple in a field somewhere and don't notice it.... People think pleasing God is all God care about. But any fool living in the world can see it always trying to please us back.

~Alice Walker, *The Color Purple*, 1982

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Summary

Over the last century, Southeast Asia lost almost half of its dipterocarp rainforests to anthropogenic activities, resulting in an increasingly common landscape of fragmented old growth forests and secondary re-growth from abandoned plantations or logged areas. Degradation of forest habitats has contributed to the loss of species and loss of ecological services performed by these species. Here, I focused on the impacts of anthropogenic disturbance on forest insect species and the ecosystem function they perform in tropical Southeast Asia. I used Scarabaeine dung beetles as my focal taxon as they are good ecological indicators of forest disturbance and perform well-defined roles such as nutrient recycling and secondary seed dispersal in tropical forest ecosystems. I first concentrated on the relationships between forest disturbance, dung beetle communities and dung removal in the forests of Johor (Peninsular Malaysia) and Singapore and addressed questions on (1) differences in species richness, abundance, and body size of dung beetle communities (2) dung beetle response to environmental variables along a gradient of forest disturbance and (3) dung removal function by dung beetles with increasing forest disturbance. Disturbed forest fragments in Singapore harboured dung beetle communities of lower species diversity and abundance, and with smaller body sizes, compared to the undisturbed, continuous forests of southern Peninsular Malaysia. My analyses revealed that dung beetle distribution was associated with shrub cover and three soil characteristics - pH, moisture and temperature. Furthermore, results from my dung removal experiment indicated that dung removal function decreased with increasing forest disturbance. These disturbance-mediated changes in dung beetle diversity and the ecosystem functions they perform highlight the urgent need to prioritize forest preservation in South-East Asia to ensure their long-term persistence. My second study focused on possible dung beetle extinctions on a small, isolated nature reserve in Singapore – the Bukit Timah Nature Reserve. I examined dung beetle species collected in the Bukit Timah Nature Reserve from the 1960s to 1970s and compared them with species collected from the same forest patch today. I employed two trapping methods – baited pitfall traps and flight interception traps for my survey. Out of the nine species collected from the past, three species – *Cartharsius molossus, Onthophagus deliensis* and *O. mentaweiensis* may be extinct. One of these species, *Cartharsius molossus*, a large-bodied dung beetle, plays an important role in nutrient recycling in the forest ecosystem. The possible extinctions of dung beetles within a span of 30 years in BTNR highlights the recurring events of species loss in Southeast Asian forests today and the need to preserve whatever remaining refuges of biodiversity.

Chapter 1. General Introduction

An estimated 27.2 million hectares of humid tropical forests were cleared between 2000 and 2005, representing a 2.36% reduction in the area of humid tropical forest (Hansen *et al.* 2008). Over one-third of this deforestation occurred in Asia. Forest clearing "hotspots" were increasingly prominent in insular Southeast Asia where forests were cleared to make way for agro-industrial purposes such as oil palm industries. Over the last century, Southeast Asia has lost almost half of its primary dipterocarp rainforests (Brooks *et al*. 1999), from anthropogenic activities including logging, subsistence and commercial agriculture, and urbanization (Sodhi & Brook 2006). The resulting landscape of fragmented old growth forests and secondary re-growth from abandoned plantations or logged areas are an increasingly common sight in the Southeast Asian tropics. Degradation of forest habitats have contributed to the loss of species, at rates comparable to those of massive extinctions in the past (Pimm & Askins 1995, Brooks *et al*. 1997, 1999). If deforestation rates in Southeast Asia continue unabated, the region could stand to lose up to a quarter of its total biodiversity over the next hundred years (Brook *et al.* 2003). Ecological studies on various taxa from insects (Liow *et al.* 2001, Koh & Sodhi 2004) to birds and mammals (Laidlaw 2000, Castelleta *et al.* 2005, Peh *et al*. 2005) in Southeast Asia have shown dramatic declines in species populations and richness following the conversion of forests to human-dominated landscapes. The impacts of altered species richness and composition may also lead to severe consequences on ecosystem processes such as primary productivity, nutrient cycling, decomposition, pollination and seed dispersal (Loreau *et al.* 2001, Hooper *et al*. 2002). Hence, it is imperative to study the ecological impacts of forest disturbance on Southeast Asia's tropical biotas.

The Republic of Singapore represents an extreme example of deforestation in Southeast Asia, having undergone major ecological transformations over the last two centuries. Singapore lost more than 95% of its original vegetation, first to cash crop cultivation during the British colonial rule and subsequently to urbanization due to industrialization and rapid development in the 1970s (Corlett 1991, 1992, Turner *et al.* 1994). The remaining forests in Singapore consist of a range of old-growth to young secondary forests, all of which have been exposed to human disturbance of varying intensities (Corlett 1997). The presence of a range of forest types in Singapore presents a natural laboratory where anthropogenic impacts on biodiversity have been examined and tested on different terrestrial taxa including plants (Turner *et al.* 1994), frogs (Ng 2007), moths (Koh 2007), butterflies (Koh & Sodhi 2004), bees (Liow *et al.* 2001) and birds (Castelleta *et al.* 2005). Singapore's biodiversity has been well-documented by amateur naturalists and professional biologists over a century, providing crucial historical documentation of the natural communities in Singapore, an important source of information for measuring species extinctions in the tropics (Brook *et al.* 2003). Therefore, the dramatic loss of forests in Singapore presents an opportunity to study the impacts of habitat disturbance in tropical humid forests (Corlett 1992, Brook *et al.* 2003).

Dung beetles comprise a small number of families in the superfamily Scarabaeoidae, of which the three main families are Scarabaeidae, Geotrupidae and Aphodiidae (Cambefort 1991a). The morphology of dung beetle mandibles reveals an evolution from saprophagy (humus, roots) to coprophagy (dung) (Cambefort 1991a). Because of the patchiness of such resources, competition within dung beetle communities is usually intense and this results in many species displaying resource specialization (Hanski & Cambefort 1991a, Peck & Forsyth 1982) and various physiological adaptations (Bartholomew & Heinrich 1978, Chown *et al.* 1995). Several dung beetle species specialize as phoretic beetles on mammals such as sloths and monkeys (Halffter & Matthews 1966, Jacobs *et al.* 2008) some live in nests or burrows where there is a constant supply of dung (Halffter and Matthews 1966) and others take advantage of dung from the canopy of forests (Gill 1991). In some cases, dung beetles may not feed on dung at all. *Onthophagus rouyero* Boucomont, may only feed on figs and not on dung at all (Davis & Sutton 1997). In Peru, *Deltochilum valgum* was shown to prey on live millipedes, using their modified mouthparts to decapitate their prey before feeding on them (Larsen *et al.* 2009). Dung beetles have also evolved certain thermo-regulatory features, which can increase their resource-finding capabilities. In the case of several Kenyan dung beetle species, the beetles were endothermic during flight, ball rolling and ball making (Bartholomew & Heinrich 1978). Higher temperatures allow for more effective flight activity by dung beetles and also enabled them to increase their speed of ball rolling. Dung beetles that survive in arid and dry areas like the savannahs have lipid-metabolizing capabilities to supplement body water and improve desiccation tolerance (Chown *et al.* 1995).

The use of Scarabaeine dung beetles as indicator taxon for tropical forest disturbance has been well studied in the last two decades (Klein 1989, Halffter & Favila 1993, McGeoch *et al*. 2002). Dung beetles have shown significant changes in species composition and community assemblage following forest fragmentation and habitat disturbances (Nichols *et al.* 2007), making them excellent biodiversity indicators for examining the responses of species communities to anthropogenic disturbance (Gardner *et al.* 2008a; Gardner *et al.* 2008b). Dung beetles are also ecologically valued for performing important ecosystem services such as dung removal (Klein 1989, Horgan 2005), secondary seed dispersal (Andresen 2002, Vulinec 2002), and biological control of vertebrate parasites (Doube 1986, Bishop *et al*. 2005). Dung pads have been described as useful model systems to study related diversity-function questions due to their ephemeral and patchy occurrence in natural surroundings (Finn 2001). Dung pads occur in natural environments as spatially and temporally delimited resources and such resource patches are easily manipulated, replicated and sampled in experiments (Finn 2001). Quantitative measurements of dung removal rates are logistically simple and are a reliable means of documenting changes in ecosystem processes in response to changes in dung beetle diversity (Klein 1989, Horgan 2005, Slade *et al*. 2007). The taxonomy of dung beetles is generally well established (Halfter & Favila 1993) and functional guilds of dung beetles are well defined by their method of manipulating dung, diel activity and body size (Doube 1990, Hanski & Cambefort 1991b, Feer & Pincebourde 2005). Thus in this study, I chose dung beetles to examine the impacts of anthropogenic disturbance on tropical forest biotas in two different aspects.

Species richness and ecosystem functioning of dung beetles.

The alteration of forests into human-dominated landscapes has led to dramatic changes in the biotic structure and composition of ecological communities, which can lead to major changes in the functioning of ecosystems (Hooper *et al.* 2005). The system of nutrient recycling through dung disposal by dung beetles is a useful model to study such questions in the natural world (Finn 2001). In Chapter 2, I report on dung beetle communities present in forests disturbed to varying degrees and identified the environmental variables that influenced the distribution of dung beetle communities. I then employed dung removal set-ups to test the level of dung removal rates in the different forest types and examined the relationships between forest disturbance, dung beetle diversity and dung removal rates.

Possible extinction of dung beetles in an isolated forest fragment.

The bulk of insect extinctions through tropical deforestation often go unnoticed due to lack of information and historical records of insects in the tropics (Dunn 2005). IUCN (International Union for Conservation of Nature) estimates of threatened insect percentages lie within the broad range of 0.07% to 50% (IUCN 2008), thus contributing to misleading estimates of insect species extinctions (McKinney 1993). Hence, historical documentation of species present in the past is valuable in calculating more accurate rates of insect extinctions in the tropics (Sodhi *et al.* 2009). In Chapter 3, I assessed the level of dung beetle extinctions in a small nature reserve in Singapore – the Bukit Timah Nature Reserve, by comparing dung beetle records from the 1970s to the present – 2008. Within the short span of thirty years, Bukit Timah Nature Reserve has undergone several disturbances caused by human factors and the absence of any dung beetles from the reserve may be a result of such human-induced disturbances.

As dung beetle ecology is not well studied in Southeast Asia, especially on the Malay Peninsula, I believe that my study may contribute to the scientific database of dung beetle taxonomy and ecology in this region. Such knowledge can be used to highlight the importance of dung beetles in the forest ecosystem and the need to preserve forests from further degradation by human activities.

Chapter 2. Species richness and ecosystem functioning of dung beetles[*]

2.1. Introduction

Research on ecosystem processes has largely focused on primary productivity and plant diversity (Chapin III *et al*. 1997, Finn 2001, Tilman *et al*. 2001, Loreau *et al*. 2002). The effects of disturbance-mediated changes in species communities on complex interactions between species are less well understood (Huston 1997 Schwartz *et al.* 2000, Loreau *et al*. 2001, Larsen *et al*. 2005). These effects may have important implications for the long-term persistence of forests and biodiversity in Southeast Asia, where human-dominated landscapes are becoming more prominent (Sodhi & Brook 2006). A good understanding of the relationships between human disturbance, biodiversity and ecosystem processes is urgently needed to improve the management of natural resources and inform land-use strategies and policies in the region. In this chapter, I aim to examine these relationships in naturally occurring communities of dung beetles along a gradient of forest disturbance in Southeast Asia.

The two most common forms of human disturbance to tropical forest habitats are habitat modification by human activities such as logging, agriculture or tourism, and fragmentation of natural habitats into smaller, isolated patches within a matrix of modified habitats (Turner 1996). The influence of habitat modification on dung beetle communities leads to a reduction in species richness and body size, and smaller fragment sizes show increased dominance and lower species richness and abundance (Nichols *et al.* 2007). Previous studies on the effects of forest modification on dung beetles show lower species richness and/or abundance (Howden & Nealis 1975, Klein 1989, Scheffler 2005). Larger dung beetles that use larger amounts of dung resources

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(Doube 1990) are also shown to be more susceptible to population declines following conversion of primary rainforests to secondary or plantation forests (Gardner *et al.* 2008a). Some studies show that changes in dung beetle species richness by anthropogenic disturbances result in reduced rates of dung burial (e.g. Klein 1989, Larsen 2005) and seed burial (e.g. Andresen 2003).

Research on dung beetle ecology in tropical rainforests has largely been concentrated in the Neotropics (see Nichols *et al*. 2007 and references therein) and relatively less so in Southeast Asia (Hanski 1983, Davis *et al*. 2001, Boonrotpong *et al*. 2004, Shahabuddin *et al*. 2005, Slade *et al*. 2007). How human modification of forest habitats affect local dung beetle communities and subsequent ecological services is still relatively unknown (but see Slade *et al*. 2007). No known study has been published on dung beetle ecology from the Malay Peninsula. In this study, I address the following questions:

a. Are there differences in dung beetle communities, in terms of species richness, abundance, and body size, between disturbed and undisturbed forest sites? I test the hypothesis that old growth forests contain dung beetle communities of higher species richness and abundance, and with bigger body sizes.

b. Do dung beetles respond to any environmental variables along a gradient of forest disturbance?

c. Is dung removal function affected by forest disturbance? I test the hypothesis that dung removal activity of dung beetles is reduced in more disturbed forests compared to less disturbed forests.

2.2. Materials and Methods

2.2.1. Study sites

My study location is in southern Peninsular Malaysia (latitude 1º38’N, longitude 103º40’E), and includes four forest fragments on the main island of Singapore, two on the offshore island of Pulau Ubin, Singapore and two continuous forests in the Malaysian state of Johor. Deforestation over the last 200 years in Singapore has removed over 95% of its original vegetation, leaving behind a mosaic of forest fragments that has been modified by humans to varying extents (Corlett 1992). Since all forests in Singapore have been subjected to human disturbance, I selected two continuous forest sites from the nearest state of Johor in Peninsular Malaysia to represent a baseline for dung beetle communities. Peninsular Malaysia and Singapore are part of the shallow Sunda Shelf (Voris 2000), and share similar biogeographic history and pre-colonial biotic communities (Brook *et al*. 2003). However, there have also been suggestions that there is a lack of historical records of similar mammalian fauna between Singapore and Peninsular Malaysia (Corlett 1988), which may subsequently affect the type of dung beetle community present in both sites. Considering that Singapore is an island-state, there is also a possibility that lower species richness may occur due to the ‘island effect’. Nevertheless, Peninsular Malaysia remains the best comparable site for this study and one has to interpret the results of this study in light of the above-mentioned assumptions.

The eight sites established (Fig. 1) represent a range of tropical lowland dipterocarp forests with varying levels of human disturbance. I estimated the level of disturbance of individual sites by considering the forest type, the impact of human modification on the forest based on past and present land use by humans, as well as the level of forest fragmentation based on the area, corrected perimeter to area ratio (Patton 1975) and matrix quality around the sites (Table 1). Sites were ranked with increasing level of human disturbance from 1 to 4. Reference sites in my study were from Belumut and Bekok, the last remaining pristine forests in Johor, southern Peninsular Malaysia. The two old growth forest sites were continuous lowland and hill dipterocarp forests, which had never been logged. Based on the presence of dung samples in the forest and local knowledge from the guides, these forests still retained most of their mammalian fauna such as the Malayan tapir *Tapirus indicus*, Wild boar, *Sus scrofa*, Pig-tailed macaque *Macaca nemestrina*, Sambar deer *Cervus unicolor* and the Tiger *Panthera tigris*. Sites from Singapore contained a more depauperate mammalian fauna, consisting of mostly small to medium sized mammals such as the Long-tailed macaque *Macaca fasicularis*, Wild boar *Sus scrofa*, Plantain squirrel *Callosciurus notatus* and Common treeshrew *Tupaia glis* (Teo & Rajathuran 1997).

2.2.2. Dung beetle sampling

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae, Aphodiinae) were sampled using pitfall traps (7 cm diameter, 9 cm depth) buried flush with the ground and baited with *ca*. 20 g of fresh cattle dung, collected from the Singapore Zoological Gardens. Baits were suspended 5 cm from the mouth of the traps using a piece of twine tied to a 20 cm wooden skewer and were covered with a large leaf that acted as a rain cover. Cattle dung was kept for a maximum of 4 days for dung beetle trapping. Each trap was filled with a mixture of detergent and saturated salt solution (25%, v/v). Depending on the area of the site, two to six standard-length transects (120 m) were randomly located at least 200 m apart at each site (Table 1). Five traps were placed at 30 m intervals along each transect. Trapping was conducted over three cycles at each site between 3 September 2007 and 13 March 2008. Each trapping cycle was conducted over a month and was carried out before, during and at the end of the Northeast monsoon season, which occurs from December to March (NEA 2008). A different set of transects was randomly sited during each sampling cycle (Table 1). Although my study transects were sited at least 200 m apart, I recognize that I could not exclude the possibility that transects and sites are not statistically independent from one another. In my data analysis, I minimize the potential effects of pseudo-replication by including "site" and "transect" as control factors in my models (see Data analysis).

Traps were collected after 48 hours in the field. Captured dung beetle individuals were preserved in 100% ethanol, and were processed and identified in the laboratory. Where individuals could not be identified, a series of morphospecies numbers were assigned to the genus. The mean body length of each dung beetle species was measured from 10 randomly selected individuals using a ruler (± 0.1 cm). To obtain the mean biomass of each dung beetle species, up to 10 individuals of each species were dried in an oven for three days at 70°C, until constant weight of beetles was achieved. Each individual was weighed on an electronic balance accurate to ± 0.001 g. For species that had less than 10 individuals caught, all individuals caught were measured and weighed. For species that were too small to register on the weighing scale, their collective biomass was taken and an average weight was used. Dung beetle species were also assigned to functional guilds according to their size (large beetles ≥ 10 mm or small beetles < 10 mm) and manner of dung manipulation (roller, tunneller or dweller; Hanski & Cambefort 1991b). Rollers (telocoprids) form balls of dung, which are rolled away from the source and buried for nesting purposes. Tunnellers (paracoprids) construct tunnels directly under the dung source and supply dung into the tunnels for nesting. Dwellers (endocoprids) do not move away from the dung source, but rather, stay inside the dung pad and utilize the dung for feeding or nesting purposes. All specimens collected are deposited at the Raffles Museum of

Biodiversity Research (RMBR) in the National University of Singapore and the Leiden Natural History Museum Naturalis, Netherlands (RMNH).

2.2.3. Environmental variables

To determine whether environmental characteristics influence dung beetle species distribution, the following variables were measured at every sampling unit (i.e. at 30 m intervals) along each transect: temperature and humidity point readings, using a digital thermohygrometer (Control Company Traceable$^{®}$ Humidity/Temperature Pen) and soil temperature, moisture and pH readings using a soil thermometer (Forestry Supplies Inc.) and soil probe (Kelway$^{®}$ Soil pH and Moisture Meter). The following vegetation characteristics were also measured within a circular plot with a radius of 5 m from every sampling point: i) canopy cover of the forest using a spherical densiometer (Lemmon 1957), ii) the number of dead trees and palms as a representation of the vegetation structure of the forest, iii) percentage ground and shrub cover by visual estimation and iv) leaf litter depth, the average of five random points measured using a metal ruler. The subsequent characteristics were only measured at the first, third and fifth sampling point along each transect: diameter at breast height (dbh) and total number of trees. Values of habitat environmental variables were averaged for each transect.

To observe how habitat disturbance influence the climatic conditions in the forests, correlation tests between environmental variables and habitat disturbance were carried out using R statistical software (R Development Core Team 2008). Mean environmental values for each transect were tested for normality and subjected to Pearson's product-moment correlation test. Variables that did not follow a normal distribution were tested using both Kendall's rank correlation and Spearman's rank correlation tests.

2.2.4. Dung removal experiments

Dung removal experiments were conducted twice (3 September to 7 October 2007 and 31 January to 13 March 2008) using standardized dung piles to determine if dung removal activity varied across a gradient of disturbance. Depending on the area of the site, two to six transects of 90 m each were set up (Table 1). Transects involved in dung removal experiments were used for dung beetle sampling a day later to detect dung beetle species which were closely associated in the removal of dung. Three dung piles were placed at 30 m intervals within a transect and transects were separated from each other by 200 m. Standardized dung piles were made with *ca*. 50 g of fresh cattle dung using a container (7 cm diameter, 4 cm depth). At each experimental set up, a pair of dung piles were placed 10 cm apart and were subjected to either of these two treatments: (1) caged dung pile covered with a 2 mm by 2 mm green netting to exclude the smallest dung beetle from entering and (2) exposed dung pile without netting to allow complete access to dung beetles. The dung piles were left under a rain cover in the field and collected after 24 hours. Any dung beetles found were removed by hand and dung piles were subsequently air-dried for a week before being oven-dried until constant mass was achieved. Dung piles were weighed using an electronic balance accurate to ± 0.01 g. Mass loss of dung was a better representation of dung removal compared to visual estimations (Klein 1989, Larsen *et al*. 2005) as some of the dung piles were largely colonized by small tunnellers (*Onthophagus* sp.) in Southeast Asia rainforests and visual estimations on the effect of their removal are not as easily characterized compared to rollers typically found in the Neotropics.

2.2.5. Data analysis

I collected dung beetles from both dung baited pitfall traps and the experimental dung pads. I selected dung beetles captured only from dung baited pitfall traps for data analysis on species richness, abundance, biomass and body length among sites, hierarchical cluster analysis and non-metric multidimensional ordination techniques. Dung beetles collected from my pitfall traps provided a better representation of the dung beetle community in sampling locations as both diurnal and nocturnal beetles could be sampled from this method. Dung beetles collected from dung pads were used only in the analysis of dung removal experiments.

Mean values for dung beetle abundance and species richness per transect were compared across all study sites and tested for any significant differences using the Kruskal-Wallis (KW) test. The mean values were ranked and Duncan's multiple range test was used to determine which sites were different from the rest. To compare body size of dung beetles across sites, I applied the same analysis to total biomass per transect and mean body length of beetle per transect.

Species richness was computed using a binomial mixture model (Colwell 2005), and any heterogeneity or patchiness in the sample data was removed by averaging the values over repeated randomizations (Gotelli & Colwell 2001). Nonparametric species richness estimators were generated to estimate the total number of species undetected by the surveys. An average of the estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap) was used as a measure of the species richness in each habitat, accounting for species that may have not been detected using my sampling techniques. Values for species richness and nonparametric estimators were generated using EstimateS version 8.0 (Colwell 2005). Species diversity indices (Fisher's alpha, Shannon index and Simpson index) were calculated to obtain a measure of dung beetle community diversity and evenness among sites. Species diversity indices were calculated using Primer version 5.0.

I used non-metric multidimensional scaling (NMS) to determine how dung beetle species respond to various environmental variables (e.g. soil moisture) along a disturbance gradient. NMS is an indirect gradient analysis that uses information from biotic communities to represent the environmental conditions (McCune & Grace 2002); contrary to other methods (e.g. canonical correspondence analysis; ter Braak 1986), which select biologically relevant environmental variables prior to analysis (Beal 1984). Since NMS is an indirect analysis and selects the environmental variables using species community information, environmental variables were not subjected to Pearson's correlation prior to analysis. Species and abundance data for each transect were used as the primary matrix for NMS analysis and NMS ordination was performed on PC-ORD version 4.14 (McCune & Mefford 1999) using the "autopilot (slow and thorough)" mode and Sorensen distance as a dissimilarity measure. NMS utilizes this information to conduct a computational-intensive iterative optimization of the best orientation of *n* objects (transect samples) on *k* dimensions (axes) which minimizes the divergence from monotonicity in the association between the actual dissimilarity data of the *n* samples and the diminished *k*-dimensional ordination space of these samples (McCune & Grace 2002). The next step of this analysis utilizes 16 environmental variables of each transect (ambient and ground temperature, ambient and ground humidity, canopy cover, ground and shrub cover, palm density, soil temperature, pH and moisture, number of dead trees standing and on the ground, leaf litter depth, tree density and average dbh of trees) by correlating each variable to the two axes of the final optimal two-dimensional ordination space. The positions of samples along the ordination axes are therefore explained by the Spearman correlation coefficients of each environmental variable. Significantly correlated ($R > 0.50$) environmental variables were retained and plotted together with the sample and species scores as vectors to show their influence on the biotic communities.

To investigate dung removal rates in different habitats, a set of four candidate models were generated representing competing hypotheses to explain variations in dung biomass along the disturbance gradient (1 to 4):

Null model: There is no relation between dung biomass and degree of habitat disturbance or experimental treatment.

Model 1: Dung mass is affected by disturbance, treatment, as well as the interaction between disturbance and treatment.

Model 2: Dung mass is affected by disturbance and treatment, but there is no interaction effect.

Model 3: Dung mass is affected by disturbance only.

All candidate models were fitted to the data as generalized linear mixed-effects models (GLMM) using the lmer function in the R statistical software, assigning each model a normal error distribution and an identity link function. Candidate GLMMs were fitted by coding dung mass ($\log_{\text{natural}}$-transformed) as the response variable, and various combinations of disturbance (ordinal variable) and treatment (either caged or exposed) as fixed effects in the linear predictor. Each candidate model also includes beetle biomass ($\log_{\text{natural}}$-transformed) as a continuous control variable, as well as site, transect (nested in site) and sampling cycle as random effects.

The first step of the model selection procedure was to calculate the Akaike's information criterion corrected for small sample sizes (AIC_c) for each candidate model. The AIC_c is an estimate of the relative Kullback-Leibler (K-L) distance between each fitted model and the unknown true mechanism that generated the data. Next, the Akaike weight and McFadden's pseudo-R^2 were calculated for each model. The Akaike weight reflects the weight of evidence in support of a particular model relative to the entire model set, and varies from 0 (no support) to 100% (complete support). The McFadden's pseudo-R^2 of each candidate model reflects the additional variance explained by the fixed effects (i.e. predictor variables of interest), compared to the null model (which only includes the random effect). The candidate model with the highest Akaike weight was selected as the K-L most parsimonious model.

2.3. Results

A total of 1 604 individuals and 44 species of dung beetles using dung baited pitfall traps were captured from three sampling cycles. The three most abundant species in the eight sites combined were *Sisyphus thoracicus*, *Onthophagus rorarius* and *O.* sp. 16 with 349, 245 and 205 individuals, respectively. *Copris doriae* and eight other species of *Onthophagus* were found in the baited pitfall traps only once during the collection period. Dung beetles that occurred in three or more of the study sites include *Onthophagus* sp. 2, *O. crassicollis*, *O.* sp. 10, *O.* sp. 11 and *Paragymnopleurus maurus*. Dung beetles hand collected from dung pads amounted to 561 individuals from 35 species. Beetle species collected from dung pads yielded eight more beetle species that were not found in dung traps including *Oniticellus pictus*, *Onthophagus* sp. 1, *O.* sp. 6, *O.* sp. 14, *O.* sp. 15, *O. phanaeides*, *O.* sp. 3 and *O. batillifer*. Out of these eight species, only *O. phanaeides* and *O.* sp. 1 have more than one specimen collected (see Appendix).

Among the eight study sites, Bekok had the highest mean number of species and mean number of individuals and MacRitchie had the lowest mean number of species and mean number of individuals in baited pitfall traps within a single transect

(Figs 2a and 2b). Mean number of individuals and species collected per transect differed significantly among sites (KW = 70.31, df = 6, $P < 0.0001$ and KW = 71.06, df = 6, $P < 0.0001$, respectively). Duncan's multiple range tests showed that the mean number of species and individuals per transect was significantly higher ($P < 0.0001$) in Malaysia compared to Singapore sites and showed no significant differences among Singapore sites (Table 2). There were no dung beetles caught at Kent Ridge, Singapore. The total biomass of dung beetles per transect followed a similar trend with mean number of species and individuals across sites. Mean body length of dung beetles in Malaysia sites were significantly higher than Singapore sites. Among the sites in Singapore, dung beetles from Lower Pierce had a significantly higher mean body length compared to the rest of the Singaporean sites (Table 2).

2.3.1. Dung beetle species diversity

Based on species diversity indices calculated (Table 3), the site with the most diverse dung beetle community was Belumut, an old growth, continuous forest. Species richness for both Bukit Timah and MacRitchie, tall secondary forests in Singapore, were comparable to Pulau Ubin Plantation forest, a former rubber plantation (Table 3). These three sites had the lowest species diversity. Sampling coverage varied from 59.91% in Pulau Ubin secondary forest to 99.57% in Bukit Timah forest (Table 3). Dung beetle species diversity in individual sites were calculated using only beetles collected from baited pitfall traps. However, there are some disparities in the dung beetles caught using baited pitfall traps and dung pads, e.g. dung pads in MacRitchie yielded 6 species and 207 individuals of dung beetles compared to just 1 species and 1 individual from traps. There are obvious limitations to the dung beetle sampling employed in this study, which will be addressed later.

2.3.2. Dung beetle response to environmental variables

Among the 16 environmental variables, nine variables were correlated with habitat quality (Table 4). These include ambient temperature, percentage ground and shrub cover, palm density, soil temperature, soil pH, soil moisture, number of dead trees on the ground and leaf litter depth. All variables, excluding ambient temperature, soil temperature and number of dead trees on the ground, showed negative correlations with increasing habitat disturbance (Table 4).

The first and second axis of the NMS ordination explained 25.4% and 24.9% of variation within the datasets, respectively. Dissimilarities in species composition between two transects are reflected in the distances between them in the ordination of sample scores. Grouping of transects based on their habitat type show a distinction between the old growth, continuous sites (Forest type 1) and the rest of the forest types (Fig. 3a). Graphical overlay of functional groups of dung beetles show the predominance of large tunnellers associated with transects from old growth, continuous forests and a single large roller, *Paragymnopleurus maurus* (sp38) and three small tunnellers, *Onthophagus crassicollis* (sp15), *O.* sp. 11 (sp23) and *O.* sp. 12 (sp25), associated with the forests of Singapore (Fig. 3b). Among the 16 environmental variables used, shrub cover, soil temperature, soil pH and soil moisture showed strong correlations ($R > 0.50$) with dung beetle species distribution. Transects from old growth, continuous forest types and species (e.g., sp39, *Sisyphus thoracicus*, sp11, *Onthophagus aphodiodes*, sp42, *O.* sp. 18) in the upper right quadrant were positively correlated with shrub cover and soil moisture. Transects from old growth forest types and species (e.g., sp2, *Caccobius unicornis* and sp1, *Aphodius* sp.1) in the upper left quadrant were positively correlated with soil pH (Fig. 3a and Fig. 3b). Transects from forest types 2, 3 and 4 and species sp15, *Onthophagus crassicollis*, were correlated with soil temperature.

2.3.3. Dung removal and habitat disturbance

The most parsimonious model for explaining variations in dung biomass along the disturbance gradient includes disturbance, treatment and their interaction effect (Table 5; Fig. 4). This model accounted for 91.6% of the Akaike weights in the model set and explained 9.8% of variations in dung biomass. This model is described by the following equation:

$$\log(\mathrm{D.BIOMASS})=2.763-0.193\times\mathrm{DISTURB}-0.997\times\mathrm{TREAT[exposed]}$$
$$+0.242\mathrm{DISTURB}*\mathrm{TREAT[exposed]}+0.597\times\mathrm{B.BIOMASS},$$

whereby D.BIOMASS is dung biomass, DISTURB is disturbance rank, TREAT[exposed] is exposed treatment, and B.BIOMASS is beetle biomass. In this model, disturbance affects dung piles according to the treatment they had been subjected to (i.e. exposed or caged) and the difference between these two treatments provides us with an estimate of the dung removal function performed by the dung beetle community in each forest habitat. This fitted model shows that there is an increase in dung biomass in exposed treatments with increasing disturbance, which suggests a lower proportion of dung removed in disturbed habitats (e.g., Pulau Ubin Secondary) compared to less disturbed habitats (e.g., Belumut) (Fig. 4). The model also indicates a decrease in dung biomass in caged treatments with increasing disturbance, suggesting that the rate of dung decomposition likely increase with increasing disturbance (Fig. 4).

2.4. Discussion

2.4.1. Dung beetle communities in forests of varying disturbance

The results from my study demonstrate that human disturbance on forested habitats result in depauperate dung beetle communities. The negative influence of forest disturbance on insect diversity has also been shown in several other taxonomic groups in the tropics (Holloway *et al*. 1992, Hill *et al*. 1995, Lawton *et al*. 1998 Schulze *et al*. 2004, Beck *et al*. 2002, Koh & Sodhi 2004). My results show a great contrast in the level of dung beetle diversity and abundance between the old growth, continuous forests and the modified forest fragments in Singapore. Within the disturbed forest types, there was no significant difference in dung beetle diversity and abundance. The effectiveness of my bait, cattle dung, may have led to exclusion of other dung beetle species that are more specialized in omnivorous dung. However, I assume my comparisons of dung beetle communities to be fair as the type and amount of dung used throughout the study was standardized.

The general consensus from several studies conducted in the region suggests that dung beetle species richness and abundance in disturbed forests is lower than that of undisturbed forests (Davies *et al*. 2001, Boonrotpong *et al*. 2004; Shahabuddin *et al*. 2005). Davies *et al*. (2001) found a graded response in species diversity to forest disturbance in Danum Valley (Sabah, Malaysia) whereby dung beetle species richness was highest in old growth forests, followed by logged forests and finally plantation forests. A study by Shahabuddin *et al.* (2005) in Sulawesi (Indonesia) found that abundance and species richness was also highest in natural, least disturbed forests, but did not differ significantly in young secondary forests and agroforestry systems, a result similar to my study.

The impoverished mammalian fauna in Singapore forests compared to Malaysian contiguous forests may be the result of a lack of dung from mid- to large-size mammals as the general abundance of such mammals decline with forest loss, fragmentation and isolation (Laidlaw 2000). The only mid-size mammals still occurring in the forests of Singapore are the Wild boar *Sus scrofa* and the Long-tailed macaque *Macaca fasicularis*. Although there is reason to believe that the depauperate dung beetle community in Singapore may be the result of reduced mammalian abundance (Nichols *et al*. 2009), the result may also be attributed to the 'island-effect' as mentioned earlier. Hence, these results are to be interpreted cautiously.

2.4.2. Biomass and body length of dung beetles

The decline in mean values of biomass and body length of dung beetles from primary continuous forests to other disturbed forest types, is consistent with results from Scheffler (2005) and Gardner *et al*. (2008a) showing that larger body sized beetles are more susceptible to population declines due to increasing disturbance, compared to smaller bodied beetles. Including traits such as biomass and body length in data analysis is useful in complementing abundance data on dung beetles as they provide more ecological understanding on the loss of species due to habitat changes (Peck & Forsyth 1982, Gardner *et al*. 2008). Larger bodied beetles may be more susceptible to changes in environmental conditions that follow drastic habitat alterations. My study showed an increase in ambient temperature and a decrease in ground and shrub cover as forest disturbance increased (Table 4). Large dung beetles dissipate excess heat slower (Bartholomew & Heinrich 1978) so that they have a competitive foraging advantage over other beetles due to higher body temperatures. However, such an advantage only persists in a cool, humid forest and quickly becomes a disadvantage in a hotter and drier climate, characteristic of disturbed forest habitats (Chown 2001).

Environmental correlations from my study show that soil temperature increases and soil moisture decreases with increasing disturbance (Table 4). This trend in low soil humidity may be disadvantageous for large dung beetles as high soil humidity is suggested to be important for these beetles to burrow deep underground nests (Anduaga 2004) as well as prevent desiccation of their larvae in the soil (Fincher

1973). Apart from microclimatic differences, it is hypothesized that large dung beetles are attracted to bigger dung piles (Peck & Howden 1984) as they consume a much greater proportion of dung resource (Doube 1990, Larsen *et al*. 2005). The lack of large mammals in disturbed forest habitats in Singapore could have led to a shortage of resource and consequently, reductions in the large bodied dung beetle populations (Gardner *et al*. 2008).

2.4.3. Response of beetles to environmental variables

Previous studies have shown that dung beetle distributions may be influenced by environmental factors such as tree cover (Halffter & Matthews 1966, Halffter & Arellano 2002) and soil characteristics (Fincher 1973, Vessby & Wiktelius 2003). From my results, shrub cover, soil temperature, soil moisture and soil pH appear to have significant influence on the dung beetle communities found in forest transects (Fig. 3a). All four variables have also been shown to correlate with increasing habitat disturbance (Table 4). Shrub understory (0.5 m - 1.5 m above ground) is an important habitat for dung beetles, which exhibit leaf-perching behavior (Davis 1999). Medium to small sized dung beetles perch on leaves to regulate body temperatures (Young 1984) and leaf-perching has been postulated to function as a form resource partitioning (Howden & Nealis 1978) and even a predator-avoidance strategy (Young 1982). I did not record any observations of beetles perching on leaf surfaces in Peninsular Malaysia and Singapore, though there have been records of perching behavior by dung beetles from Borneo (Davis 1999). Studies on soil characteristics on dung beetles have typically focused on soil moisture (Fincher 1973, Anduaga 2004) as well as soil type (Doube 1983, Davis 1987, Osberg *et al*. 1994), both of which can be explained through physiological and oviposition behavior of dung beetles. Soil moisture is especially important for ensuring that larvae of large bodied beetles do not dry up too quickly (Anduaga 2004). My analysis shows soil moisture and soil pH to be closely related to transects from forest type 1. Soil pH is a novel environmental characteristic to be related to dung beetle diversity. Only one beetle, *Ochicanthon neglectus*, has been associated with alkalinity and are found only in limestone areas (Hanski 1983). A study by Bertone (2004) mentioned how increase in dung beetle activity has a positive effect on soil pH and cation exchange capacity of soils. Currently, no research has been conducted on how the acidity or alkalinity of the soil may affect dung beetles.

2.4.4. Dung removal in disturbed forest habitats

Dung removal and subsequent mixing with the soil layer by dung beetles for breeding and feeding purposes is the first step towards critical ecosystem services such as nutrient recycling, bioturbation, plant growth enhancement, secondary seed dispersal and parasite suppression (Nichols *et al*. 2008). The process of dung removal by dung beetles has shown to decrease with increasing fragmentation and disturbance of forests in the Neotropics (Klein 1989, Horgan 2005). My results support similar findings in previous studies and suggest that forests with greater disturbance have lower dung removal function performed by dung beetles (Fig. 4). The species richness, abundance and body size of dung beetle communities decreased strongly from old growth, continuous forests (forest type 1) to the other forest types (2, 3 and 4) and it is likely that this alteration in dung beetle communities resulted in a significant difference in dung removal function between undisturbed and disturbed forests. The old growth continuous forests also support a greater variety of large tunneller species (*Cartharsius molossus, Copris agnus, C. doriae, C. haroldi, C. ramosiceps*) (Fig. 3b and Appendix), which play an important role in providing ecosystem services as they have been shown to contribute up to 75% of dung removal function in tropical dipterocarp forests (Slade *et al*. 2007). Altered dung beetle communities in disturbed forests may result in a change in ecosystem services provided by dung beetles during the process of dung removal. In relation to parasite suppression, a study in Peru demonstrated that dung beetles reduced the number of flies emerging from dung pads in forested compared to deforested areas (Horgan 2005). In Brazil, a study on secondary seed dispersal by dung beetles found that a significantly higher proportion of seeds were buried by dung beetles in continuous forests than in forest fragments for two of the three seed species but did not show any significant difference in the number of seedlings established among forest sites (Andresen 2003). Research on the effects of human disturbance on dung beetle-mediated ecosystem services is still much needed and will be a very useful model for us to examine the importance of biodiversity to ecosystem functions in natural surroundings.

From my results, I also observed a more than expected decline in predicted dung mass of caged dung piles along the disturbance gradient (Fig. 4). It is important to note that my optimal model explains only 9.8% of the overall variation in observed dung mass, hence I am cautious in interpreting the absolute model predictions. Caged dung piles in disturbed forests may be exposed to warmer and drier conditions compared to undisturbed forests and the differences in drying rates, temperatures and light intensities may have an effect on the biochemical processes involved in dung decomposition and influence the level of demineralization and decomposition (Horgan 2002). However, most research on the decomposition process of dung has been carried out in pasture systems and not in disturbed forests (Buschbacher 1987, Herrick & Lal 1996, Dickinson *et al*. 1981) and a basic understanding of the breakdown of dung in tropical forest can be looked into for future studies.

2.4.5 Caveats

The major drawback of my study is the unusually poor catch of dung beetles from the baited pitfall sampling. Dung beetles appear to be caught in different number of species and abundance using baited pitfall traps and from the dung pads collected (e.g., MR, LP and PUP under Appendix). I am apprehensive of the numbers collected using baited pitfall traps as they reflect a rather inaccurate picture of the dung beetle species richness and abundance especially in the forest fragments of BT and MR (Forest type 2). A separate study (see Chapter 3) involving 100 g of cow dung as bait in baited pitfall traps and flight intercept traps in BT caught 19 species and up to 800 individuals of dung beetles between the months January to March 2008 (after the third round of sampling for this study). Despite this major drawback in my study, I base my comparisons and conclusions of dung beetle diversity and ecosystem functioning on standardized methods employed throughout the study and across all sites. Another drawback of my study is the use of cattle dung as bait and results for this study may be very different if human or monkey dung was used instead. Nevertheless, I assume that comparisons of dung beetle communities across sites are reasonable due to the standardized dung type used in my experiments.

2.4.6. Conclusion

My results demonstrate that disturbed forest fragments of Singapore, whether primary or secondary forests, harbor depauperate dung beetle communities in terms of species diversity and abundance compared to the undisturbed, continuous forests of southern Peninsular Malaysia. Larger bodied dung beetles collected in this study were mostly confined to primary continuous forests in Malaysia, with the exception of *Paragymnopleurus maurus*, a large roller still present in disturbed forest fragments of Singapore. The impacts of human disturbance on dung beetles in Southeast Asian forest may be attributed to the change in environmental variables in the forest following disturbance. Another possible explanation is the lack of dung resources as these forests become less suitable to support medium to large sized mammal populations. My study also shows a reduction in dung removal function between undisturbed and disturbed forests, illustrating the effect of human disturbance on ecosystem functions through the alteration of dung beetle communities. The drastic reduction in dung beetle biodiversity and the resulting impact on ecosystem functions due to human disturbance highlights the need for prioritizing the preservation of primary continuous forests in Southeast Asia.

Chapter 3: Possible extinctions of dung beetles[*]

3.1. Introduction

Tropical forest loss and degradation by human activities continue to threaten earth's biodiversity (Brooks *et al*. 2002, Brook *et al*. 2003, Sodhi *et al*. 2007). This loss of forest habitats may lead to an unprecedented level of species extinctions as forest loss continues to accelerate in the most biodiverse regions (Myers *et al*. 2000, Pimm & Raven 2000). The extinction of forest dwelling fauna has been better studied for more charismatic and larger mammal and bird species compared to insects (Dunn 2005) despite the fact that more than 57% of described living species are insects (Stork 1997, IUCN 2008) and that insects perform critical roles in the ecosystem (Didham *et al*. 1996). The lack of assessment of insect survivability has led to broad estimations of the percentages of threatened insects between 0.07% and 50% (IUCN 2008). Hence the lack of insect knowledge especially in highly threatened tropical forests may contribute to misleading levels of insect extinctions occurring (McKinney 1993). Previous assessments of insect extinctions were often carried out at a local scale, in island systems or isolated forest reserves with a history of biodiversity inventories (Brook *et al*. 2003, Thomas *et al*. 2004, Hanski *et al*. 2007, Sodhi *et al*. 2009). An example is the fauna of Singapore, which has been well studied since 1819 by British natural historians. In Brook *et al*. (2003), insects such as butterflies have a similar extinction rate of 38% as compared to commonly studied taxa such as mammals (43%), birds (34%) and vascular plants (26%).

Here, I aim to determine the possible extinctions of dung beetles (Coleoptera: Scarabaeinae) from a small isolated forest fragment, Bukit Timah Nature Reserve

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(hereafter BTNR), Singapore, by comparing historical documentation of dung beetles from the 1960s to 1970s with an intensive collection carried out in present day. The reduction of forest size and its isolation from a larger tract of forest can result in the decrease in middle to large sized mammal populations (Corlett 1992, Laidlaw 2000). This decline in mammalian populations may have cascading effects on animals such as dung beetles, which are generally reliant on mammalian dung for nutrition and nesting (Cambefort & Hanski 1991). Hence, dung beetle species richness and abundance can be used as a possible indicator of mammal populations in a forest habitat (Andresen & Laurance 2007). A review by Nichols *et al*. (2008) also show that dung beetles perform a myriad of ecological processes such as nutrient recycling (Yokoyama *et al*. 1991), controlling pest populations (Bornemissza 1970) and secondary seed dispersal (Andresen & Feer 2005), emphasizing the usefulness and importance of dung beetles in ecosystems. Based on the list of beetles from the 1960s to 1970s, I aim to determine the absence or presence of each individual species and find out if there has been any apparent extinction of dung beetles in BTNR over the last 40 years.

3.2. Materials and Methods

3.2.1. Study site

The Republic of Singapore is a highly urbanized city-state at the southern tip of the Malay Peninsula (1°14N, 103°55E). Rapid deforestation in Singapore occurred in two phases, firstly the cultivation of cash crops which was completed by the end of the nineteenth century and secondly, urbanization which led to rapid development and economic success to the country (Corlett 1992). Much of Singapore’s original vegetation has been cleared and the largest remnant of primary hill dipterocarp rainforest lies in the Bukit Timah Nature Reserve (Corlett 1992). The total size of

BTNR is 163 ha, of which approximately 71 ha consists of primary forests disturbed to varying extents. Records of isolation of the forest on Bukit Timah stretch back to 1843, with accounts of gambier and pepper plantations separating Bukit Timah from other forests (for more details, see Corlett 1988). Legal protection was more strictly enforced in 1939 where Bukit Timah was gazetted to be a nature reserve under the British colonial law (Corlett 1988). Several legislations were passed to protect both flora and fauna in the early 20th century, though these were not sufficient to prevent illegal hunting and logging (Corlett 1988). At present, BTNR is surrounded by a matrix of urban housing and a major expressway, which separates BTNR from a larger forest fragment (ca. 3,043 ha), the Central Catchment Nature Reserve (Fig. 5). A total of 843 forest angiosperm species have been recorded in BTNR, with the most species coming from the following plant families: Euphorbiaceae, Orchidaceae, Rubiaceae and Moraceae (Corlett 1990).

The fauna history of BTNR has also been recorded albeit not as well studied than the flora. The primary forests in BTNR are different from the rest of Southeast Asia namely because all its large mammals, e.g. the Tiger *Panthera Tigris corbetti*, Leopard *Panthera pardus*, Sambar *Rusa unicolor*, have gone extinct (Tan *et al*. 2007). Mammals that are extant in BTNR include small to medium sized mammals such as the Long-tailed Macaques, *Macaca fasicularis*, Common Treeshrews *Tupaia glis* and Slender Squirrels *Sundasciurus tenuis*. The last published survey of mammals found in BTNR was conducted from 1993 to 1997 as part of a larger survey of fauna diversity in the nature reserves of Singapore (Teo & Rajathurai 1997).

3.2.2. Historical collection of dung beetles

I searched the Raffles Museum of Biodiversity Research in the National University of Singapore for any past collections of dung beetles made in the forest interior of

BTNR. Dr. D. H. Murphy, a retired entomology professor, made most of the dung beetle collection during the period of 1960s to 1970s. I interviewed Dr. Murphy regarding the methods used for collection of the dung beetles and the exact locations where he made his collections. The beetles were collected with a variety of techniques, such as glycol pitfall traps, light traps and malaise traps. All the beetles were collected opportunistically and there was no systematic sampling design, which could be replicated. Dung beetle specimens collected from 1960s to 1970s are currently held at the National History Museum Naturalis in Leiden, Netherlands.

3.2.3. Dung beetle survey

Since past collections of dung beetles were carried out opportunistically using a variety of methods, I decided to carry out an intensive dung beetle survey using well-used sampling techniques for dung beetles such as dung baited pitfall traps and flight interception traps (Davis *et al*. 2001). I identified five valleys of BTNR (Lasia Valley, Taban Valley, Jungle Fall Valley, Fern Valley and Seraya Valley) as forest interiors of BTNR and placed both trap types in all these valleys. This study was conducted between January 2008 and March 2008.

Each baited pitfall trap consist of a 500 ml plastic cup (diameter = 8.5 cm and height = 12 cm) buried flushed with the ground. A 15 cm by 15 cm corrugated plastic board served as a rain cover and was supported 10 cm above the surface of the cup by steel wires. Cow dung collected from the Singapore Zoological Gardens was used as bait for my traps. The cow dung was kept in an airtight container for at least 4 days at room temperature so as to obtain a more pungent smell of the decomposing dung. I used approximately 100 g of cow dung and wrapped it in a 2 mm by 2 mm green mesh, secured with rubber bands and suspended from the surface of the trap by 5 cm with cotton twine. Each pitfall trap contained formalin, filled to a depth of 3 cm, to kill and preserve trapped dung beetles. Traps were organized in quadrants where one trap was 10 m away from the other and the distance between each quadrant was 50 m. The number of quadrants in each valley differed according to the size of the valley (Table 6). Traps were set up during the morning and left in the field for two nights before collection. Beetles were collected and stored in 100 % ethanol and brought back to the laboratory for species identification.

Flight interception traps are a form of passive trapping and are able to catch dung beetles that specialize on rotting fruits or other types of dung (Davis 2000). All flight interception traps were constructed using a black fabric 2 m wide by 1.3 m long and suspended tautly across a forest trail using raffia strings. The black fabric intercepts beetles flying along forest trails and these beetles fall into collecting trays half-filled with a saturated salt solution with a small amount of detergent. A large ground sheet secured with raffia strings above each flight interception trap acted as a rain cover and prevented the collecting containers from being flooded. One flight interception trap was set up in each valley, except for Fern Valley, which had two such traps set up (Table 6). All traps were visited every 7 days and left in the forest for a period of 21 days. Captured dung beetle individuals were preserved in 100% ethanol, and were processed and identified in the laboratory. Where individuals could not be identified, a series of morphospecies numbers were assigned to the genus. The dung beetle specimens collected from the intensive survey are held in the Raffles Museum of Biodiversity Research, National University of Singapore.

3.3. Results

Dung beetles that were not found in this survey could not be labeled as ‘extinct’ since this study was conducted approximately 30 years later. Conventional definition of extinct species requires that species should not have been reported or seen in the last

50 years (IUCN 2008). Hence, dung beetles that were not found in this 2008 survey were classified as “possibly extinct”. Based on the historical collection in RMBR, I collated a list of nine dung beetle species and 30 individuals collected from the forest interior of BTNR between 1960s and 1970s. I checked for the presence of any of these species in our pitfall and flight interception traps conducted in February and March 2008. Out of the nine species from the historical records, three (33%) were absent and possibly extinct in BTNR (Table 7). Species not caught in traps and possibly extinct include *Cartharsius molossus*, *Onthophagus deliensis* and *Onthophagus mentaweiensis* (Table 7).

Using both baited pitfall traps and flight interception traps, a total of 19 species and 871 individuals was collected (Table 8). I recorded 13 new species of dung beetles from BTNR in 2008 *(Bolbochromus* sp. 1*, Haroldius* sp. 1*, Ochicanthon peninsularis, Onthophagus angustatus, Ont. deflexicollis, Ont. pedator, Ont. rutilans, Ont.* sp. 4*, Ont.* sp. 5*, Ont.* sp. 6*, Ont.* sp. 7*, Ont.* sp. 8*,* and *Ont.* sp. 9*)*. The number of species sampled using flight interception traps was higher, 18 species compared to 7 species which were found in baited pitfall traps (Table 8). Similarly, the number of individuals from flight interception traps exceeded the number of individuals from baited pitfall traps, 768 beetles compared to 103 beetles. The majority of dung beetle individuals came from these three dung beetle species *Onthophagus* sp. 1, *Ont.* sp. 2 and *Ont.* sp. 3, which made up 68% of the total number of individuals caught in flight interception traps. There was also a great disparity in the catch of dung beetle species *Onthophagus* sp. 1 and *Ont.* sp. 2, where more than a hundred beetles were caught in flight intercept traps and only one or no beetles caught using baited pitfall traps (Table 8).

3.4. Discussion

Deforestation and alteration of natural habitats have been shown to cause insect population decline and extinction in studies from tropical (e.g. Brook *et al*. 2003, Hanski *et al*. 2007, Sodhi *et al*. 2009) as well as temperate regions (Lobo 2000, Brandmayr *et al*. 2008). The loss of forests can lead to a deterioration of habitat conditions (e.g. greater predation risks and microhabitat changes), which are less conducive for certain insect species (Sodhi *et al*. 2007).

In the case for dung beetles, larger bodied beetles may be more prone to microclimatic changes as they dissipate heat slower (Bartholomew & Heinrich 1978) and may find themselves vulnerable to over-heating or desiccation in a hotter and drier forest habitat (Chown 2001). The drier forest can also lead to lower soil humidity that correlates with increased desiccation of large dung beetle larvae in the soil (Anduaga 2004). Effects of deforestation are also associated with a decline in middle and large mammals, important dung producers in the tropical forests (Laidlaw 2000) and this has ramifications on the availability of sufficient dung resources for beetles with higher biomass (Larsen *et al*. 2005). Hanski *et al*.'s (2007) study on dung beetle extinctions in Madagascar cited the reduction in the population of lemurs as a possible reason for the dramatic decline of *Helictopleurus undatus*, a relatively large dung beetle that was common in the past. In this study, a single large dung beetle *Cartharsius molossus* (*ca*. 0.572 g in dry mass), a nocturnal tunneller was identified to be possibly extinct in BTNR. *C. molossus* is a widespread species in Southeast Asia and is commonly found in the interior of primary lowland forests in Johor but not present in the forest fragments of Singapore (see Appendix). According to Slade *et al*. (2007), the presence of large, nocturnal tunnellers account for approximately 75% of dung removal and the loss of these beetles may have serious consequences on nutrient recycling and secondary seed removal processes in BTNR and forests of

Singapore. Other dung beetle species that were absent from our 2008 survey included dung beetle species of the genus Onthophagus - *Onthophagus deliensis* and *Ont. mentaweiensis*. Little is known about both of these species except that they are small tunnellers (*ca.* 4 – 6 mm in length) and have very low biomass. *Ont. deliensis* is suggested to be a canopy dung beetle due to its curved and elongated hind metatarsus, which is used to carry dung from the canopy, such as monkey dung, to the forest floor (Davis *et al.* 1997, J. Huijbregts pers. comm.).

Dung beetle species richness in BTNR is much lower in comparison to a similar study by Davis (2000) in Ulu Segama Reserve, Sabah, Malaysia. Flight interception traps set up over 7 days in reduced impact logging and conventionally logged lowland dipterocarp forests collected 57 species and 48 species respectively. In contrast, only 18 species of dung beetles were collected using the same methods but three times the trapping period in BTNR. The thirteen new species recorded from this 2008 survey together with the six previously recorded species from BTNR brings the total number of dung beetle species in BTNR to 19 species. Newly recorded species were most likely missed out due to the opportunistic nature of sampling between 1960s and 1970s. It is unclear if their presence may be due to colonization of the forest fragment after 1970s. Out of the collected 19 species, only one species was not found in flight interception traps and the other 18 species found in either flight intercept traps exclusively or in both trap types. Since flight interception traps are passive in nature and collect dung beetles that have a more diversified diet, they serve as an important complementary trap type to survey dung beetle species diversity in a locality. Some dung beetle species such as *Onthophagus sp. 1*, *Ont. sp. 2* and *Ont. sp. 3* are found in much higher abundance in flight intercept traps than in baited pitfall traps (Table 8). Considering that flight intercept traps are left in the field for three consecutive weeks and baited pitfall traps are set out only three days for each sampling period, this disparity in abundance may be a result of the difference in effective trapping period rather than the efficiency or appropriateness of the trap itself. The use of cattle dung instead of human dung as bait for the pitfall traps might also be another reason for the disparity in species and number of individuals between the two trap types. Since human dung is representative of an omnivorous diet, using human dung as bait may have been able to attract a wider range of dung beetle species and a larger number of individuals (J. Huijbregts pers. comm.).

Since the early 19th century, the forest of BTNR has undergone several anthropogenic disturbances ranging from the clearance of land for agriculture and plantation to the modern day influences of human developments for recreation, housing and transport (Corlett 1988). Between the time of our sampling and the time of collection of dung beetles from the museum, one major disturbance to BTNR was the construction of the Bukit Timah Expressway from 1983 to 1986. This six-lane expressway provides an effective barrier between BTNR and the Central Catchment Nature Reserve, restricting the movement of most terrestrial animals especially mammals between the two forests. Furthermore, walking trails that allow access to all parts of BTNR subdivide the forests into smaller areas and expose the forests to increased drying effects from the external environment (Corlett 1988). All these human disturbances could have resulted in possible extinctions of the three dung beetles species from BTNR since the 1970s. However, we are cautious not to rule out any possible extinction from faunal relaxation due to earlier disturbance events in the early 19th century.

This study focuses on BTNR, a small, isolated forest fragment in Singapore and hence, its results may not be widely applicable. However, this localized example can still serve as an illustration of the ongoing effects of human disturbance on Southeast Asian forest species (Sodhi *et al*. 2004) and especially less well-documented insect groups. The preservation of forests in BTNR and conservation of mammals therein has important consequences for the continued survival of dung beetles in the forests.

General conclusions

In Chapter 2, I show that dung beetle communities in disturbed forest fragments of Singapore had a much lower level of species richness, number of individuals and body size compared to the less disturbed, old-growth forests in Johor. Most dung beetles remaining in Singapore were small tunnellers belonging to the genus *Onthophagus*, with one exception of a large roller, *Paragymnopleurus maurus*. Environmental conditions such as shrub cover and soil characteristics including temperature, moisture and pH were demonstrated to correlate significantly with the distribution of dung beetle communities. Environmental variables such as ambient temperature, percentage ground and shrub cover, palm density, soil temperature, soil pH, soil moisture, number of dead trees on the ground and leaf litter depth were correlated with changes in forest disturbance. All variables, excluding ambient temperature, soil temperature and number of dead trees on the ground, showed negative correlations with increasing forest disturbance. The dung removal experiments show that forests with greater disturbance had lower dung removal function performed by dung beetles, which is possibly due to the lack of large tunneller species such as *Cartharsisu molossus* and *Copris ramosiceps.*

In Chapter 3, I report the absence of three dung beetle species from a small nature reserve in Singapore based on the comparisons of a 2008 survey with past records of dung beetle collections. The loss of one of these dung beetles, *Cartharsius molossus*, is a significant loss to the dung beetle community in a forest as these large tunnellers also contribute most to dung removal in forest ecosystems within Southeast Asia. The use of flight intercept traps in this Chapter greatly enhanced the number of species caught using cow-baited dung pitfall traps and is an important complementary trapping method for conducting dung beetle surveys.

One limitation to be addressed is the great difference in number of dung beetle species in Bukit Timah collected in Chapter 2 compared to Chapter 3. This is due to the differences in the amount of dung used for baited pitfall traps and an additional trapping method – flight interception traps. In Chapter 2, only 20 g of cattle dung was used as bait, compared to 100 g of cattle dung used in Chapter 3. Previous studies carried out in the Neotropics have cited 20 g or less human or cattle dung to be sufficient for trapping dung beetles (Larsen & Forsyth 2005, Shahabuddin *et al.* 2005). However, in the forests where dung beetle communities are adversely affected by human modification and fragmentation, it is perhaps important to use a higher quality and quantity of dung to have a better representation of dung beetles in the forests. Therefore, the volume of dung used for trapping dung beetles is critical in the number of species and individuals of dung beetles caught. The use of flight interception traps in Chapter 3 greatly enhanced the diversity of species caught within the same location as Chapter 2 (19 species compared 2 species). Perhaps the use of a high quality of dung such as human dung may collect just as many species. But faced with restraints within the regulations of the nature reserves of Singapore, using flight interception traps may be a way of overcoming the problem of not being able to use human dung for the collection of dung beetles. I acknowledge the limitations to interpreting the results in Chapter 2 due to the assumption that Singapore's dung beetle fauna would have been similar to that of the undisturbed Malaysian sites in the past. A better study design could include study sites from mainland Peninsular Malaysia using forests disturbed to varying degrees. Given that oil palm cultivation is rapidly affecting biodiversity in Southeast Asia (Fitzherbert *et al.* 2008), it would also be useful to study the effects of forest conversion to oil palm plantations on dung beetle communities.

In this study, I have shown the various impacts of anthropogenic disturbance on tropical forest dung beetles in a relatively less-studied region of Southeast Asia and highlight the importance of preserving remaining old-growth forests as they continue to harbor the richest source of biological diversity. The remaining forest fragments in Singapore, still continue to support a few species of dung beetles within the forest, but the chances of reviving or increasing the number of species and their populations depend heavily on the number of mammals present in the forests. Re-introductions of mammals may have a positive impact on dung beetle communities in the forest but there are many other considerations such as feasibility of re-introductions, ability to survive and propagate in current forest systems, impacts of re-introductions on other fauna and flora species, which need to be carefully studied beforehand. Another option is to reintroduce a population of *Cartharsius molossus* into the forests and 'subsidise' their diet using mammalian dung collected from the Singapore Zoological Gardens. Theoretically, this option might help restore the ecological service of nutrient recycling and even seedling regeneration if seeds from native plants are embedded in the dung (see Andresen 2003). However, these ideas need to be empirically tested first. Recovery of dung beetle communities in fragmented tropical forests may also occur after the regrowth of secondary vegetation within approximately one decade (Quintero & Roslin 2005). Thus, preservation of secondary vegetation and forest fragments in Singapore may be useful in the recovery of dung beetle communities.

The future of dung beetle ecology research can focus on filling the gaps of Southeast Asian dung beetle biology and taxonomy as much remains unknown especially in the Malay Peninsula and Philippines. With a history of forest exploitation through plantations and logging within Southeast Asia, more research on forest regeneration through the function of secondary seed dispersal by dung beetles is certainly warranted.

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Tables

Table 1 - Summary information of eight study sites in Peninsular Malaysia and Singapore.

Name and location of study site	Forest habitats	Forest type	Area (ha)	Corrected perimeter to area ratio	Matrix quality	Past land use by humans	Present land use by humans
Belumut Forest Reserve, Malaysia (BL)	1	Old growth dipterocarp forests	>30,000	NA	Logged forests and mixed-agricultural systems	Never logged	Recreation
Bekok Forest Reserve, Malaysia (BK)	1	Old growth dipterocarp forests	>80,000	NA	Logged forests and mixed-agricultural systems	Never logged	Recreation
Bukit Timah Nature Reserve, Singapore (BT)	2	Tall secondary forest with fragments of old growth forest	134	2.11	Urban areas, abandoned quarries	Logging, gutta percah and rubber plantations	Recreation, telecommunication tower
MacRitchie Forest, Singapore (MR)	2	Tall secondary forest with fragments of old growth forest	415	2.55	Urban areas, grassland, reservoir	Logging	Recreation
Lower Pierce Forest, Singapore (LP)	3	Tall secondary forest	85	1.34	Urban areas, golf course, reservoir	Logging and rubber plantations	Recreation
Pulau Ubin Secondary Forest, Singapore (PUS)	3	Young secondary forest and abandoned rubber plantation	174	1.18	Secondary vegetation, abandoned quarries	Human settlements and rubber plantations	Outward Bound training school
Pulau Ubin Plantation Forest, Singapore (PUP)	4	Young secondary forest and abandoned rubber plantation	93	1.55	Secondary vegetation, abandoned quarries	Human settlements and rubber plantations	Recreation, rural villages
Kent Ridge Forest, Singapore (KR)	4	Young secondary forest and open parkland	14	1.98	Urban areas, secondary vegetation	Logging and rubber plantations	Recreation, housing

Table 2 - Summary of information of dung beetle catch per transect across sites. Mean values within a column with different superscripts are statistically different from each other (Duncan's multiple range test, $P < 0.05$). Highest and lowest mean values within a column are in bold. For site abbreviations, see Table 1.

		Mean no. species per transect		Mean no. individuals per transect		Total biomass per transect (g)		Mean length of beetle per transect (mm)	
Forest habitats	Sites	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.
1	BL	9.78^{a}	± 1.18	40.06^{a}	± 7.91	1.90^{a}	± 0.41	7.26^{a}	± 0.23
1	BK	**10.39**^{a}	± 0.56	**47.50**^{a}	± 3.97	**2.38**^{a}	± 0.29	**8.12**^{a}	± 0.19
2	BT	0.50^{b}	± 0.23	1.33^{b}	± 0.66	0.012^{b}	± 0.0060	1.75^{b}	± 0.75
2	MR	**0.056**^{b}	± 0.056	**0.056**^{b}	± 0.056	**0.00039**^{b}	± 0.00039	**0.34**^{b}	± 0.34
3	LP	0.42^{b}	± 0.19	0.42^{b}	± 0.19	0.029^{b}	± 0.012	3.75^{c}	± 1.61
3	PUS	0.17^{b}	± 0.11	0.25^{b}	± 0.18	0.0046^{b}	± 0.0036	0.89^{b}	± 0.60
4	PUP	0.17^{b}	± 0.11	0.25^{b}	± 0.18	0.011^{b}	± 0.0076	0.96^{b}	± 0.65
4	KR	No beetles collected							

Table 3 - Absolute number of individuals (N), dung beetle species richness (S) collected at each site (see Table 1 for abbreviations) and diversity indices, α = Fisher's alpha diversity index, H' = Shannon's index and $1-\lambda$ = Simpson's index. Highest and lowest values within a column are in bold.

Forest habitats	Site	N	S	S_{obs}[a]	S_{est}[b]	Coverage[c]	α	H'	$1-\lambda$
1	BL	721	**38**	**38**	**50.47**	75.29	**8.55**	**2.60**	**0.88**
1	BK	**855**	32	32	49.06	65.23	6.56	2.20	0.81
2	BT	16	**1**	2	2.01	**99.57**	**0.24**	**0**	**0**
2	MR	**1**	**1**	**1**	1.45	69.10	NA	**0**	**0**
3	LP	5	2	2	2.77	72.13	1.24	0.50	0.32
3	PUS	3	2	2	3.34	**59.91**	2.62	0.64	0.44
4	PUP	3	**1**	**1**	**1.05**	95.24	0.53	**0**	**0**
4	KR	0	0	0			NA		

[a] Number of species expected in the pooled number of samples given empirical data.

[b] Estimated species richness obtained by averaging the following non-parametric estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap means).

[c] Number of species observed as a percentage of the estimated species richness.

Table 4 - Correlation results between forest types and environmental variables measured.

	Pearson's		Kendall's tau		Spearman's	
Variable	*t*	correlation coefficient	*z*	tau	*S*	rho
Canopy	-0.341	-0.0331				
Ambient temperature	2.264	0.222*				
Ground temperature	1.282	0.128				
Ambient humidity	1.233	0.123				
Ground humidity	1.6	1.588				
Understory Ground			-4.47	-0.329**	300194.2	-0.43**
Understory Shurb	-3.998	-0.362***				
Palm density			-5.524	-0.406***	320152.2	-0.525***
Soil temperature			4.83	0.37***	112056.6	0.466***
pH soil			-3.881	-0.301***	214289.1	-0.409***
Moisture	-2.5746	-0.254*				
Ground dead trees			2.534	0.193*	158808.5	0.244*
Standing dead trees	-0.0091	-0.000881				
Leaf litter			-2.597	-0.189*	267533.3	-0.274*
Tree density	-1.051	-0.115				
Average dbh	-1.217	-0.129				

* $P < 0.05$
** $P < 0.001$
*** $P < 0.0001$

Table 5 - The full set of candidate models to explain variations in dung biomass ($\log_{\text{natural}}$-transformed) along a disturbance gradient (number of observations = 144). Each candidate model also includes beetle biomass ($\log_{\text{natural}}$-transformed) as a continuous control variable, as well as site, transect (nested in site) and sampling cycle as random effects. Definitions of abbreviations used are as follows: *-LL* = negative loglikelihood of fitted model; *k* = number of parameters; AIC_c = Akaike's information criterion corrected for small sample sizes; ΔAIC_c = difference in AIC_c value of each candidate model from the most parsimonous model; w_i = Akaike weight; E_{ratio} = Evidence ratio against candidate model; R^2 = McFadden's pseudo-R^2 for generalized linear models; NULL = null model (including only control variables and random effects); DISTURB = disturbance rank/class; TREAT = treatment (either caged or exposed).

Candidate model	*-LL*	*K*	AIC_c	ΔAIC_c	w_i	E_{ratio}	R^2
NULL	-141.51	5	293.44	21.15	0.00%	39126.61	0.00%
DISTURB+TREAT+ DISTURB:TREAT	-127.61	8	272.30	0.00	91.58%	1.00	9.82%
DISTURB+TREAT	-131.12	7	277.07	4.77	8.42%	10.88	7.34%
DISTURB	-140.91	6	294.43	22.13	0.00%	63916.70	0.42%

Table 6 - Number of quadrants and flight interception traps in each valley of Bukit Timah Nature Reserve.

Site	Number of Quadrants	Number of Flight Interception Traps
Seraya Valley	2	1
Jungle Fall Valley	2	1
Fern Valley	6	2
Lasia Valley	3	1
Taban Valley	4	1

Table 7 - List of nine dung beetles which were collected between 1965 and 1976 and their presence or absence in the pitfall traps (PFT) or flight intereption traps (FIT) set up between January and March 2008. Functional guild refers to the size and mode of dung removal based on Cambefort (1991b).

Species	Functional Guild *	Biomass (g)	PFT	FIT	Present/Absent (+/-)
Catharsius molossus	LT	0.5719± 0.0670	0	0	-
Onthophagus deliensis	ST	0.003	0	0	-
Onthophagus sp. 1	ST	0.0037±0.0019	1	1	+
Onthophagus sp. 2	ST	0.0027±0.0002	0	1	+
Onthophagus sp. 3	ST	0.0110±0.0010	1	1	+
Onthophagus mentaweiensis	ST	0.0040±0.0020	0	0	-
Onthophagus semicupreus	ST	0.005	1	1	+
Onthophagus semifex	ST	0.0393±0.0040	1	1	+
Paragymnopleurus maurus	LR	0.0840±0.0241	1	1	+

* Functional guild of dung beetles include size (L = large, S = small) and mode of dung removal (T = tunneller, R = roller).

Table 8 - List of dung beetle species found in pitfall traps (PFT) and flight interception traps (FIT).

Family	Species	PFT	FIT
Geotrupidae	*Bolbochromus* sp. 1	0	3
Scarabaeinae	*Haroldius* sp. 1	0	1
	Ochicanthon peninsularis	0	4
	Onthophagus angustatus	0	11
	Onthophagus deflexicollis	0	16
	Onthophagus pedator	0	30
	Onthophagus rutilans	3	0
	Onthophagus semicupreus	7	6
	Onthophagus semifex	41	86
	Onthophagus sp. 1	1	198
	Onthophagus sp. 2	0	140
	Onthophagus sp. 3	40	186
	Onthophagus sp. 4	7	25
	Onthophagus sp. 5	0	1
	Onthophagus sp. 6	0	6
	Onthophagus sp. 7	0	2
	Onthophagus sp. 8	0	24
	Onthophagus sp. 9	0	27
	Paragymnopleurus maurus	4	2
	Total species	7	18
	Total individuals	103	768

Figures

Fig. 1 - Map showing the eight study sites. Belumut (BL), Bekok (BK), Bukit Timah (BT), Mac Ritchie (MR), Lower Pierce (LP), Pulau Ubin Secondary (PUS), Pulau Ubin Plantation (PUP) and Kent Ridge (KR).

Fig. 2 - Comparison of (a) mean number of individuals and (b) mean number of species collected using baited pitfall traps per transect among the eight study sites.

Fig. 3 - Non-metric multidimensional ordination vector plots of (a) sample scores and (b) species scores with four significantly (R > 0.50) correlated environmental variables, shrub cover, soil moisture, soil pH and soil temperature.

Fig. 4 - Predicted dung mass (remaining after 24 hours) for the experimental treatments – exposed or caged – along a disturbance gradient (1 to 4). Predicted mean values were calculated based on the AIC *c*-selected most parsimonious model (DISTURB+TREAT+DISTURB:TREAT; see Table 5).

Fig. 5 - Map showing geographical location of Bukit Timah Nature Reserve in Singapore and location of traps used in the 2008 dung beetle survey.

Fig. 1 - Map showing the eight study sites. Belumut (BL), Bekok (BK), Bukit Timah (BT), Mac Ritchie (MR), Lower Pierce (LP), Pulau Ubin Secondary (PUS), Pulau Ubin Plantation (PUP) and Kent Ridge (KR).

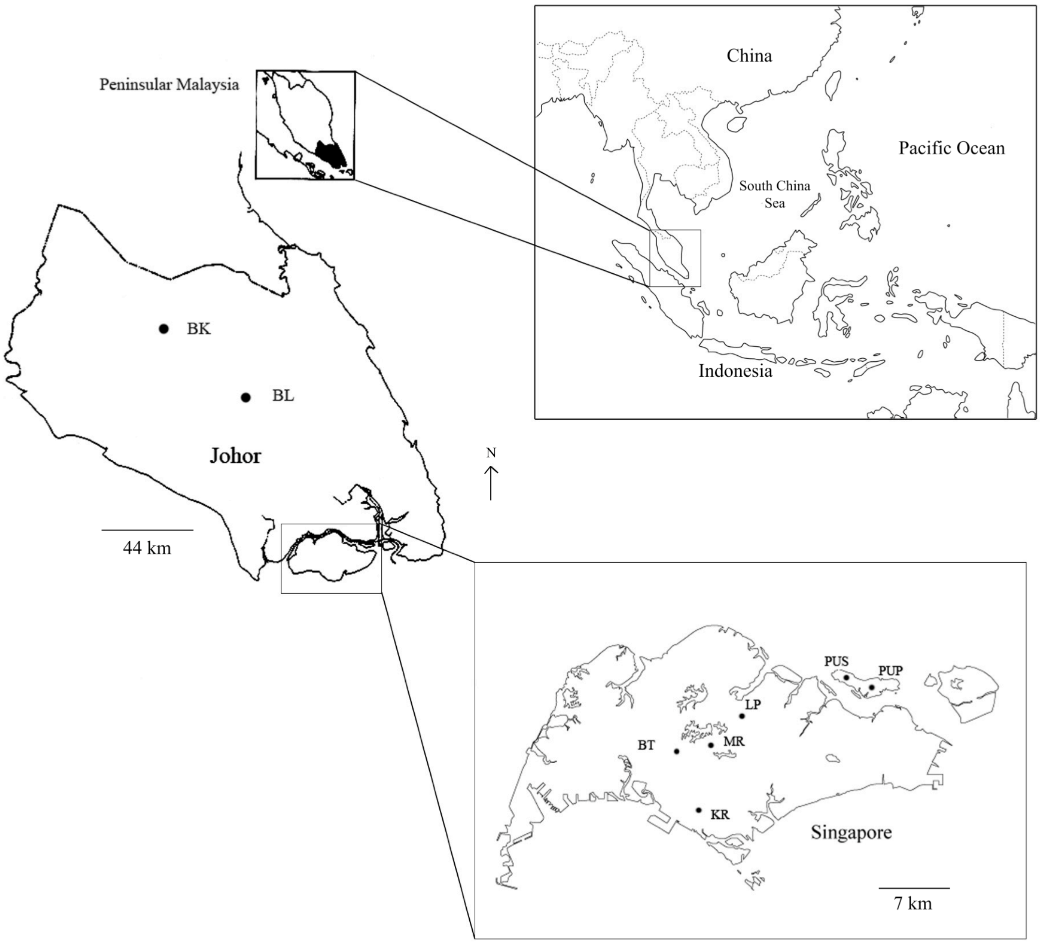
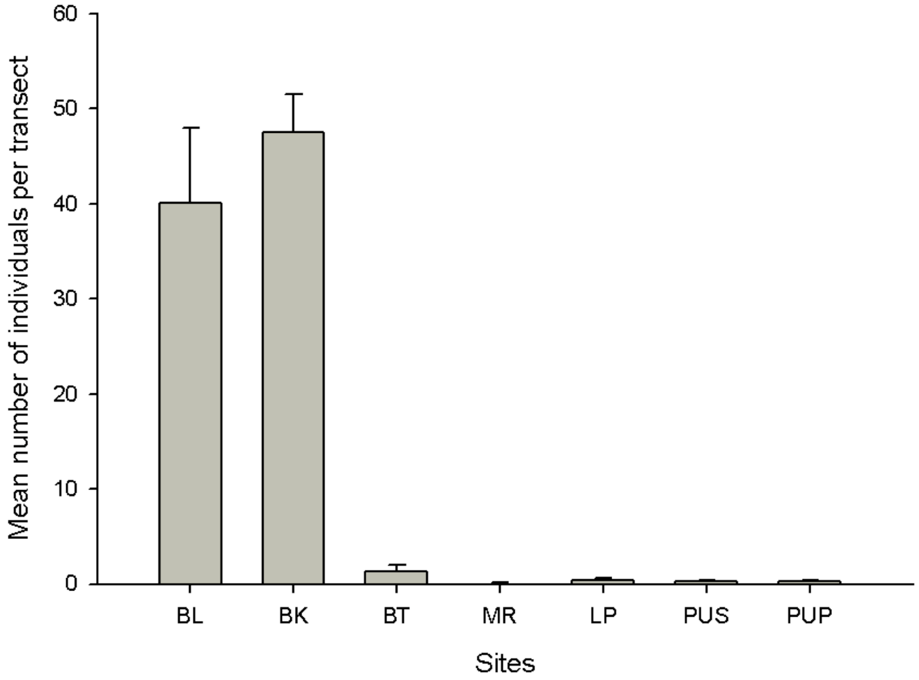


Fig. 2 - Comparison of (a) mean number of individuals and (b) mean number of species collected using baited pitfall traps per transect among the eight study sites.

(a)



(b)

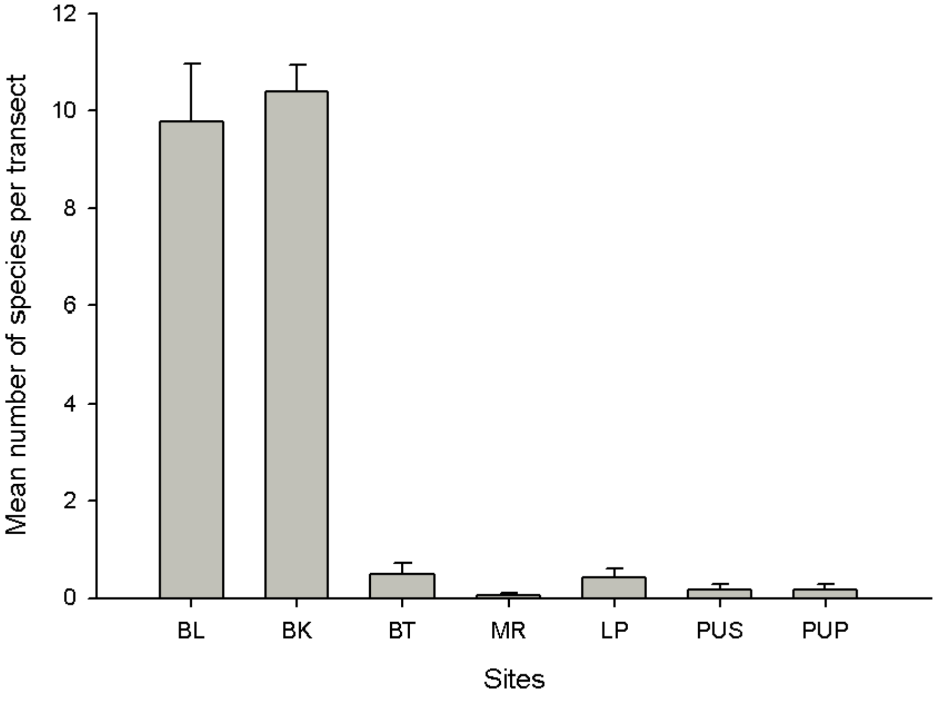
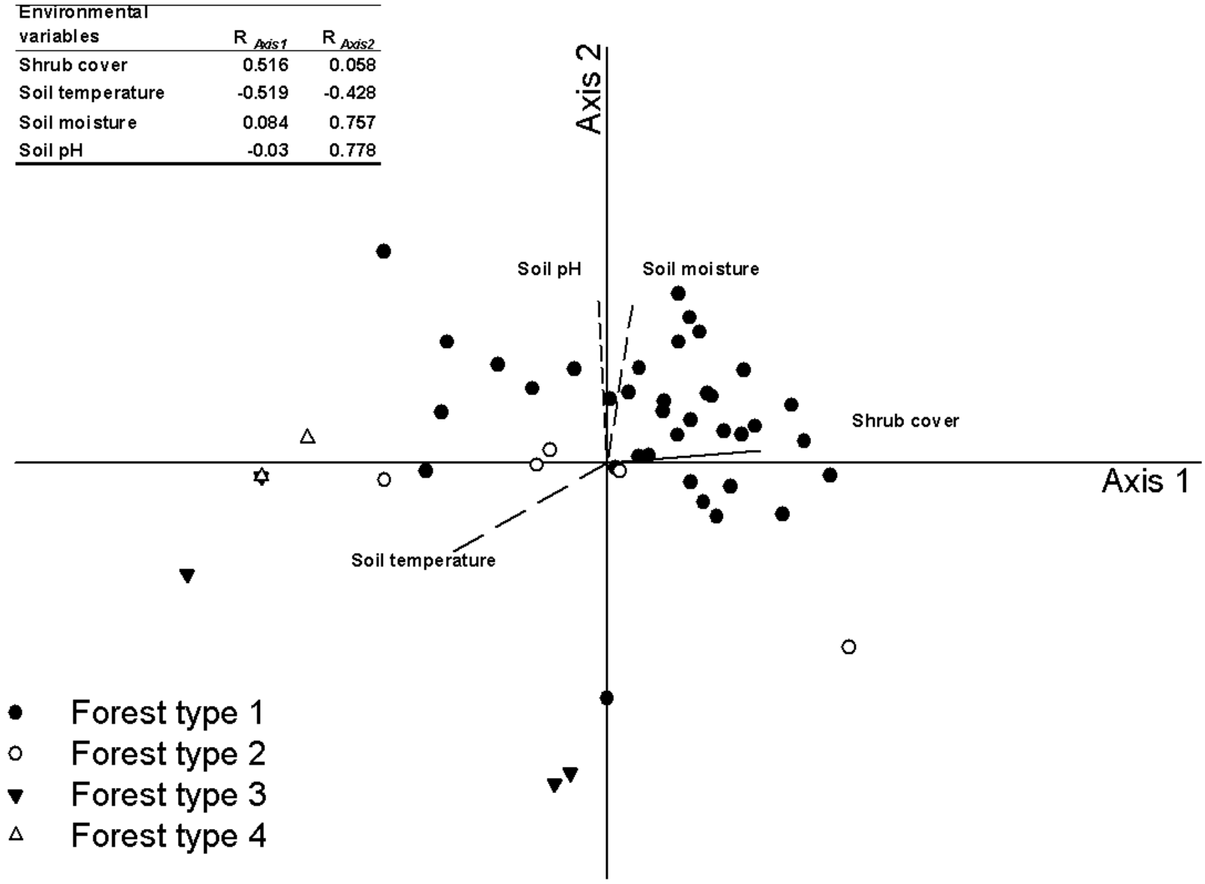


Fig. 3 - Non-metric multidimensional ordination vector plots of (a) sample scores and (b) species scores with four significantly ($R > 0.50$) correlated environmental variables, shrub cover, soil moisture, soil pH and soil temperature.

(a)



Environmental variables	R_{Axis1}	R_{Axis2}
Shrub cover	0.516	0.058
Soil temperature	-0.519	-0.428
Soil moisture	0.084	0.757
Soil pH	-0.03	0.778

(b)

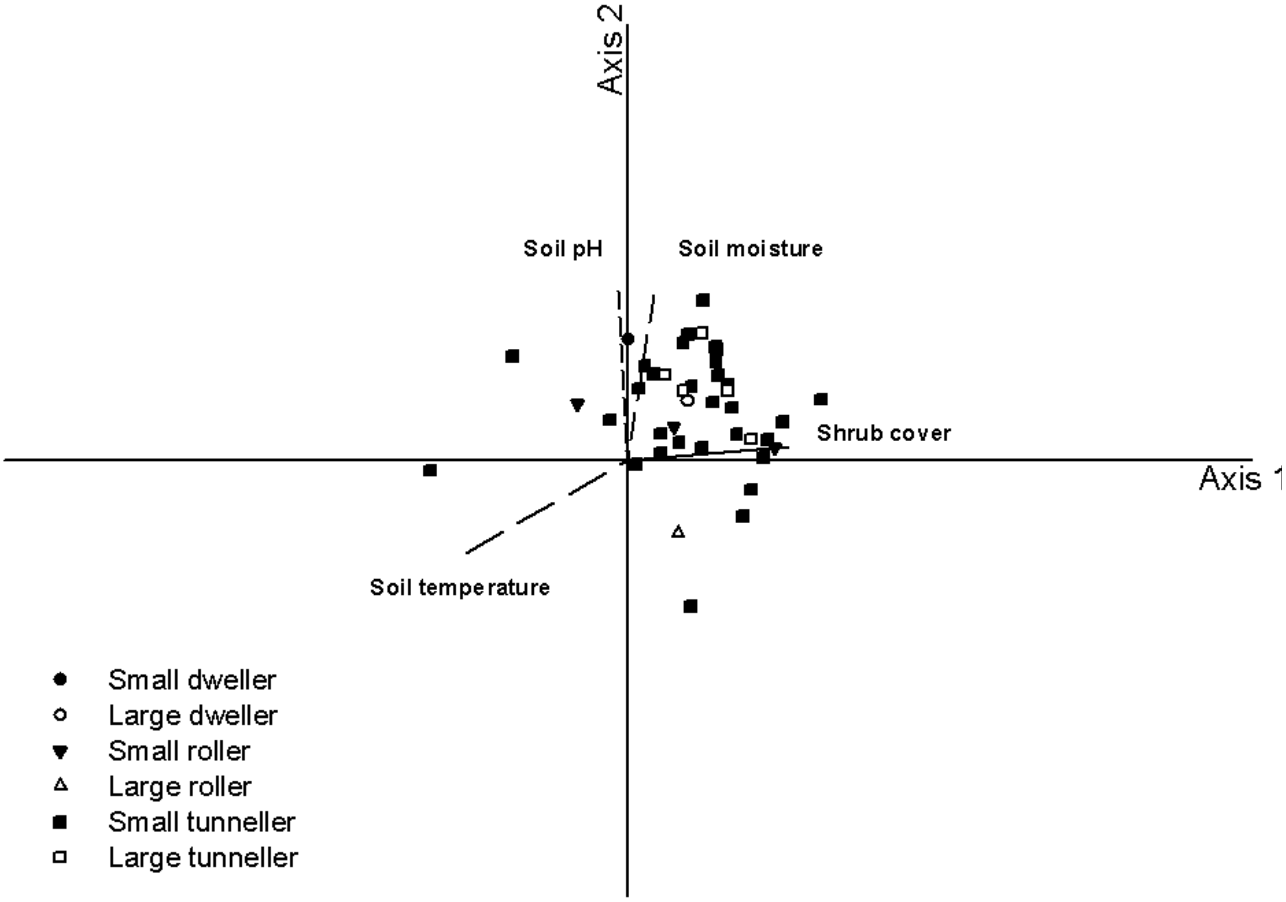

Axis 2
Axis 1
Soil pH
Soil moisture
Shrub cover
Soil temperature
● Small dweller
○ Large dweller
▼ Small roller
△ Large roller
■ Small tunneller
□ Large tunneller

Fig. 4 - Predicted dung mass (remaining after 24 hours) for the experimental treatments – exposed or caged – along a disturbance gradient (1 to 4). Predicted mean values were calculated based on the AIC *c*-selected most parsimonious model (DISTURB+TREAT+DISTURB:TREAT; see Table 5).

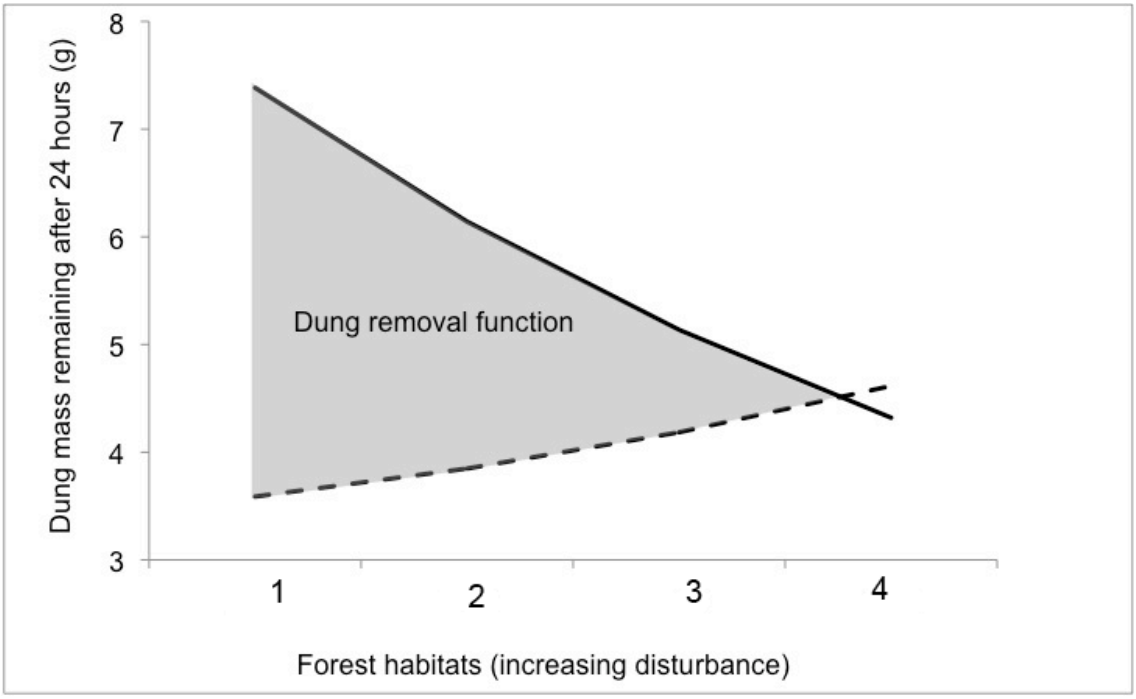
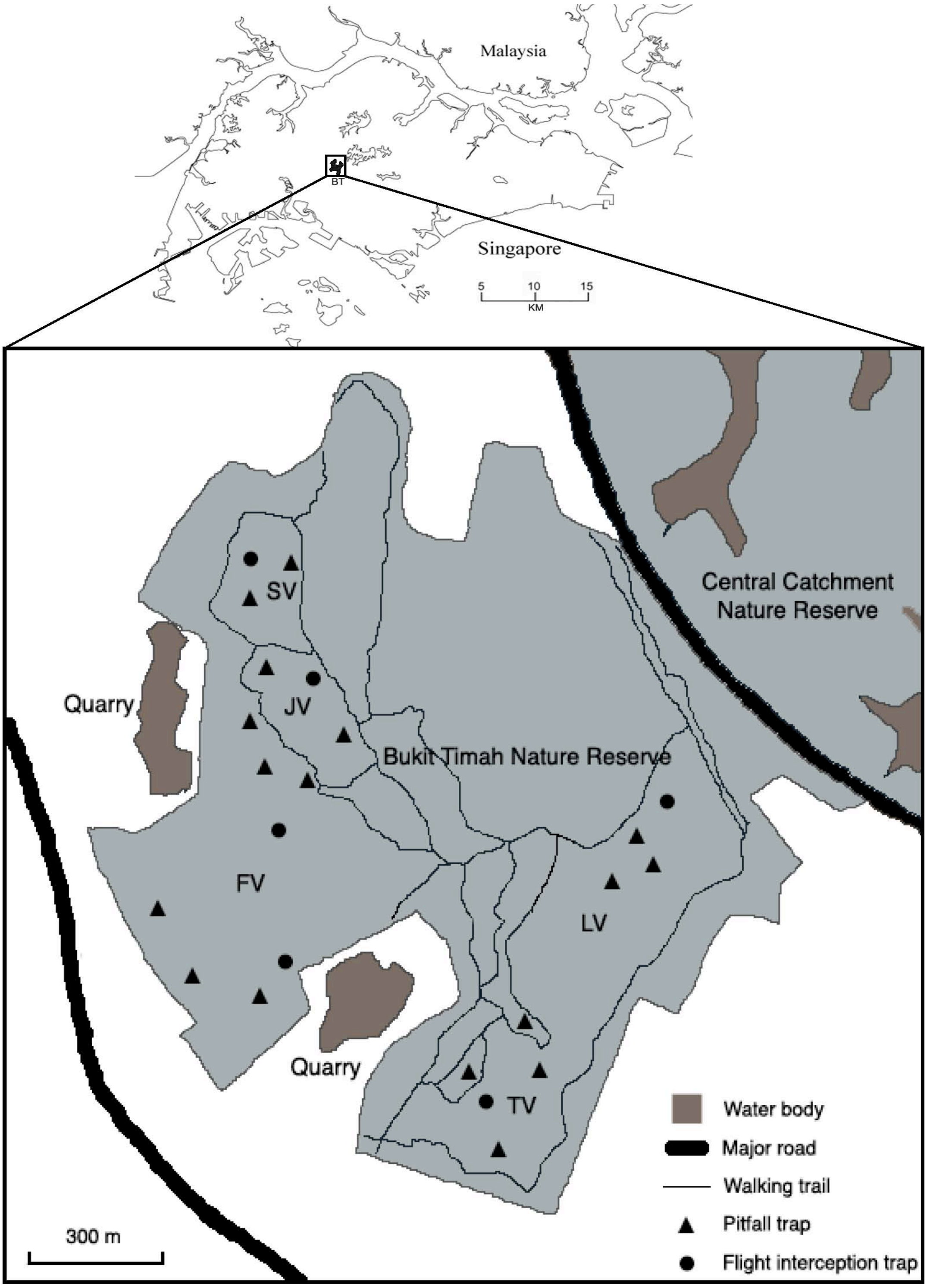


Fig. 5 - Map showing geographical location of Bukit Timah Nature Reserve in Singapore and location of traps used in the 2008 dung beetle survey.



Appendix - Total number of dung beetles collected from dung pads and dung baited pitfall traps in the eight study sites. Functional group abbreviations: S = small, L = large, D = dweller, T = tunneller, R = roller.

				Belumut		Bekok		Bukit Timah		MacRitchie		Lower Pierce		Pulau Ubin Secondary		Kent Ridge		Pulau Ubin Plantation	
Genus	Species	Author	Functional group	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps
Aphodius	*Aphodius* sp. 1		SD	10	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caccobius	*Caccobius unicornis*	Fabricius, 1798	ST	1	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Catharsius	*Catharsius molossus*	Linnaeus, 1758	LT	0	16	1	34	0	0	0	0	0	0	0	0	0	0	0	0
Copris	*Copris agnus*	Sharp, 1875	LT	8	44	8	12	0	0	0	0	0	0	0	0	0	0	0	0
	Copris doriae	Harold, 1877	LT	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Copris haroldi	Lansberge, 1886	LT	0	32	0	14	0	0	0	0	0	0	0	0	0	0	0	0
	Copris ramosiceps	Gillet, 1921	LT	0	9	0	41	0	0	0	0	0	0	0	0	0	0	0	0
Ochicanthon	*Ochicanthon* sp. 1		SR	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Ochicanthon peninsularis	Krikken & Huijbregts, 2007	SR	0	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Oniticellus	*Oniticellus pictus*	Harold, 1879	ST	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus	*Onthophagus angustatus*	Boucomont, 1914	ST	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus aphodiodes	Lansberge, 1883	ST	1	18	0	3	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 1		ST	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus batillifer	Harold	ST	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 2		ST	77	89	33	47	0	0	0	0	0	0	26	1	0	0	21	3
	Onthophagus sp. 3		ST	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 4		ST	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus cervicapra	Boucomont, 1914	ST	17	24	1	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus crassicollis	Boucomont, 1913	ST	0	2	0	1	0	0	0	0	2	0	1	2	0	0	7	0
	Onthophagus deflexicollis	Lansberge, 1883	ST	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus deliensis	Lansberge, 1885	ST	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 5		ST	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 6		ST	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	Onthophagus sp. 7		ST	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 8		ST	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 9		ST	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0

				Belumut		Bekok		Bukit Timah		Mac Ritchie		Lower Pierce		Pulau Ubin Secondary		Kent Ridge		Pulau Ubin Plantation	
Genus	Species	Author	Functional group	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps	Pads	Traps
	Onthophagus sp. 10		ST	2	4	3	10	19	16	194	0	6	0	0	0	0	0	5	0
	Onthophagus sp. 11		ST	0	1	0	3	0	0	3	1	0	0	0	0	0	0	0	0
	Onthophagus laevis	Harold, 1880	ST	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 12		ST	0	2	0	0	0	0	2	0	0	1	0	0	0	0	0	0
	Onthophagus sp. 13		ST	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 14		ST	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 15		ST	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	Onthophagus sp. 16		ST	19	189	0	16	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 17		ST	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus pedator	Sharp, 1875	ST	2	17	0	1	0	0	6	0	6	0	0	0	0	0	0	0
	Onthophagus phanaeides	Frey, 1956	ST	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0
	Onthophagus rorarius	Harold, 1877	ST	5	67	1	178	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus rudis	Sharp, 1875	ST	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus rugicollis	Harold, 1880	ST	0	2	4	49	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus rutilans	Sharp, 1875	ST	1	54	1	50	0	0	1	0	0	0	0	0	0	0	0	0
	Onthophagus semicupreus	Harold, 1877	ST	0	0	0	2	0	0	1	0	1	0	0	0	0	0	0	0
	Onthophagus semifex	Krikken & Huijbregts, 2008	ST	0	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sideki	Krikken & Huijbregts, 1987	ST	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus uenoi	Ochi, 1995	ST	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus vulpes	Harold, 1877	ST	12	74	2	55	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 18		ST	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 19		ST	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Onthophagus sp. 20		ST	1	4	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Paragymnopleurus	*Paragymnopleurus maurus*	Sharp, 1875	LR	0	6	0	10	0	0	0	0	0	4	0	0	0	0	0	0
Sisyphus	*Sisyphus thoracicus*	Sharp, 1875	SR	1	19	1	300	0	0	0	0	0	0	0	0	0	0	0	0
Yvescambefortius	*Yvescambefortius sarawacus*	Gillet, 1926	LD	5	6	0	3	0	0	0	0	0	0	0	0	0	0	0	0
			Individuals	170	721	61	855	19	16	207	1	17	5	27	3	0	0	44	3
			Species	22	38	15	32	1	1	6	1	6	2	2	2	0	0	4	1