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Environmental and geographic factors driving dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in the dipterocarp forests of Peninsular Malaysia

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Abstract. Despite a good understanding of dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) ecology in Southeast Asia, little is known about dung beetles in Peninsular Malaysia. No general study of dung beetle diversity has been carried out in Peninsular Malaysia, and we lack an understanding of how environmental and geographic factors, such as floristic zone, affect dung beetle community diversity. We sampled dung beetle diversity at eight different sites distributed throughout Peninsular Malaysia that encompass primary and secondary lowland, hill, and upper hill dipterocarp forests. We collected 4,313 dung beetles of 64 different species that represent six tribes (Coprini, Oniticellini, Onthophagini, Gymnopleurini, Deltochilini, and Sisyphini) in the subfamily Scarabaeinae. The number of our sampling locations and the range of floristic zones and forest conditions represented by these sites allow us to present a general overview of dung beetle diversity in Peninsular Malaysia and to begin to analyse trends in dung beetle composition throughout the peninsula.

Key words. dung beetles, beta diversity, virgin jungle reserves

INTRODUCTION

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) comprise a well-studied and widely distributed group that plays key roles in tropical forest ecosystem functioning, such as contributing to nutrient cycling and secondary seed dispersal. Feeding, living, and breeding primarily in pads of mammal dung, but also known to feed on carrion, detritus, and fungi, dung beetles are found in high diversity and abundance in areas that are also rich in mammals, particularly herbivores (Hanski & Cambefort, 1991; Davis, 2000b). Since these food sources are often unevenly distributed within a forest, competing dung beetle species partition resources differently. Dung beetles are divided into three main functional groups based on their practices: rollers (roll balls of dung away from dung pats and bury them for feeding and breeding), tunnelers (build underground chambers beneath dung pats and construct nests), and dwellers (breed in dung pats) (Hanski & Cambefort, 1991; Vinod & Sabu, 2007).

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The close associations between dung beetles and mammals allow researchers to reach preliminary conclusions regarding mammal abundance in an area by trapping dung beetles rather than by investing the time and money needed to track or capture the mammals themselves. Dung beetles' associations with mammals are so close, in fact, that severe disruptions to mammal species' populations caused by subsistence or commercial hunting in tropical forest systems may in turn have major impacts on the diversity and abundance of dung beetle communities due to changes in the availability of dung resources (Nichols et al., 2009).

Dung beetles have been studied throughout Southeast Asia, including Thailand, Indonesia, and Singapore (e.g., Shahabudin et al., 2003; Lee et al., 2009b), and thorough studies have been carried out in Sabah in Malaysian Borneo (e.g., Davis, 2000a, b; Davis et al., 2001; Ochi et al., 2009; Slade et al., 2011). Davis (2000b) identified 97 different dung beetle species in Danum Valley, Sabah, Malaysian Borneo, significantly more than the global average of 57.9 dung beetle species per rainforest site. This makes Danum Valley, a lowland rainforest with an 80 percent dipterocarp canopy, the most species-rich rainforest site for dung beetles that has been identified to date.

However, despite the widespread study of dung beetle ecology in other parts of Southeast Asia, very little is known about dung beetles in Peninsular Malaysia (but see Balthasar, 1963; Chan, 1997). As far as we are aware, no general study of dung beetle diversity has ever been carried out in Peninsular Malaysia. The few times that dung beetles have been collected in Peninsular Malaysia, the collections were for small surveys carried out at a limited number of sites. Ochi et al. (2009) identified nine new species and two new subspecies of *Onthophagus* in a combined study of dung beetles in Peninsular Malaysia, Borneo, and Sumatra, but they did not make a concerted effort to describe overall dung beetle diversity in Peninsular Malaysia. In an attempt to analyse changes in dung beetle communities in the small, disturbed patches of forest remaining in Singapore, Lee et al. (2009a) conducted a small study of dung beetle communities at two forested sites in the state of Johor at the very southern tip of Peninsular Malaysia. They surveyed in Johor in order to provide a comparison of natural and undisturbed forest for their disturbed forest sites in Singapore, but once again the authors did not assess dung beetle diversity throughout Peninsular Malaysia. Tregidgo et al. (2010) assessed the effects of forest fragmentation on the vertical stratification of arboreal dung beetles in Lake Kenyir, a hydroelectric reservoir in northeastern Peninsular Malaysia. Qie et al. (2011) analysed dung beetle diversity on small islands that formed in Lake Kenyir when the reservoir was created. They specifically sought to study the effects of many small islands on community composition and ecosystem function, rather than to survey diversity in many locations. Most recently, Kudavidanage et al. (2012) utilised data from Lee et al. (2009a) and Qie et al. (2011), as well as data from Sri Lanka, to investigate the impacts of habitat disturbance on dung beetle ecosystem function in Sri Lankan, Malaysian, and Singaporean forests. Additionally, Qie et al. (2012) continued work at Lake Kenyir. There, they studied how providing dung supplementation to existing dung beetles would affect their population sizes and also assisted dung beetle dispersal to previously uninhabited land-bridge islands within the lake. However, while these studies shed some light on dung beetle communities in Peninsular Malaysia, we still lack dung beetle species occurrence data for Peninsular Malaysia. Additionally, we lack an understanding of which environmental and geographic factors (e.g., elevation, size of forest area) affect their distribution.

Widespread land-use change continues to occur throughout Peninsular Malaysia, and if we are to employ dung beetles as bio-indicators and as clues to overall forest health, we need to better understand their diversity and which environmental and geographic factors affect their distribution. We sampled dung beetle diversity at eight sites distributed throughout Peninsular Malaysia that encompass primary and secondary lowland, hill, and upper hill dipterocarp forests. To our knowledge, this paper presents the most geographically large-scale survey of dung beetle diversity ever conducted in Peninsular Malaysia. The number of our sampling locations and the range of floristic zones and conditions represented by these sites allow us to present a general overview of dung beetle diversity in Peninsular Malaysia and to begin to analyse trends in dung beetle composition throughout the peninsula. Our extensive dataset can be utilised as a baseline checklist of known dung beetle diversity in dipterocarp forests by researchers who study dung beetle communities in Peninsular Malaysia and Singapore.

MATERIAL AND METHODS

Data for this study were collected between November 2007 and October 2009 in and around six Virgin Jungle Reserves (VJRs) (BFR = Berembun Forest Reserve, GAFR = Gunung Angsi Forest Reserve, GTFR = Gunung Tebu Forest Reserve, KSFR = Kledang Saiong Forest Reserve, SFR = Semangkok Forest Reserve, and UGFR = Ulu Gombak Forest Reserve) and in two primary forests (TFR = Temengor Forest Reserve and RBFR = Royal Belum Forest Reserve) that vary in size and are distributed throughout Peninsular Malaysia (see Table 1 and Fig. 1 for full site information).

VJRs are pristine forests that were set aside by states in Peninsular Malaysia. They serve as protected biodiversity gene pools and as sources of tree seeds for natural dispersal within a production forest landscape that has been managed intensively for timber extraction (Wyatt-Smith, 1950; Laidlaw, 1999). The primary forests of each VJR are located adjacent to secondary forest stands, which were harvested as early as the 1930s but mostly in the 1960s and 1970s. All secondary forest stands we surveyed for dung beetles were harvested under an uneven-aged management system at least 30 years prior to data collection.

TFR and RBFR are not VJRs, but rather sampling at these sites occurred entirely in primary forest. Our sampling in TFR occurred in a 9765-ha timber concession within the Temengor Forest Reserve, which is 148,870 ha total. Our plots were located in Compartment 44, Block 5 of the Perak Integrated Timber Complex, which was 200 ha of unlogged forest at the time of sampling. RBFR is part of the Belum-Temengor forest complex and is a 117,500-ha area protected under the Malaysian National Forestry Act. Basic site descriptions and geographical data for each site are provided in Table 1. ("Site" hereafter refers to the primary forest and the adjacent secondary forest within each VJR or to the entirety of the two other primary forest sites.) Overall, the eight sampling sites were chosen for their complementary range in sizes, elevations, floristic zones, and topology, as well as their accessibility.

Dung beetles were captured using standardised baited pitfall trapping (e.g., Davis & Sutton, 1998; Davis, 2000a, b; Davis et al., 2001; Andersen, 2005). Pitfall traps (12 cm tall, 8 cm diameter) were baited with one dessert spoon (approximately two teaspoons or 10 ml) of elephant dung from a local zoo, because elephants are native to primary forests in Peninsular Malaysia. While the diet of captive elephants is not the same as that of wild elephants, dung from captive elephants was used in this study for practical purposes (i.e., ease of collection, large supply available). Bait was placed in a pocket made from mosquito netting and suspended approximately 5 cm above each trap using a bamboo skewer. Large leaves were positioned to protect the traps from rain. Traps were filled with a mixture of detergent and salt, which acted as a killing detergent and prevented captured beetles from escaping from the traps. All traps

Table 1. Description of the eight dipterocarp forest study sites.

Site	Location	Size (ha)	State	Elevation (m asl)	Floristic Zone[a]	Site Type	Trapping Effort (days)
Berembun Forest Reserve (BFR)	2°48'N, 102°01'E	1834.3	Negeri Sembilan	200–700	Lowland and Hill	VJR	162
Gunung Angsi Forest Reserve (GAFR)	2°39'N, 102°06'E	143.3	Negeri Sembilan	200–500	Lowland and Hill	VJR	162
Gunung Tebu Forest Reserve (GTFR)	5°37'N, 102°39'E	50.0	Terengganu	244–472	Lowland and Hill	VJR	162
Kledang Saiong Forest Reserve (KSFR)	4°38'N, 101°01'E	814.0	Perak	100–600	Lowland and Hill	VJR	162
Semangkok Forest Reserve (SFR)	3°37'N, 101°44'E	28.0	Selangor	379–472	Hill	VJR	162
Ulu Gombak Forest Reserve (UGFR)	3°21'N, 101°46'E	449.0	Selangor	457–1128	Hill and Upper Hill	VJR	162
Temengor Forest Reserve (TFR)	5°24'N, 101°33'E	148,870	Perak	550–810	Hill and Upper Hill	Primary Forest	432
Royal Belum Forest Reserve (RBFR)	5°48'N, 101°23'E	117,500	Perak	600–800	Upper Hill	Primary Forest	162

[a]Whitmore (1990) defines lowland dipterocarp forest as lying below 300 m asl. Hill dipterocarp forest stretches from 300–650 m asl and upper hill dipterocarp forest ranges from 650–1200 m asl.

were collected after 48 h. After every sampling period, all elephant dung baits were carried out of the forest, in order to avoid introducing foreign seeds to the sampling sites.

At each of the VJR sites and at RBFR, three sets of three 300 m sampling transects were established (nine transects total per site). At TFR, eight sets of three transects were established (24 transects total). Transects ran approximately parallel to each other following topographic contours with approximately 500 m between them. In each location, one transect was established on a ridge, one ran along a slope, and one was established in a valley. At the two primary forest sites, all transects were established in primary forest. At the VJR sites, the first set of three transects was located in the primary forest of each VJR, and the remaining two were in adjacent secondary forest that was logged >30 years before this study (one in secondary forest located >500 m from the pristine forest, and the second in secondary forest located >1,000 m from the pristine forest). Nine baiting points were established along each transect (offset to the side of transects by 0.5–1.0 m) at approximately 30 m intervals. We acknowledge that due to size and topological limitations of the sampling sites, this is short of the 50 m between baiting points recommended to minimise interference among traps (Larsen & Forsyth, 2005). It is thus possible that there was some overlap and interference among the traps along each transect. Trapping effort at seven of the sites (the six VJRs and RBFR) was 162 d, while trapping effort at the eighth site, TFR, was more than double (432 d) due to the greater number of sampling transects established at this site (24 compared to nine).

All beetles collected in the pitfall traps were pinned out for identification at the Forest Research Institute Malaysia. Pinned specimens were identified to species by referring to Ochi et al. (1996) and Bouchard et al. (2011) and by comparing them to voucher specimens at the Sabah Research Centre.

Due to the difference in trapping effort between TFR and the other sites, which would affect quantitative comparisons of the diversity and abundance of beetles trapped at the different sites, we rarefied our beetle capture data by trap using the "specaccum" function with the "rarefaction" method available in the Vegan package (Oksanen et al., 2009) for R (R Development Core Team 2011). To create ordinations of the species data, we used non-metric multidimensional scaling (NMDS) in Vegan. Ordinations that incorporated abundance data were created using the Bray-Curtis dissimilarity metric with a maximum of 1,000 random starts. When captures were grouped at the species, genus, and tribe levels, two convergent solutions were found after one try. These NMDS ordinations allow for the comparison of community composition (abundance, richness, and taxa identity) at each of the eight sites. The plots are based on relative similarities between communities, and they may be rotated in any direction, so their axes have no intrinsic meaning and are not labeled. Functional group classifications (tunneler, roller, or dweller), body size range, and diel activity (diurnal or nocturnal) were assigned to the 15 most abundant species based on previously published literature.

RESULTS

We collected 4,313 dung beetles of 64 different species across the eight collection sites (Table 2). The beetles collected represented six tribes (Coprini, Oniticellini, Onthophagini, Gymnopleurini, Deltochilini, and Sisyphini) in the subfamily Scarabaeinae. Only two of the 64 species were found at all eight sites (*Onthophagus vulpes* and *Sisyphus thoracicus*), while two species were found at seven of the eight sites (*Yvescambefortius sarawacus* and *Onthophagus pacificus* (B)). Twenty-eight of the 64 species were only collected at one site each; of these 28 species, 13 were captured at TFR. Three sites, BFR, KSFR, and UGFR, did not have any unique species that were not also caught at other sites. Thirty-three of the 64 species had 10 or fewer total individuals captured, and 10 species were singletons.

The most abundant species in our study was *Onthophagus vulpes* (724 individuals) followed by *Sisyphus thoracicus* (518 individuals). *O. vulpes* captures occurred relatively evenly across the four forest types sampled (32% in primary forest sites, 24% in pristine forest within VJRs, 17% in previously

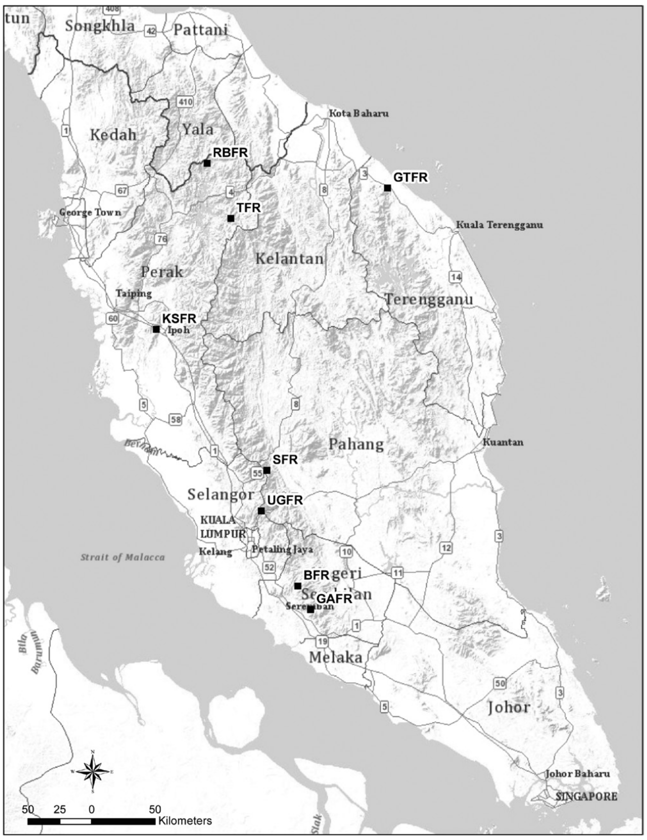

Fig. 1. Locations of the eight dipterocarp forest sites where dung beetle sampling occurred in Peninsular Malaysia: BFR = Berembun Forest Reserve, GAFR = Gunung Angsi Forest Reserve, GTFR = Gunung Tebu Forest Reserve, KSFR = Kledang Saiong Forest Reserve, RBFR = Royal Belum Forest Reserve, SFR = Semangkok Forest Reserve, TFR = Temengor Forest Reserve, and UGFR = Ulu Gombak Forest Reserve.

logged forest >500 m from pristine forest in VJRs, and 27% in previously logged forest >1,000 m from pristine forest in VJRs) (Table 3). In contrast, *S. thoracicus* was primarily captured in primary forest sites (72%). In addition to these two species, more than 200 individuals were captured of four other species (*Copris doriae*, *Onthophagus babirussoides* Krikken & Huijbregts, MS, *Onthophagus cervicapra*, and *Paragymnopleurus maurus*), and nine other species had between 100 and 200 individuals captured. A functional characterisation of the 15 most abundantly trapped species shows that 12 were tunnelers while three were rollers, 11 were diurnal while four were nocturnal, and nine were small/medium species while six were medium/large species (Table 4).

The greatest number of individual dung beetles was captured at TFR (1914 individuals), where a greater sampling effort was carried out than at the other seven sites, followed by SFR (595), GTFR (541), and UGFR (537). The fewest individual beetles were captured at BFR (21 individuals). None of the eight sampling sites possessed all 64 species. The greatest number of species (41) was also collected at TFR. Dung beetles from 30 species were collected at SFR, and 27 species were found at GTFR. The fewest number of species was found at BFR (6 species). When capture data for all eight sampling sites were rarefied to 80 traps, in order to account for the greater sampling effort at TFR, abundance patterns were similar across the sites (Fig. 2). The expected species richness was still highest at TFR (~40 expected species), followed by SFR (~30 expected species). BFR had the fewest expected species (<10).

Rank abundance curves of dung beetle species at each of the eight sampling sites show very different community structures among the sites (Fig. 3). The most abundant species at GAFR and BFR accounted for approximately half of the total dung beetle abundance at those two sites, while the most abundant species at TFR, RBFR, KSFR, and GTFR accounted for only about 20 percent of the total abundance at those sites. GTFR had the most evenly structured community, with many species accounting for between 10 and 20 percent of overall abundance, while the rank abundance curve for TFR had the longest tail showing many species accounting for less than 5 percent of total abundance at that site.

The NMDS ordinations based on the Bray-Curtis distance metric show how similar the composition of the dung beetle communities at each of the eight sites are to each other. The NMDS ordination based on species level diversity (stress: 7.38, dimensions: 2; Fig. 4a) shows that the community at BFR is the least like any of the other communities; it is located far to the right of the NMDS1 axis, while all the other communities loosely cluster to the left. The community at GAFR is also slightly removed from the other sites, as it is the located more to the right than any site except BFR, and it is located higher on the NMDS2 axis than any other site. The genus (stress: 6.52, dimensions: 2; Fig. 4b) and tribe (stress: 4.55, dimensions: 2; Fig. 4c) level ordinations show similar trends, with BFR being located far away from the other sites and GAFR located slightly away from the other

Table 2. Complete species list and abundances of dung beetles collected in eight dipterocarp forest sites in Peninsular Malaysia.

Tribe	Species	Site[a]								
		BFR	GAFR	GTFR	KSFR	RBFR	SFR	TFR	UGFR	Total
Coprini	*Catharsius* sp. 1					18	17	9	18	62
	Copris agnus				5	15	25	80	1	126
	Copris cf. agnus (A)							4		4
	Copris cf. agnus (B)							5		5
	Copris doriae	10		7	2	28	13	296		356
	Copris spinator		8	67		4		78	17	174
	Copris ramosiceps		1					3		4
	Copris sp. 1		1							1
	Copris sp. 2					1				1
	Microcopris sp. 1							5		5
	Synapsis sp. 1	1				29	12	45	16	103
Oniticellini	*Liatongus femoratus*					6		6		12
	Oniticellus tessellatus	1	3	1		9		55	1	70
	Yvescambefortius sarawacus		6	1	9	10	1	61	7	95
Onthophagini	*Onthophagus angustatus*			1				1		2
	Onthophagus aphodioides			1			23	18		42
	Onthophagus babirussoides Krikken & Huijbregts, MS			73	4	3	11	190	7	288
	Onthophagus cervicapra			43	11	37	15	87	85	278
	Onthophagus cf. deflexicollis						21	10		31
	Onthophagus cf. deliensis							5		5
	Onthophagus cf. incisus						2			2
	Onthophagus cf. laevis		1			2		5		8
	Onthophagus cf. pedator						18	6		24
	Onthophagus cf. penicillatus							3		3
	Onthophagus cf. peninsularis							6		6
	Onthophagus cf. rudis							3	1	4
	Onthophagus cf. rutilans			11	16	19	25	38	4	113
	Onthophagus leusermontis			5				62		67
	Onthophagus pacificus (A)		2	1	5		17	19	3	47
	Onthophagus pacificus (B)		1	4	11	10	97	48	4	175
	Onthophagus peninsularis							17		17
	Onthophagus pseudoholzi Krikken & Huijbregts, MS			1						1
	Onthophagus pseudotaeniatus Krikken & Huijbregts, MS							10		10
	Onthophagus rorarius			4		41	16	48		109
	Onthophagus rotoculus Krikken & Huijbregts, MS							1		1
	Onthophagus rugicollis		11	74		3	14	3	4	109
	Onthophagus sp. 1	3	7	68	2		22			102
	Onthophagus sp. 2		2						1	3
	Onthophagus sp. 3			2						2
	Onthophagus sp. 4		1	1			3			5

Table 2. Cont'd.

Tribe	Species	Site[a]								
		BFR	GAFR	GTFR	KSFR	RBFR	SFR	TFR	UGFR	Total
	Onthophagus sp. 5		1							1
	Onthophagus sp. 6			1			3			4
	Onthophagus sp. 7						2			2
	Onthophagus sp. 8						13			13
	Onthophagus sp. 9		1							1
	Onthophagus sp. 10						2			2
	Onthophagus sp. 11			2			13		10	25
	Onthophagus sp. 12			1	27		18		2	48
	Onthophagus sp. 13			1	3					4
	Onthophagus sp. 14		2							2
	Onthophagus sp. 15						1			1
	Onthophagus sp. 16						3			3
	Onthophagus sumavejenis							2		2
	Onthophagus unknown					11		35		46
	Onthophagus venzoi			17						17
	Onthophagus vulpes	5	82	1	13	74	165	160	224	724
Gymnopleurini	*Paragymnopleurus maurus*			96	12	50	9	2	90	259
	Paragymnopleurus striatus				11	20		104	9	144
Deltochilini	*Ochicanthon cf. peninsularis*		2	6			4	5	1	18
	Ochicanthon sp. 1							1		1
	Ochicanthon sp. 2		1							1
	Ochicanthon sp. 3							5		5
Sisyphini	*Sisyphus thoracicus*	1	30	51	19	2	10	373	32	518
Total Abundance		21	163	541	150	392	595	1,914	537	4,313
Species Richness		6	19	27	15	21	30	41	21	64

[a]BFR = Berembun Forest Reserve, GAFR = Gunung Angsi Forest Reserve, GTFR = Gunung Tebu Forest Reserve, KSFR = Kledang Saiong Forest Reserve, RBFR = Royal Belum Forest Reserve, SFR = Semangkok Forest Reserve, TFR = Temengor Forest Reserve, and UGFR = Ulu Gombak Forest Reserve

sites in both plots. However, these two plots show different patterns in how the remaining sites cluster when compared to the species ordination. In the genus ordination, UGFR clusters more closely to SFR than in the other ordinations. In the tribe ordination, UGFR and GTFR as well as RBFR and KSFR are plotted close together, and the remaining sites are less tightly clustered.

DISCUSSION

We conducted a large-scale survey of dung beetles at forested sites in Peninsular Malaysia, which provides dung beetle species occurrence data and allows us to analyse the environmental and geographic factors (e.g., elevation, floristic zone, size of forest area) that may affect their distribution. Pitfall trapping with elephant dung bait at six different primary and secondary VJR sites and two primary forest sites in Peninsular Malaysia resulted in the collection of 4,313 dung beetles from 64 different species. We did not record all 64 species at any one of the sampling sites, indicating that trapping dung beetles at multiple sites throughout the peninsula was necessary to provide a representative sample of dung beetle diversity in Peninsular Malaysia.

We captured 10 or fewer individuals of 33 of the 64 total species we collected, including singletons of 10 species. Twenty-eight of the 64 species were only collected at one site each. These large numbers of singletons and species collected at only one of the eight sites indicate the great diversity of dung beetles throughout Peninsular Malaysia. They also show that while our study provides an informative picture of what dung beetle diversity in Peninsular Malaysia is like, our sampling was likely far from exhaustive. For instance, the dung beetles attracted to our traps were likely

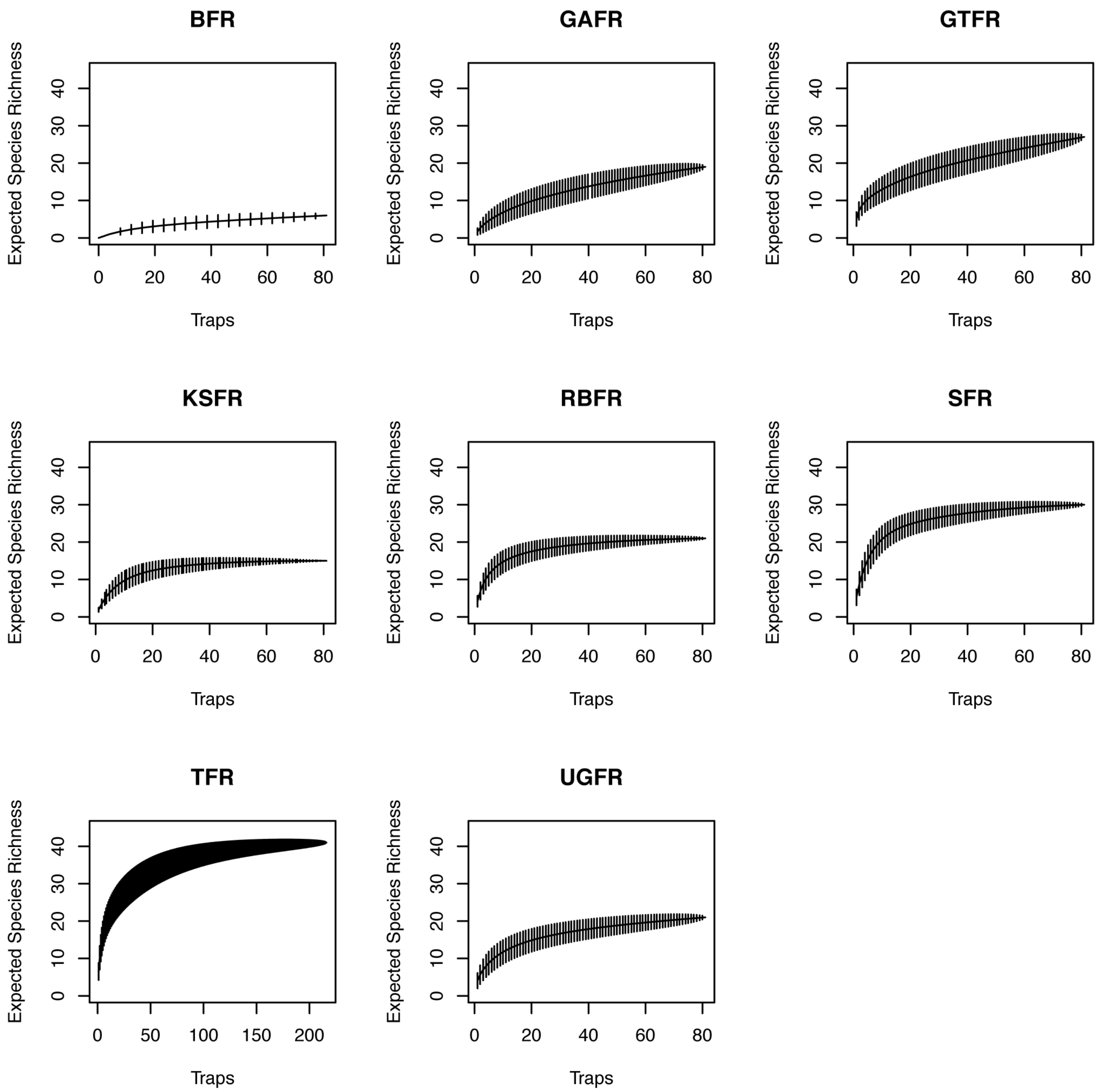

Fig. 2. All dung beetle capture data for the eight sampling sites rarefied by trap.

Table 3. Capture data listed by forest type for the 15 most abundant dung beetle species, reported in species counts and percentage of total captures for each species.

Species	Primary Forest[a]		VJR		>500m from VJR		>1,000m from VJR		Total
1. *Onthophagus vulpes*	234	(32%)	173	(24%)	121	(17%)	196	(27%)	724
2. *Sisyphus thoracicus*	375	(72%)	38	(7%)	13	(3%)	92	(18%)	518
3. *Copris doriae*	324	(91%)	19	(5%)	3	(1%)	10	(3%)	356
4. *Onthophagus babirussoides* Krikken & Huijbregts, MS	193	(67%)	39	(14%)	19	(7%)	37	(13%)	288
5. *Onthophagus cervicapra*	124	(45%)	79	(28%)	12	(4%)	63	(23%)	278
6. *Paragymnopleurus maurus*	52	(20%)	18	(7%)	4	(2%)	185	(71%)	259
7. *Onthophagus pacificus* (B)	58	(33%)	107	(61%)	4	(2%)	6	(3%)	175
8. *Copris spinator*	82	(47%)	29	(17%)	28	(16%)	35	(20%)	174
9. *Paragymnopleurus striatus*	124	(86%)	8	(6%)	3	(2%)	9	(6%)	144
10. *Copris agnus*	95	(75%)	18	(14%)	12	(10%)	1	(1%)	126
11. *Onthophagus cf. rutilans*	57	(50%)	41	(36%)	3	(3%)	12	(11%)	113
12. *Onthophagus rorarius*	89	(82%)	8	(7%)	10	(9%)	2	(2%)	109
13. *Onthophagus rugicollis*	6	(6%)	33	(30%)	16	(15%)	54	(50%)	109
14. *Synapsis* sp. 1	74	(72%)	13	(13%)	0	(0%)	16	(16%)	103
15. *Onthophagus* sp. 1	0	(0%)	50	(49%)	32	(31%)	20	(20%)	102

[a]Note that trapping effort at all VJR sites and at RBFR was 162 days, while trapping effort at TFR was more than double (432 days). The trapping at TFR falls into the Primary Forest category in this table, while the other three categories (VJR, >500m from VJR, and >1,000m from VJR) had equal trapping effort.

limited by our choice of elephant dung as bait. Some dung beetle species are more attracted to human or pig dung baits, therefore our choice of dung may have limited our captures of these species. In contrast, some species, such as *Yvescambefortius sarawacus*, are large herbivore dung specialists, and our traps were biased toward their capture. Additionally, we did not include other types of bait besides dung (e.g., carrion, fruit) or other types of traps (e.g., flight interception traps) in our study, which may have also limited our captures. Lastly, our study was not designed to explore the effects of seasonality on dung beetle diversity. Peninsular Malaysia is generally considered aseasonal, although wetter and dryer periods do exist and vary in intensity from year to year (Tani et al., 2003; Kumagai et al., 2005). Sampling at our sites was done randomly throughout the year, although we did avoid sampling during the wettest part of the year (December through mid-January). Thus, while our forest sites should not have been subject to strong temporal changes during the study period, it is possible that our results were affected by untested seasonal changes to dung beetle community diversity. Future dung beetle sampling in Peninsular Malaysia should test for seasonal changes to communities by trapping beetles simultaneously at multiple sites, in order to avoid confounding possible seasonal changes with site effects.

A more detailed picture of dung beetle diversity that encompasses more species would likely emerge by taking potential seasonal changes into account, by utilising additional bait types and sampling techniques, as well as by increasing sampling effort and trapping. The advantage of increasing sampling effort is evinced by the fact that the sampling effort at TFR was more than double that at the other seven sites, and of the 28 species that were only collected at one site, 13 were found at TFR. The greatest species richness, both in terms of absolute number of species and rarefied expected number of species, was collected at TFR.

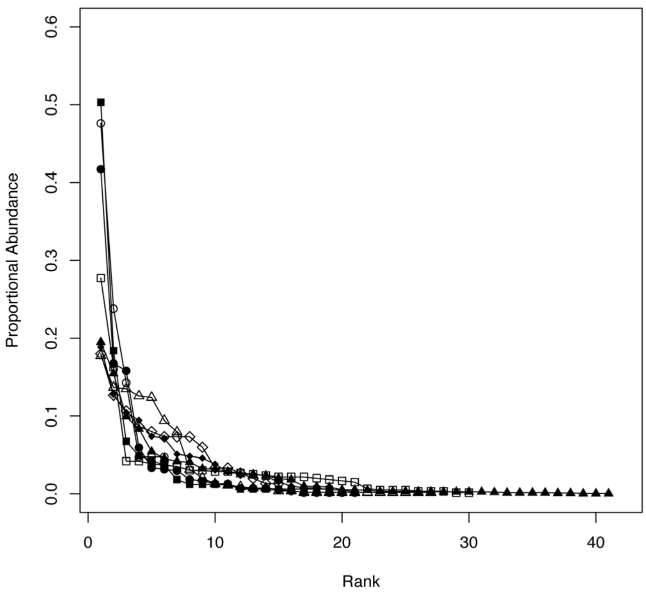

Fig. 3. Rank abundance curves of dung beetle species at each of the eight sampling sites: ○BFR, ■GAFR, △GTFR, ◇KSFR, ◆RBFR, □SFR, ▲TFR, and ●UGFR.

The two most abundant species in our study were *Onthophagus vulpes* (collected at all eight sites; 724 individuals) and *Sisyphus thoracicus* (collected at all eight sites; 518 individuals). *O. vulpes* was previously found to be common in primary lowland dipterocarp forest but to be less common in logged forest at the Danum Valley Field Centre on Borneo (Edwards et al., 2011). Similarly, Slade et al. (2011) trapped *O. vulpes* across six sites in Malaysian Borneo and found this species in approximately equal numbers in two undisturbed forest sites (39 and 37 individuals) and two forest sites that had undergone low-intensity selective logging (42 and 38 individuals), but in lower numbers at two sites that had undergone high-intensity logging (32 and 5 individuals). In this study we found that 32 percent of *O. vulpes* individuals were trapped in primary forest sites, 24 percent were trapped in pristine forest within VJRs, 17 percent were trapped in previously logged forest >500 m from pristine forest within VJRs, and 27 percent were trapped in previously logged forest >1,000 m from pristine forest (Table 3). It is important to remember that there was greater sampling intensity at TFR, which is a primary forest site, and we would thus expect to find more *O. vulpes* beetles there than in the other forest types. However, we did trap more *O. vulpes* at VJR sites in previously logged forest >1,000 m from pristine forest than in pristine forest in the VJRs. This points to the possibility that this species can thrive in secondary forest areas better than previously thought. *S. thoracicus* has been previously found to be common in both primary and secondary lowland dipterocarp forest in the Danum Valley Field Centre (Edwards et al., 2011). The majority of our *S. thoracicus* captures were in primary forest, but we did capture this species across all forest types we sampled.

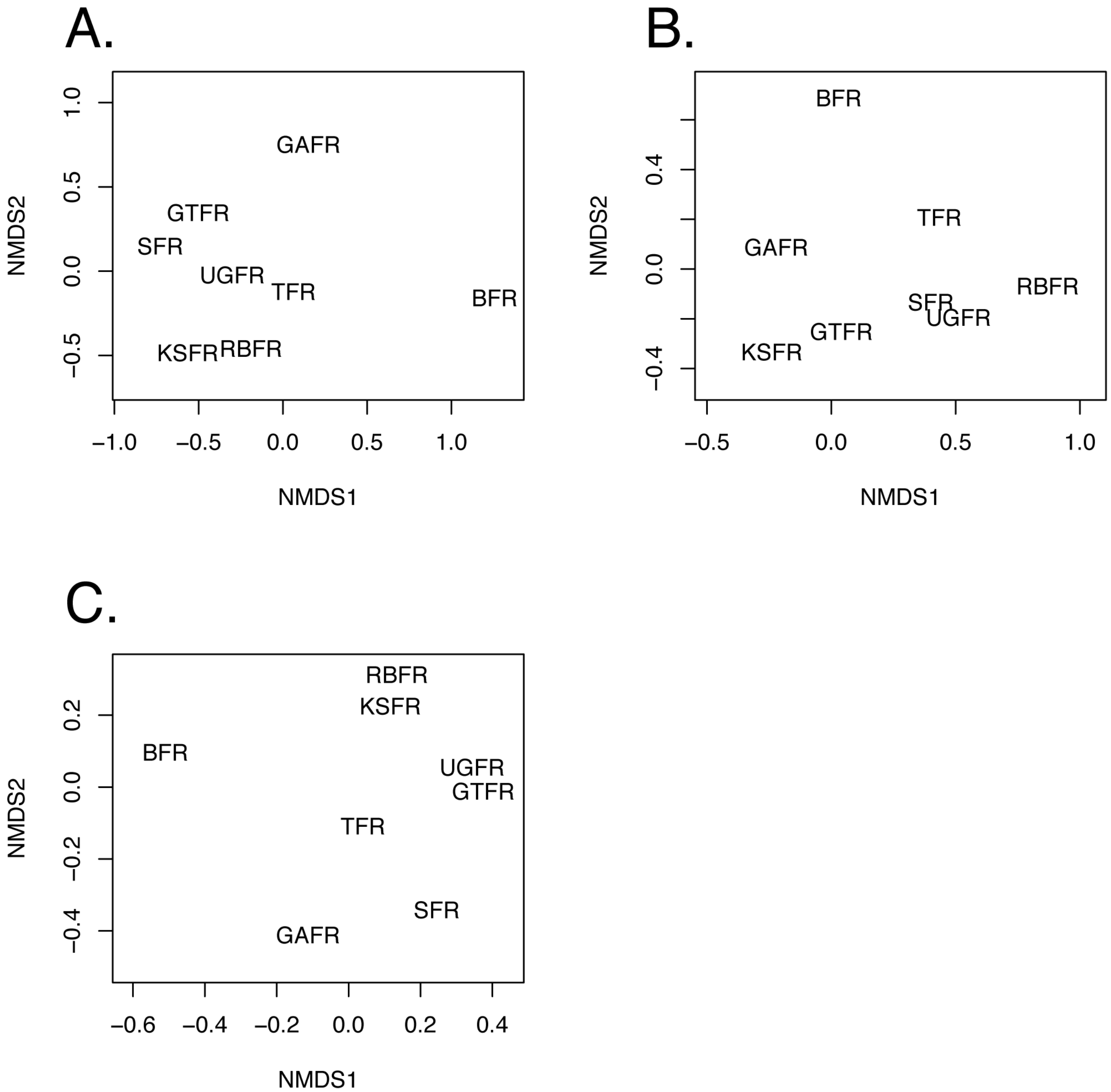

Fig. 4. NMDS ordination based on the Bray-Curtis distance metric with beetle captures grouped by species (A), genera (B), and tribes (C). Note that the sampling effort at TFR was much greater than sampling effort at the other seven sites.

Table 4. Functional characteristics of the 15 most abundant dung beetle species.[a]

Species	Functional Group	Size Range (mm)	Diel Activity
1. *Onthophagus vulpes*	Small/medium tunneler	3.5–12.0	D
2. *Sisyphus thoracicus*	Small roller	5.5[b]	D
3. *Copris doriae*	Medium/large tunneler	13.0–18.0	N
4. *Onthophagus babirussoides* Krikken & Huijbregts, MS	Small tunneler	21 mm^2 [c]	D
5. *Onthophagus cervicapra*	Small/medium tunneler	3.5–12.0	D
6. *Paragymnopleurus maurus*	Large roller	14.0–19.0	D
7. *Onthophagus pacificus* (B)	Small/medium tunneler	3.5–12.0	D
8. *Copris spinator*	Large tunneler	98.8 mm^2 [c]	N
9. *Paragymnopleurus striatus*	Large roller	14.0–19.0	D
10. *Copris agnus*	Large tunneler	14.8[b]	N
11. *Onthophagus cf. rutilans*	Small tunneler	13.3[b]	D
12. *Onthophagus rorarius*	Small/medium tunneler	3.5–12.0	D
13. *Onthophagus rugicollis*	Small/medium tunneler	3.5–12.0	D
14. *Synapsis* sp. 1	Large tunneler	25.0[b]	N
15. *Onthophagus* sp. 1	Small/medium tunneler	3.5–12.0	D

[a]Species functional characteristics adapted from Davis (1999), Qie (2010), Slade et al. (2011), and Larsen (2013).
[b]Range not available. Representative size reported by Davis (1999) or Larsen (2013).
[c]Size only available in mm^2 (Qie, 2010).

After these two widespread species, two other species were found at seven of the eight study sites, *Yvescambefortius sarawacus* and *Onthophagus pacificus* (B). Edwards et al. (2011) found that both *Y. sarawacus* and *O. pacificus* were rare in the primary and logged forest of Danum Valley, while we found that they were both very widespread across our sites. However, as noted above, *Y. sarawacus* is a large herbivore dung specialist, and our sampling was biased towards attracting this type of species due to our bait choice. In contrast, Edwards et al. (2011) used human dung baits, so the differences between our captures of this species (and others) may be due to sampling artifacts rather than true differences in the communities that we sampled.

An analysis of the functional characteristics of the 15 most abundantly trapped species provides some insight into the ecosystem functioning of the eight sampling sites (Table 4). Twelve of these 15 species were tunnelers, only three were rollers, and there were no dwellers. Previous studies have found that tunnelers—particularly nocturnal tunnelers—are more efficient than rollers at removing dung and seeds, and that tunnelers are thus the most important group in maintaining these ecosystem functions (Estrada & Coates-Estrada et al., 1991; Slade et al., 2007). Additionally, Slade et al. (2007) found that other functional groups were unable to compensate for the loss of this group in short-term removal experiments. Thus, the high presence of tunnelers in our sampled communities implies efficient removal of dung and seeds across these sites. However, while four of these tunneler species are nocturnal, they were not the very most abundant species. The most abundant species in our study, *O. vulpes* (724 captures), is a small/medium diurnal tunneler. The second most abundant species, *S. thoracicus* (518 captures), is a small diurnal roller, and the third most abundant species, *Copris doriae* (356 captures), is a medium/large nocturnal tunneler. Slade et al. (2007) found that small beetles have a relatively limited effect on dung and seed removal compared to larger beetles; therefore, the presence of *C. doriae*, a medium/large nocturnal tunneler, in relatively high numbers most likely represents a large amount of the cumulative dung and seed removal that takes place across these eight sites. Additionally, the fact that the three most abundant species represent non-overlapping functional guilds is a clear demonstration of complementarity between functional groups and of the resource partitioning that occurs among different beetle species in these habitats. It has been previously found that functional group richness correlates positively with dung and seed removal (Slade et al., 2007).

When comparing the structure of the eight different dung beetle communities, NMDS ordinations show that some sites that are geographically close to each other do cluster closely together in the graphs (e.g., UGFR and SFR). However, it seems that, overall, the sites' geographic locations, sizes, and elevations have only limited influences on dung beetle community composition. For instance, the ordinations show that the community at BFR was the least like any of the other communities, and the community at GAFR was also slightly removed from the other sites. The uniqueness of the BFR and GAFR communities could possibly be explained by location, since BFR and GAFR are the southernmost located sites. However, despite the fact that they are located farther south than the other sites, they are still situated close to SFR and UGFR, and they are not nearly as far from other sampling sites as GTFR is (the only site located on the east coast of the peninsula), which clusters closely to other sites. Of the VJRs, BFR is the biggest site (1,834.3 ha), so size could potentially be a possible explanation for why its dung beetle community was so different from the communities at the other sites. However, the BFR community was unique due to its very low number of captures, which is unlikely to be explained by the large size of the reserve. In addition, GAFR is an intermediate size, and both BFR and GAFR are located at intermediate elevations in the Lowland/Hill Forest floristic zone.

Given the seemingly limited effects of the sites' geographic locations, sizes, and elevations on dung beetle community composition, other factors should be considered. Dung beetle diversity at a given site is likely largely determined by mammal diversity, which in turn is likely to be determined and affected by a number of factors beyond distance and dispersal capabilities, such as proximity to human settlements. Evidence for this comes from the fact that the least number of individuals and unique dung beetle species were captured at BFR. A lack of visible signs of mammals was noted during sampling at this site, and it is located near a settlement of the indigenous Orang Asli people who may hunt mammals in the reserve. Additionally, it is possible that certain compositional similarities between sites may be due to sampling artifacts. For example, some communities may appear to be more similar to each other than others due to similar weather conditions during trapping nights.

It is also important to recognise the potential impact of the peninsula effect on the dung beetle communities we surveyed. Our eight study sites were located throughout Peninsular Malaysia, which is aptly named for its location on the Malay Peninsula that narrows from mainland Southeast Asia in Southern Myanmar and Southern Thailand and runs to the Straits of Johor and the Straits of Malacca. The peninsula effect predicts that the number of species of a given taxa will decline from a peninsula's base down to its tip (Simpson, 1964; MacArthur & Wilson, 1967; Cook, 1969). Our data show some evidence of the peninsula effect impacting the diversity of our sampled dung beetle communities. In terms of rarefied expected species richness, BFR was the least diverse site, and it is the site that is second farthest south down the peninsula (after GAFR). Additionally, of the three most diverse sites in terms of expected species richness (TFR, SFR, and GTFR), TFR and GTFR are among the three northern most sites; SFR is located much farther south. However, we did not design our study to specifically test the peninsula effect. Rather, sites were chosen for their range in sizes, elevations, floristic zones, and topologies, as well as their accessibility. Thus, in our study, the peninsula effect is most likely confounded by many other factors, such as some of the environmental variables we measured (e.g., size of forest area, elevation), as well as others we did not measure (e.g., distance to urbanisation or roads). In order to specifically test for the peninsula effect on dung beetle diversity in Peninsular Malaysia, future studies should sample dung beetle diversity in multiple replicated plots that are established at the same latitude throughout the peninsula and that control for other environmental variables.

This paper presents the most geographically large-scale study of dung beetle community diversity in a variety of primary and secondary forest reserves located throughout Peninsular Malaysia. It reports how dung beetle community composition varies as related to various environmental and geographic factors. Our data can be used as a reference for studies that compare dung beetle diversity in forest reserves in Peninsular Malaysia to diversity in anthropogenically altered ecosystems in the area, such as recently logged forests or oil palm plantations.

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