

## The habitat preference of dung beetle species associated with elephant dung of the Malay Peninsula

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**Abstract.** Dung beetles are often used as indicators of forest health. However, not much is known about the non-forest dwelling dung beetle species of the Malay Peninsula and the species in this habitat have not been compared to communities recorded in anthropogenically altered habitats in South East Asia. Grassland along forest edges is the habitat of grazing megafauna and the dung produced by these mammals is a potentially large resource to dung beetles that can adapt to non-forest habitats. In this study, we classified 25 dung beetle species associated with elephant dung based on their habitat preference. We sampled six different localities on the Malay Peninsula, placing transects within forests and along forest edges. Elephant dung baited traps were deployed at regular intervals along these transects. Forest sampling points had higher abundance, species richness and Shannon diversity than forest edge sampling points, but there was no significant difference in species accumulation curves or rarefied species richness. Hierarchical cluster analysis and ordination indicated a clear division between forest and forest edge species. A binomial generalised linear mixed model further showed that 14 species preferred forest habitats and eight preferred forest edge habitats. These classifications largely agreed with previous habitat preference studies conducted in Borneo and Sulawesi. It is likely that habitat preference in dung beetles is dependent on abiotic factors such as temperature as well as biotic factors such as forest cover and mammalian diversity. The lack of records of non-forest species in literature indicates that non-forest habitats may be neglected in terms of dung beetle studies.

**Key words.** community structure, edge species, bioindicators, habitat change, diversity

### INTRODUCTION

Dung beetles are an important component of the nutrient cycling system in tropical habitats (Nichols et al., 2008). These beetles have a close association with mammalian fauna, and it is believed that the evolution and diversification of dung beetles has been in response to the adaptive radiation of mammals in the Cenozoic Era (Hanski & Cambefort, 1991). Dung beetles have been proposed as a bioindicator due to the response of these beetles to anthropogenic disturbances in the form of habitat change and loss of mammalian biomass (Spector, 2006). Aside from burying dung, these beetles also act as secondary seed dispersers, increase soil aeration through bioturbation, suppress pest and parasite animals such as flies and enteric parasites, enhance plant growth and pollinate plants (Nichols et al., 2008).

Dung beetle community studies in Southeast 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 85% (Hanski & Krikken, 1991). We define the Malay Peninsula as Singapore, Peninsular Malaysia, and portions of Southern Thailand that are below the Isthmus of Kra. 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 Peninsular Malaysia, 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 made by logging with the surrounding forest matrix and found that there was a significant difference between beetles found in forest clearings and 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

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of large tunnelers declined when forests are altered to other habitats, and roller abundance tends to peak in agroforestry systems while dwellers are 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, open patches created by intense logging may have a lasting effect on the community structure of dung beetles. 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 estimated 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.

In this study, we explored how dung beetle communities respond to grassy non-forest areas adjacent to forests and classified dung beetle species based on their habitat preference.

## MATERIALS AND METHODS

**Localities.** This study was conducted in six localities in Peninsular Malaysia (Table 1). All localities were mature, lowland secondary forests with an altitude range of 100 m to 400 m. These forests are classified as Virgin Jungle Reserves, which are a mix of unlogged primary forest stands and secondary forest stands that have regenerated following logging in the 1970s (Doll et al., 2014). Sampling was conducted between July 2016 and December 2017.

**Sampling design.** In this study, we divided our sampling points into two categories: forest and forest edges. We defined forest edges as areas bordering forests, where there is a mix of *Imperata cylindrica* grassland or small stands of early succession plants. In this habitat type, there are few or no large trees and little canopy cover. This category is analogous to the “open areas” category of Shahabuddin et al. (2010) and the “grassland” category of Ueda et al. (2017). We defined forest points as points with 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).

Burrowing Interception Traps (BIT) (Goh & Hashim, 2018) were used as pilot studies showed that these traps could easily be baited with large amounts of elephant dung; they were capable of trapping dweller dung beetles that rarely occur in pitfall traps but are known to inhabit megafaunal dung (Goh et al., 2014). It should be noted that these traps have limited ability to collect roller dung beetles (Goh & Hashim, 2018). This trap consisted of a 16 × 11 × 4.5 cm plastic container filled with soil, with a single (~1 kg) bolus of Asian elephant (*Elephas maximus*) dung placed directly in contact with the soil. This trap functions by preventing beetles from burrowing further into the ground and traps them within the container. The dung and soil were then manually inspected for beetles after being left for 24 hours. The elephant dung was freshly collected from captive elephants.

Table 1. GPS coordinates, forest types, number of transects, number of sampling points for all localities.

Name	Coordinates		Forest Type	No. of Transects	Sample Size	Forest Sampling Points	Forest Edge Sampling Points
Kenyir	N 5°09'59.4"	E 102°37'28.8"	Mature Secondary Forest	6	61	31	30
Bukit Lanchang	N 3°35'29.4"	E 102°10'48.4"	Mature Secondary Forest	6	60	30	30
Gombak	N 3°19'28.7"	E 101°45'09.6"	Mature Secondary Forest	6	60	30	30
Kuala Gandah	N 3°35'40.1"	E 102°08'39.1"	Mature Secondary Forest	6	60	30	30
Templer's Park	N 3°17'12.8"	E 101°38'34.1"	Mature Secondary Forest	2	20	10	10
Temenggor	N 5°32'41.6"	E 101°18'46.9"	Mature Secondary Forest	1	10	–	10

In each locality, we placed up to three paired 500 m transects in the forest and along the neighbouring forest edges. Forest transects were placed at least 200 m from the forest edges. Ten to 11 trapping sampling points were placed at 50m intervals on each transect. A single BIT was set up in each site. 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. Due to safety reasons, only one transect could be placed in forest edge habitat in the Belum-Temenggor locality. A total of 271 sampling points were sampled over a total of 813 trap nights (Table 1).

**Identification.** Identification of beetle species was carried out by comparing specimens to reference collections deposited in the Museum of Zoology, University of Malaya. Balthasar (1963) and Arrow (1931) 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.

**Analysis.** As BITs are inefficient at collecting roller dung beetles (Goh & Hashim, 2018), we removed this functional guild from our analysis. We then compared the mean of each habitat type 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, we could not use parametric tests. 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 (Oksanen et al., 2017).

For the subsequent analysis, we removed species with an abundance of less than 10 as conclusions made on such a limited number of samples were likely to be unreliable,

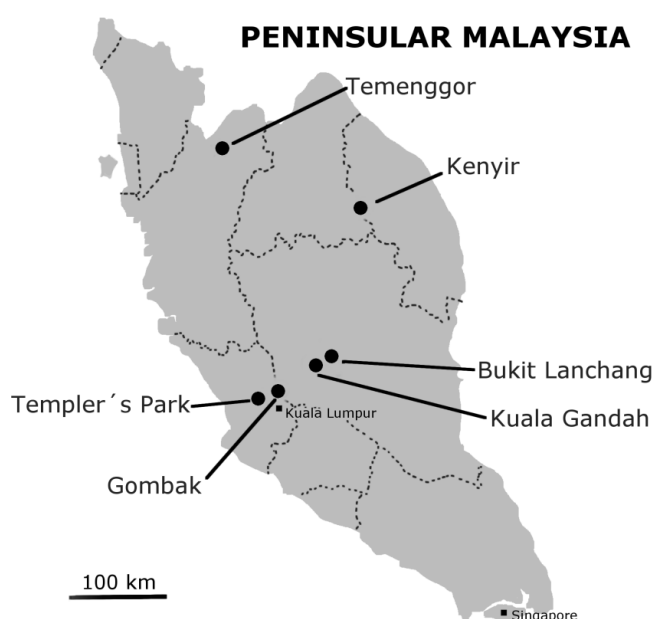


Fig. 1. Map of all the localities where dung beetle sampling was carried out.

which resulted in a dataset of 25 species. We categorised each species 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 (Oksanen et al., 2017) was used to calculate the distance measures used for cluster analysis and NMDS. We then modelled habitat preference of each species as Generalised Linear Mixed Models (GLMMs) that described the relationship between habitat type and abundance. The binomial GLMM had the following predictors: abundance of a single species as a fixed effect and localities as a random effect. This response variable was habitat type, which we coded as a dummy variable with 0 representing forests while 1 represented forest edges. The lme4 package was used for this analysis (Bates et al., 2015).

All analysis was performed using R 3.5.1 (R Core Team, 2018).

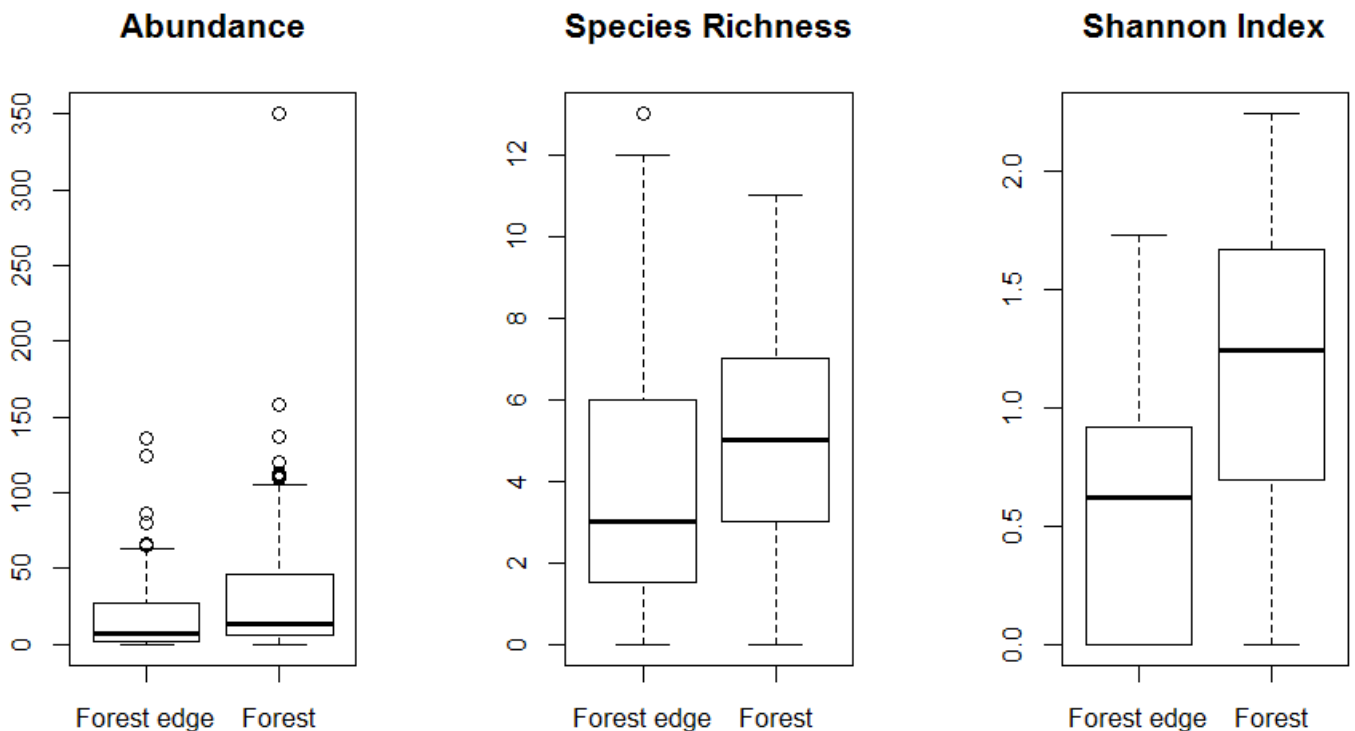


Fig. 2. Boxplots of the dung beetle relative abundance, species richness, and Shannon diversity for forest ( $n = 131$ ) and forest edge ( $n = 140$ ) sampling points.

The distribution range of each species was categorised using categories adapted from Ueda et al. (2017). These categories were: Malay Peninsula Endemic, Southeast Asia mainland (Malay Peninsula + Thailand, Laos, Cambodia, and/or Vietnam), Sundaland (Borneo + Malay Peninsula, Sumatra, Java, and/or Palawan), Sundaland and Indochina (Sundaland + Thailand, Laos, Cambodia, and/or Vietnam), Southeast Asia (Sundaland and Indochina + Myanmar, Philippines, and/or Sulawesi), and Widespread (Southeast Asia + India, Taiwan, China, Japan, New Guinea, and/or Australia). Distributional records were retrieved from Arrow (1931), Balthasar (1963), Davis et al. (2001), Dellacasa et al. (2001), Doll et al. (2014), Goh et al. (2014), Gray et al. (2014), Hosaka et al. (2014), Kabakov & Napolov (1999), Ochi & Kon (1996), Ochi & Kon (2009), Ochi et al. (2009), Masumoto et al. (2008), Slade et al. (2014), and Qie et al. (2011).

## RESULTS

A total of 5,413 tunnelling and dwelling beetles from 50 species were collected. Overall, forest sampling points had higher means and medians for all measures compared to forest edge sampling points (Fig. 2). The mean abundance of forest edge sampling points was  $17.16 \pm 23.13$  while the mean for forest sampling points was  $32.24 \pm 44.67$ . In terms of species richness, the mean was  $4.01 \pm 3.23$  for forest edge sampling points and  $4.96 \pm 2.67$  for forest sampling points. For Shannon's Diversity Index, forest edge sampling points had a mean of  $0.56 \pm 0.50$  while forest sampling points had a mean of  $1.35 \pm 0.64$ . A Mann-Whitney test indicated that there was a significant difference between the medians of both habitat types for abundance ( $U_{\text{abundance}} = 6,620.5$ ,  $df = 270$ ,  $p < 0.001$ ), species richness ( $U_{\text{species richness}} = 7,032.5$ ,  $df$

$= 270$ ,  $p < 0.001$ ) and Shannon's Diversity Index. ( $U_{\text{diversity}} = 1,040$ ,  $df = 270$ ,  $p < 0.001$ ).

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  $45.75 \pm 4.20$  and all open sites was  $41.50 \pm 3.16$ . 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. 3A). Rarefied species richness estimated 39.0 species in forest edge sites against 38.6 species in forest sites (Fig. 3B).

The sample of 25 beetle species was clearly divided into two groups by hierarchical cluster analysis (Fig. 4). One cluster represented beetles that preferred forest edge habitats, characterised by *Megatelus brahminus*, *Onthophagus crassicolis*, *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 forest group was further divided into two subgroups: a group of species that were less common and with restricted distribution amongst the localities, which contained *O. leusermontis*, *O. laevis*, *O. rorarius*, *O. dayacus*, and *Copris spinator*, and a group containing the remainder of the species that consisted of common and widely distributed species. The overall pattern indicates a demarcation between preference for forest and for forest edge habitat types.

The NMDS also indicated a similar pattern with forest species clustering together towards positive values of the NMDS1

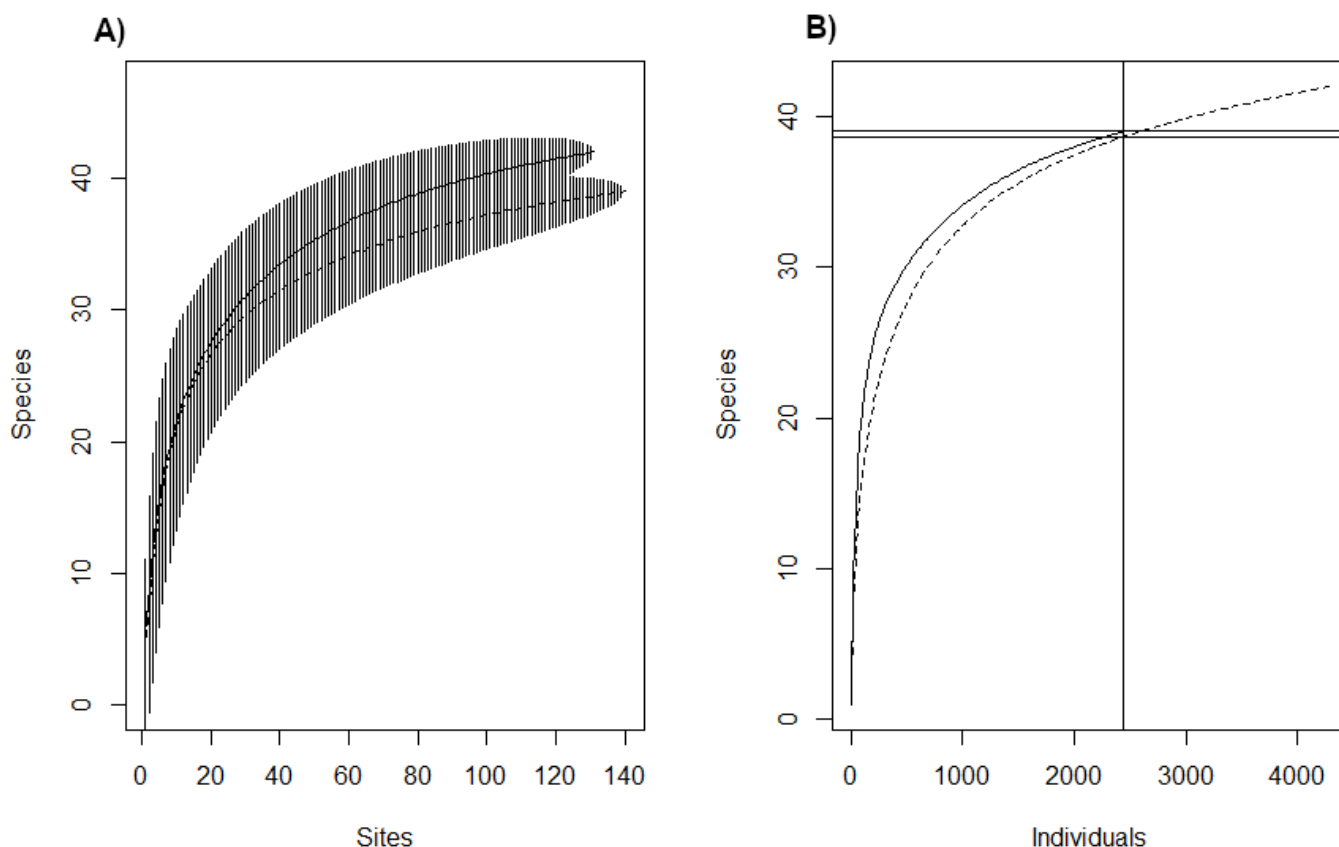


Fig. 3. A, Species accumulation curves for dung beetle species in 271 sampling points; B, Rarefaction curves comparing forest and forest edge samples. The solid line represents forest sampling points while the dotted line represents forest edge sampling points.

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. 5). There was no overlap between the forest edge and forest species clusters, which supports segregation between the species of both clusters.

The categorisation of the GLMM corroborated the classification of all the species through hierarchical clustering and ordination (Table 2). However, some of the models could not reach convergence for three species: *O. rorarius*, *O. laevis*, and *O. viridicervicapra*. The presence of species that were categorised as having a preference for forest habitats in previous analysis were correlated to forest habitats and vice versa. Positive coefficients for model corresponded to a preference for forest edge habitats while negative coefficients corresponded to a preference for forest habitats (Table 2). We used these coefficients to categorise the habitat preference of these species. *Onthophagus orientalis* and *Cc. unicornis* showed a small coefficient towards forest edge habitats; this may indicate that this species is close to being evenly distributed in both forest and forest edge habitats.

## DISCUSSION

Forest sampling points had a higher abundance of beetles compared to forest edge sampling points, 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 sampling points to forest edge sampling points, 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 sampling points 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 correlated with dung beetle diversity (Nichols et al., 2009).

The classification first proposed by Davis et al. (2001) 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

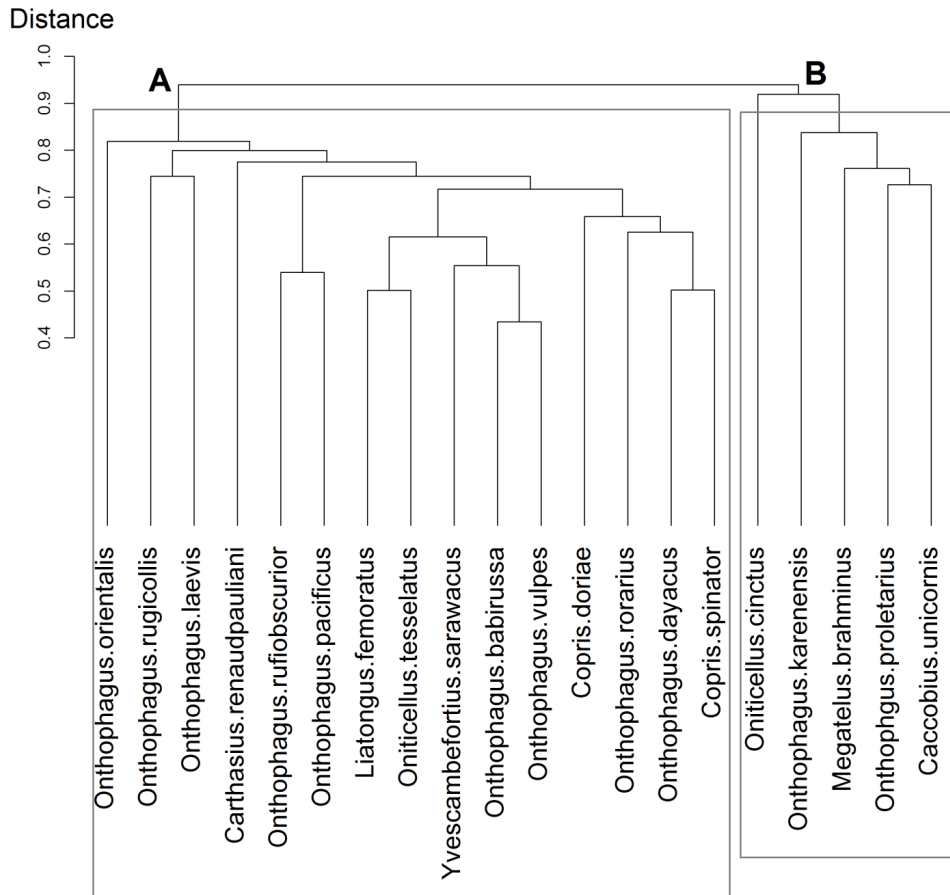


Fig. 4. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) hierarchical clustering with Bray-Curtis distances of the 25 dung beetle species. Two major clusters are indicated, dung beetles that prefer (A) forest sampling points and (B) forest edge sampling points.

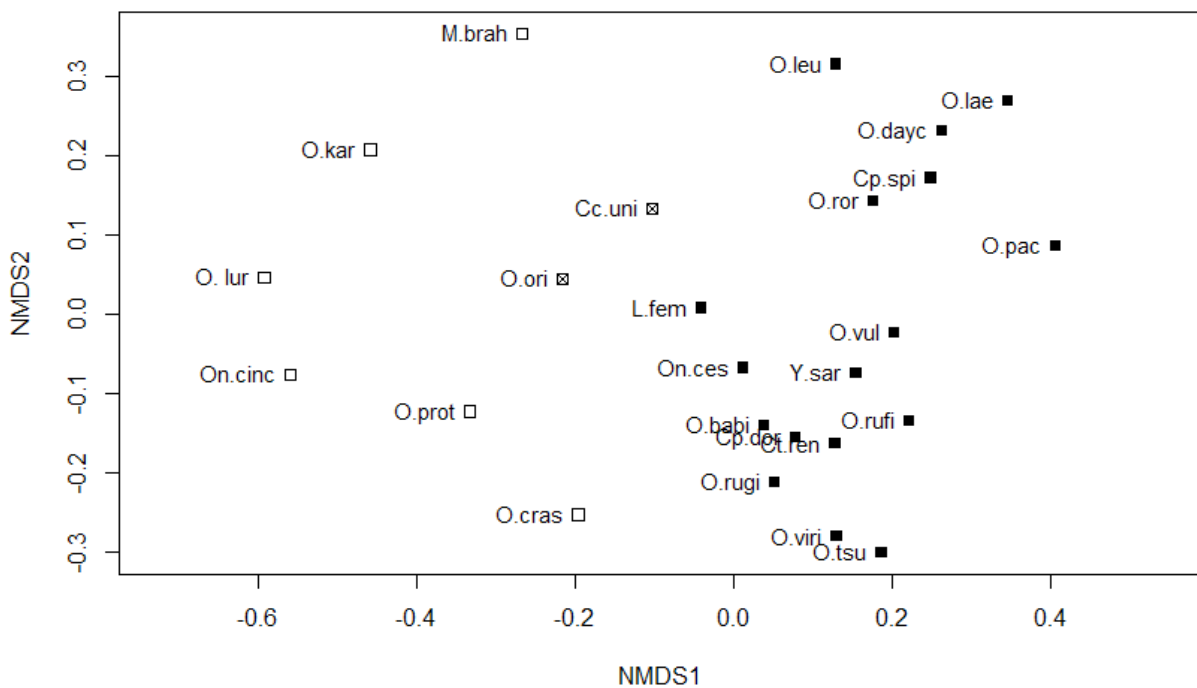


Fig. 5. The Non-metric multidimensional scaling (NMDS) ordination of 25 species of dung beetle from 271 forest and forest edge sampling points. Filled squares represent species that prefer forest habitats, open squares represent species that prefer forest edge habitats, and crossed squares represent 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. crasscollis*, 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*.

Table 2. Coefficients and standard errors for binomial Generalised Linear Mixed Model (GLMM) for the habitat preference of each species. The abundance of each species was used as a fixed effect, while localities were included as a random effect. Additional information on their biogeographical distribution are included in the last column. Malay Peninsula endemic (MP), Sundaland (SU), Sundaland and Indochina (IN), Southeast Asia (SEA), Widespread (W).

Species	Intercept	SE	Abundance	SE	Category	Distribution
<i>Liatongus femoratus</i>	0.8900	0.4592	-0.3604	0.0874	Forest	IN
<i>Oniticellus tessellatus</i>	0.9507	0.3875	-0.8795	0.1624	Forest	IN
<i>On. cinctus</i>	-0.0508	0.1288	0.5619	0.2313	Edge	W
<i>Yvescambefortius sarawacus</i>	0.5131	0.1420	-1.4505	0.3006	Forest	SU
<i>Onthophagus babirusa</i>	1.3403	0.7511	-0.1403	0.0322	Forest	SU
<i>O. crassicollis</i>	0.0038	0.126	0.4097	0.2496	Edge	W
<i>O. dayacus</i>	0.1932	0.1265	-1.8619	0.7164	Forest	SU
<i>O. karenensis</i>	-0.0648	0.1265	1.8221	0.7461	Edge	IN
<i>O. leusermontis</i>	0.1496	0.125	-1.7765	0.7372	Forest	SU
<i>O. luridipennis</i>	-0.0818	0.1274	1.2455	0.4805	Edge	W
<i>O. orientalis</i>	0.0392	0.1292	0.1148	0.1859	Edge	W
<i>O. pacificus</i>	0.1814	0.1257	-2.4585	1.0159	Forest	W
<i>O. proletarius</i>	-0.2309	0.1345	1.6557	0.4129	Edge	W
<i>O. rufiobscurior</i>	0.1594	0.1283	-0.3983	0.1949	Forest	MP
<i>O. rugicollis</i>	0.1658	0.132	-0.2691	0.1441	Forest	SU
<i>O. tsubakii</i>	0.1252	0.1275	-0.3501	0.2345	Forest	MP
<i>O. vulpes</i>	0.402	0.1381	-0.5699	0.141	Forest	SU
<i>Carthasius renaudpauliani</i>	0.3269	0.2428	-0.4725	0.2011	Forest	SU
<i>Copris doriae</i>	0.3982	0.2246	-0.3016	0.0941	Forest	SU
<i>Cp. spinator</i>	0.2258	0.1273	-2.6446	0.9936	Forest	SU
<i>Megatelus brahminus</i>	-0.1744	0.3935	1.0607	0.3398	Edge	W
<i>Caccobius unicornis</i>	0.0205	0.131	0.1487	0.1599	Edge	W

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 *Liatongus 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* species that prefer forest clearings.

Most of the species that we recorded in forest habitats were present in species lists of community level studies from the Malay Peninsula. However, the forest edge species that we 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 dung beetle studies. Perhaps non-forest habitats should not be viewed as disturbed or

damaged habitats but as alternative stable 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. 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., 2010). 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 (, pers. comm.). In our 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 e.g., Doll 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 Aphodinae. Also, the trap used in this study did not collect roller dung beetles efficiently (Goh & Hashim, 2018), and therefore an important functional group was not examined. 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 that we used in this study.

## CONCLUSION

Tunnelling and dwelling elephant dung associated dung beetle species of the Malay Peninsula showed strong habitat preference in relation to non-forest habitats. Forests sampling points had more individuals and were more diverse, compared with forest edge sampling points. 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.

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