THE ECOLOGY OF ELEPHANT DUNG ASSOCIATED DUNG BEETLES IN PENINSULAR MALAYSIA

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FACULTY OF SCIENCE
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THE ECOLOGY OF ELEPHANT DUNG ASSOCIATED DUNG BEETLES IN PENINSULAR MALAYSIA

ABSTRACT

The loss of large mammals such as Asian Elephants (*Elephas maximus*) can potentially disrupt the trophic structure for ecosystems that depend on the dung produced by these animals. This can cause a restructuring of the dung beetle community as it may result in less resources for food and breeding and higher intra- and interspecific competition. Dung beetles utilise dung in different manners, and this leads them to be categorised as dwellers, tunnelers or rollers. These categories of beetle likely have different reactions to changes in resource availability. For this study I 1) Designed a method to collect large numbers of dwelling and tunnelling dung beetles, 2) examined the effects of habitat type on the diversity and abundance of elephant dung visiting dung beetles, 3) determined the effects of elephant removal on the community structure of dwelling and tunneling dung beetles and 4) quantified if changes in resource availability affects the phenotype of six common dung beetle species. A novel dung beetle trap, the burrowing interception trap, was designed and the dung beetle collecting performance was compared with conventional pitfall traps. For objectives (2) and (3), dung beetles were sampled from six localities in Peninsular Malaysia, half of which had elephants absent because of human elephant conflict relocations. Both forest edges and forests were sampled to take into account the effects of habitat. Dung beetles were categorised as forest edge or forest species based on their distribution amongst the two habitat types. Between two localities with similar forest structure and elevation but different presence/absence of elephants, I compared intraspecific pronotum sizes of six species of dung beetles. Burrowing interception traps could collect higher abundance, species richness and Shannon diversity but were not effective in collecting roller dung beetles compared to pitfall traps. A total 5413 individuals from 50 tunnelling and dwelling dung beetle species were collected in all localities. Habitat selection of dung beetles played an important role in community assembly, with 10 species categorised as preferring forest edge environments to forests. Forests also had higher abundance and species richness compared to forest edges. Generalised linear models indicated a a positive relationship between the abundance of dwellers and the presence of elephants. At least two species, *Megatelus brahminus* and *Copris numa,* were found to be absent when elephants were removed, both were forest edge species. When the intraspecific pronotum widths were examined, two dweller species, *Liatongus femoratus* and *Oniticellus tessellatus,* had significant differences in pronotum size, while four tunneler species did not. The loss of elephant dung likely causes a shift from dweller dominated to tunneler dominated communities as an environment with excess resources changes to one of limited and rapidly depleted resources. Aside from extinction, it is possible that some species undergo phenotypic change in order to survive the change in resource availability. This study indicates that the relationship between elephants and dung beetles is a complex interaction that depends on behavioural adaptations of all species and environmental factors.

Keywords: trophic collapse, megafauna, disturbance, adaptation

EKOLOGI KUMBANG NAJIS YANG BERKAIT DENGAN NAJIS GAJAH DI SEMENANJUNG MALAYSIA

ABSTRAK

Kepupusan mamalia besar seperti Gajah Asia (*Elephas maximus*) boleh menganggu struktur trofik ekosistem yang bergantung kepada najis yang dikeluarkan oleh haiwan ini. Ini mungkin boleh menyebabkan penstrukturan semula komuniti kumbang najis, kerana ia mungkin mengakibatkan kekurangan sumber makanan dan tempat pembaikan dan peningkatan persaingan intra- dan inter-spesifik. Kumbang najis mengunakan najis dengan pelbagai cara dan berdasarkan tingkahlaku ini spesis kumbang najis dikategorikan sebagai *dweller*, *tunneler* atau *roller*. Setiap kategori ini mungkin mempunyai reaksi yang berbeza terhadap perubahan kepada kehadiran sumber makanan. Untuk kajian ini, saya telah 1) merekabentuk kaedah baru untuk mengumpul kumbang najis *dweller* dan *tunneler* dalam kuantiti yang besar, 2) Memeriksa kesan habitat keatas kepelbagaian dan bilangan kumbang najis yang mengunakan najis gajah 3) Menentukan kesan penyingkiran gajah keatas struktur komuniti kumbang najis *dweller* dan *tunneler* dan 4) mengkuantifikasikan jika finotaip enam spesis kumbang najis mengalami perubahan jika berlaku perubahan dengan sumber makanan yang ada. Cara menangkap kumbang yang baru, *Burrowing Interception Trap*, telah direka dan dibandingkan dengan prestasi pengumpulan kumbang *pitfall trap*. Untuk objektif (2) dan (3), kumbang najis telah disampel dari enam kawasan di Semenanjaung Malaysia, separuh daripadanya tiada gajah kerana penempatan semula gajah liar akibat konflik manusia-gajah. Hutan dan kawasan pesisiran hutan disampel untuk mengambil kira peranan habitat. Kumbang najis dikategorikan sebagai spesis hutan atau pesisiran hutan berdasarkan taburannya diantara dua habitat tersebut. Diantara dua kawasan yang mempunyai struktur hutan dan ketinggian yang sama tetapi kehadiran gajah yang berbeza, saya membandingkan lebar pronotum intraspecific enam spesis kumbang najis. Berbanding dengan pitfall trap, Burrowing interception trap dapat mengumpul bilangan kumbang, bilangan spesis dan Shannon Diversity yang lebih tinggi, tetapi tidak berkesan dalam mengumpul kumbang najis *roller*. Sebanyak 5413 indiviu daripada 50 spesis kumbang najis tunnelling dan dwelling dikumpulkan daripada semua kawasan. Pemilihan habitat mempengaruhi pembentukan komuniti kumbang najis, dengan 10 spesis dikategorikan sebagai spesis persisiran hutan. Hutan juga mempunyai bilangan kumbang dan spesis yang lebih tinggi berbanding dengan persisiran hutan. Menurut GLM, bilangan kumbang najis *dweller* mempunyai hubungan positif. Dua spesis persisiran hutan, *Megatelus brahminus* dan *Copris numa* tidak dapat dijumpai di kawasan tanpa kehadiran gajah. Bila lebar pronotum intraspecific dibandingkan, dua spesis *dweller*, *Liatongus femoratus* dan *Oniticellus tessellatus,* mempunyai perbezaan signifikan di dalam saiz pronotum, manakala empat spesis *tunneller* tidak mempunyai perbezaan. Kehilangan najis gajah daripada ekosistem mungkin menyebabkan peralihan daripada komuniti yang didominasikan oleh kumbang *dweller* kepada komuniti yang didominasikan oleh kumbang *tunneler* akibat daripada perubahan persekitaran yang mengandungi sumber makanan yang berlebihan kepada persekitaran yang mengandungi sumber makanan yang terhad dan dihabiskan dengan cepat.Selain daripada kepupusan, mungkin ada spesis yang mengalami perubahan fizikal untuk bertahan dengan perubahan keadaan sumber makanan. Kajian ini menunjukan bahawa hubungan diantara gajah dan kumbang najis adalah satu interaksi yang kompleks yang melibatkan adaptasi tingkah laku setiap spesis dan faktor persekitaran.

Kata kunci: runtuhan trofik, megafauna, ganguan, adaptatasi

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LIST OF SYMBOLS AND ABBREVIATIONS

AIC	:	Akaike's Information Criterion
BIT	:	Burrowing Interception Trap
DWNP	:	Department of Wildlife and National Parks
GLM	:	Generalised Linear Model
NMDS	:	Non-metric Multidimensional Scaling
PERMANOVA	:	Permutational analysis of variance
Q-Q plot	:	Quantile-Quantile plot
SNE	:	Balanced variation (Sorenson dissimilarity decomposition)
SIM	:	Abundance gradient (Sorenson dissimilarity decomposition)
UPGMA	:	Unweighted Pair Group Method with Arithmetic Mean

1.0 GENERAL INTRODUCTION

Very little is known about the association of dung beetles with megafauna such as elephants within Asia. In the Malaysian context a short checklist of species which were found in elephant dung has been published (Goh *et al*., 2014), which concluded that several rare species, which included large tunnelers from the genus *Copris*, the very large tunneler *Heliocopris* and the dweller *Megatelus* were found in elephant dung (Goh *et al*., 2014). These results were in contrast to a survey conducted by Doll *et al*. (2014), which using elephant dung baited pitfall traps reported the dominance of various medium tunneler Onthophagini species. Further literature searches uncovered records from India that suggested that medium sized dwellers from the tribe Oniticellini may be specialists of elephant dung (Sabu *et al*., 2006; Vinod & Sabu, 2007). In this thesis I expand on Goh *et al*. (2014) and explore the dung beetles associated with elephant dung. What is the effect of habitat selection? What is the actual community structure of dung beetles visiting elephant dung? What was the cause of the differences between communities described by Goh *et al*. (2014), Doll *et al*. (2014), Sabu *et al.* (2006) and Vinod and Sabu (2007)? Which of these groups specialised or were totally endemic to elephant dung? How do these beetles utilise this unique dung type? With the current conservation crisis, are dung beetles in danger of extinction?

Large mammals in South East Asia are facing the increasing threat of extinction due to habitat loss and poaching (Ripple *et al*., 2016). It has been argued that many large mammals act as keystone species, and the loss of such species leads to a chain reaction of changes to ecological systems (Nicols *et al*., 2009; Terborgh & Estes, 2010). Asian elephants (*Elephas maximus*) have poor digestion and require a large amount of food to sustain their large body size, consequently they produce massive amounts of dung (Sukumar, 2003). This dung is utilised by dung beetles, which incorporate it back into the nutrient cycle by burying it back into the soil (Nicols *et al*., 2008). When there is a loss of elephants due to relocation or poaching, a large amount of potential resources for the dung beetle community is removed and this leads to less available food and breeding sites (Nichols *et al*., 2009). Increased competition for resources, restructuring of the existing community structure or loss of ecosystem functions can be results of this perturbation to the system (Nichols *et al*., 2009).

This study was conducted in the zoogeographical subregion of Sundaland. While this study was conducted fully in the political unit of Peninsular Malaysia, the political boundaries of Malaysia do not accurately depict the biogeography of the Malay Peninsula. In this study I refer to 'Peninsular Malaysia' as a political entity while 'Malay Peninsula' corresponds to the biogeographic zone. Here I define the Malay Peninsula following the Northern Sundaland boundary proposed by Kloss (1929) of latitude 10°N. This includes Peninsular Malaysia, portions of Southern Thailand that are below the Isthmus of Kra and the islands surrounding the Peninsula (the largest of which are Penang, Singapore and Langkawi). These areas share a similar climate, but with some variations in seasonality due to the central mountain range that runs along the center of the Peninsula (Elliot *et al*., 1992).

In order to study certain aspects of the dung beetle community, new sampling protocols had to be devised. While the current method of dung baited pitfall traps is useful for targeting tunnelling and rolling species (Hanski & Cambefort, 1991), it tends to miss some target species that are usually found in wild elephant dung (Goh *et al*., 2014). In order to survey components of the dung beetle community that are of interest, a new method that could combine the detection of manually surveying intact bolii of elephant dung with a standardised replicable size so was required. Additionally, this method had to detect dweller beetles and very large dung beetles, which Goh *et al*., (2014) and Vinod & Sabu (2007) believed were characteristic of elephant dung. It also had to be relatively easy to set up large numbers of traps with a limited amount of manpower. There exists informal discussion and limited records of traps which may fulfil these requirements, but they have never been tested in South East Asia (Bernon, 1980; Doube & Giller, 1990). Therefore, formally describing this type of trap, and comparing these traps to pitfall traps is a prerequisite to further study.

As elephants are capable of altering their environment through feeding and seed dispersion (Terborgh, 2017; Campos-Arceiz & Blake, 2011) there is a large possibility that the pre-existing habitat requirements of dung beetles may be a factor in their response to elephant removal. It has recently been recognised that elephants are edge specialists that prefer forest edges to forest interiors, likely due to the presence of more abundant food items for grazing (Wadey *et al*., 2018). Unlike elephants, which have a very wide niche due to their large body size and versatile feeding habits (Sukumar, 1991), dung beetles are relatively much smaller and are therefore physiologically limited to smaller habitat niches (Davis *et al*., 2001). While there has been some study of how dung beetles in Borneo react to changes in habitat type (Davis *et al*., 2001), the habitat preferences of many species of the Malay Peninsula are still undocumented.

There is no information on what happens to dung beetles when Asian elephants are removed from a habitat. While the effects of the loss of very large megafauna on forest structure has been explored (Terborgh *et al*., 2017), little is known about the changes to animal communities when elephants are removed. There are few species documented to feed on elephant dung, but it has been noted that several rare beetles can be found within this type of dung (Goh *et al*., 2014). In terms of community structure, Vino & Sabu (2007) noted that in India, elephant dung tends to be dominated by dwellers as opposed to tunnelers and rollers. Dwelling beetles, which have a close association with herbivorous mammals, are relatively neglected in dung beetle studies in South East Asia. Even less is known about how the loss of megafauna would affect this group of beetles. It is unknown if a trophic collapse occurs following the removal of elephants, or if there is a shift from one stable state to another.

It can be hypothesised that two patterns of community reassembly could result from the loss of elephants, 1) if elephants are a keystone species the trophic collapse would result in an overall loss in abundance and species richness of both tunneler and dweller dung beetles or 2) if only specialised species can exploit elephant dung, there would be a pattern of species turnover in which only certain species are lost from the community. It is worth asking whether the large tunneling beetles in South East Asia are associated with elephant dung due to the amount of resources required to build nests, which appears to be the case in the Afrotropical region (Cambefort, 1991). Another possible interaction that may arise from the presence of large amounts of persistent dung is the presence of dwelling beetles, which may be outcompeted by tunnelers when the supply of dung is smaller.

Since elephant dung is a very coarse and high fibre dung that is not high in nutrient density, like other herbivorous mammal dung it is a poor resource for dung beetles to use as a breeding medium (Emlen, 1994). While some beetles may visit elephant dung or be caught in elephant dung baited traps, elephant dung may not be an obligate requirement for the development of some species of dung beetles. Differences in pronotal widths, which can be used as a proxy measure for the amount of dung provisioned during the larval stage (Emlen, 1994), may be a useful way to determine if there are any changes to resource availability of a beetle species following the removal of elephants from a habitat.

1.1 Objectives

1) To compare the effectiveness of burrowing interception traps (BITs) and pitfall traps.
2) To determine the effects of forest edges on dung beetle communities.
3) To quantify changes in tunneler and dweller dung beetle communities following the removal of elephants.
4) To determine associations between dung beetle species and elephants.
5) To compare the differences in pronotal width in dung beetles in forests with and without elephants.

1.2 Research questions:

1) What is the difference in performance between burrowing interception traps (BITs) and pitfall traps?
2) What are the habitat preferences of dung beetle communities?
3) Is there a change in tunneler and dweller dung beetle communities following the removal of elephants from an ecosystem?
4) Are there any associations between dung beetle species and elephants?
5) Is there a difference in intraspecific pronotal widths of dung beetle species in forests where elephants are present or absent?

2.0 LITERATURE REVIEW

2.1 General literature review:

2.1.1 Asian elephants:

The Asian elephant (*Elephas maximus*) is the sole living representative of the genus *Elephas*, one of only three species of extant Proboscidea in the world (Sukumar, 1996). Weighing up to 4 tons and with a shoulder height of 2.75 m the Asian elephant is the largest extant land animal on the Asian continent (Harisson, 1966). Asian elephants are social animals where the females and young live in matriarchal herds while the males live a more solitary existence (Sukumar, 1996). The gestation period of 18-22 months is extremely long even for a mammal, and combined with the long suckling period of up to three years results in a birth interval of four to five years (Sukumar,1996). Low birth rates, combined with food requirements due to large body sizes puts elephants at a high risk of extinction due to perturbations to the environment (Ripple *et al*., 2016). Elephants are hindgut fermenters and unlike ruminant fermenters like cows, their dung does not go through much processing, this leads to dung with large amounts of poorly digested fibre (Sukumar, 2003).

2.1.1.1 Status of elephants and human wildlife conflict:

Peninsular Malaysia has an estimated wild elephant population size of 1223 to 1677 individuals which are mainly distributed in the northern states of Kelantan and Terengganu, the central states of Perak and Pahang, and the Southern state of Johor (Saaban *et al*., 2011). There have been very low numbers of elephants killed by humans legally and illegally, with incidents of poaching relatively low compared to the other countries in the region (Saaban *et al*., 2011). However, deaths do occur through road accidents (David, 2017) or accidents during conflict with humans (Bedi, 2018). Some young elephants are injured by snares targeted at other wildlife (Saaban *et al*., 2011).

The largest threat to elephants however has been that of encroachment into human spaces which fuels Human Elephant Conflict (HEC) (DWNP, 2006; Saaban *et al*., 2011). While this conflict is mainly driven by the destruction of the lowland forests that are typically inhabited by elephants (Clements *et al*., 2010) recently there has been evidence that it is not the lack of food that pushes elephants towards human plantations, but it is the abundance of resources and preferred food plants that can be found near roads or monoculture plantations relative to the unfavourable woody plants in pristine forests that draw elephants towards human plantations (Wadey *et al*., 2018; Yamamoto-Ebina *et al*., 2017; Campos-Arceiz, 2013). In this sense, HEC is caused by the increased area of interface between humans and elephants instead of the destruction of suitable habitat and feeding grounds (Campos-Arceiz, 2013). The Department of Wildlife and National Parks (DWNP or in its Malay acronym PERHILITAN), manages cases of HEC in Peninsular Malaysia (DWNP, 2006) and has established several action plans for the mitigation of such conflict, such as the Elephant Management Plan (2006), and the Action Plan for Wildlife Conflict Management (2010-2015). The DWNP employs several methods to prevent elephants from entering human settled areas. Amongst these are to scare the elephants away with firearms, to prevent entry in plantations through the use of electric fences and the relocation of elephants to forests that are far from human habitation (DWNP, 2006). Due to proper implementation, HEC in Peninsular Malaysia are rarely lethal to either side of the conflict. However, the relocation of elephants from forest fragments or forests that are near human habitation has resulted in forests where elephants are absent and locally extinct (Saaban, 2011).

2.1.1.2 Elephants as bioengineers and Megagardeners:

The presence of megafauna is a distinct feature of South East Asia that is only shared by the Afrotropical region. Of these megafaunas, elephants represent a unique influence on forest structure and diversity due to their large body size and very wide dispersal ability in the range of hundreds of square kilometers. (Sukumar, 2003; Campos-Arceiz & Blake, 2011). Through their feeding activities, elephants influence the seed dispersal (Campos-Arceiz & Blake, 2011) as well as the survivability of saplings (Terborgh, *et al.*, 2017). In the long term, these activities cumulatively affect the biodiversity and forest structures of the South East Asian rainforests (Campos-Arceiz & Blake, 2011). Additionally, elephants and wild cattle act as bioengineers in the management of grazing grounds as these animals are capable of suppressing the growth of secondary forests by trampling and clearing shrubs and saplings (Scheffer *et al.*, 2001). Feeding grounds that are regularly visited by elephants are usually covered in tall grasses as opposed to secondary forest successional plants, and elephants are known to strip the bark of young early succession trees, an act which may change the succession patterns of forests (Goh, T.G., pers. obs). Elephants from the Malay Peninsula show a preference towards grassy habitats with monocotyledonous plants (Wadey *et al.*, 2018) and analysis of plants fragments in elephant dung show that fast growing grasses, bamboos, gingers and bananas are preferred food items of elephants (Yamamoto-Ebina *et al.*, 2016). There is still no proper study as to whether elephants are creating and maintaining these environments or merely attracted to them, but large tusked males and matriarchs are capable of toppling trees or killing trees through browsing or striping bark which leads to the creation of new forest gaps (Sukumar, 2003). Areas with intense elephant activity such as salt licks are often quite barren due to the intense disturbance of these animals (Pers. obs.). As a whole, elephants affect what is in the forest and where the borders of the forest lie through the acts of seed dispersal (Campos-Arceiz & Blake, 2011) and their actions of stripping bark and feeding on trees along the forest border (Sukumar 2003; Wadey *et al*., 2018).

2.1.2 Dung beetles:

In contrast to the single species of the Asian elephant, dung beetles are an entire community that is composed of various subfamilies, tribes, genera and species. Dung beetles comprise of two subfamilies of Scarabaeidae, Scarabaeinae and Aphodiinae which combined have over 5000 species described worldwide as of 2004 (Spector, 2006). The sizes of dung beetles vary between 2mm to 50mm, ranging from very small to relatively large beetles (Hanski & Cambefort, 1991). Like elephants, some dung beetles practice parental care and raise a single larva at a time, while other species of dung beetles lay masses of eggs which they abandon (Hanski & Cambefort, 1991). Due to their size and relatively rapid development, dung beetles can achieve several generations in a year in tropical conditions (Hanski & Cambefort, 1991). Some dung beetles are relatively resilient to changes in habitat, while others are sensitive to alterations to their microhabitat (Boonrotpong *et al*., 2004; Doll *et al*., 2014; Hosaka *et al*., 2014; Lee *et al*., 2009; Shahabuddin *et al*., 2010). Unlike elephants, little is known of the ecology of many species of dung beetle. Some species are merely known by museum specimens and have never been observed alive (Arrow, 1930; Balthasar, 1963).

The subfamily Scarabaeinae or true dung beetles feed mainly on dung (Triplehorn & Johnson, 2005). Since this resource is pre-digested and rich in nutrients, these beetles have shorter digestion tracts and hence shorter abdominal sternites compared to the herbivorous subfamilies of Scarabaeidae (Arrow, 1931; Hanski & Cambefort, 1991). Almost all these beetles have some sort of adaptation to fossorial movement such as flattened and shovel like heads and front tibia which are furnished with tooth-like projections that are used for digging (Hanski & Cambefort, 1991). Some of these beetles have become extremely adapted to specialized modes of living, with some beetles with extremely short limbs and almost spherical bodies that specialize in tunneling to beetles with long spider like legs that specialize in rolling dung balls (Arrow, 1931; Hanski & Cambefort, 1991).

Of these two subfamilies, Aphodiinae or Aphodian dung beetles are considerably less conspicuous than Scarabaeinae (Triplehorn & Johnson, 2005). This subfamily usually has dull colouration of browns, dark reds and blacks, does not display any specialized behaviours such as rolling dung balls and rarely possesses impressive horns (Hanski & Cambefort, 1991). As they are rarely attracted to lights, the only way to encounter them is through manually searching dung or by targeting them with traps (Hanski & Cambefort, 1991). This subfamily is distinguished from all other subfamilies of Scarabaeidae by the elytra which completely cover their pygidium (Triplehorn & Johnson, 2005). Among dung feeding Scarabaeidae, they are further distinguished by the presence of two terminal spurs on their hind tibia, as opposed to the single terminal spur found on Scarabaeinae (Balthasar, 1963).

2.1.2.1 Breeding behaviour of dung beetles:

Scarabaeid dung beetles display the typical breeding behaviour of provisioning a nest of larvae with some form of decaying material. According to (Hanski & Cambefort, 1991) beetles can be divided into the following functional groups: Dwellers, Tunnelers and Rollers. The terms endocoprid, paracoprid and telocoprid correspond to these functional groups, but essentially mean the same thing while adding unnecessary jargon. These categories describe how the beetles utilize dung; dwellers build nests of dung balls within the dung pat itself or within shallow excavations, tunnelers build deep tunnels that end with a nesting chamber filled with dung provisions and rollers make dung balls, roll them a distance away, and then bury them in a relatively simple tunnel nest (Hanski & Cambefort,1991). All these behaviours achieve the same result of building a protected, provisioned and climate-controlled environment to raise larva until adulthood. However, while these breeding behaviours describe traits of how individual species manipulate dung in their environment, these categories do not describe phylogenetic lineages of beetles accurately, as some tribes have both dwelling and tunneling species (Hanski & Cambefort,1991).

Dwellers are mostly limited to the Aphodiinae, which are usually small to medium sized beetles that utilize large amounts of dung such as the large dung pads of Bovidae (Hanski & Cambefort, 1991). The entire life cycle of these beetles occurs within a single dung pat. These beetles are quite rare in environments where more competitive Scarabaeinae tunnelers and rollers are found, as the intense competition from Scarabaeinae typically removes the entire dung pat within a few hours (Hanski & Cambefort, 1991). It might be that dwellers can only survive when there is more dung available than can be buried through competition. One notable genus from a typically tunneling tribe is *Oniticellus*, which builds shallow nests that are functionally similar to dwellers (Hanski & Cambefort, 1991). This shows that dwelling is not a wholly primitive trait, but it may be advantageous under certain conditions. On the Malay Peninsula, there are far fewer records of dwelling Aphodiinae than tunneling Scarabaeinae, mostly due to the lack of taxonomic interest in the group and the limited distribution of Aphodiinae in South East Asia. For *Oniticellus* species, *On. cinctus* has a cosmopolitan distribution but is mostly limited to pastures (Hanboonsong, 1999; Arrow, 1931; Balthasar, 1967) while *On. tessellatus* is found throughout Indochina, Thailand, Sumatra, Borneo and the Malay Peninsula and appear to prefer forested environments (Balthasar, 1963b; Slade *et al*., 2014; Gray *et al*., 2014; Doll *et al*., 2014; Kabakov & Napolov, 1999).

Tunnelers are the most common functional group of dung beetles and this type of behavior is believed to be the ancestral behavior of the basal Scarabaeinae dung beetle (Hanski & Cambefort, 1991). Tunnelers form the majority of dung beetle diversity in South East Asia, with many belonging to the species rich genus *Onthophagus* (Hanski, 1991). Most *Onthophagus* are small to medium sized tunnelers and can range in terms of abundance from rare to very common, while other larger tunnelers such as *Catharsius*, *Copris* and *Heliocopris* tend to be less abundant.

These beetles construct nests at the end of tunnels that they dig under the dung (Hanski & Cambefort, 1991). Tunnels can be shallow or deep, consisting of a single chamber or multiple chambers, and protected by parents or abandoned after the eggs are deposited (Hanski & Cambefort, 1991). Eggs are laid in the dung provisioned in nest, with a single egg to a single dung ball or sausage (Hanski & Cambefort, 1991). These tunnels are then sealed off and the eggs develop to adulthood in a safe environment. Construction of the tunnels are usually done by the female which digs the tunnel and begins provisioning the nest, but a few species conduct this work as male-female pairs, a form of sub-social parental care that is rare in insects (Hanski & Cambefort, 1991). While joint parental care is relatively uncommon, almost all male beetles guard the entrance of the tunnel to prevent other males from mating with the female (Emlen, 2014). This needs to protect nests from the intrusion of other males has driven an evolutionary arms race that has produced an amazing variety of horns in tunneling species (Emlen, 2014).

Rollers avoid direct duels for nesting sites by removing a portion of dung, fashioning it into an easily transportable ball and rolling it away to a new site where a shallow tunnel and nest can be constructed (Emlen, 2014). It is believed that rolling evolved as a way to avoid the immense competition for nesting sites that occurs under dung (Hanski & Cambefort, 1991). These beetles have several adaptations to rolling balls of dung, with longer legs, curved tarsi or tibia and longer spurs for gripping dung balls (Hanski & Cambefort, 1991). Typically, rollers roll balls of dung away on their hind legs; however some genera such as the African *Scarabaeus* push dung balls with their front legs (Hanski & Cambefort, 1991). South East Asia is not particularly species rich in rollers; on the Malay Peninsula only four genera and 10 species of rollers have been recorded. These genera are *Paragymnopleurus* (three species), *Sisyphus* (one species), *Synapsis* (three species) and *Ochicanthon* (three species) (T. G. Goh, unpublished data).

2.1.2.2 The development of dung beetles:

The typical development of a dung beetle begins when a single fertilised egg is laid in a piece of provisioned dung (Hanski & Cambefort, 1991). These provisions are typically ball, pear or sausage shaped (Hanski & Cambefort, 1991). As with most Scarabaeidae, dung beetles undergo three larval stages or instars in which ecsdysis or moulting occurs at the end of the stage (Arrow, 1930). The larva of Scarabaeinae can be identified by the distinctive hump shape on their abdominal segments (Balthasar, 1963). In this larval stage they are fully dependent on the dung within their provision. Experimental studies have shown that the amount of dung provisioned for the larva have a large impact on its adult life, larva provisioned with more dung tend to become adults with larger pronotums and longer horn, traits which are linked to better combat performance in tunnels (Emlen, 2014).

After the final larval stage, the larva becomes a pupa. It is at this stage that the stored nutrients during the larval stage are used to create the integument of the adult form (Emlen, 2014). The newly formed adult beetles then emerge from their protective nest and begin their lives as adults (Hanski & Cambefort, 1991). It should be noted that when nesting beetles emerge, they are relatively light and frail (Hanski & Cambefort, 1991). These beetles must feed for several weeks or even months to compensate for the nutrient poor conditions that results from the limited resources of nesting. This is known as *Reifungsfrassperiode*, or the Maturation Feeding Period (Hanski & Cambefort, 1991). It is during this time that these beetles may be attracted to different types of protein rich bait such as rotting fish (Hanski & Cambefort, 1991). It is important to take this behavior into account when interpreting information from baited traps, as some beetles may facultatively feed on a wider range of food items than they use for nesting. When the muscles and reproductive organs have obtained sufficient size, the beetles can then search for dung and begin the mating process (Hanski & Cambefort, 1991). Unlike the competition free larval period, this portion of the life cycle involves desperate competition for mates and resources (Hanski & Cambefort, 1991).

2.1.2.3 Utilisation of other resources:

Dung beetles in Southeast Asia are also known to utilise resources other than dung as food. This corresponds with observations by Gill (1991) of Neotropical dung beetles utilising resources other than dung. These include: saprophagy, frugivory, necrophagy and parasitism. Several species have been observed feeding on plant detritus

(Masumoto, 2001a) or fleshy fruits such as figs (Davis and Sutton, 1997), persimmons (Masumoto, 2001a) or jackfruit (Masumoto, 2001a). The *Onthophagus* species that were observed feeding on fruits were related within the same species group as *O. deflexicollis* (Davis & Sutton, 1997). Other beetles species have adapted to exploit other nutrient rich food sources such as vertebrate carrion (Goh, 2014) and dead millipedes (Masumoto, 2001b). Most necrophagus species are from the *Onthophagus* subgenus *Parascatonomus* or the genus *Ochicanthon*, which are reportedly be rare when trapped using dung but easily collected using rotten meat (Ochi & Araya, 1997). However, even dung feeding species are known to be attracted to carrion, this is likely a post-eclosion feeding behaviour in which the dung beetles are obtaining the necessary proteins required to develop mature sexual organs (Hanski & Cambefort, 1991).

Table 2.1: Records of beetles directly feeding on non-dung material.

Non-dung food item:	Species:	Reference:
Carrion:		
Rat Carrion	*Onthophagus babirussa* *O. semifex* *O. vulpes* *O. rudis* *Copris ramosiceps* *Paragymnopleurus maurus*	Goh (2014)
Dead Millipedes	*O. penicilatus*	Masumoto (2001b)
Plant matter:		
Plant detritus	*O. deflexicollis*	Masumoto (2001a)
Rotten jackfruit	*O. deflexicollis*	Masumoto (2001a)
Rotten wild persimmons	*O. bonarae*	Masumoto (2001a)
Figs	*O. deflexicollis* *O. batillifer* *Microcopris reflexus*	Davis and Sutton (1997)

2.1.2.4 Classification of dung beetles:

It was previously assumed that dung beetle phylogeny could be divided into two monophyletic groups based on how they exploit dung: The Scarabaeinae, which roll dung into balls for transport to nesting sites with less spatial competition, and the Coprinae, which build nesting tunnels beneath the dung (Balthazar, 1963; Cambefort & Hanski, 1991). Each group consisted of six tribes according to Balthazar (1963) (Table 2.2). The underlying assumption of this classification was that both nesting systems were so complex that they must have evolved only once (Halffter & Matthews, 1966; Halffter & Edmonds, 1982). A competing view of the phylogeny, but based on a similar assumption, is that of Janssens (1949) which divides Scrabaeninae into six tribes: Coprini, Eurystenini, Oniticellini, Onitini, Onthophagini and Scarabaeini. In this classification only Scarabaeini exhibits the dung rolling behaviour. Lawrence and Newton (1995) later proposed a revision of Balthazar (1963) in which Coprinae was synonymous with Scarabaeinae and that all 12 tribes be placed within Scarabaeinae. Most modern workers tend to classify all non-Aphodine dung beetles as Scarabaeinae and maintain the Balthazar's (1963) tribes, this is more due to convenience and tradition rather than proper phylogenetic study. Cambefort (1991) organized these tribes into rollers and tunnelers, and based on biogeography categorized them as old, intermediate and modern tribes (Table 2.3).

The hypothetical division between tunneling Coprinae and rolling Scarabaeinae however has not stood up to some morphological and genetic studies of the phylogeny of dung beetles. Phylogenies constructed using morphological (Zunino, 1983; Luzatto, 1994; Montriel, 1998) and molecular methods (Villalba *et al*., 2002; Phillips, 2004, Emlen & Phillips, 2006; Monaghan *et al*., 2007) all point toward rolling behavior being polyphyletic and developing independently in multiple lineages. Consequently, Davis

(2002) proposed a classification based on the biogeographical distribution of the genera, dividing the tribes into four distribution clusters: Madagascan, Gondwanaland, Afro-Eurasian and American (Table 2.4). Tarasov and Genier (2015) noted that the current tribe classification needed revision due to the polyphyletic nature some tribes, and Tarasov and Demitrov (2016) subsequenly used molecular and morphological characters to attempt to redefine problematic tribes such as Deltochilini (Canthonini), Dichotomiini and Coprini and Sisyphini. Of the species that were relavant to Southeast Asia, Coprini was redefined as a monophyletic group that excluded Heliocopris, Synapsis and Catharsius.

In this thesis, the tribal classification proposed by Davis (2002) is adopted, but taking into account recent developments in Davis (2011). Gymnopleurini, Sisyphini, Canthonini and Onitini of the Malay Peninsula are monogeneric and used to describe the corresponding genera of *Paragymnopleurus*, *Sisyphus*, *Ochicanthon* and *Onitis*. Oniticellini has three genera; *Oniticellus*, *Liatongus* and *Yvescambefortius*, but Breeschoten *et al*. (2017) indicates that the representatives in the Oriental region form a monophyletic group and this thesis will use this as a valid tribe. Dichotominii and Coprini are likely to be polyphyletic (Davis, 2011), therefore these tribes will not be referenced directly and this thesis will refer to the individual genera of *Heliocopris*, *Copris*, *Synapsis* and *Catharsius* when necessary. Onthophagini are acknowledged to likely to be polyphyletic (Davis, 2011) and several subgenera may be elevated to generic status in the future, but due to the complexity of the task it is likely that this group will not be phylogenetically resolved anytime soon. Therefore, any reference to Onthophagini in this thesis will be referring to the genera *Onthophagus* and *Caccobius*.

Table 2.2: List of tribes according to Balthazar (1963) and their worldwide distribution. (distribution from Cambefort & Hanski 1991)

		Distribution:
Rollers:	Canthonini*	Afrotropical, Australian Madagascar, Nearctic, Neotropical, Oriental, Palearctic
	Eucraniini	Neotropical
	Eurysternini	Nearctic, Neotropical
	Gymnopleurini*	Afrotropical, Oriental, Palearctic
	Scarabaeini	Afrotropical, Oriental, Palearctic
	Sisyphini*	Afrotropical, Nearctic, Oriental, Palearctic
Tunnellers:	Dichotomiini*	Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palearctic
	Onitini*	Afrotropical, Oriental, Palearctic
	Phanaeini	Nearctic, Neotropical
	Coprini*	Afrotropical, Australian, Nearctic, Neotropical, Oriental, Palearctic
	Oniticellini*	Afrotropical, Madagascar, Nearctic, Neotropical, Oriental, Palearctic
	Onthophagini*	Afrotropical, Australian Madagascar(?), Nearctic, Neotropical, Oriental, Palearctic

* Tribes found in the Malay Peninsula

Table 2.3: The classification of tribes by Cambefort (1991).

Category:	Tribe
Roller:	
Old	Canthonini
Intermediate	Scarabaeini
	Gymnopleurini
	Eucraniini
	Eurysternini
Modern	Sisyphini
Tunneler:	
Old	Dichotomiini
Intermediate	Onitini
	Phanaeini
Modern	Coprini
	Oniticellini
	Onthophagini

Table 2.4: Classification of tribes by Davis *et al*. (2002)

Distribution cluster:	Genera:
Madagascar	Oniticellini:
	Helictopleurina
Gondwanaland	Canthonini
	Dichotomiini
Afro-Eurasian	Oniticellini:
	Drepanocerina
	Sisyphini
	Onitcellini:
	Oniticellina
	Coprini
	Onthophagini
	Scarabaeini
	Gymnopleurini
	Onitini
Americas	Phanaeini
	Eucraniini
	Eurysterini

2.1.2.5 A taxonomic review of dung beetles in the Southeast Asian region:

Studies into the diversity of dung beetles in South East Asia have been rather scattered. Modern reference materials begin with Arrow (1931), which summarised the extent of species found in the Indian subcontinent and other British Colonies, recording about 354 species in British India. Due to the large number of species and often inadequate keys and illustrations, this work is very difficult to use for identification purposes. This effort was followed up by Balthazar's (1963) revision of the Scarabaeinae of the Paleoarctic and Oriental regions, which remains one of the main references of Scarabaeid diversity in the Oriental region. Unfortunately, this relatively comprehensive work was written in German and has never been translated.

The description of species from the region then went dormant until the 1980s work of the Dutch team of Huijbregts and Krikken, who did the identification for the Hanski's (1983) landmark study on South East Asian dung beetles (Appendix 1). Concurrently, the Japanese team of Ochi and Kon, released publications on the taxonomy of several species groups in the South East Asian region (Appendix 1). Currently, both teams are still actively working on species from the Malay Peninsula. In the 1990s, the Russian taxonomist Kabakov and Japanese Masumoto began independently surveying the Indochinese and Thai regions respectively (Appendix 1). All the taxonomy work that has been done has been rather traditional in its methods, often relying solely on morphological characters.

A majority of the fragmented work done thus far has been lacking in keys (Appendix 1). However, resolving entire genera of dung beetles is too daunting a task, especially for the genus *Onthophagus* which is estimated to have 400 species in the entire region. Additionally, both groups have not done much work on the Malay Peninsula. The Japanese and Dutch groups apparently did not communicate outside of journal publications, resulting in synonyms exclusive to each group. Both groups also preferred to publish in obscure local journals, making it a difficult task to track down references. Consequently, species level identification can only be done by experts who have access to a relatively complete reference collection, but the identifications are almost always contradictory.

Conflicts in nomenclature have found their way into many publications, for example Lee *et al*. (2009a), Lee *et al*. (2009b), Qie *et al*. (2011), Doll *et al*. (2014) and Ong *et al*. (2013) referred to the *Catharsius* species present in the Malay Peninsula as *Catharsius molossus*, while Niino *et al*. (2014) recorded it as *Catharsius renaudpauliani*, a species described in Borneo by Ochi and Kon (1996a). Hosaka *et al*. (2013) collected an unusually large number of *Onthophagus pauper*, a species previously only recorded in Java, while Qie *et al*. (2011) recorded a species very similar in appearance in the same locality, *O. leusermontis*, which was described by Huijbregts and Krikken (2011). Until the taxonomy for these species is resolved, all species identifications for ecological studies in the region should be taken with a healthy dose of skepticism. One of the most common beetles of the Malay Peninsula is referred to as the undescribed manuscript name *O. babirussoides* in Lee *et al*. (2009a), Lee *et al*. (2009b), Qie *et al*. (2011), Doll *et al*. (2014), Goh (2014); and as *O. obscurior* in Niino *et al*. (2014). In this thesis it will be refered to as *O. babirussa*.

2.1.3 Trophic collapse

Trophic cascades are observed when there is a disturbance to a food web, it can be described as the indirect consequences following the loss of a predator or a component of a food web (Terborgh & Estes, 2010). Ecosystems have top-down pressures, which are predators that keep lower trophic levels in check, and bottom-up pressures, which deal with the provisioning of resources for higher levels of the food web (Terborgh & Estes, 2010). ffects of trophic cascades can be rapid in terrestrial ecosystems, for example the removal of predators can result in the hyperabundance of certain species in other trophic levels, this in turn leads to cascades that can threaten the ecosystem functions of an entire ecosystem (Terborgh et al. 2001). The term "trophic collapse" was described by Dobson et al. (2006) as a rapid loss of species within a community following change to the food web structure. Trophic collapse as modeled by Dobson et al. (2006) are initiated by the thinning of a species within a food web, followed by a rapid shortening of the food web. In the case of this study, observing changes to the community structure, especially the loss of species compared to a baseline, may be sign that a trophic cascade or trophic collapse is taking place within the dung beetle community.

2.2 Dung beetle specimen collection for ecological study:

Baited pitfall traps have long been the preferred trap in the field of dung beetle ecology (Hanski & Cambefort, 1991; Larsen and Forsyth, 2005). As such, this trap is recommended as a standard method for the collection of dung beetles, as this aids in comparative studies and meta-analysis (Nichols *et al.* 2007). However, attempts to collect the target genera of *Heliocopris* and *Megatelus* using conventional baited pitfall traps were largely unsuccessful, these species were also rarely recorded in diversity surveys that used pitfall traps (Hanski, 1983; Hanski & Niemela, 1989; Davis *et al.*, 2001; Lee *et al.*, 2009; Qie *et al.*, 2011; Gray *et al.*, 2014). This necessitated the use of a trapping method that closely resembled physically examining the bolli of wild elephants as described in Goh *et al*. (2014). This type of trap had to share the advantages of pitfall traps, i.e. be relatively inexpensive, can be quickly set up and collect a comparably large sample of beetles (Spector, 2006).

There exists another type of trap that has similar advantages to pitfall traps, but these traps are rarely mentioned in the literature. The general design of these traps involves placing dung on soil in a container and preventing dung beetles from burrowing out of the container, these traps are termed as burrowing interception traps. These traps have the additional advantage of collecting specimens alive but permit the movement of beetles in and out of the traps. The earliest mention of such traps was by Bernon (1980), who outlined a method for collecting dung beetles and phoretic mites that mimics the natural conditions of dung. Doube and Giller (1990) described a trap of the following design: “1 litre dung pads were placed at ground level on several litres of sieved soil in an excavation approximately 50 cm wide and 30 cm deep and lined with gauze to prevent the beetles tunnelling into the soil beneath the trap”. This trap showed similar performance to pitfall traps in collecting pastoral South African tunnelling species (Doube & Giller 1990). However, there are no records of how these traps perform in relation to pitfall traps in tropical settings.

2.3 Dung beetle habitat preference:

Not much has been recorded about the preferences of dung beetles to the disturbed habitats which elephants prefer. But the effects of habitat type may be a factor in the distribution of dung beetles and the habitat type might become a confounding variable in any analysis on the community structure unless it is accounted for. A bulk of dung beetle community studies which deal with the effects of habitat in South East Asia have mostly been conducted in the Malay Peninsula, Sulawesi, and Borneo. The most recent estimate of the shared species between the Malay Peninsula and Borneo is 25%, while that of the Malay Peninsula and Sulawesi is less than 10% (Hanski & Krikken, 1991).

Studies in the Malay Peninsula tend to compare overall community structure of habitat types rather than examine the response of individual species to habitat disturbance. Lee *et al*. (2009) surveyed undisturbed forests and disturbed forests and concluded that species richness, abundance and biomass decreased along a disturbance gradient. Doll *et al*. (2014) conducted a comprehensive study of dung beetles in forests within the Malay Peninsula, surveying a mix of primary and secondary forests. While the community data was analysed using ordination, Doll *et al*. (2014) did not categorise species according to different habitat types. Hosaka *et al*. (2014) compared forest clearings from logging to the surrounding forest matrix and found that there was a significant difference between beetles found in forest clearings and intact forests. Boonrotpong *et al*. (2004) listed the response of ten *Onthophagus* species to the parameters of canopy cover, light intensity and temperature. Compared to Borneo, the habitat preference of many species of the Malay Peninsula is relatively unknown, especially in open habitats with little tree cover.

In Sulawesi, Shahabuddin *et al*. (2010) explored the dung beetle communities in forests, agroforestry systems and open areas. Generally, it was found that the response of dung beetles was tied to their behavioural guild, the abundance of large tunnelers declined when forests are altered to other habitats, and roller abundance tended to peak in agroforestry systems while dwellers were abundant only in open areas. The isolation of Sulawesi compared to the other islands in the Malay Archipelago and the relatively small number of native large mammal species is likely the cause for a high number of dung beetle species endemic to Sulawesi (Shahabuddin *et al*., 2010). In Northern Borneo, Davis *et al*. (2001) sampled river edges, forest interiors, logged forests and plantation forests and categorised the habitat preference of dung beetles into riverine, interior forest and even subgroups. Logged and plantation forests were found to be a mix of riverine and forest interior subgroups but with a strong representation of riverine species. These riverine species are interpreted to be edge specialists that have higher tolerances to environmental disturbance than forest interior species. The effect of logging on dung beetle community structure was also investigated by Slade *et al*. (2011), which compared unlogged forests, low intensity selectively logged forests and high intensity selectively logged forests. Overall abundance and species diversity was similar across all sites, but high intensity logged forests had lower rarefied species richness. This suggests that even after regrowth, intense logging and forest clearing may have a lasting effect as the community structure of dung beetles may never recover. In terms of functional traits, the higher soil temperatures of oil palm estates compared to forests are believed to act as an environmental filter that reduces the abundance of large nocturnal foragers, increases the proportion of small species and leads to a complete loss of roller dung beetles (Edwards *et al*., 2014). In Southeast Borneo, Ueda *et al*. (2017) surveyed several forests types and disturbed areas and described the diet and habitat preferences of 44 species. From this total, 36 species were found to be rare in anthropogenically-changed forests, plantation forests and open habitats while seven species were found to prefer these habitats. It was noted that species that were abundant in forests had a relatively narrow distributional ranges, while many open area species were distributed outside of Sundaland. Ueda *et al*. (2017) suggested that the wide range of habitat tolerance of open area species may be a cause for their distribution beyond Sundaland. Studies such as Davis *et al*. (2001) and Ueda *et al*. (2017) were able to identify the habitat preference of individual species and this allowed for a more nuanced understanding of how individual species responded to changes in their environment. This nuance may be lost when species identities are not included in analysis and only gross measurements such as total species richness or species diversity are used.

It should be noted that studies conducted in the Malay Peninsula tend to take place within forests, largely ignoring localities with few trees such as tropical scrubland or grassland. The sole exception was Hosaka *et al*. (2014) that also surveyed bare lumber camps, log yards, skid trails and logging roads. Grassland, however, is not foreign to Sundaland; changes in the climate since the Holocene have given rise to drier savannah type habitats during glaciation periods (Whitmore, 1984). These grassy areas have persisted along the edges of forests, and there are records of mammalian megafauna inhabiting these habitats, such as the Asian elephant (*Elephas maximus*) (Wadey *et al*., 2018), the Javan rhinoceros (*Rhinoceros sondaicus*), and gaur (*Bos javanicus*) (Harrison, 1966). Long grasses are the preferred food source of megafauna such as elephants (Wadey *et al*., 2018), and these vegetation types also provide cover for dung beetles. Considering the close association between dung beetles and mammals, it is possible that several species may be attracted to grassland habitat because of the presence of resources created by megafauna.

2.4 Dung beetle community structure:

The effect local extinctions on the community structure of animals that depend on resources created by elephants is thus far unknown as most research into trophic cascades deal with the photosynthetic energy and primary production pathways of the 'Green world' component of ecosystems as opposed to the 'Brown world' of decomposition and detrital pathways (Moore *et al*., 2004). Theoretically, tropical ecosystems are known to have multiple functional redundancies and trophic pathways that minimise the effect of trophic cascades caused by the removal of a single species (Terborgh & Feely, 2010). Alternatively, the removal a species that produces a large amount of resources could cause the population collapse of throphically dependent species within the community, thus leading the community to restructure into a new alternative state.

As previously mentioned, in tropical South East Asia, dung beetle communities have been shown to respond to changes in ecosystem structure. In general, disturbances by habitat alteration such as logging or agriculture produces communities that are less species rich (Davis, 2001; Qie *et al*., 2011; Hosaka *et al*., 2014) and have reduced ecological functions (Gray *et al*., 2014). The relationship between large herbivorous mammal presence and dung beetle communities is less clear. In South East Asia, Slade *et al*. (2014) demonstrated that the presence of large mammals such as domestic cattle in oil palm plantations leads to higher dung beetle abundance and dung removal. Several studies in the Neotropics indicate decreasing mammalian biomass and biodiversity leads to a loss of dung beetle diversity and abundance (Feer & Boissier, 2014; Anderson & Laurence 2007; Culot *et al*., 2013). However natural tropical forests in the Neotropics lack the diversity of mammalian megafauna such as rhinoceros, wild cattle and elephants (Amezquita & Favila, 2010) that are found in South East Asian forests and the results could differ.

2.5 Dung beetle species associated with elephants

Thus far little is known is about elephant-dung beetle associations in South-East Asia. In dung beetle inventories, Hanboonsong *et al*. (1999) records 22 species and Goh *et al*. (2014) recorded 11 species of dung beetles feeding on elephant dung. A general survey of Malay Peninsula was conducted by Doll *et al*. (2014) using small amounts of elephant dung in eight different forests whereby 64 species were recorded. A summary of all species is listed in Table 2.5. Unlike other records of dung beetles in elephant dung, Doll *et al*. (2014) notes a large diversity of small tunnelling *Onthophagus* attracted to elephant dung. As Elephant dung has a very large proportion of coarse fibre compared to other large mammal species (Yamamoto-Ebina *et al*., 2016), Goh *et al*. (2014) posited that some species of beetle may have evolved to exclusively feed on elephant dung.

Aside from South East Asia, the only records of dung beetles visiting the dung of Asian elephants are from India (Sabu *et al*., 2006; Vinod & Sabu, 2007). Sabu *et al*. (2006) reported a high incidence of dwellers and tunnelers in elephant dung, with the dwellers *Drepanoceros setosa* and *Liatongus indicus* being the dominant dwellers while the small tunnelers *Onthophagus bronzeus* and *O. cervus* were the dominant tunnelers, the very large tunneler *Heliocopris dominus* was also present. Sabu *et al*. (2006) also conducted a succession study, where it was found that several species of *Copris* and *Onitis* were attracted to older dung.

Records of Afrotropical elephant dung visiting dung beetles were collected from forests in Zaire, the Ivory Coast, Gabon, Liberia and Uganda, most of which are summarised in Cambefort (1991). Afrotropical forests are the only one of the two tropical forests in which elephants occur, the other tropical forest being within the Oriental region. There are two different groups of dung beetles in these forests, categorised by how the type of dung that they exploit: Beetles that specialise on smaller omnivorous droppings and beetles that exploit larger elephant dung. Despite the diversity of large mammals in Africa, only the forest elephant is a true tropical forest dwelling large mammal. Other mammals such as hippopotamus and buffalo tend to occur on the edge of the forests or clearings. Species richness was reportedly lower in buffalo dung placed in African forests, where it rarely occurs naturally. This difference between Afrotropical and Sundaland forests, which can have gaur or tapirs as well as elephants, should be noted (Harisson, 1966). Dung left by elephants tends to exist in excess, with many piles left untouched by beetles. When beetles do access these dung piles, they are only able to bury 1/5th of the total mass (Cambefort, 1991). This is opposed to beetles that visit omnivorous dung in the same forests, which were able to completely bury human droppings (which are used as a standard reference for omnivorous dung in dung beetle studies) (Cambefort, 1991).

The unique biogeographic and phylogenetic history of the African region leads to a unique assemblage of dung beetle –elephant interactions there. The African continent is the center of diversity for both dung beetles (Hanski & Cambefort, 1991) and elephants (Sukumar, 2003), therefore both groups have been able to develop complex interactions through a long co-evolutionary period. It has been reported that elephant dung is very rapidly buried by the activity of African dung beetles (Cambefort, 1991; Heinrich & Bartholomew, 1979); clouds of thousands of dung beetles are known to descend on single dung patches (Hanski & Cambefort, 1991). The action of dung beetles on elephant dung is so intense that it tends to leave only a residual mat of coarse fibres (Heinrich & Bartholomew, 1979); these structures are not observed in South East Asian forests. Instead, elephant bolii tend to remain intact until termites break down the fibrous balls (Pers. Obs.). The genera usually associated with African elephant dung are typically not found in South East Asia, except for a few widespread genera like *Catharsius*, *Heliocopris*, *Copris*, *Proagoderus*, *Onthophagus* and *Sisyphus* (Doube, 1991; Cambefort, 1991).

Table 2.5: Dung beetle species recorded to visit Asian elephant dung.

Tribe	**Species**
Coprini	*Copris angusticornis* [A]
	Copris bellator [C]
	Cp. corpulentus [A]
	Cp. iris [A]
	Cp. laevigatus [A]
	Cp. numa[C]
	Cp. agnus [B]
	Cp. spinator [B]
	Cp. (Paracopris) cariniceps [A]
	Cp.(P.) punctulatus [A]
	Cp. (P.) furciceps [A]
	Cp.(P.) ramosiceps [B]
	Copris (Microcopris) doriae [BC]
	Cp. (M.) hosakai [C]
	Cp. (Microcopris) reflexus [A]
	Cp.(Microcopris) vitalisi [A]
	Catharsius renaudpauliani [B]*
	Catharsius molossus [A]
	Catharsius birmanensis [A]
	Synapsis sp. [B]
Dichotomiini	*Heliocopris tyrannus* [C]
	H. buecephalus [A]
Gymnopleurini	*Paragymnopleurus maurus* [BC]
	Pg. striatus [B]
Sisyphini	*Sisyphus thoracicus* [BC]
Oniticellini	*Liatongus affinis* [A]
	Liatongus gagatinus [A]
	Liatongus femoratus [BC]
	Liatongus tridentatus [A]
	Oniticellus tessellatus [B]
	Yvescambefortius sarawacus [B]
Onthophagini	*Caccobius unicornis* [B]
	Onthophagus angustatus [B]
	Onthophagus babirussa [B]*

Table 2.5: Continued

Tribe	**Species**
	Onthophagus balthasari [A]
	Onthophagus banasus [A]
	O. cervicapra [B]
	O. cf. deflexicollis [B]
	O. cf. deliensis [B]
	O. cf. incisus [B]
	O. laevis [B]*
	O. mulleri [C]
	O. pedator [B]*
	O. cf. penicillatus [B]
	O. cf. peninsularis [B]
	O. cf. rudis [B]
	O. cf. rutilans [BC]
	O. leusermontis [B]
	O. pacificus [B]
	O. rorarius [B]
	O. rugicollis [B]
	O. venzoi [B]
	O. vulpes [B]
	O. seniculus [A]
Onitini	*Onitis* sp. [B]
	Onitis bordati [A]
	Ot. excavatus [A]
Canthonini	*Ochicanthon cf. peninsularis* [B]
Aphodiinae	*Megatelus* braminus [C]*

References: [A] Hanboonsong et al. (1999), [B] Doll et al. (2014), [C] Goh et al. (2014)

*Species identification has been revised.

2.6 Intraspecific responses to elephant loss:

Traits are defined as a surrogate measure of organismal performance, a trait connects the physical characteristics of an organism with the genetic, ecological and environmental parameters that affect the trait (Violle *et al*., 2007). Life history related traits such as body size can be used to observe how species adapt in response to ecological problems (Berven & Gill, 1983). In relation to insect fauna, morphological traits have been used to understand aspects of species ecology and ecosystem functions (Fountain-Jones *et al*., 2015). Several traits, such as body length, thorax length/width/depth and elytral length/width/depth, and related ecological parameters have been suggested for beetles (Fountain-Jones *et al*., 2015).

While thorax size has been described as a morphological trait (Fountain-Jones *et al*., 2015), it also has a relationship with the developmental physiology of dung beetles and the ecological conditions in which they reside. Dung beetle larva are not free living, but they are provisioned with a fixed amount of dung by their parents, which is dependent on how much dung is available in the ecosystem (Emlen, 1994). The relationship between the resulting body size of *Onthophagus acuminatus* and different quantities of food has been examined; beetles supplied with more dung when young were larger in terms of pronotum width compared to beetles which were supplied with smaller quantities of dung during the larval stage (Emlen, 1994). If the growth response rate to food quantity is assumed to be constant within a species, comparison of the difference between the pronotum widths of two populations can give a relative measure of the quantity of larval resources available in the ecosystem.

The ability to adapt to different dung resources of varying quality has been recorded in *O. taurus* which indicates that dung beetles are able to switch between different resources of varying qualities (Moczek, 1998). When resources are not optimal, the dung beetle species can alter the balance between primary (Aedegus size) and secondary (Horn length, body size) sexual characteristics to suit the level of competition and availability of resources of the habitat (Parzer & Moczek, 2008). The reduction of aedegal size is believed to carry less of a competitive penalty compared to body size or horn length, which is why some populations of Australian O. taurus are known to have a high variation of aedegus length (Parzer & Moczek, 2008). Experiments by Moczek (1998) and Moczek (2002) showed that the growth and horn development of O. taurus varied according to the type of dung provisioned to larvae, larva that were given cow dung had larger body sizes and horns than larva given horse dung.

Several studies utilising functional traits have been conducted on dung beetles at the community level. Typically, trait based studies applied to dung beetles are done using categorical variables based on nesting behaviour (rollers, tunnelers, dwellers), feeding preferences (coprophages, necrophages, generalists), activity times (diurnal, nocturnal, crepuscular) and relative body size (large, medium, small) (Edwards *et al*., 2014; da Silva & Hernandes, 2015; Barragan *et al*., 2011). It has been found that the abundance of large tunnelers and rollers are negatively associated with conversion of forests into oil palm estates (Edwards *et al*., 2014). Human activity such as hunting has also been found to affect the functional diversity of dung beetles (Barragan *et al*., 2011). Both studies concluded that disturbance affects the functional diversity at community level. Intraspecifically, dung beetles are known to display phenotypic plasticity in response to different environments; it has been observed that introduced populations of *Onthophagus taurus*, in North America and Australia differ in their pronotal size, horn expression and genitalia despite only 40 years of isolation from the native Mediterranean populations (Moczek, 2003).

Dung beetles are adapted to feeding on mammalian dung and therefore are susceptible to trophic collapse caused by the removal of mammalian fauna by human activities (Nichols *et al*., 2009). In the Malay Peninsula where this study was conducted, megafauna such as Asian elephants and wild cattle have experienced local extinctions in some forests due to hunting and human-animal conflict relocation programs (Saaban *et al*., 2011). However, in many of these forests that have lost large herbivorous mammals, dung beetles still persist (Doll *et al*., 2014). Likely these species are either capable of switching to alternative food sources or not solely dependent on large herbivorous mammal dung. There have also been records that indicate that some tribes such as Oniticellini and Onitini may have a preference in the dung of large mammalian herbivores (Hanboonsong *et al*., 1999). Pronotal widths therefore are a good proxy measure of the extent of resource deprivation caused by megafauna loss.

3.0 MATERIALS AND METHODS

3.1 Study sites:

This study was conducted in six localities in Peninsular Malaysia (Fig, 3.1), elephants were still present in 3 of these localities: the Tembat Forest Reserve next to the Kenyir Lake and the Belum-Temenggor Forest Complex, both located in Northern Peninsular Malaysia and the Kuala Gandah Elephant Sanctuary in Central Peninsular Malaysia. The localities where elephants were absent were the Gombak Forest Reserve and Templer's Park Forest Reserve, where elephants were last sighted in 1961 (Earl of Cranbrook, Per. Comm.) and the Bukit Lanchang Forest Reserve, where the last elephants were relocated in the 1990s (Saaban *et al*., 2011). All elephant absent localities were located in Central Peninsular Malaysia. All localities were mature secondary forests.

Fig. 3.1: Map of study localities. Circles represent localities used for model trainingdata, stars represent localities used as model test data. Open symbols represent sites with elephant presence, closed symbols represent sites with elephant absence.

3.2 Burrowing Interception Trap (BIT):

3.2.1 Trap Construction:

The BIT was composed of a plastic container, soil, and dung. The soil was placed in the container, and the dung was left in direct contact with the surface of the soil (Fig. 3.2). A rain cover, made from plastic or leaves found at the sampling site, was placed over the trap to prevent the container from becoming flooded due to rain. Small holes were also be made in the bottom of the trap to allow for drainage. The trap was placed on top of the ground. It was left for 24 hours to allow dung beetles to burrow into the soil beneath the dung. The plastic container prevents the burrowing beetles from escaping the trap, since they tend to settle at the bottom of the soil in the container. To remove the collected dung beetles, the soil was manually examined or the contents of the trap were placed into a basin of water and the beetles collected from the water surface.

To assess the effectiveness of BITs, traps were constructed using plastic containers measuring 16 × 11 × 4.5 cm. These containers were half-filled with soil collected at the location where the trap was placed. Traps were buried level with the ground. About 50 g of fresh cow dung were placed on the soil. Pitfall traps were plastic cups with a diameter of 12 cm. About 50 g of fresh cow dung were placed into a perforated plastic bag and suspended above the cup with bamboo skewers. The cup was filled with a brine and soap solution.

Dried leaves found in the field were used as rain covers over both trap types. Dried leaves do not warp due to dehydration and are therefore more reliable rain covers than fresh leaves, they also help to hide the traps from scavengers. All cow dung used in our study was from a single homogenized source of dung. While the cow dung was obtained from domesticated cattle (*Bos taurus indicus* Linnaeus), its structure and consistency were similar to native Southeast Asian cattle species, such as the gaur (*Bos gaurus* Smith) and banteng (*Bos javanicus* d'Alton) (E. Slade, Pers. Comm.).

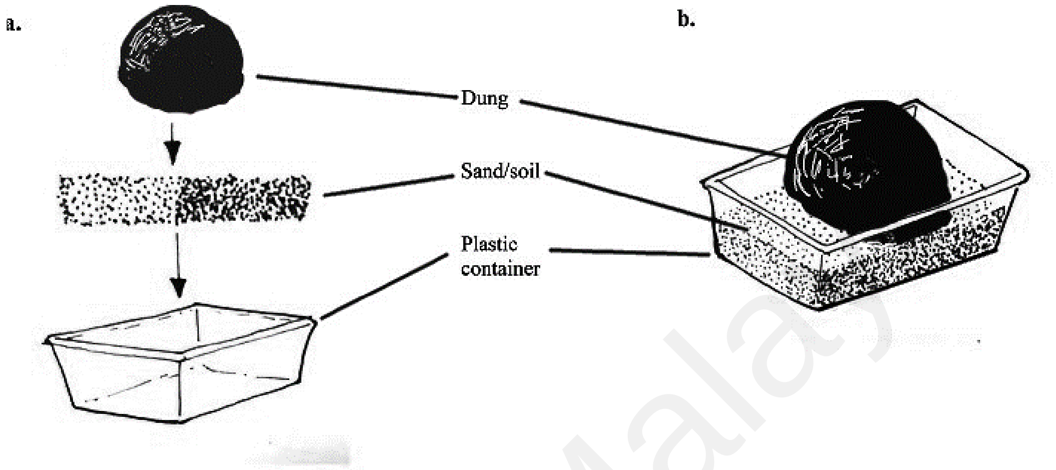


Fig. 3.2: a) Construction diagram of Burrowing interception trap. b) The completed trap.

3.2.2 Comparative Study:

The study site was a homogenous rainforest patch located adjacent to the Ulu Gombak Field Studies Centre, which is within the Ulu Gombak Forest Reserve in Peninsular Malaysia. This study was conducted during August 2016. Two levels of randomization were done for the sampling design. A systematic 5 × 6 grid of 50 × 50 m quadrats was placed from a random starting point, and a single trap type was randomly assigned to the center of each quadrat. Thirty traps were put in place, divided into 15 BITs and 15 pitfall traps. The relatively small site and sample size were chosen so that all the quadrats would be within dense tree cover of a secondary forest stand and away from forest edges to minimize the effects of microhabitats and forest types. All traps were put in place on the same day and examined at the end of 24 hours. A short trapping period was used to ensure that weather and other temporal effects were equal for all traps. Traps were placed at the centre of the quadrat, with a minimum distance of 50 m apart to prevent interference with other traps (Larsen & Forsyth 2005).

3.2.3 Analysis:

Six measures were used to quantify the differences between the two trap types at a scale of individual traps: abundance; species richness; number of tribes present in a sample (tribal richness); number of rollers present; Shannon's Diversity Index; and Simpson Diversity Index. Tribal richness was used to determine if the traps were catching a variety of phylogenetically distinct groups or merely attractive to a group of closely related species. Shannon's Diversity index ($-\sum_{i=1}^{s} p_i \ln p_i$) was used as a measure of how well the traps collected species relative to the number of beetles collected, while Simpsons Diversity Index ($1/(\sum_{i=1}^{s} {p_i}^2)$) was used to measure the dominance of single species relative to the number of beetles collected. For each of the six measures: abundance; species richness; number of tribes present in a sample (tribal richness); number of rollers present; Shannon's Diversity Index; and Simpson Diversity Index, a generalized linear model (Poisson regression model) was constructed with the type of traps as a binary dummy predictor variable. This was used to determine if there were any significant differences between the type of traps as well as measure the effect size for any differences. A Poisson model was used because most of the data was count data and the distributions of the data were fitted to Poisson distributions. To measure the cumulative effects of the differences in species detected, species accumulation curves and rank abundance curves were constructed for both trap types. All analysis was conducted in R 3.5.1 software with the vegan package (Oksanen *et al.*, 2017)

3.3 Habitat preference and elephant dung association for dung beetles:

3.3.1 Sampling design:

All 6 localities were sampled for dung beetles (Fig. 3.1). In each locality, two to six 500 m transects were placed in the forest and along the neighbouring forest edges. Forest transects were placed at least 200 m from the forest edges. Ten to 11 sites were placed at 50m intervals on each transect to avoid trap interference (Larsen & Forsyth 2005). A single BIT was set up in each site, using plastic containers measuring 16 × 11 × 4.5 cm and baited with a single bolii of captive elephant dung. The trap in each site was collected after 24 hours. Each site was sampled three times within the same month to ensure temporal consistency and the samples were pooled to reduce the effect of single outlier samples. See table 3.2 for definitions of smapling units. Due to safety reasons, only one transect could be placed in forest edge habitat in the Belum-Temenggor locality. A total of 271 sites were sampled over a total of 813 trap nights (Table 3.1).

The sites were divided into two categories: forest and forest edges. Forest edges were defined as areas within 10m of fully covered forest borders, where there is a mix of *Imperata cylindrica* grassland or small stands of early succession plants such as *Malestoma malebactrichum*, *Macaranga* spp., *Acacia* spp. and *Dicranopteris linearis*. In this habitat type there are few or no large trees and little canopy cover, mostly caused by human disturbance but sometimes maintained by elephant feeding. This category is analogous to the "open areas" category of Shahabuddin *et al*. (2010) and the "grassland" category of Ueda *et al*. (2017). Forest sites were defined as sites within mature forests characterised by saplings, forest trees, palms and lianas that are typical of tropical lowland forests. This habitat type has intact canopies and is analogous to the "logged forest" category of Shahabuddin *et al*. (2010), Davis *et al*. (2001), Gray *et al*. (2014) and the "secondary forest" category of Ueda *et al*. (2017).

The timeframe of the sampling was within a 12 months period (Table 3.3). The main portion of the sampling was conducted from July 2016-November 2016. To increase the sample size some resampling was conducted the following year in the Kuala Gandah, Templer Park and Temenggor localities. To control for possible temporal differences, sampling was done during similar weather conditions (heavy rain and thunderstorms) for all the sites.

Table 3.1: GPS coordinates, forest types, number of transects, number of sites for all localities.

Name	**Coordinates**		**Forest type:**	**No. of transects**	**Forest sites:**	**Forest edge sites:**	**Total sites:**
Kenyir	N 5°09'59.4"	E 102°37'28.8"	Mature Secondary Forest	6	31	30	61
Bukit Lanchang	N 3°35'29.4"	E 102°10'48.4"	Mature Secondary Forest	6	30	30	60
Gombak	N 3°19'28.7"	E 101°45'09.6"	Mature Secondary Forest	6	30	30	60
Kuala Gandah	N 3°35'40.1"	E 102°08'39.1"	Mature Secondary Forest	6	30	30	60
Templer’s Park	N 3°17'12.8"	E 101°38'34.1"	Mature Secondary Forest	2	10	10	20
Temenggor	N 5°32'41.6"	E 101°18'46.9"	Mature Secondary Forest	1	-	10	10
			TOTAL	27	131	140	271

Table 3.2: The following terminology regarding units of physical space used in this thesis:

Terminology:	**Definition**
Locality:	A large geographical area, usually representing a forest.
Transect	A 500-550m transect with 10-11 sites spaced out at 50m intervals
Site:	A single sampling point within a transect that has been sampled consecutively for 3 days.
Replicate:	A single sampling point that has been sampled for a single day.
Habitat type:	The type of habitat in which a transect has been placed. Habitat type is either forest or forest edge.
Elephant presence:	Whether a locality has a current elephant or not. Elephant presence is recorded as either present or absent.
Training locality:	Localities in which the data from each site will be used to train classification models.
Testing locality:	Localities in which the data from each site will be used to test classification models.

Table 3.3: The sampling period for each locality.

Name	**Season:**	**Weather conditions**	**Sampling period**
Kenyir	Inter monsoon	Heavy Rain/ Thunderstorms	4.viii.2016 - 13.viii.2016
Bukit Lanchang	Southwest monsoon	Heavy Rain/ Thunderstorms	20.ix.2016 – 2.x.2016
Gombak	Southwest monsoon	Heavy Rain/ Thunderstorms	1.xi.2016 - 14.xi.2016
Kuala Gandah	Southwest monsoon	Heavy Rain/ Thunderstorms	20.ix.2016 - 30.ix.2016 24.1.2017 (Additional sampling)
Templer's Park	Inter monsoon	Heavy Rain/ Thunderstorms	20.v.2017 - 22.v.2017
Temenggor	Inter monsoon	Heavy Rain/ Thunderstorms	17.iv.2017-20.iv.2017

3.3.2 Habitat preference Analysis:

As BITs are inefficient at collecting roller dung beetles (Section 4.1), this functional guild was removed from subsequent analysis. The mean of each habitat type was then compared using three metrics: abundance, species richness and Shannon's Diversity Index. Shannon's Diversity Index was chosen as it is widely used in dung beetle studies because the evenness component of this index can reveal competitive asymmetries in high competition taxa such as dung beetles (Davis *et al*., 2001). As the samples were not normally distributed, parametric tests could not be used. The medians and quartiles for each of these metrics were described using box plots and the medians were compared using Mann-Whitney tests. The estimated species richness was then compared using Chao1 estimates, species accumulation curves and rarefaction curves which were evaluated with the vegan package in R Software (Oksanen *et al*., 2017).

For the subsequent analysis of habitat preference, species with an abundance of less than 10 were removed as conclusions made on such a limited number of samples were likely to be unreliable, which resulted in a dataset of 25 species. Each species was categorised with hierarchical cluster analysis which used Bray-Curtis distances calculated from abundance and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm. Further support for our classification was gained with a Non-metric Multidimensional Scaling (NMDS) ordination also using Bray-Curtis distances. The vegan package in R Software (Oksanen *et al*., 2017) was used to calculate the distance measures used for cluster analysis and NMDS.

3.3.3 Dung beetle community structure analysis:

The total abundance, species richness and dweller abundance for elephant absent sites and elephant present sites were summarised as boxplots. To compare between localities, the rarefied species richness of each locality was determined using the vegan package in R Software (Oksanen *et al*., 2017).

To detect if spatial autocorrelation was present within the dung beetle community dataset, a Mantel test was conducted. This test compared a Bray-Curtis distance matrix of summed species abundance in each locality with a Euclidean distance matrix of the geographical distance between localities.

An NMDS ordination was conducted on a Bray-Curtis distance matrix of the dung beetle community dataset after removing singleton species and sites without any records. A Permutational multivariate analysis of variance (PERMANOVA) was then conducted on the same dataset with Elephant presence and absence and forest types coded as dummy variables, while locality was used as a categorical variable.

Chao-Sorensen pairwise distances were calculated for each locality using the summed dung beetle community dataset for each locality. Hierarchical cluster analysis was used to compare the clustering of the localities based on the distance matrices each of these components. The distances were then decomposed into its balanced variation (SNE), which measures species turnover and abundance gradient (SIM), which measures nestedness, components using the bray.part function from the vegan package (Balsega, 2010). This was to detect if the community composition of dung beetles in localities where elephants were absent was a subset of localities where elephants were present (indicating a loss of species), if this was the case then it could be interpreted as evidence that some form of extinction or trophic collapse has occurred.

3.3.4 Dung beetle -elephant association analysis:

In order to test the hypothesis that there is a shift from dweller dominated to tunneler dominated communities, a logistic model was built with the proportion of dwellers in a sample as a predictor and the presence or absence of elephants as the response variable. In order to estimate the effect of elephant loss on the species size, a logistic model which used the number of small sized species and number sized of large species as predictor variables and the presence or absence of elephants as the response variable was created. Both models treated this as a classification problem, in which a model was trained to predict the presence of elephants based on the respective dataset of a sample. By placing the binary variable of elephant presence as the response variable, a log-link function could be used to satisfy the assumption of linear response between response and predictor variables. The predictor variables also satisfied the distribution or reisduals and specification of variance structure required by a GLM. The assumption that all samples are independent was also made. The model could then be tested against a real test dataset to quantify how reliable the dweller proportion is as a predictor to elephant presence. In order to test the logistic models accuracy against real data, the dataset was divided into training and test datasets. Four localities were used in the training dataset: Kenyir, Gandah, Lanchang and Gombak. There was a total of 231 sites in this dataset. The test dataset consisted of four localities as well: Kenyir, Gandah, Temenggor and Templer’s Park. As forests could not be entered in Temenggor for safety reasons, 10 forest site samples were randomly selected from the Kenyir and Gandah localities to represent elephant present forest sites. The total number of sites for this dataset was 40. The resulting models were then used to predict the presence of elephant in the test sites. The predictions were then tabulated and compared to the actual presence/absence of elephants in the test sites using confusion matrices. The error rate of the model, which is the proportion of wrong predictions that were made by the model, was calculated to determine the accuracy of the model.

Apriori association rules (Toomey, 2014) were generated by comparing the occurrence of a species with the presence of elephants. This generates three values: Support, which is the percentage of sites that contain both the species and elephant presence; Confidence, which is the percentage of sites in which there is a co-occurrence between the species and elephant presence; and Lift, is the ratio of confidence to the percentage of sites containing elephant presence, in which a lift larger than one indicates positive association between a species and elephant presence (Toomey, 2014). This analysis was conducted with the arules package in R Software (Hashler *et al*., 2018).

3.4 Intraspecific trait comparison:

3.4.1 Sample selection:

The beetles from two localities were compared, Kenyir and Gombak. Both forests were of similar elevation, climate, logging histories and human disturbance patterns. Elephants were present in Kenyir but extripated in Gombak. All the beetles used in this study were collected from forested microhabitats with intact canopies and collections were done during the wet season between June and November 2016 to minimise the effect of environmental variables. In cases where the total number of collected beetles exceeded a sample size of 40, a sample of 40 specimens was randomly selected.

Six different species were used in this study: *O. babirussa, O. vulpe, On. tessellatus*, *L. femoratus*, *Y. sarawacus* and *Cp. doriae*. These species were selected on the basis of having sufficient sample sizes for comparisons in both localities and little to no sexual dimorphism in regards to the pronotum. Due to the lack of sexual dimorphism on the pronotum (Arrow, 1931; Balthasar, 1963), both males and females were pooled for this study. The sample sizes for each species are indicated in Table 3.4. These species were selected in order to obtain a variety of body sizes, functional groups, and tribes.

3.4.2 Measurement:

In this study, the pronotum width was defined as the distance between the two widest points of the pronotum. All beetles were measured three times with a digital calliper and the mean was taken to increase the precision of the measurement. All beetles were dried in an oven at 50°C prior to measurement.

3.4.3 Analysis:

Histograms, q-q plots and Shapiro-Wilks tests indicated that some of the samples were not normally distributed due to the presence of outliers. As these violated the normality assumptions of parametric t-tests, a Mann-Whitney test was used to determine if there was a significant difference between the medians of the samples. Bootstrapped means and 95% confidence intervals were also compared to determine if there was a significant difference between means. All analysis was done with R Software ver. 3.5.1 and the boot package (Canty & Ripley, 2018).

Table 3.4: The body size category, functional group, tribe and sample size of each species used for intraspecific pronotum width comparisons.

Species	Body Size (Length, mm)	Functional Group	Tribe	Sample size	
				Elephants Present	Elephants Absent
Onthophagus babirussa	7mm, Medium	Tunneler	Onthophagini	40	40
Onthophagus vulpes	9mm, Medium	Tunneler	Onthophagini	40	31
Liatongus femoratus	10mm, Medium	Dweller	Oniticellini	40	25
Oniticellus tesselatus	7mm, Medium	Dweller	Oniticellini	40	40
Yvescambefortius sarawacus	14mm, Large	Tunneler	Oniticellini	24	31
Copris doriae	15mm, Large	Tunneler	Coprini	27	31

3.5 Identification:

Identification of beetle species was carried out by comparing specimens to reference collections deposited in the Museum of Zoology, University of Malaya. Balthasar (1967) and Arrow (1950) were used to verify the identification of some species. Beetles which could not be identified in this manner were referred to Johannes Huijbregts of the Naturalis Biodiversity Centre, Leiden, the Netherlands and Marco Dellacasa of *Museo di Storia Naturale e del Territorio dell'Università di Pisa*, Italy.

4.0 RESULTS

4.1 Dung beetle specimen collection for ecological study:

For the preliminary study of BIT performance compared to pitfall traps, a total of 1034 Individuals were captured with both types of traps, BITs captured 733 beetles and pitfall traps captured 301 beetles in the 24 hours sampling period (Table 4.1). The most abundant species was *O. babirussa*, which was 587 individuals or 80% of all beetles caught. In pitfall traps the abundance of *O. babirussa* was smaller than in BITs, with 155 individuals or 52% of all beetles caught. BITs also collected more species, with a cumulative total of 32 species as opposed to the 22 species found in pitfall traps. There was a relatively similar proportion of singleton species collected in both traps, with 15 singleton species (47%) were collected in BIT traps, while 9 singleton species (41%) were collected in pitfalls. Both traps were capable of collecting beetles from the tribes Onthophagini, Coprini, Oniticellini, Sisyphini and Gymnopleurini.

Table 4.1: Species list of beetles collected in pitfall traps and Burrowing Interception traps for the comparative study. Activity period information from Davis (1999) and Niino *et al.* (2014).

Species	Abundance		Activity period
	Pitfall	BIT	
Onthophagus angustatus	0	5	Diurnal
O. aphodiodes	0	2	Diurnal
O. babirusa	155	587	Diurnal
O. crassicollis	2	10	Diurnal
O. fujiii	1	1	Diurnal
O. karenensis	0	1	Diurnal
O. leusermontis	6	13	Diurnal
O. nigriobscurior	2	1	Diurnal
O. orientalis	8	12	Diurnal
O. pacificus	1	2	Diurnal
O. rorarius	1	0	Diurnal
O. rudis	0	1	Diurnal
O. rufiobscurior	3	1	Diurnal
O. rugicollis	8	25	Diurnal
O. semifex	0	1	Diurnal
O. viridicervicapra	0	4	Diurnal
O. vulpes	2	6	Diurnal
Onthophagus Sp. bA	1	1	
Onthophagus Sp. bB	1	1	
Onthophagus Sp. bC	4	2	
Onthophagus Sp. bD	1	3	
Onthophagus Sp. bE	0	1	
Onthophagus Sp. bF	0	1	
Onthophagus Sp. bG	0	1	
Onthophagus Sp. bH	0	1	
Sisyphus thoracicus	67	13	Diurnal
Paragymnopleurus maurus	1	1	Diurnal
Cartharsius renaudpauliani	1	1	Nocturnal
Copris doriae	6	10	Nocturnal
Cp. ramosiceps	25	24	Nocturnal
Cp. spinator	4	5	Nocturnal
Oniticellus tesselatus	1	2	Diurnal
Phaeochroops rattus	0	1	Nocturnal

The means and standard deviation of individual traps is summarised in Fig. 4.1. The performance of individual traps showed a significant difference in total abundance and roller abundance (Table 4.2). There were more species caught per BIT compared to pitfall trap, however this difference was not significant to 0.05 (But still significant to 0.055). The Poisson Regression model indicated that in terms of raw abundance, for every one beetle caught in a pitfall trap a BIT caught 2.45 more beetles. For every species detected in a pitfall trap, a BIT detected 1.33 more species. Conversely for every roller caught in a pitfall trap, a BIT caught 0.342 less beetles.

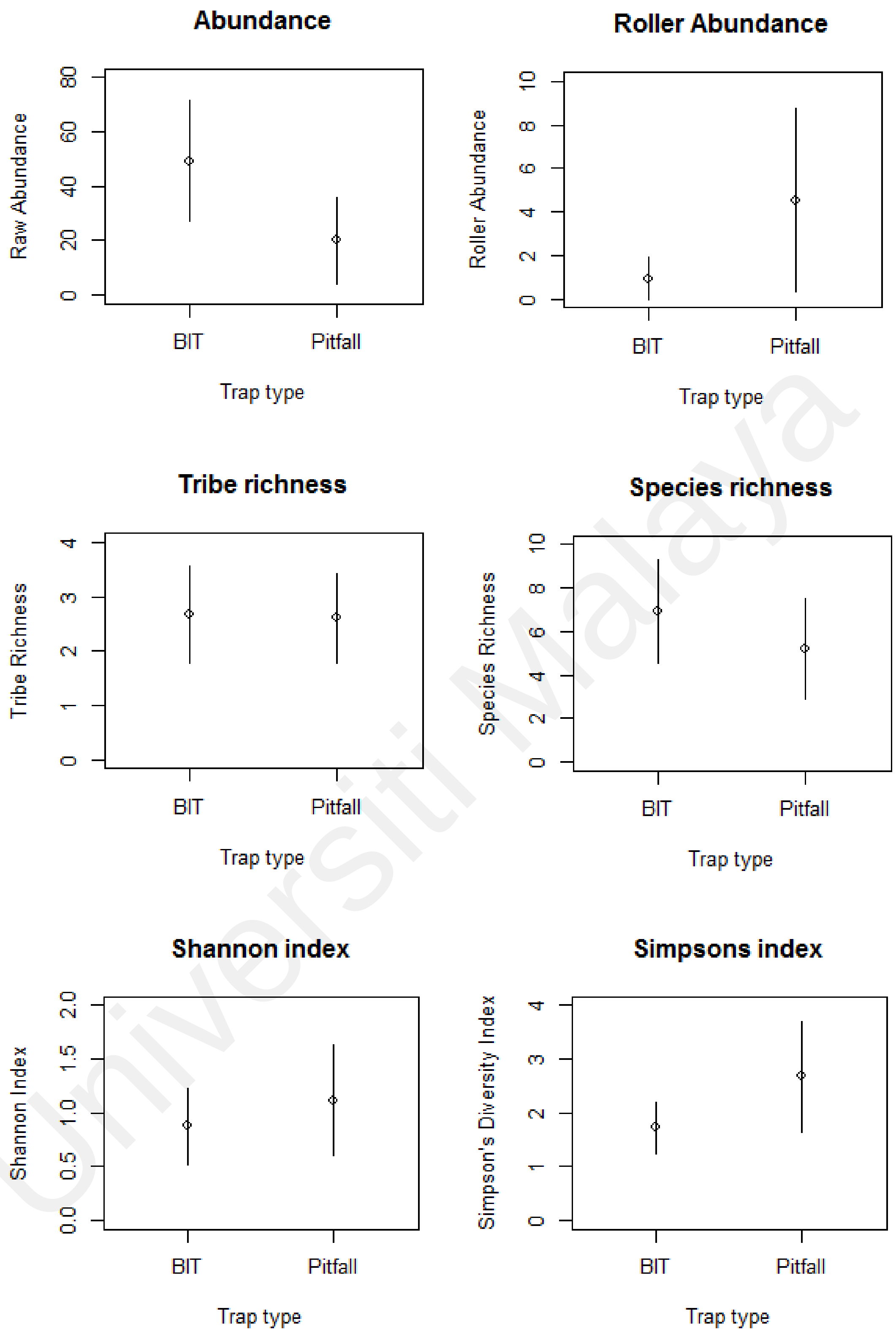


Fig. 4.1: Mean and standard deviations for different measures of individual burrowing interception trap (BIT) and pitfall trap performance.

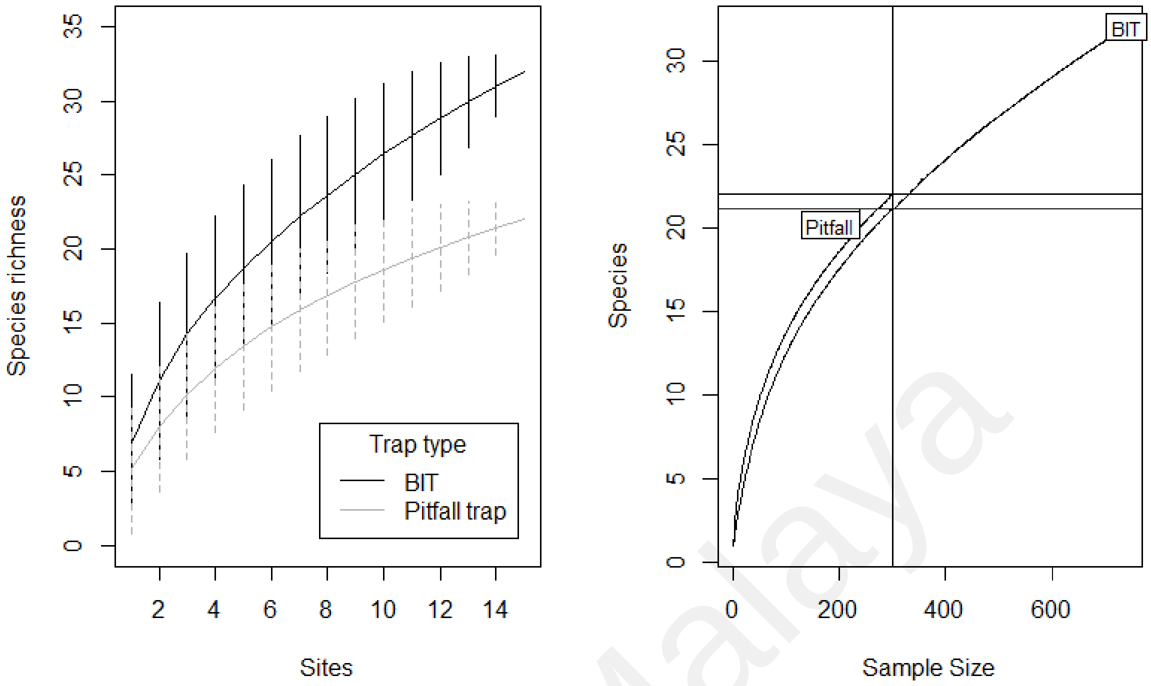


Fig. 4.2: a) Species accumulation curve comparing BIT (in gray) and Pitfall traps (in black). b) Rarefaction curves comparing Pitfall to BIT traps.

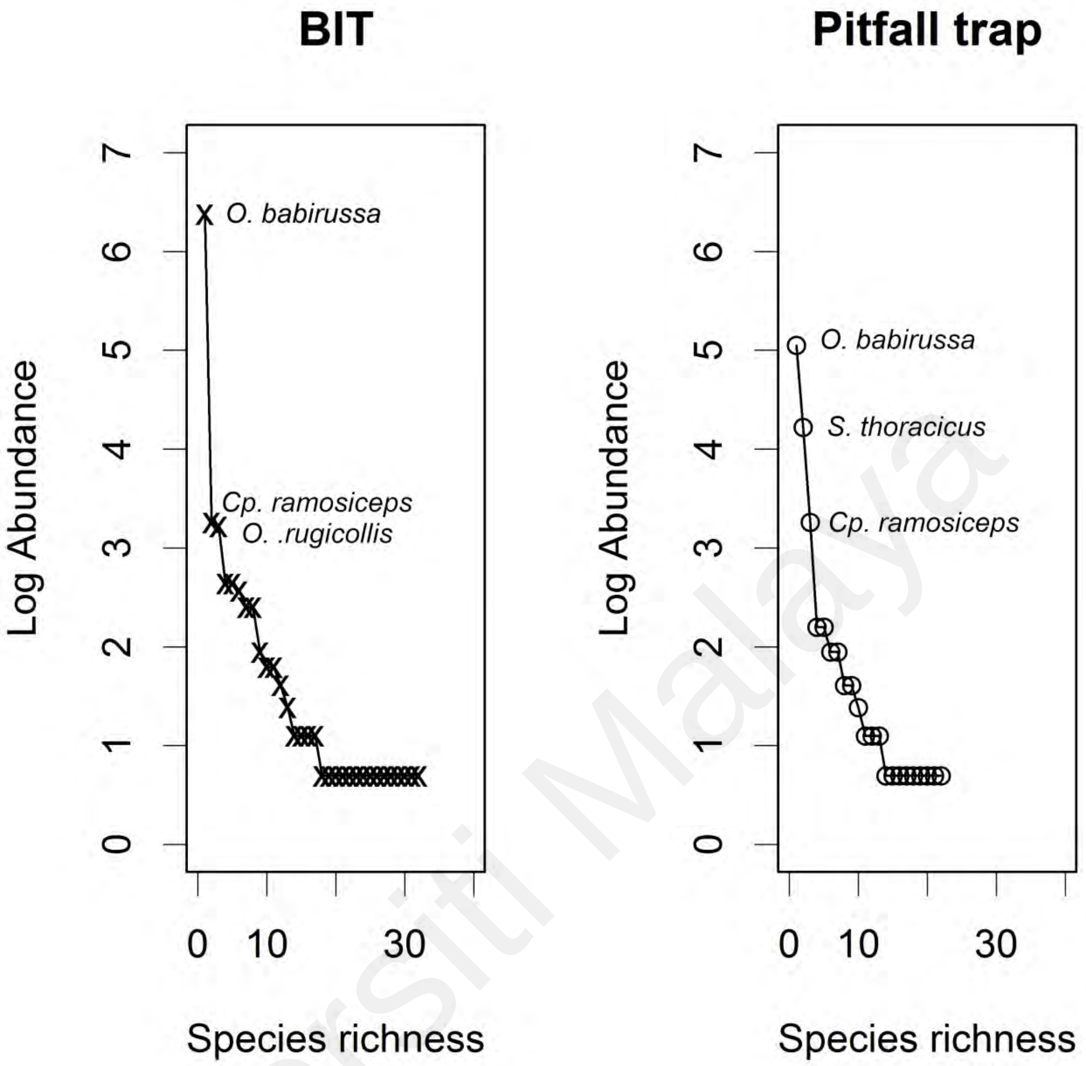


Fig. 4.3: Rank abundance curves for BIT and pitfall traps, the three most abundant species are labeled.

Table 4.2: Least square estimates for the Generalised Linear Model coefficients. The BIT coefficient is a dummy variable coded 0 = pitfall trap and 1= BIT. * Significant to 0.05, ** Significant to 0.01, *** Significant to 0.001

Model:	Raw abundance ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	2.9991	0.0576	52.03	>0.001 ***
BIT	0.8995	0.0684	13.16	>0.001 ***

Model:	Species Richness ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	1.6487	0.1132	14.56	>0.001 ***
BIT	0.2877	0.1498	1.92	0.0548

Model:	Tribe Richness ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	0.9555	0.1601	5.97	>0.001 ***
BIT	0.0253	0.2250	0.11	0.91

Model:	Roller abundance ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	1.5404	0.1195	12.89	>0.001 ***
BIT	-1.0704	0.2365	-4.53	>0.001 ***

Model:	Shannon Index ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	0.1069	0.2448	0.44	0.662
BIT	-0.2406	0.3689	-0.65	0.514

Model:	Simpsons Index ~ Trap type			
	Coefficient	Std. Error	z value	p-value
Intercept	0.9828	0.1580	6.22	>0.001 ***
BIT	-0.4343	0.2519	-1.72	0.085

Species accumulation curves show that BITs collect more species at a faster rate per trap than pitfall traps (Fig 4.2a). However, at sizes below 10 traps, there is no significant difference due to the 95% confidence intervals overlapping (Fig 4.2a). Rarefaction curves indicate that the higher number of species collected by the BITs is likely to be attributed to the higher number of individuals collected. At a similar sample size of 301 specimens, pitfall traps collect more species per individual, although the difference is only one more species (Fig 4.2b). Rank abundance curves produced by both trap types produce relatively similar shaped logistic curves, however they differ at the extremes with BIT traps having a higher peak (reflecting a large number of *O. babirussa* collected) and a longer tail of singleton species (Fig 4.3).

4.2 Overall collection:

A total of 5413 tunneling and dwelling beetles from 50 species were collected and used for the subsequent analysis (Table 4.3). The highest abundance of beetles was collected in Gombak with 3422 beetles while the smallest abundance of beetles was collected in Temenggor with 47 beetles (Fig 4.4). The highest number of species was recorded in Kenyir, with 35 species while the lowest was in Temenggor with only three species (Fig 4.5). Almost half of the beetles collected, at 2436 individuals, were from a single tunnelling species: *Onthophagus babirussa*. The dweller with the highest abundance was *Megatelus brahminus*, with 821 individuals. *Onthophagus babirussa* was found in all localitiess, while *M. brahminus* was exclusive to localities where elephants were present. In general, dwellers such as *Liatongus femoratus*, *M. brahminus*, *Caccobius unicornis* and various Aphodiinae were more common in localities with elephant presence. Tunnelers such as *O. babirussa*, *Copris doriae*, *Catharsius renaudpauliani* were found with higher abundance in localities with no elephant presence.

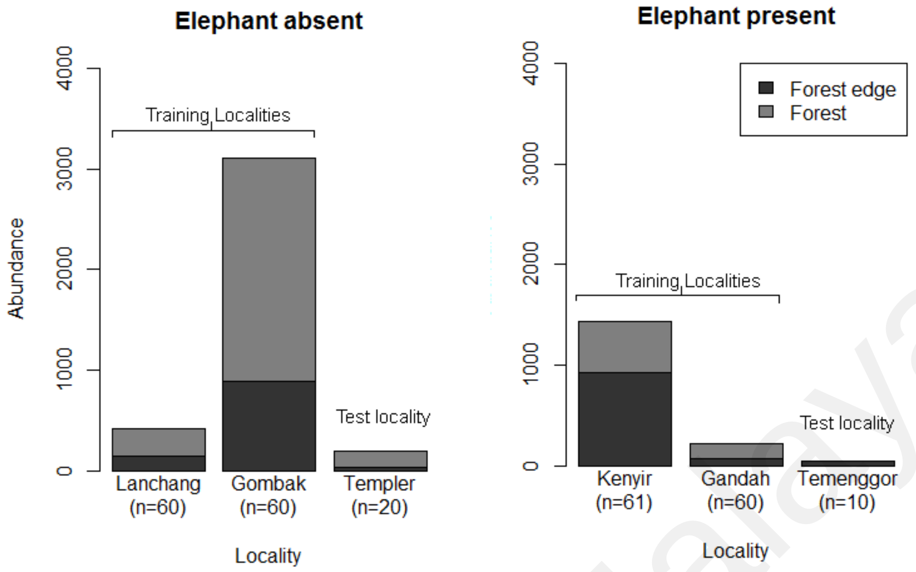


Fig 4.4: Total abundance of tunnelling and dwelling dung beetles collected from each locality.

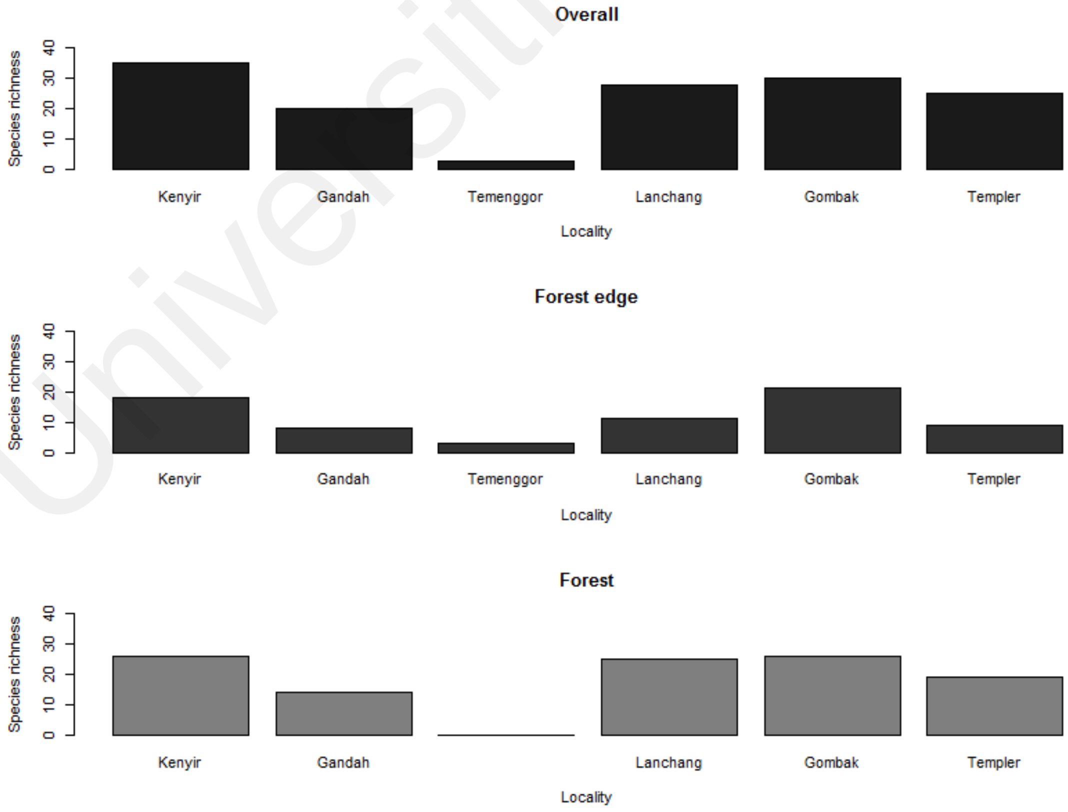


Fig 4.5: Species richness of tunnelling and dwelling dung beetles of each locality.

Table 4.3: Mean and standard deviation dung beetle abundance per site for all localities.

	Total	**Forest**	**Forest Edge**
	Mean ±S.D.	Mean ±S.D.	Mean ±S.D.
Elephant absent			
Lanchang	8.52±6.73	11.60±6.96	5.43±4.90
Gombak	56.15±51.23	81.10±59.83	32.20±21.71
Templer	10.00±11.60	16.60±13.48	3.40±2.32
Elephant present			
Kenyir	38.74±33.80	43.55±28.05	33.77±38.73
Gandah	4.18±4.63	5.9±5.67	2.47±2.33
Temenggor	4.7±4.99	--	4.7±4.99

The Mantel test indicates that there was no spatial autocorrelation between localities (p=0.2563). This indicates that localities did not have similar community structures to other nearby localities and spatial distribution of localities is likely to not be a major confounding variable.

4.3 Dung beetle species habitat preference:

Overall, forest sites had higher means and medians for all measures compared to forest edge sites (Fig 4.6). The mean abundance of forest edge sites was 17.16 ± 23.13 while the mean for forest sites was 32.24 ± 44.67. In terms of species richness, the mean was 4.01 ± 3.23 for forest edge sites and 4.96 ± 2.67 for forest sites. For Shannon's Diversity Index, forest edge sites had a mean of 0.56 ± 0.50 while forest sites had a mean of 1.35 ± 0.64. A Mann-Whitney test indicated that there was a significant difference between the medians of both habitat types for abundance ($U_{abundance} = 6{,}620.5$, df = 270, $p<0.001$), species richness ($U_{species\ richness} = 7{,}032.5$, df = 270, $p<0.001$) and Shannon's Diversity Index. ($U_{diversity} = 1{,}040$, df = 270, $p<0.001$).

However, at community level, there was little difference between the species accumulation curves, rarefaction curves, and estimated number of species for both habitat types. The Chao1 estimate for all forest sites were 45.75 ± 4.20 and all forest edge sites was 41.50 ± 3.16. The overlap in standard errors suggested that there was no significant difference between the total number of species. Species accumulation curves indicated that there was no difference between the communities at 124 sites (Fig. 4.7A). Rarefied species richness estimated 39.0 species in forest edge sites against 38.6 species in forest sites (Fig. 4.7B).

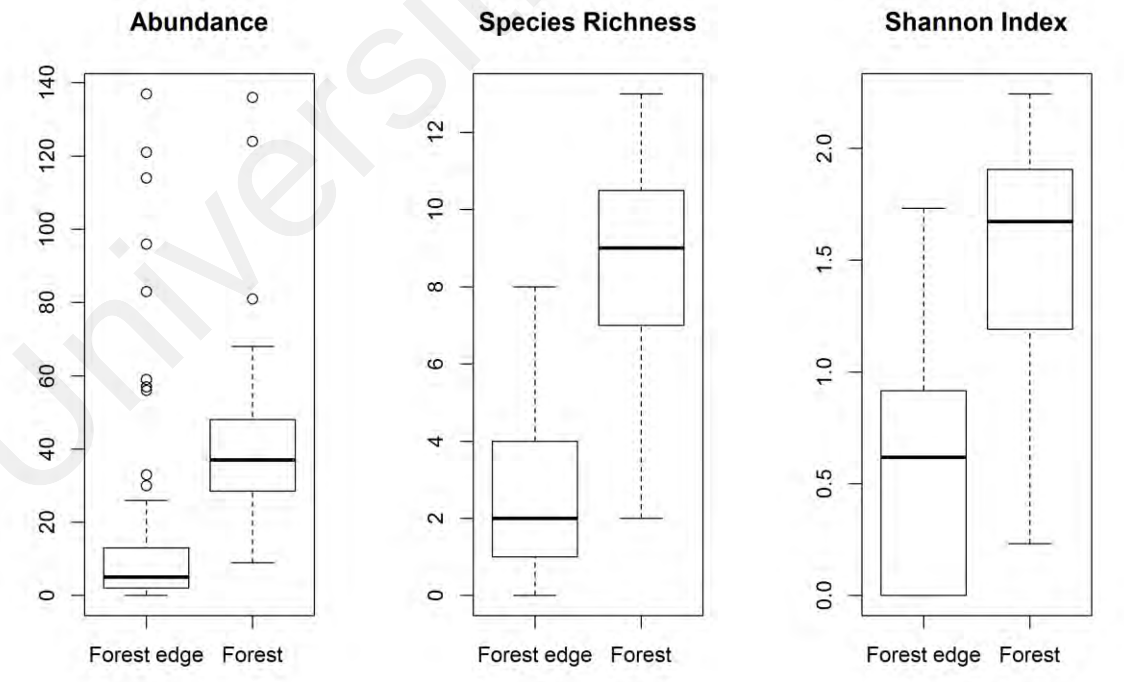


Fig. 4.6: Boxplots of the dung beetle relative abundance, species richness, and Shannon diversity for forest (n = 131) and forest edge (n = 140) sites.

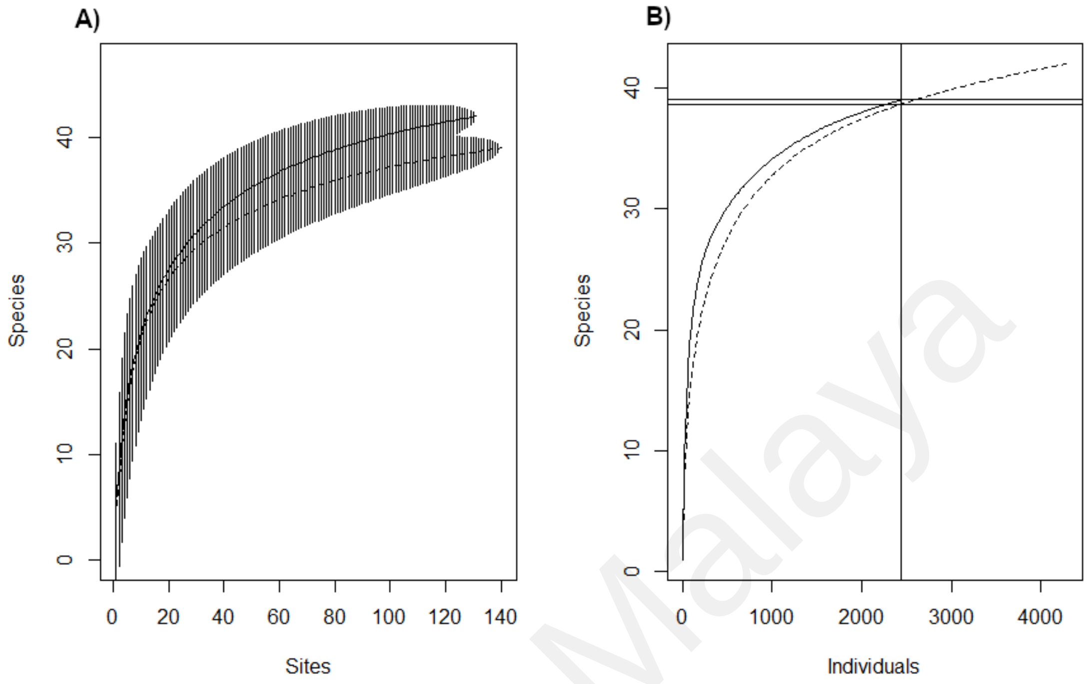


Fig. 4.7: A, Species accumulation curves for dung beetle species in 271 sites; B, Rarefaction curves comparing forest and forest edge samples. The solid line represents forest sites while the dotted line represents forest edge sites.

The sample of 25 beetle species was clearly divided into two groups by hierarchical cluster analysis (Fig. 4.8). One cluster represented beetles that preferred forest edge habitats, characterised by *Megatelus brahminus*, *Onthophagus crassicollis*, *O. karenensis*, *O. luridipennis*, *O. orientalis*, *O. proletarius, Caccobius unicornis*, and *Oniticellus cinctus*. The second cluster is composed of the remaining 15 species with a preference for forest habitats. The overall pattern indicates a demarcation between preference for forest and for forest edge habitat types.

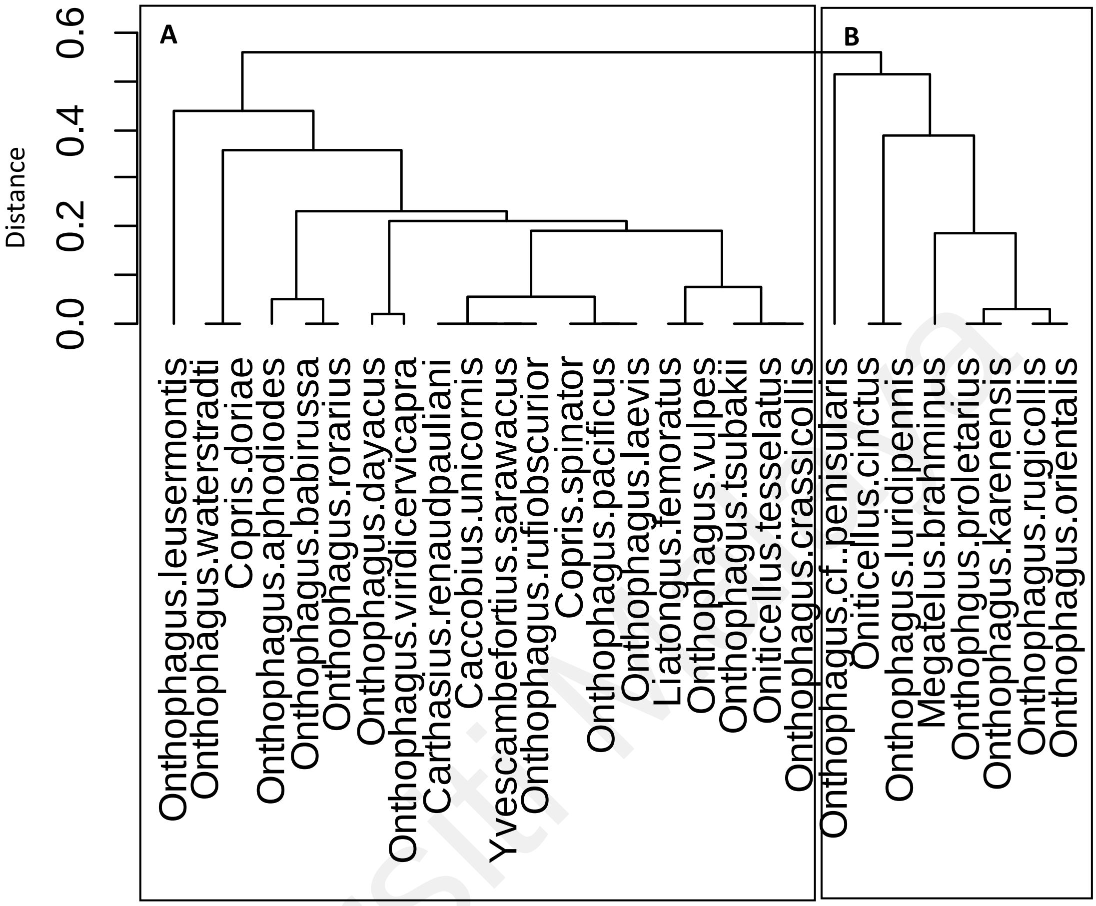


Fig. 4.8: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) hierarchical clustering with Chao-Soerensen distances of the 25 dung beetle species. Two major clusters are indicated, dung beetles that prefer (A) forest sites and (B) forest edge sites.

The NMDS also indicated a similar pattern with forest species clustering together towards positive values of the NMDS1 axis. Forest edge species were scattered along the negative values of the NMDS1 axis. The NMDS2 axis was influenced by the distribution of each species amongst localities; species that were present in few localities had positive values, while species which were widespread amongst localities had negative values (Fig. 4.9). There was no overlap between the forest edge and forest species clusters, which supports segregation between the species of both clusters.

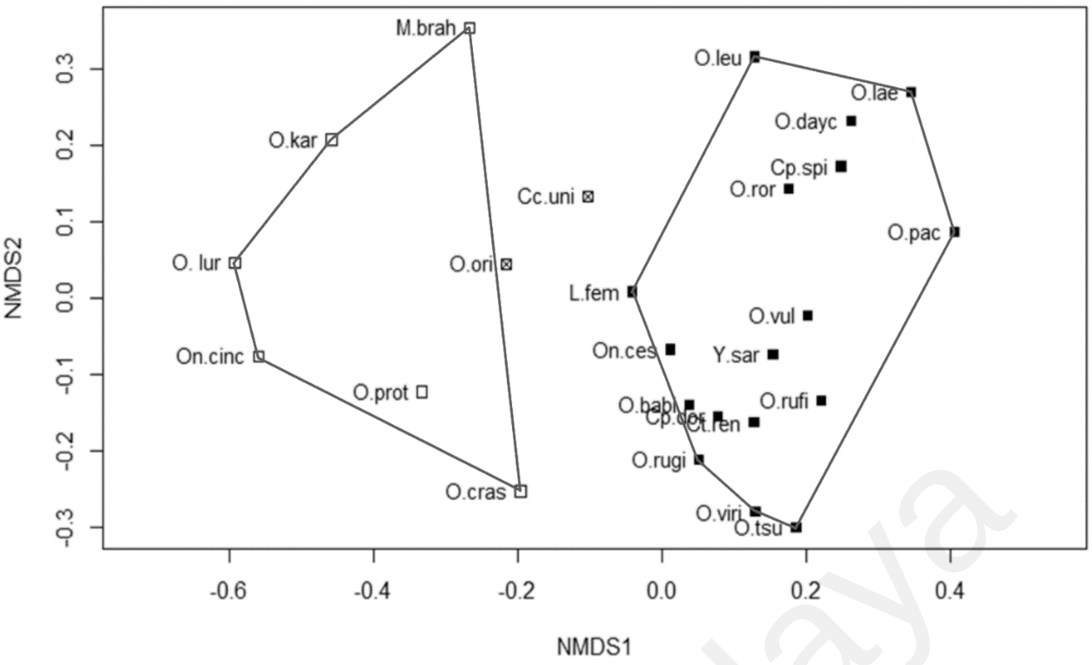


Fig. 4.9: The Non-metric multidimensional scaling (NMDS) ordination of 25 species of dung beetle from 271 forest and forest edge sites. Filled squares represent species that prefer forest habitats, open squares represent species that prefer forest edge habitats, and crossed squares represent species that are evenly distributed among habitat types. Species codes: L.fem: *Liatongus femoratus*, On.tes: *Oniticellus tessellatus*, On.cinc: *On. cinctus*, Y.sar: *Yvescambefortius sarawacus*, O.babi: *Onthophagus babirussa*, O.rufi: *O. rufiobscurior*, O.vul: *O. vulpes*, O.ror: *O. rorarius*, O.prot: *O. proletarius*, O.pac: *O. pacificus*, O.rugi: *O. rugicollis*, O.ori: *O. oreintalis*, O.cras: *O. crassicollis*, O.lae: *O. laevis*, O.dayc: *O. dayacus*, O.kar: *O. karenensis*, O. lur: *O. luridipennis*, O.leu: *O. leusermontis*, O.viri: *O. viridicervicapra*, O.tsu: *O. tsubakii*, Cc.un: *Caccobius unicornis*, Ct.ren: *Catharsius renaudpauliani*, Cp.dor: *Copris doriae*, Cp.spi: *Cp. spinator*, M.brah: *Megatelus brahminus*.

4.4 Dung beetle Community structure:

Sites with elephant presence had lower mean and median abundance and species richness. Sites where elephants were present had a mean abundance of 12 ± 21 beetles, and a median abundance of 5 beetles (Fig 4.10). Sites where elephants were absent had a mean abundance of 26.6 ± 39.5 beetles, and a median abundance of 11 beetles (Fig 4.10). Shapiro-Wilk normality tests indicate that the total abundance, species richness and dweller abundance of elephant present and elephant absent samples were not normally distributed ($p<0.01$). In terms of species richness, elephant present sites had less species with a mean of 3.26 ± 2.73 species per site and a median of 3 species per site whereas elephant absent sites had a mean of 4.57 ± 2.65 species per site and a median of 5 species per site. There was no obvious pattern between elephant present and absent sites in terms of rarefied species richness (Table 4.4).

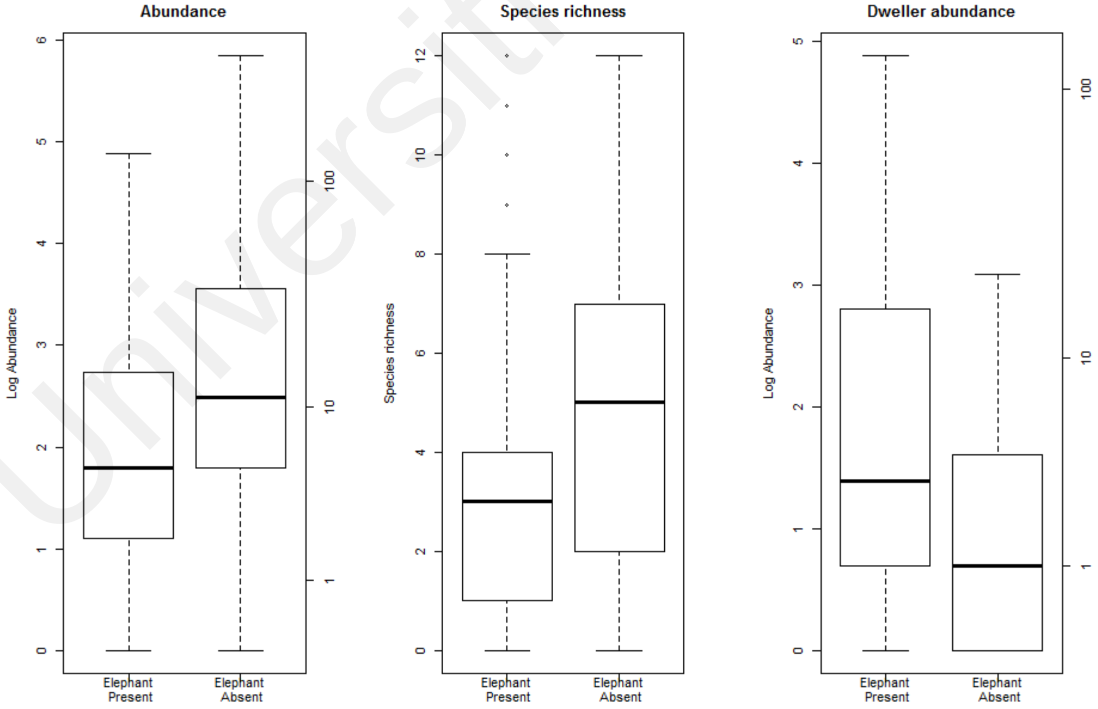


Fig 4.10: Boxplots of total abundance, species richness and dweller abundance for sites where elephants were present and absent.

Table 4.4: Rarefied species richness for all localities, separated by habitat type and breeding behaviour. Abundance for each rarefaction is given under each category.

	Forest			Forest Edge		
	Total (N=166)	Tunneler (N=148)	Dweller (N=29)	Total (N=34)	Tunneler (N=34)	Dweller (N=27)
Elephant absent						
Lanchang	22.20	20.54	3.00	8.64	6.28	3.64
Templer	20.00	18.55	--	9.00	9.00	--
Gombak	12.45	10.45	1.99	9.19	8.24	2.00
Elephant present						
Kenyir	18.35	19.67	2.29	5.10	9.07	2.35
Kuala Gandah	15.68	14.00	2.00	9.04	5.72	4.00
Temenggor	--	--	--	3.98	--	3.93

While PERMANOVA indicated that there was a significant difference between elephant present and elephant absent community structures (Table 4.5), the low R^2 value of 0.094 indicated that variance explained by this variable was very low. This is more clearly seen in the Non-metric multidimensional scaling (NMDS) of the same dataset, which showed no pattern between species and the presence of elephants (Fig. 4.11). Sites with and without elephant presence were tightly clustered and most common species were within this cluster while singleton species were loosely distributed surrounding it. The pattern of the species in the NMDS is however reflective of the previous habitat preference results.

Table 4.5: PERMANOVA table for the effects of elephant presence and forest type on the Bray-Curtis distance matrix of the dung beetle community. Dummy variables coded as follows; Elephant: 0= Elephants absent, 1=elephant present; Forest: 0= forest, 1=forest edge. Locality was recorded as a categorical variable.

	Df	Sums Of Sqs	Mean Sqs	F. Model	R^2	Pr(>F)
Elephant	1	7.587929	7.587929	34.62483	0.09492	0.001
Forest	1	5.595435	5.595435	25.53279	0.069995	0.001
Locality	4	12.88258	3.220645	14.69628	0.161152	0.001
Elephant:Forest	1	2.87075	2.87075	13.09965	0.035911	0.001
Forest:Locality	3	7.393675	2.464558	11.24614	0.09249	0.001
Residuals	199	43.61026	0.219147		0.545533	
Total	209	79.94063			1	

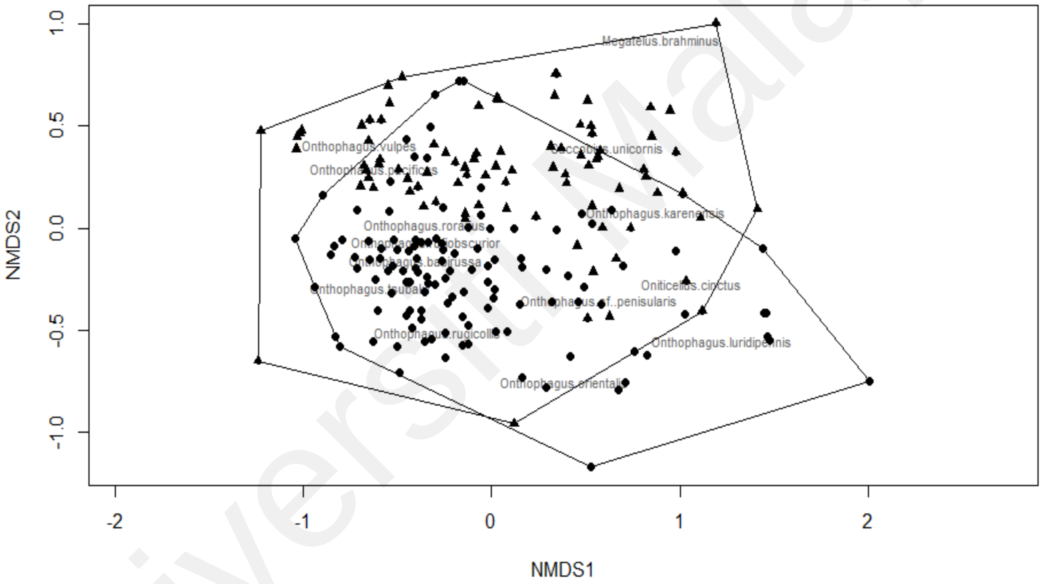


Fig. 4.11: Non-Metric Multidimensional Scaling (NMDS) results for species and sites. Circles represent elephant absent sites, while triangles represent elephant present sites.

Cluster analysis did not indicate any patterns based on elephant presence. Pairwise Sorenson Dissimilarity between localities showed low dissimilarity between localities, with the exception of Temenggor which had much lower sampling effort. Excluding Temenggor, the average pairwise Sorenson dissimilarity was 0.30±0.04, which indicates a large species overlap between localities. Cluster analysis based on Chao-Soerensen dissimilarity indicates that the different localities did not form distinct clusters based on presence of elephants (Fig. 4.12). Partitioning the beta diversity into nestedness and turnover components failed to show any distinct patterns. In group pairwise comparisons of Sorenson dissimilarity of elephant present sites revealed that the dissimilarity was largely a nestedness pattern (Fig. 4.13), while elephant absent sites had a largely turnover pattern due to the presence of various *Onthophagus* species. Pairwise comparisons of Sorenson dissimilarity between elephant present and elephant absent localities revealed an overall turnover dominated pattern (Fig. 4.13). With the exception being comparisons between Kenyir-Templer and Kuala Gandah-Gombak, which showed larger nestedness components.

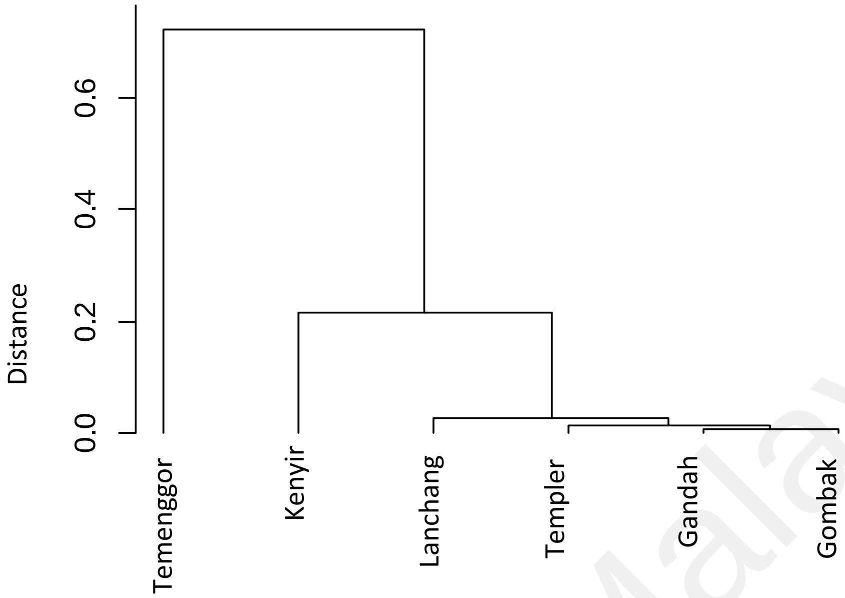


Fig 4.12: Unweighted pair-group method using arithmetic averages (UPGMA) Cluster analysis of localities using Chao-Soerensen distance measures

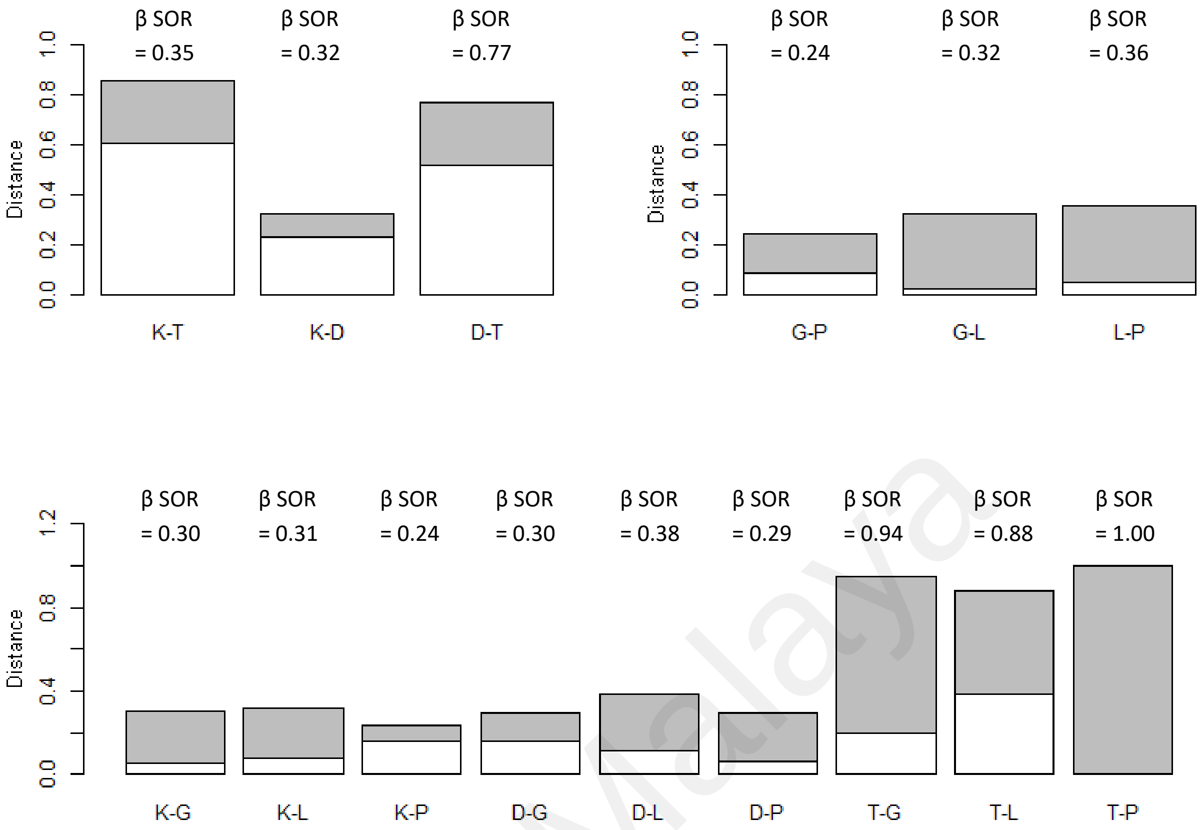


Fig. 4.13: Beta diversity partitioned using pairwise Sorenson distance, grey represented the nestedness component while white represents the turnover component. Locality code is as follows: K: Kenyir, T: Temenggor, L: Lanchang, D: Kuala Gandah, P: Templer, G: Gombak

4.5 Elephant dung beetle associations:

Dweller proportion was shown to be a good predictor for the presence of elephants. Localities where elephants were present had a higher proportion of dwellers (Table 4.6) compared to localities without elephants. The logistic regression model had a 17.5% error rate in predicting the presence of elephants based on the dweller/tunneler proportion in the dung beetle community (Table 4.7). Conversely the size class of the dung beetles did not show a clear response to the loss of elephants. The species richness of large beetle species and small beetle species was not a good indicator for the presence of elephants, with an error rate of 52.5% (Table 4.7).

Table 4.6: The coefficients for the binomial generalised linear models that predict elephant presence based on dweller proportion and dung beetle size.

Model:	**Elephant presence ~ dweller proportion**			
	Coefficient	**Std. Error**	**z value**	**p-value**
Intercept	-0.9037	0.2018	-4.859	<0.001 ***
Dweller proportion	2.814	0.4756	5.917	<0.001 ***
Model:	**Elephant presence ~ Large beetle species richness + Small beetle species richness**			
	Coefficient	**Std. Error**	**z value**	**p-value**
Intercept	0.6618	0.2521	2.625	<0.001 ***
Large species	-0.1625	0.1645	-0.988	0.3231
Small species	-0.0963	0.0725	-1.327	0.1845

Table 4.7: Binomial generalised linear model confusion matrixes for the dweller proportion model and the beetle size model.

Dweller Proportion model			
	True elephant presence		
Predicted elephant presence		0	1
	0	20	7
	1	0	13

Beetle size Model			
	True elephant presence		
Predicted elephant presence		0	1
	0	5	6
	1	15	14

Apriori association rules were more informative regarding the relationship between elephant presence and dung beetle species. A few species were closely associated with the presence of elephants with a lift score of 2.069 (Table 4.8). A confidence score of one indicates that these species exclusively co-occur with elephants. Species with low support and count score co-occur with elephants in a small number of sites, and therefore any indication of association could be due to random factors. Of all the 50 species tested, only *M. brahminus* has a high count of exclusive co-occurrences with elephants. *Cp. numa*, *Aphodius* sp. B and *Cp. punctulatus* had a high confidence, but low support due to the small amounts of individuals collected, the pattern seen in these species may be influenced by the small number of meaningful samples. *Onthophagus dayacus* and *O. laevis* were also positively associated with the presence of elephants with a lift score of 1.742 and 1.724 respectively, however both species had a confidence score that was less than one, indicating that were also present in sites without elephants. Other species indicated no association with elephants.

Table 4.8: Apriori association rules results species associated with elephant presence.

Species	**Support**	**Confidence**	**Lift**	**Count**
Megatelus brahminus	0.173	1	2.069	47
Onthophagus dayacus	0.059	0.842	1.742	16
Onthophagus laevis	0.037	0.833	1.724	10
Copris numa	0.022	1	2.069	6
Aphodius sp.B	0.011	1	2.069	3
Copris punctulatus	0.007	1	2.069	2

4.6 Intraspecific trait comparison:

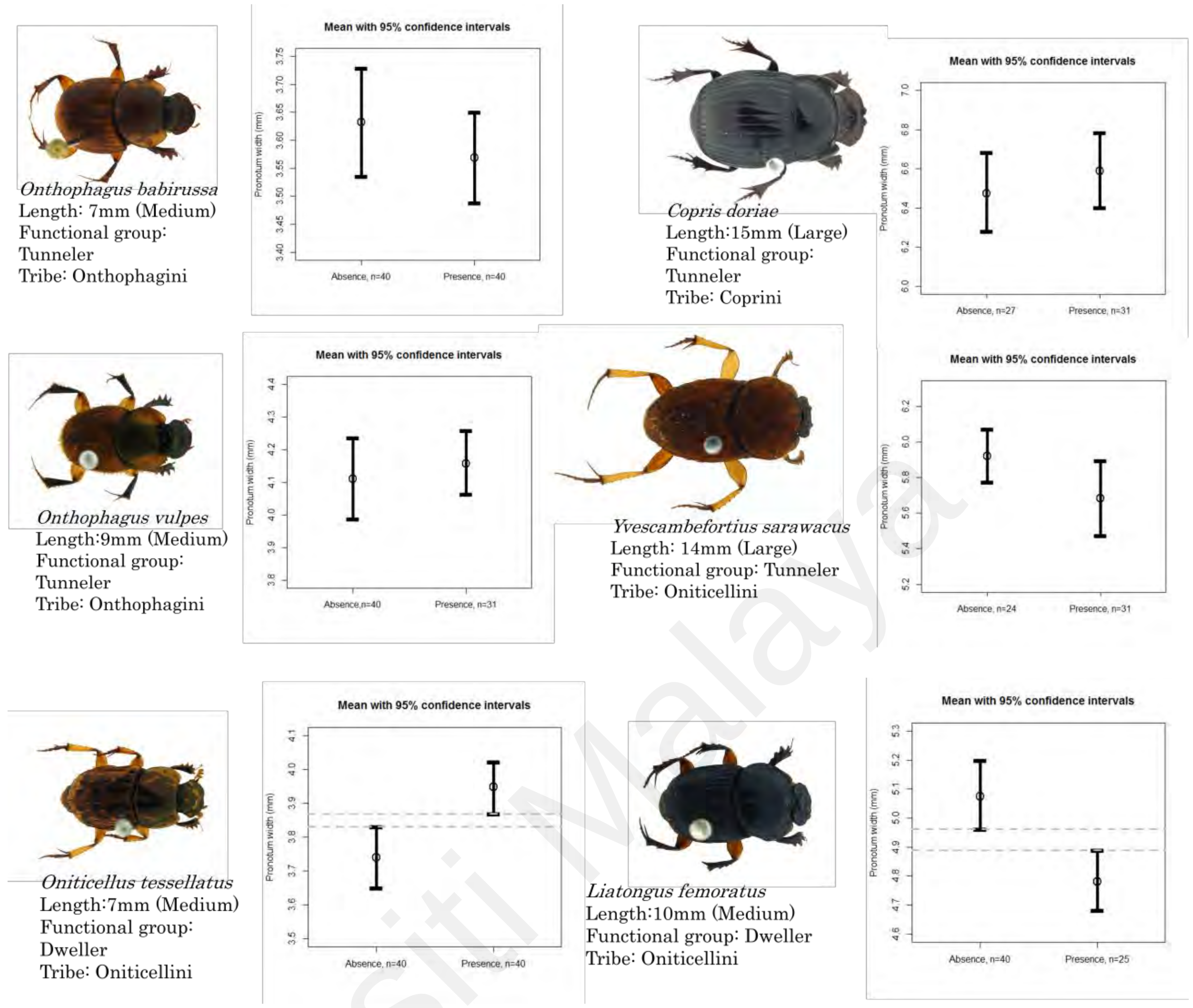
Histograms, q-q plots and Shapiro-Wilks tests (Table 4.9) indicated that some of the samples were not normally distributed due to the presence of outliers. Four of the six dung beetle species did not show any significant difference between the means or medians of each locality, while two species showed a significant difference between both localities. *Liatongus femoratus* and *On. tessellatus* had significant differences between the medians, as indicated by the Mann-Whitney test (Table 4.10). Bootstrapped means and confidence intervals further support this result, with only *L. femoratus* and *O. tessellatus* having significant differences between the means due to non-overlapping confidence intervals (Fig. 4.14). *Liatongus femoratus* had a bootstrapped mean of 4.78 and 95% confidence intervals of 4.68 mm and 4.89 mm in the locality with elephant presence and bootstrapped mean of 5.07 and 95% confidence intervals of 4.96 mm and 5.20 mm in the locality with elephant absence. This indicates that *L. femoratus* in localities without elephants were significantly larger than those in locality without elephants. The difference between means was 0.29 mm. *Oniticellus tessellatus* had a bootstrapped mean of 3.94 mm and 95% confidence intervals of 3.86 mm and 4.02 mm in the locality with elephant presence and a bootstrapped mean of 3.74 mm and 95% confidence intervals of 3.65 mm and 3.83 mm in the locality with elephant absence. *Oniticellus tessellatus* in localities without elephants were significantly smaller than localities with elephants. The difference between means was 0.21mm.

Table 4.9: Results of the Shapiro-Wilks Normality test on pronotum widths of each species. * indicates a significant difference from a normal distribution.

Species	Treatment	Shapiro-Wilks statistic	p-value
Onthophagus babirusa	Absent	0.9736	0.4653
	Present	0.9637	0.2245
Onthophagus vulpes	Absent	0.9181	0.0240*
	Present	0.9479	0.0643
Liatongus femoratus	Absent	0.8411	0.0015*
	Present	0.9434	0.0450*
Oniticellus tessellatus	Absent	0.9647	0.2414
	Present	0.9525	0.0859
Yvescambefortius sarawacus	Absent	0.9655	0.4043
	Present	0.9660	0.5694
Copris doriae	Absent	0.9071	0.0109*
	Present	0.9754	0.7460

Table 4.10: Results of the Mann-Whitney test comparing pronotal widths of dung beetles in forests where elephants were present and absent. ** indicates a significant difference between medians to 0.01, *** indicates a significant difference between medians to 0.001, nd indicates no significant difference was detected between medians.

Species	U-Statistic	DF	p-value
Copris doriae	433.5	79	0.821 nd
Liatongus femoratus	214.5	70	<0.001***
Onthophagus babirusa	698.5	64	0.331 nd
Oniticellus tessellatus	1155	79	<0.01**
Onthophagus vulpes	623.5	54	0.785 nd
Yvescambefortius sarawacus	298.5	57	0.215 nd



Onthophagus babirussa
Length: 7mm (Medium)
Functional group: Tunneler
Tribe: Onthophagini

Copris doriae
Length:15mm (Large)
Functional group: Tunneler
Tribe: Coprini

Onthophagus vulpes
Length:9mm (Medium)
Functional group: Tunneler
Tribe: Onthophagini

Yvescambefortius sarawacus
Length: 14mm (Large)
Functional group: Tunneler
Tribe: Oniticellini

Oniticellus tessellatus
Length:7mm (Medium)
Functional group: Dweller
Tribe: Oniticellini

Liatongus femoratus
Length:10mm (Medium)
Functional group: Dweller
Tribe: Oniticellini

Fig. 4.14: Boostrapped means and 95% confidence intervals for the pronotal width of six species of dung beetle from the Kenyir (Elephant present) and Gombak (Elephant absent) localities. Overlap between 95% confidence intervals indicates a significant difference between the means. Dotted lines were added to show the lack of overlap between the 95% confidence intervals.

5.0 DISCUSSION

5.1 Dung beetle specimen collection for ecological study:

Compared to pitfall traps, BITs appear to be more efficient at collecting larger numbers of tunneling beetles but at the expense of rollers. In terms of species collected per trap, the results were relatively similar but a larger sample would be needed to conclusively determine if there is a difference in the number of species detected per trap. Shannon’s Diversity index tends to give more weightage to the number of species, while Simpson’s Diversity Index is better at detecting cases of single species dominance. There were no significant differences between traps for both diversity indexes, indicating that both traps collect similar community structures of beetles.

While BITs only collected 1.33 species per trap, the cumulative effect of this is felt at larger sample sizes. Once more the sample size is larger than 10 traps, BITs collect a significantly larger number of species. This is also be related to the larger abundance of beetles collected in BITs, as generally the larger the abundance collected, the higher the chance of catching rarer species. This partially explains why the BIT was capable of collecting 6 more singletons than pitfall traps.

BITs proved to be inefficient in collecting rollers. The only rollers collected were caught in the act of rolling. In some traps, the abandoned balls of rollers could be found. Pitfall traps however managed to collect 70 individuals of roller dung beetle, compared to the 24 found in BITs. Modification of an additional water filled bowl that collects rollers or integrated traps for roller as described in Bernon (1980) may be made to increase the catch of rollers.

Doube and Giller (1990) reported that there was no significant differences in the number of individuals for most species of African crepuscular/nocturnal tunnelers collected in BITs compared to pitfall traps. *Onthophagus* species which are mostly diurnal in habit (Davis 1999, Niino *et al.*, 2014) contributed to most of the individuals collected in BITs in this study. However, beetles collected from the previous night remained in the trap, as evident by the presence of nocturnal beetles recorded by Davis (1999) and Niino *et al.* (2014) such as *Copris ramosiceps*, *Cp. doriae*, *Cp. spinator* and *C. renaudpauliani* in the traps.

Davis *et al.* (2001) characterised the disturbance of a forest by the shape of rank abundance curves, with the assumption that steeper and shorter curves indicate less species and higher dominance and therefore a more damaged environment. It can be shown here that varying the trap types in the same habitat and same environmental conditions can produce curves that could be misinterpreted as evidence of disturbed environments. While the sample is relatively small, this demonstrates that comparisons between studies that use different types of traps should be done with care.

A small amount of dung was used to bait the BITs in the comparative study due to the logistics of obtaining a sufficient amount of fresh dung to bait a large number of traps in a single day. An interesting observation in the BITs was that the small amount of dung (50 g) in all traps was not exhausted after 24 hours. This is in contrast to Slade *et al.*, (2011) which placed 780 g of cow dung because "It was the smallest amount that could be used without total removal in 24 hours." A likely explanation for this is the lack of large nocturnal tunnelers in this sample, only two *Catharsius renaudpauliani* were collected in all the BIT and pitfall traps. Slade *et al.* (2011) stated that large nocturnal tunnelers were positively correlated with of dung removal and responsible for the removal of large amounts of dung. It is possible that larger beetles are attracted to larger quantities of dung and hence increase the rate of dung removal. Larger numbers (>14) of *C. renaudpauliani* were collected in field trials of BITs that used larger quantities of dung. The effects of size of dung on the attraction of certain species are still unknown.

It is not known why there was such a large difference in the abundance of *O. babirussa* between traps. *Onthophagus babirussa* is a generalist species that is commonly found in forests throughout the Malay Peninsula and Borneo (Davis *et al.*, 2001; Slade *et al.*, 2011; Doll *et al*., 2014). It should be noted that the soil used in the traps smelled strongly of dung beetles when it was being examined and no provisioned *Onthophagus* nests were found even when there are large numbers of beetles. Perhaps the BIT mimics the natural sub-social conditions of these beetles better, and hence there may be some sort of signalling that attracts more members of the same species. However, it has not been established if there is any long distance pheromonal signalling in dung beetles (Hanski & Cambefort, 1991). As this study cannot explain this observation, this may represent an interesting avenue for further research.

The lack of documented uses of BITs makes them a more unreliable trap type than conventional pitfall traps because a lot of unforeseen complications of their use have not been recorded. This lack of information also reduces the interpretability and comparisons between studies. While having a slightly faster set up time compared to pitfall traps, BIT traps are much more tedious to collect, since beetles are manually collected and there is a larger number of individuals to collect. In terms of research design, emigration from the trap (especially from beetles such as rollers) is another confounding parameter is added to data collected from BITs. This emigration also reduces the effectiveness of BITs as a long terms trap, as beetles may be able to escape the trap if it is left in the field for prolonged periods of more than 48 hours.

BITs have the advantage of collecting live specimens. This is useful for DNA studies, given the fast DNA degradation of dead specimens in warm, humid environments (conventional pitfalls in the tropics). Live specimens can also be used for capture-recapture studies and population estimation. The higher yield of species in more intensive sampling is also advantageous for the collection of taxonomic material. As digging a hole is not necessary for this trap, it can be used on habitats with rocky or hard substrates that prevent the use of pitfall traps, such as limestone karsts. During other field tests of this trap, it was found that very large (65 mm) species such as *Heliocopris tyrannus* could be caught in relatively shallow (4.5 cm depth) traps. Attempts to trap this species using pitfall traps have largely been unsuccessful. Practically, BITs are less cumbersome to carry compared to pitfall traps due to the absence of liquids. This is advantageous in situations with limited manpower.

The design of BITs depends entirely on the environment that they are deployed in, where considerations such as the composition of the dung beetle community, sample sizes, logistics and manpower limit the design that can feasibly be deployed. Depth of traps appears to not be much of a factor, large (20-35 mm) and very large (65 mm) sized beetles could be caught in traps with the depth of 4.5 cm. However deeper traps may be used to observe the nesting behaviour of the beetles attracted to the bait. Soil or sand can be obtained from the site itself, this reduces the amount of materials that needs to be carried to the trapping site and ensures that the soil type is the same as the microhabitat. Beetles are usually only found in the bottom layer of soil once the trap is examined. Because of this the container is recommended to be only half filled with soil, since beetles are rarely found in the upper layers of the soil and the gap reduces the chances of beetles from escaping. The amount of dung used is a factor for some species, when large elephant dung was used with these traps larger sized beetles were found per trap than when smaller amounts of cow dung were used. Amount of dung may be factor here as opposed to the type animal producing the dung, Vinod and Sabu (2007) report overlap between the beetles that visit elephant and gaur dung, which indicates that cow dung is a suitable proxy for collecting most generalist herbivore dung feeding beetles.

5.2 Habitat preference of dung beetle species:

Forest sites had a higher abundance of beetles compared to forest edge sites, however the lack of significant difference in species accumulation curves and rarefaction indicated that there is some plasticity in habitat preference, with some species being found in both habitat types albeit at lower abundances. Ordination, clustering and modelling showed a clear divide between species that prefer forest edges and species that prefer forest habitats. Most species preferred forest sites to forest edge sites, but there were a few forest edge specialists that were rarely found in forest habitats. It was previously suggested by Hosaka *et al*. (2014) and Boonrotpong *et al*. (2004) that dung beetles are sensitive to the loss of canopy cover, which causes fluctuations in light intensity, temperature, and humidity. It is likely that the higher abundance and diversity at forest sites is due to a more stable environment compared to the fluctuating physical environment of forest edge habitats. Forest edge specialists probably have a wider tolerance to the conditions encountered in environments outside the forests. Additionally, Southeast Asia generally has higher mammalian diversity within forests as opposed to large grazing mammals at forest edges (Harrison, 1966). Therefore, the response of beetle diversity to forests may be affected by this factor as mammalian diversity has been positively correlated with dung beetle diversity (Nichols *et al*., 2009).

The classification first proposed by Davis *et al*. (2001), which was riverine (riparian or forest edge habitats), even (no preference to any habitat) or forest interior (Preference to forest interior habitats), is applicable to our sample of beetle species. In this case, our forest edge species corresponded with the riverine category, while forest species corresponded with the forest interior category. The habitat preference of most of the species documented in this study does not contradict previous reports; however, there are several exceptions. Davis *et al*. (2001) categorised *O. rugicollis* and *Y. sarawacus* as riverine and even categories, respectively. Both species were found in disturbed shaded habitat (e.g., riparian reserves, logged forests, and oil palm estates) by Gray *et al*. (2014) and this agrees with our classification as forest species. Ueda *et al*. (2017) recorded *O. crassicollis* as a species found in burnt forests, *C. renaudpauliani* in secondary forests and burnt forests, and *On. tessellatus* in cattle pasture. In this study, these species were recorded as a forest edge, forest, and forest species, respectively. The species categorised as forest species matched previous records of these species being found in disturbed but shaded habitats such as riparian reserves (Gray *et al*., 2014), logged forests (Edwards *et al*., 2014; Gray *et al*., 2014) and oil palm estates (Slade *et al*., 2014; Gray *et al*., 2014) It is likely that Oniticellini such as *L. femoratus*, *On. tessellatus*, and *Y. sarawacus* are more common when the dung of large herbivorous mammals is used as a bait (Hanboonsong *et al*., 1999); these mammals tend to prefer open grazing grounds and possibly habitat selection of Oniticellini is somewhat influenced by the availability of such dung. The findings of Hosaka *et al*. (2014) mostly supported our classifications of *O. proletarius* and *O. orientalis* as species prefer forest clearings.

Most of the species that were recorded in forest habitats were present in species lists of community level studies from the Malay Peninsula (Lee *et al*., 2009; Doll *et al*., 2014; Hosaka *et al*., 2014; Boonrotpong, 2004). However, the forest edge species identified as *M. brahminus*, *O. proletarius*, *O. crassicollis*, *O. karenensis*, and *On. cinctus* were rarely or never recorded in the previous studies. In this study, *O. luridipennis* is a new record for the Malay Peninsula. It is a species that appears to have been overlooked in previous surveys despite being commonly associated with domestic cattle (Hanboonsong *et al*., 1999). This indicates that these non-forest habitats are relatively underrepresented in regards of dung beetle studies. Perhaps non-forest habitats should not be viewed as disturbed or damaged habitats but as alternative states that have their own unique species interactions and food webs.

As with Ueda *et al*. (2017), it appears that forest edge species have larger distributional ranges than forest species. Except for *O. karenensis*, all of the edge species were of widespread distribution, with ranges extending north to India and China, while most forest species were of Sundaland or Indochina distribution (Table 5.1). It is likely that the physiological plasticity that allows these beetles to survive in non-forest environments also allows them to adapt to a wider range of climatic conditions (Shahabuddin *et al*., 2011). There are still many unresolved species complexes in South East Asian dung beetle taxonomy: for example, *O. laevis* and *O. pacificus* are believed to be species complexes that have yet to be fully resolved (J. Huijbregts, pers. comm.). In my results, these species were classified as forest species in spite of having widespread distributions. Some caution should be taken when interpreting these results.

While the species compositions in this study were similar to other studies conducted in the Malay Peninsula (Lee *et al*., 2009; Doll *et al*., 2014; Hosaka *et al.*, 2014), the difference in trap types may be a factor in the detection of some dweller species in this study such as *L. femoratus* and various Aphodiinae. This study was also of limited geographical scope, and a wider survey that includes more types of forests and other non-forest habitats such as pastures, tropical scrubland and sub-urban areas may bring about a better understanding of how these beetles can adapt to non-forest habitats. A transect measuring the distance from the edge of the forest, similar to the design of Peyras *et al*. (2013), is likely to produce a more nuanced classification of the beetles as opposed to the dichotomous classification used in this study.

Table 5.1: The biogeographical distributions of selected species Malay Peninsula endemic (MP), Sundaland (SU), Sundaland and Indochina (IN), Southeast Asia (SEA), Widespread (W). (Arrow, 1931; Balthazar, 1963).

Species	Distribution
Caccobius unicornis	W
Megatelus.brahminus	W
Onthophagus crassicollis	W
O. karenensis	IN
O. luridipennis	W
O. orientalis	W
O. proletarius	W
Oniticellus cinctus	W
Carthasius renaudpauliani	SU
Copris doriae	SU
Cp. spinator	SU
Liatongus femoratus	IN
O. babirussa	SU
O. dayacus	SU
O. leusermontis	SU
O. pacificus	W
O. rufiobscurior	MP
O. rugicollis	SU
O. tsubakii	MP
O. vulpes	SU
On. tessellatus	IN
Yvescambefortius sarawacus	SU

5.3 Dung beetle community structure:

While a trophic collapse was not observed, in habitats where elephants were removed, there was a shift from being dominated by dwellers such as *L. femoratus* and *M. brahminus* to generalist species which specialise in rapid burial of dung such as *Onthophagus babirussa*, *Catharsius renaudpauliani* and *Copris doriae*. This may be an indication of a change from a habitat where low quality dung, which is high in fibre and low in carbohydrates, is available in excess to a habitat where only high quality dung, which is richer in carbohydrates and proteins (Frank *et al*., 2017), is available and scarce. The former system would be more conducive to less competitive dweller species that do not rapidly bury dung and prevent it from being used by competitors. The high persistence of elephant dung may also be a factor that allows dweller beetles to be present in larger numbers, as large pieces of highly fibrous dung cannot be totally cleared away by the action of tunnelers and thus it provides the necessary breeding medium for dwellers.

In the case of trophic collapse, the localities without elephants would be a nested subset of the community in which elephants are present (Balsega, 2010). This was not the case in the results, instead many localities indicated turnover instead of nestedness as the major component of the Sorenson dissimilarity. The dissimilarity between localities can thus be interpreted as other species being present due to other disturbances or random chance, and not an extinction event that leads to the community becoming a smaller subset of the original community.

Some dwellers were still able to survive in environments where elephants were absent. Nichols *et al*. (2009) demonstrated that Neotropical dung beetles were relatively resilient to trophic cascades, as multiple linkages within the trophic structure of tropical terrestrial habitats allow species to switch to other available resources when a single resource is removed. Most studies into mammalian-dung beetle co-extinctions conducted in the Neotropics reported a correspondence between the loss of mammalian biomass and the reduction of dung beetle species richness and abundance (Feer and Boissier, 2014; Anderson and Laurence, 2007; Culot, 2013). These studies dealt with an overall loss of mammalian fauna, in this study when elephants were relocated some large mammals such as wild cattle, deer, wild boar and tapirs, as well as smaller omnivores such as monkeys remained in the forest and dung beetles could still utilise the dung produced by these mammals (Clements *et al*., 2010).

5.4 Dung beetle-elephant association:

Revisiting the list of dung beetles recorded to visit elephant dung of Goh *et al.* (2014), it appears that some of the patterns that were observed matched the results of a more thorough survey, but it has also revealed more nuances to the habits of dung beetle species. *Copris* species and other large tunnelers were indeed attracted to the dung of elephants, however many small tunnelers and dwellers were also present and very large tunnelers such as *Heliocopris* were not collected in any of the traps baited with elephant dung in this study.

While both Goh *et al*. (2014) and Doll *et al*. (2014) suggested that *Copris* had a higher diversity on elephant dung, this study seems to indicate that there is not much difference in terms of *Copris* diversity compared to other studies from the Malay Peninsula (Lee *et al*., 2009; Hosaka *et al*., 2014; Boonrotpong *et al*., 2004; Qie *et al*, 2011). Upon examining the original sample from Doll *et al*. (2014), I found that the number of *Copris* species recorded by Doll *et al*. (2014) was exaggerated due to misidentifications of large males and small males as different species. Of the *Copris* species encountered in this study, *Cp. numa* was believed to co-occur with elephants due to exclusive co-occurrence in localities where elephants were present. Museum records indicate that there is an overlap between the geographic range of *Cp. numa* and elephants on the Malaya Peninsula (Pers. Obs). While *Cp. punctulatus* had a high confidence value in the apriori rules, Hanboonsong *et al*. (1999) notes that it is also found in cattle dung, these results are likely to be an artefact of the small number of beetles collected and it reflected in the small count value. Other species such as *Cp. agnus, Cp. spinator, Cp. doriae* and *Cp. ramosiceps* were not found to be associated with elephant dung. The species *Cp. bellator* and *Cp. hosakai* were not detected despite intensive sampling, both of which are very rare species (Balthasar 1963; Ochi & Kon, 2014a). The large tunneler *Ct. renaudpauliani* was present in elephant dung, but especially common in the Gombak locality where elephants were absent, this species has been observed feeding on the dung of humans, monkeys and wild boars as well as being attracted to traps baited with rotting fish (Goh, T.G., unpublished data). It is likely that this species is a generalist that prefers omnivorous dung.

The very large tunneler *Heliocopris tyrannus* was encountered during this survey, a single female was found burrowing under a pile of wild elephant dung in the Kenyir locality. Another female individual was collected from Fraser's Hill in BIT baited with horse dung. Following the statement in Goh *et al*. (2014) that this species "is rarely found in modern museum collections but quite common in older museum collections", many more specimens have been found and it has become apparent that *H. tyrannus* is an open area species with wide habitat tolerances (Goh, T.G., unpublished data). The rarity of *H. tyrannus* specimens is likely due to biases in sampling and searching in areas where they are not present, they are quite reliably attracted to lights in rural areas (Goh, T.G., unpublished data). The attraction of *Heliocopris* species to lights has been reported by Sabu *et al.* (2006). Another species, *H. bucephalus* is farmed on buffalo dung in Thailand (Leksawasdi, 2010) and generally known to feed on cattle dung

(Hanboonsong *et al*., 1999). The remaining Asian *Heliocopris* species, *H. dominus*, is reportedly exclusively associated with elephant dung (Joseph, 1998; Hanboonsong *et al*., 1999), but it was not encountered in this study.

Some species such as the small Onthophagini tunnelers recorded by Doll *et al*. (2014) are consistent with surveys in the Malay Peninsula (Lee *et al*., 2009; Hosaka *et al*., 2014; Boonrotpong *et al*., 2004; Qie *et al*, 2011). Most of these species occurred larger quantities in forested habitats, and *Onthophagus* species collected in the forest were observed in the field to die after a few minutes of exposure to direct sunlight. Even though many of these species can persist without elephants, this study shows that elephant dung may be a supplementary resource for many small tunneler species which facultatively use this dung.

The use of elephant dung and BITs resulted in a rarely observed pattern in tropical dung beetle community structure, the dominance of Oniticellini in the samples. Many of these species are very rarely recorded in standard dung beetle trapping that uses human dung baited pitfall traps (Davis *et al*., 2001). Hanboonsong (1999) noted the association of Oniticellini with large herbivorous mammals, this tribe includes *Liatongus*, *Oniticellus* and *Yvescambefortius*. The dung beetle communities observed in habitats with elephants were similar to elephant dung beetle communities in India which is typically dominated by *Liatongus indicus* (Vinod & Sabu, 2007). Cambefort and Wolter (1991) also report higher Oniticellini abundance in African forest elephant dung. Perhaps this group, along with Aphodiinae dwellers, are the most affected by the loss of megafauna as opposed to generalist Onthophagini which make up the bulk of dung beetle species in South East Asia.

Megatelus brahminus has only been recorded to visit elephant dung (Marco Dellacassa, pers. comm.) *M. brahminus* were mostly collected in forest edge or grassy areas. These beetles were at their most active in dung exposed to direct sunlight at midday, flying directly into the dung as opposed to landing a distance away and crawling towards the dung like *Onthophagus* species. This latter behaviour explains why it is not commonly found in pitfall traps. The beetles tended to congregate in large numbers on certain traps (>80 individuals in a single bolii) but avoid others, therefore at smaller sample sizes they may also be missed by chance. The combination of microhabitat, specific dung preferences and dwelling behaviour are probably why it is rarely recorded in dung beetle biodiversity surveys.

To answer the previously raised question of "What was the cause of the differences between communities described by Goh *et al*. (2014), Doll *et al*. (2014), Sabu *et al*. (2006) and Vinod and Sabu (2007)?", it can be surmised that all the studies were describing different aspects of the same community structure. Only two species have reasonable evidence of endemism to elephant dung; *Cp. numa* and *M. brahminus* (Section 4.5). Both species have almost nothing in common, with one being a large tunneler and the other being a very small dweller. Most tunneler species appear to be using elephant dung as a facultative rather than an obligate resource, and the community structure of these species was largely affected by habitat type. Dwellers were an important part of the elephant dung community, but sampling methods and the quantity of dung used for trapping are likely factors which influence their detection. How rollers utilise elephant dung is poorly known, but undoubtedly there are many interesting discoveries awaiting anyone that delves further into this topic.

5.5 Intraspecific trait comparison:

Of the six beetle species surveyed, only two species: *On. Tesselatus* and *L. femoratus;* showed any intraspecific difference between localities with different elephant presence. While all of these species have been recorded to be attracted to elephant dung (Doll *et al*., 2014), based on these results it is possible that not all species utilise elephant dung as a nesting medium for larva. Most adult dung beetles feed on a variety of dung types (Frank *et al*., 2018) and are known to have a prolonged stage of ‘maturation feeding’, in which beetles build up body reserves after eclosion (Hanski & Cambefort, 1991). While elephant dung may be a food resource for adult beetles, it is probably not used by some species for breeding. These results indicate that by looking at the variation of response in terms of morphological development on an intraspecific scale, the preferred nesting medium of dung beetle species can be explored.

In tropical Africa, it has been observed that elephant specialists can switch to other types of dung when their preferred food source is not available, however this comes with the trade off of smaller sizes (Cambefort, 1991). It may be that *L. femoratus* and *On. tessellatus* have adapted to feeding on the fibrous dung of large mammals such as wild cattle and elephants. These types of dung are believed to be of low quality as more provisioned dung is needed to produce larger sizes of beetles (Moczek, 1998). The ecology of one of these beetles supports this hypothesis as *L. femoratus* is known to occur in cattle farms across Malaysia and Southern Thailand (Hanboonsong *et al*., 1999). However, *L. femoratus* showed an increase in pronotum width in the site where these large mammals were absent. This may indicate that *L. femoratus* is capable of switching to other resources when large herbivore dung is absent. With less viable breeding sites, possibly larger individuals are more capable at competing for scarce resources, leading to directional selection towards larger sizes. The *On. tessellatus* from forests without large mammals were smaller than that of the other sample. *Oniticellus tessellatus* has been found to be capable of feeding on other sources of food aside from dung, such as rotting durian fruit (Goh, T.G., unpubl. data). It may be that loss of large mammal dung causes a switch from more nutritious dung to less nutritious options or that less available resources result in less larval provisioning, resulting in smaller pronotal widths.

The lack of a phenotypic response from *Y. cambefortius* and *Cp. doriae* was possibly due to these species being large tunnelers. Large tunnelers are believed to be more competitively advantaged in environments of scarce dung because they are able to remove large amounts of dung (Hanski & Cambefort, 1991). It is possible these large tunnelers are actually better suited for high competition/low persistence resource availability and therefore do not need to undergo phenotypic adaptation when there is a change in resource availability. Alternatively, large tunnelers displayed a larger standard deviation in pronotum size (*Cp. doriae*: 6.53±0.53mm, *Y, sarawacus*: 5.82±0.50mm), this existing variation within size could possibly buffer the effect of resource loss on these species. However, the direct causation of the variation within species is unknown unless more of the natural history is known and further study is conducted.

5.6 Caveats and limitations

As with most studies, this one was limited by available time, funds and logistic considerations. The low number of localities sampled means that there cannot be a generalised conclusion on the effects of elephant removal on dung beetle communities. The lack of existing literature on the breeding behaviour and natural history of a majority of the dung beetles proved to be a major problem in allowing interpretation of the data at habitat, community and intraspecific levels.

The 50m trap spacing is the current standard used for most dung beetle community level studies in the region. While there are some questions regarding the independence of samples separated by this spacing, there is no evidence thus far that the distance should be increased. Independent mark and recapture studies had been attempted some of my colleagues (EM Slade, Per. Comm.) and myself, but of the thousands of beetles marked and released less than a handful are recaptured. While the lack of data makes statistical analysis almost impossible, it does bring into question if the trapped beetles are actually affected by the distance of the trap.

This study used the dung of captive elephants to bait the traps. While it helped to standardise the bait between traps there may be differences in the composition of the captive elephant dung with wild dung. For the safety of the research team, close proximity to wild elephants was avoided. Therefore, closely tracking elephants and examining wild elephant dung was not a viable option. This consideration also limited the study sites to localities that were close to our source of elephant dung, and this reduced the geographical scope of the study. Further examination of this topic with a larger geographical scope that takes into account environmental variables may yield a more detailed understanding of the relationships between elephants and dung beetles.

Due to a limited budget, logistic challenges and a small team, the quality of field data recorded had to be simplified. Many environmental variables were of low resolution, eg. dummy variables were used instead to indicate different habitat types. Quantifying the habitat in terms of density of vegatation, vegetation types, canopy cover, and ambient temperature would have yielded a more accurate description of the microhabitat conditions. A gradient of change from the forest to the edge would also have been possible to examine. Physiological experiments on the heat tolerance of dung beetles would be important information that could have been corroborated with habitat preference data.

At community level, the low resolution of the presence and absence of elephants, which were treated as dummy variables as opposed to spatial occupancy data, may have also introduced limitations to the interpretability of the effects of elephants on the community structure. While climate was accounted for by sampling within the same seasonal conditions, detailed weather information such as ambient temperature or rainfall would have been valuable. Other valuable information was absent in the analysis such as elevation, geological bedrock stratum, three-dimensional forest structure, tree species composition, and the presence of wild and domestic large mammals. This limits the attribution of the absence of elephants as the cause of the differences observed in between elephant present and elephant absent sites.

However, the time-consuming nature of the field work limits the ability of a team to conduct adequate sampling at a large geographical scope within a single season. A much more ambitious project would require a larger team and more sophisticated logistics coordination. Experimentation on the effects of diet of elephant dung on dung beetles of different breeding behaviours and genera may be helpful in understanding the actual effect of the availability of this type of dung.

For the intraspecific trait study, many confounding variables were not accounted or controlled for such as the natural variation within a species or other environmental factors. There are several caveats to be acknowledged in this study. For instance, studies into the effects of forest loss on dung beetle diversity may be confounded by presence and absence different types of mammals. This is further complicated by the unequal response of dung beetle to megafauna as seen in this study. The inclusion of different categories of mammalian diversity (carnivore, omnivore, small herbivore, large herbivore) as parameters in models may yield more accurate models in the investigation of human disturbance on dung beetle diversity. This study was also conducted on only two sites with extreme differences in mammalian fauna, hence it could only produce a limited and less nuanced description of the relationship between the presence of megafauna and dung beetle larval provisioning. Expanding the geographical scope and comparing dung beetle size in multiple sites which have properly quantified mammalian surveys would likely lead to a more complete understanding of how the developmental physiology of dung beetles are affected by human caused mammalian extinctions. A common garden experiment and breeding experiments may be a better means of finding evidence in intraspecific responses to changes in food availability. While it is an indication that there may be room for further study, it is not conclusive evidence that there is trait based change in response to elephant absence?.

6.0 CONCLUSIONS

Any form of trapping has inherent biases. It is important to be able to document these biases and compare the performance of any novel trapping methods with the current baseline. Burrowing Interception Traps apparently have the advantage of collecting more specimens, but this is at the expense of catching less roller dung beetles. These traps however also collect very large beetles such as *Heliocopris* and are easier to set up compared to a larger pitfall trap.

Tunnelling and dwelling dung beetle species of the Malay Peninsula showed quite strict habitat preference in relation to non-forest habitats. Forests sites had more individuals and were more diverse, compared with forest edge sites. However, there was no difference in terms of rarefied species richness. A majority of the species surveyed were forest specialists. Seventeen species preferred forest habitats and eight preferred forest edge habitats. Few of the forest edge species have been recorded in the Malay Peninsula, indicating that this habitat type may be underrepresented in studies concerning dung beetles of the region. Forest edge species generally had a wider distributional range than forest species, but further taxonomic studies are required to resolve if this is truly a biogeographic pattern or whether these are widespread species complexes.

The species composition of dung beetle communities is relatively resilient to disturbances such as the removal of large mammals like elephants. Instead of a trophic collapse, it appears that the community is able to adapt to the loss of elephants with the loss of few species. But while the number of species showed little change between the presence or absence of elephants, the relative proportion of dwellers to tunnelers seems to be a good indicator of the availability of excess dung resources. This represents a shift from beetles that take advantage of an excess availability of dung to beetles that are adapted to high removal rates of dung.

The association of dung beetle species to elephant dung seems to be combination of factors such as the tribe, habitat type, beetle size and the breeding behaviour of the beetle. Tunnelers and dwellers both utilise elephant dung, and both types of nesting behaviour appear to have a single representative among elephant dung endemic beetles. These are the large tunneler *Cp. numa* and the small dweller *M. brahminus*. Other species appear to be attracted to or able to facultatively use elephant dung.

This study has shown that comparative trait based studies can help elucidate the effects of trophic collapses on species that may otherwise go undetected in community-level ecological studies. In our study, there were phenotypic change in beetles between the different localities.

While extinction as a direct result of the removal of elephants seems rare, the current conservation strategy in Malaysia of preserving remaining elephant habitats has a direct effect on conserving dung beetle species by reducing habitat disturbances. For the detrital trophic pathway of dung beetles, it appears that elephants do not act as a keystone species in which the removal causes large scale changes in the community structure (Terborgh & Estes, 2010). However, one of the largest threats to dung beetle diversity in the region is the habitat destruction, as most tropical dung beetle species are adapted for forest habitats (Davis, 2001; Qie *et al*., 2011; Hosaka *et al*., 2014). Elephants therefore play a role as an umbrella species for dung beetles as maintaining the forests required to sustain elephant populations protects the habitat for forest dwelling dung beetle species.

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