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LINKING BIODIVERSITY AND ECOSYSTEM FUNCTIONING OF DUNG BEETLES IN SOUTH AND SOUTHEAST ASIAN TROPICAL RAINFORESTS

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ABSTRACT. — We investigated the impacts of habitat disturbance and the resulting changes in biodiversity on ecosystem function in South and Southeast Asian forests using dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) as a focal taxon. Dung beetle sampling and dung burial experiments were conducted in intact, modified, and fragmented forest habitats in three different countries: Sri Lanka, Malaysia, and Singapore. Data analysis was split into two themes for analysis: the effect of habitat modification, and the effect of fragmentation. The proportion of dung mass removed was modelled against habitat modification, and the species richness and abundances of the entire dung beetle community, the tunneller communities, and the roller communities. Abundance and richness of tunnellers and the degree of habitat disturbance were the main determinants of dung burial in the habitat modification analysis. Total dung beetle abundance was the main determinant of dung burial in the fragmentation analysis. Through our combined analysis, we show that habitat modification and forest fragmentation impact dung removal activity, albeit through different aspects of the dung beetle community structure.

KEY WORDS. — Scarabaeinae, dung removal, tropical forests, ecosystem function, functional groups

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INTRODUCTION

Forest clearing and modification for human settlements and agricultural production is prevalent and accelerating throughout the tropics (Achard et al., 2002; Sodhi et al., 2007; Gibbs et al., 2010). Such changes in forest landscapes occur rapidly in South and Southeast Asia where a number of biodiversity hotspots are located (Myers et al., 2000; Sodhi et al., 2004; Mittermeier et al., 2005). Ecological studies on conversion of forests to human land use areas in these regions have shown dramatic declines in populations and species richness across various taxa (Sodhi et al., 2010; Kudavidanage et al., 2011). However, resulting disruption of ecosystem functions and services (MEA, 2005) are relatively less studied compared to losses in biodiversity. As degradation through anthropogenic activities (e.g., logging, conversion to agriculture) and fragmentation continues in South and Southeast Asian forests, there is a necessity to link these impacts to changes in biodiversity and ecosystem functions in order to gain a more comprehensive understanding of anthropogenic disturbances on tropical forests.

Linkages between biodiversity and ecosystem functions such as primary productivity, nutrient recycling, and decomposition have been demonstrated in various controlled and field ecological experiments as reviewed by some authors (Schwartz, 2000; Loreau et al., 2001; Naeem & Wright, 2003; Hooper et al., 2005; Proulx et al., 2010; Isbell et al., 2011). Studying these ecological processes performed by different taxa (i.e., dung beetles) can lead to an understanding of related environmental services provided by the guilds or species occupying different ecosystems (Andresen, 2003; Nichols et al., 2007; Slade et al., 2007;Aguirre & Dirzo, 2008; Amazquita & Favila, 2010; Slade, et al., 2011). Natural communities contain functional redundancy, where multiple species perform the same ecological function and fall into one functional group (Kremen, 2005). Therefore, it has been argued that the diversity of functional groups, more than that of species, governs the ecosystem functions they perform (Kremen, 2005).

Here, we investigate the linkages between biodiversity and ecosystem functions in South and Southeast Asian forests using dung beetles (Coleoptera: Scarabaeinae) as a focal taxon. Exploring a large geographic scale enables detection of common patterns across the region and hence increases the applicability of research findings. Dung beetles are key bioindicators which are sensitive to tropical forest modification and fragmentation (Halffter & Arellano, 2002; Davis et al., 2004; Nichols et al., 2007) and provide a cost-effective indicator group for tropical forest disturbances (Davis et al., 2001; Gardner et al., 2008). Feeding and breeding activities of dung beetles involve dung burial through which dung beetles perform a series of ecosystem functions. Dung burial enhances soil fertility by making the critically important nitrogen available for plant uptake (Gillard, 1967; Nichols et al., 2008). Dung burial also results in soil aeration, secondary seed dispersal, and biological control of pests and parasites (Nichols et al., 2008). All these functions are ecologically valued as important ecosystem services (Klein, 1989; Horgan, 2005), and disruption of them through habitat disturbance will cascade into many trophic levels while causing significant economic loss to mankind (Losey & Vaughan, 2006). However, the understanding of the functional importance of dung beetles is primarily supported by data from pasture and grasslands which makes ecological and economical evaluation of their role in relation to the tropical deforestation a critical need.

Habitat modification and fragmentation are the most prominent types of landscape conversion leading to disturbance (Gibson et al., 2011). Previous studies have demonstrated that decreased species richness of dung beetles caused by habitat disturbance led to reduced dung burial rates and have highlighted the disproportional importance of large-bodied dung beetles in dung removal (Larsen et al., 2005; Slade et al., 2007, 2011). In this study, we use data from three separate studies (Lee et al., 2009; Qie, 2011; Kudavidanage, 2011) to focus on linkages between changes in dung beetle communities and dung burial rates in highly fragmented and heavily modified forest landscapes in South and Southeast Asia. We hypothesize that increasing habitat modification and fragmentation will lower dung burial rates by dung beetles. As dung beetles are categorised into three functional guilds of different nesting strategies and varied performance (tunnellers, rollers, and dwellers; Halffter & Edmonds, 1982; Slade et al. 2011), we also evaluated the composition of two important guilds (tunnellers and rollers) in dung burial and tested whether the composition of functional guilds was a more important factor than total dung beetle abundance and species richness in maintaining dung removal functions.

MATERIAL AND METHODS

Study site. — Dung beetle diversity sampling and dung burial experiments were conducted in modified and fragmented forest habitats in three different countries: Sri Lanka, Malaysia, and Singapore. Kudavidanage (2011) conducted the study in and around Sinharaja, Kanneliya, and Kottawa-Kombala lowland tropical rainforests situated in the southwestern region of Sri Lanka. Rates of dung removal, dung beetle richness, and abundance were sampled on transects in four habitat types (primary forests, selectively logged forests, tea plantations, and home gardens) in each of the three above-mentioned forest sites. The three modified habitats (selectively logged forests, tea plantations, and home gardens) were compared with the primary forest habitat as the control. Lee et al. (2009) carried out the study on forest sites on the island of Singapore and in the state of Johor, Peninsular Malaysia. Five sites from Singapore represented forest fragments of varying levels of habitat modification and two control sites in Peninsular Malaysia were included as natural and undisturbed sites for comparison. Qie (2011) conducted the study in Lake Kenyir, a man-made reservoir in the state of Terengganu, northeastern Peninsular Malaysia. The flooding of dense hilly forest for the reservoir created a fragmented forest landscape consisting of over 340 land bridge islands, ranging in size from less than 1 ha to over 1,000 ha. Dung beetle trapping and dung removal experiments were carried out along transects on 11 islands of varying sizes and three mainland forest sites. Descriptions of the study sites are detailed further in the supplementary material (S1).

Sampling and experimental set-ups. — We employed baited pitfall traps in all three study sites to survey dung beetle diversity and abundance in fragmented and modified habitats. Pitfall traps (200 ml plastic cups) were buried in the ground and filled with approximately 50 ml salt water and a small amount of detergent to reduce surface tension (Larsen & Forsyth, 2005). Approximately 15–20 g of human or cattle dung was suspended above each trap, in a plastic mesh, with a rain cover above. Traps baited with cattle dung was used for the habitat modification study in Singapore and Malaysia while the study in Sri Lanka used human faeces baited traps. To minimise the impact of using two different dung types of different appeal to dung beetles, species specifically found in human faeces and not in cow dung were not included in the analysis.

Traps were arranged in a transect design, spaced a distance of 30–100 m apart and left open for 48 hours before the beetles were collected. Each transect was sampled at least once (supplementary material S1) and the Sri Lanka data were averaged between dry and wet seasons to remove the seasonal variations if any. The number of transects, transect interval, and trap interval were adjusted to best fit field conditions for each study location (see supplementary material S2 for further details). Captured dung beetle individuals were preserved in 100% ethanol and identified to species level where possible. Unidentified species were assigned a morphospecies number and were included in the analysis.

We set up dung removal experiments 24–48 hours prior to dung beetle sampling along the same transects. For each of the sampling transects, three of the five trapping points were randomly selected as dung burial experiment locations. At each location, leaf litter on the forest floor was cleared and two dung pads of 50–100 g, each on a piece of thin plastic coated paper, were placed side by side. One of the dung pads was enclosed in a polyester mesh bag with 2 mm mesh size to prevent dung beetle access but account for mass loss by other sources (i.e., flies, evaporation). Rain covers were supported above the dung pads. Dung pads were collected after 24 hours and dried to constant weight for the calculation of the dry dung mass removed by beetles. We calculated the proportion of dung mass removed by beetles within 24 hours after correcting for loss of biomass by sources other than beetles such as flies and moisture loss. The sampling durations were standardised across all three studies to sample the same community of dung beetles removing dung.

Data analysis. — Differences in study site conditions prevented a combined meta-analysis of all three sites. Hence we split data analysis into two themes for analysis: the effect of habitat modification and the effect of fragmentation on the linkage between biodiversity and ecosystem functioning. To analyse the relationship between biodiversity and ecosystem functioning under the effect of habitat modification, we pooled data on dung beetle diversity and dung removal from Kudavidanage (2011) and Lee et al. (2009). Data on dung beetle diversity and dung removal across different sites in Qie (2011) was used to analyse the relationship between biodiversity and ecosystem functioning under the effect of fragmentation. Under the habitat modification analysis, habitat classes from Lee (2009) and Kudavidanage (2011) were grouped together and categorised under two levels of modification: 'least modified' (primary forest [PF], primary continuous forests [PCF], and old secondary logged forests [OLSF]), and 'heavily modified' (primary secondary forests [PSF], young secondary forests [YSF], home gardens [HG], tea plantations [TEA], and highly degraded forests [HDF]), based on the history of anthropogenic disturbance to forest habitats. OSLF was categorised under the 'least modified' as the forests were logged 40 years ago and has since been placed under protection status. To compare dung removal and dung beetle communities across different levels of habitat modification, we analysed data at the transect level. Proportion of dung mass removed over 24 hours was averaged across the three sampling points to provide a mean proportion removal of dung mass at each transect. Dung beetle species richness and abundance data were pooled for sampling sites to provide information at the transect level (Table 1). We compared dung removal and dung beetle community variables (species richness and abundance) between low and heavily modified habitats using Wilcoxon rank sum test for non-normal data. To account for the two different types of dung baits used in the habitat modification study and to prevent any effect on the overall conclusion, "site" was used as a random effect when pooling the data from Singapore, Malaysia, and Sri Lanka. This helped to control for the intrinsic differences between the two studies to a certain extent. For the fragmentation analysis, 11 islands of different sizes from Qie (2011) ranging from 2.5 ha to 383.3 ha and three mainland sites were used. It has been shown that in Lake Kenyir, dung beetle species richness and abundance generally decreased with island area (Qie et al., 2011). Hence fragmentation is hypothesized to have influenced the dung removal function through altering dung beetle communities on these islands. To compare how changes in species richness and abundance of the dung beetle community affected dung removal at different sites, we analysed the data at a site level because transects were located in close proximity to each other on small islands due to space constraints and were therefore considered non-independent. Proportion dung mass removed and dung beetle species richness and abundance were pooled across transects to provide information at a site level (Table 1). To investigate the relationship between dung removal and dung beetle communities in the habitat modification and fragmentation studies, we used an information-theoretic approach that allows for multiple model comparisons and identifies the most parsimonious model which best explains variation in the response variable (Burnham & Anderson, 2002). This approach requires the construction of a priori candidate models using existing knowledge about factors which influence dung removal by dung beetle communities. Model comparison is carried out using the Akaike's information criterion corrected for small sample sizes (AIC_C). This index measures the Kullback-Leibler (K-L) information loss and assigns relative strengths of evidence to different competing models within each model set. The relative probability of each model being the best model is calculated using Akaike weights, $wAIC_C$, and ranging from 0 (no support) to 1 (complete support). Akaike weights can be used to identify the 95% confidence set of models and create evidence ratios which provide quantitative information about the support for one model relative to the other (Burnham & Anderson, 2002). They can also be used to calculate the relative importance of a variable by summing up the $wAICc$ of all models which include that variable. As there was no best model ($wAIC_C > 0.95$), we used model averaging of the 95% confidence set of models, using the 'zero' method for averaging model coefficients to obtain a final averaged model for prediction (Burnham & Anderson, 2002). We fitted our data using generalised linear mixed-effects models (GLMM) using the lmer function implemented in the R package (R Development Core Team, 2009), assigning each model a normal distribution and an identity link function. Candidate GLMMs were fitted by coding dung mass removed as the response variable (arcsine-transformed proportional data, to meet the linear model assumptions), and various combinations of species richness and abundances of all species, tunneller species, and roller species, and habitat disturbance, as fixed effects in the linear predictor (Table 2). Each candidate model also included study site as a random effect. Models were checked for homogeneity and normality of their residuals.

RESULTS

In the habitat modification analysis, we recorded 5551 individuals of 32 species from Sri Lankan sites and as 1604 individuals of 44 from Singapore and Malaysia (see supplementary material S3 for a full species list). Sample based species accumulation curves computed in EstimateS Version 8.2.0 (Gotelli & Colwell, 2001; Colwell, 2006)

Table 1. Mean proportion of dung mass removed and dung beetle community variables (species richness and abundance) presented at the transect level for habitat modification studies and site level for fragmentation study.

Study	Mean proportion of dung removal	Dung beetle species richness	Dung beetle abundance	Tunneller species richness	Tunneller abundance	Roller species richness	Roller abundance
Habitat modification							
Least modified	0.67 ± 0.032	13.79 ± 0.558	221.62 ± 20.043	11.29 ± 0.469	188 ± 17.679	1.31 ± 0.110	27.95 ± 3.133
Heavily modified	0.17 ± 0.021	7.06 ± 0.594	60.90 ± 0.223	6 ± 0.497	54.54 ± 7.096	0.38 ± 0.083	0.827 ± 0.223
Habitat fragmentation							
Mainland 1	15.4	14	6.0	11	2.3	2	3.6
Mainland 2	11.4	16	4.6	11	2.5	4	2.0
Mainland 3	38.4	21	12.7	18	8.1	2	4.6
Island 1	25.4	10	9.3	7	8.0	2	1.3
Island 2	34.4	5	4.3	3	1.2	2	3.0
Island 3	15.5	8	2.7	5	0.5	2	2.2
Island 4	37.2	6	3.4	4	2.1	2	1.3
Island 5	9.6	4	1.5	1	0.1	2	1.3
Island 6	12.6	1	0.1	1	0.1	0	0.0
Island 7	32.8	6	3.8	3	0.7	2	3.0
Island 8	15.1	2	1.2	1	0.1	1	1.1
Island 10	33.8	5	10.4	3	0.6	2	9.8
Island 12	15.4	2	2.4	1	0.2	1	2.2
Island 16	20.5	1	1.0	0	0.0	1	1.0

Table 2. Candidate set of models for habitat modification and fragmentation analysis. Models were tested against arcsine transformed proportion dung mass removed. Sampling site was accounted for as random effect (1|site) and included in all models during the model selection process. In the models below, ‘all’ refers to all dung beetles, ‘t’ refers to tunneller dung beetles, and ‘r’ refers to roller dung beetles.

Model no.	Candidate models	Analytical theme
Habitat modification		
1	~habitat + richness.all + abundance.all + richness.t + abundance.t + richness.r + abundance.r	global model
2	~habitat + richness.all + abundance.all	db community
3	~habitat + richness.t + abundance.t	db tunneller community
4	~habitat + richness.r + abundance.r	db roller community
5	~habitat + richness.all	db community richness
6	~habitat + richness.t	db tunneller community richness
7	~habitat + richness.r	db roller community richness
8	~habitat + abundance.all	db community abundance
9	~habitat + abundance.t	db tunneller community abundance
10	~habitat + abundance.r	db roller community abundance
11	~habitat	habitat only
12	~null	null model
Habitat fragmentation		
1	~richness.all + abundance.all + richness.t + abundance.t + richness.r + abundance.r	global model
2	~richness.all + abundance.all	db community
3	~richness.t + abundance.t	db tunneller community
4	~richness.r + abundance.r	db roller community
5	~richness.all	db community richness
6	~richness.t	db tunneller community richness
7	~richness.r	db roller community richness
8	~abundance.all	db community abundance
9	~abundance.t	db tunneller community abundance
10	~abundance.r	db roller community abundance
11	~null	null model

Table 3. Model ranking, number of parameters (*k*), difference in Akaike's information criteria from the minimum value (ΔAIC_C), model weight (*w*), and coefficient estimates for 95% set of the candidate models for a) habitat modification studies (Lee, 2009; Kudavidanage, 2011) and b) fragmentation study (Qie, 2011). The relative importance for variables and model-averaged coefficients are based on the 95% confidence set of models.

Model ranking	Intercept	$ABUND_{all}$	$ABUND_{roller}$	$ABUND_{tunneller}$	MOD_{low}	$RICH_{all}$	$RICH_{roller}$	$RICH_{tunneller}$	k	ΔAIC_C	w
a) Habitat modification											
1	0.189			0.001	0.384			0.015	6	0	0.444
2	0.193	0.001			0.377	0.012			6	0.93	0.279
3	0.278			0.001	0.393				5	2.38	0.135
4	0.280	0.001			0.385				5	2.76	0.112
Model-averaged	0.206	0.0003		0.0005	0.372	0.003		0.007			
Relative importance		0.391		0.579	0.970	0.279		0.444			
b) Fragmentation											
1	0.396	0.02							3	0	0.739
2	0.416	0.03				–0.01			4	1.85	0.116
3	0.419		0.026						3	2.28	0.075
4	0.487								2	2.89	0.041
Model-averaged	0.393	0.018	0.002	0		0					
Relative importance	0.855	0.077				0.003					

were used to evaluate sampling adequacy for all sites. It was observed that species richness reached at least 80% of the asymptotic value for all sites in Sri Lanka and Lake Kenyir, Malaysia, but ranged between 60–99% for sites in Singapore and Johor, Malaysia. The comparison of dung removal and dung beetle community variables (species richness and abundance) between less and highly modified habitats showed less modified habitats having significantly higher proportion of dung removal (W = 90, $P < 0.001$, df = 2) and higher species richness and abundance for the entire dung beetle community (W = 262, $P < 0.001$, df = 2 and W = 254, $P < 0.001$, df = 2, for species richness and abundance respectively), as a well as the tunneller (W = 301, $P < 0.001$, df = 2 and W = 282.5, $P < 0.001$, df = 2) and roller communities (W = 346, $P < 0.001$, df = 2 and W = 24.5, $P < 0.001$, df = 2). The most parsimonious model for explaining variations in dung removal between the less modified and highly modified habitats include disturbance and the abundance and species richness of tunnellers (Table 3a). This model accounted for 44.4% of the Akaike weights in the model set. The 95% confidence set includes four models, and the relative importance of predictor variables present in all four models are the level of habitat modification, abundance of tunnellers, and species richness of tunnellers, abundance of all species, and species richness of all species, in the order of descending importance. The averaged model is represented by the following equation:

$$\text{arcsine(D.REMOVAL)} = 0.0003 \times \text{ABUND}_{\text{all}} + 0.0005 \times \text{ABUND}_{\text{tunneller}} + 0.372 \times \text{MOD}_{\text{low}} + 0.003 \times \text{RICH}_{\text{all}} + 0.007 \times \text{RICH}_{\text{tunneller}} + 0.206$$

Where D.REMOVAL = proportion dung removal; ABUND = abundance of dung beetle community; MOD = modification level of habitats; and RICH = species richness of dung beetle community.

In the fragmentation analysis, we recorded 1491 individuals of 28 dung beetles species across all 11 islands and three mainland forest patches. Among the 11 islands, species richness decreased significantly with island area (Spearman's rho = 0.70, $P = 0.02$). Although beetle abundance generally decreased with island area, this correlation was not significant (Spearman's rho = 0.41, $P = 0.2$). The most parsimonious model explaining dung removal across a gradient of forest fragments includes abundance of all dung beetle species as a single predictor (Table 3b). This model accounts for 73.9% of the Akiake weights in the model set. The 95% confidence set includes four models, containing the main effect of abundance of all beetles (relative importance = 0.855) and weak effects of abundance of rollers (relative importance = 0.077) and richness of all species (relative importance = 0.003). The averaged model is represented by the following equation:

$$\text{arcsine(D.REMOVAL)} = 0.018 \times \text{ABUND}_{\text{all}} + 0.002 \times \text{ABUND}_{\text{rollers}} - 0.001 \times \text{RICH}_{\text{all}} + 0.393$$

Overall, the best community level predictors for dung burial rate across pristine and modified habitats were tunneller beetle species richness and abundance, although other factors, such as total species richness and abundance also had positive effects. In both analyses, abundance rather than richness of dung beetles was a stronger predictor of level of dung removal across study sites. The role of tunnellers in dung removal was more important in modified habitats compared to fragmented forests.

DISCUSSION

Habitat modification and forest fragmentation in tropical South and South East Asia have strong negative impacts on dung beetle communities and dung removal function as indicated by the low rates of dung removal, species richness, and abundance in modified habitats and fragments. Previous work in the Neotropics and Borneo report similar findings, where rates of dung removal was found to be decreasing with increasing disturbance and alteration of forest habitats (e.g., Klein, 1989; Horgan, 2005; Nichols et al., 2007; Slade et al., 2011). Modifications of pristine forest habitats cause changes in environmental conditions and could increase predation of vulnerable species by natural enemies which in turn may affect dung beetle communities (Andresen & Laurance, 2007; Nichols et al., 2007). Forest habitat modification also reduces the abundance of mammals (Laidlaw, 2000) that provide the main food source for a majority of dung beetle species (Estrada & Coates-Estrada, 1991).

The importance of functional guilds in determining the rates of removal was one of the main findings of the study. Dung removal was primarily influenced by the species richness and abundance of tunnellers in the modified habitat analysis. As observed during sampling, pristine forest and protected old continuous and selectively logged forests contain more large mammals than the highly modified habitats, and therefore possibly support a greater variety of dung beetles which may explain the high rates of dung removal activity. Tunnellers consist of the major proportion of the dung beetle communities in the study sites of Sri Lanka, Singapore, and Malaysia. For example, out of the 32 species recorded in Sri Lankan study sites, 26 species were tunnellers (supplementary material S3). In tropical Dipterocarp forests of Southeast Asia, tunneller species are known to contribute up to 75% of dung removal, and large nocturnal tunnellers are most efficient in dung burial within these habitats (Slade et al., 2007). In general, it can be established that across Southeast and South Asia, tunnellers play the most significant role in removing dung masses. However in specific findings for the wet zone of Sri Lanka, a single species of large roller was abundant in forest habitats and was important in dung removal in pristine and old selectively logged forest habitats while tunnellers that were dominant in species richness and abundance were the most important in modified habitats and open areas (Kudavidanage, 2011). In contrast, large rollers were less abundant in Singapore and the dung beetle communities were dominated by tunnellers in abundance (Lee et al., 2009).

In the fragmentation study, the total abundance of dung beetles (rather than functional guilds of dung beetles) had a stronger effect on dung removal activity. The importance of roller species in the fragmentation analysis was very weak and this may be due to the disproportionately higher abundance of rollers present in most sites within the fragmentation analysis (Table 1). Therefore for these altered communities in forest fragments, dung removal is primarily determined by the number of beetle individuals. Abundance and biomass of dung beetles are often determined by the resource availability in a habitat (Horgan, 2005) which was a main limitation for dung beetles in small islands (Qie et al., 2011). On small islands depauperate with beetles, dung burial rate was as low as 10%. The tunneller community in land bridge island forest fragments primarily consisted of small diurnal beetles (Qie, 2011) and these were not found to be an important predictor of dung removal in the best model for the fragmentation study. The majority of tunneller species found here were relatively small and may have less influence on dung removal activity within the forests. Slade et al. (2007) found that in large continuous forests in Sabah, Borneo, large nocturnal tunnellers were the primary determinants of dung removal. Conversely, the large nocturnal tunneller group was the least abundant in islands, consisting of only three species in the cattle dung community (Qie, 2011). In this case, it appears that as large continuous forests become fragmented, large beetles found within these forests disappear and the small sized beetles tend to dominate the community (Larsen et al., 2005; Slade et al., 2007).

Highly modified habitats of these studies showed decreased abundance in comparison to the primary forest, although increasing habitat modification is known to be complemented by the increase in the abundance of species characteristic of more open habitats, a phenomenon that is dependent on the context of the landscape (Howden & Nealis, 1975; Nichols et al., 2007). Similar findings have been presented previously in other regions (e.g., Klein, 1989; Vulinec, 2002; Larsen et al., 2005; Scheffler, 2005; Gardner et al., 2008). Although dung beetle abundance is not acknowledged as a successful measure of land use change or fragmentation (Nichols et al., 2007), we found that it was highly correlated with the rate of dung removal across our study sites. In the absence of large dung beetles in the community, the abundance of dung beetles may take the place of representing biomass of the beetle community in these sites and be important in accounting for dung removal activity.

One important caveat in our study presented here is the use of different proportions of cow dung and human faeces baits for dung beetle trapping in the three studies. Human faeces is shown in several studies to be the best bait type to attract a great diversity of dung beetles in Southeast Asia (Hanski, 1983), South Asia (Kudavidanage, 2011), and elsewhere (Doube & Wardhaugh, 1991; Larsen et al., 2005). To minimise this effect, necrophagic beetles and beetles found exclusively in human faeces were excluded during the analyses, hence controlling for the differences between sites sampled with different bait types.

CONCLUSIONS

From the combined analysis of three studies conducted in South and Southeast Asia, it can be concluded that dung beetle communities and their dung removal function are negatively impacted by habitat modification and fragmentation regardless of the differences in countries and sites. The dung removal process was more influenced by the functional guild tunnellers which were predominant in the habitat modification analysis, while the abundance of dung beetle communities was more important for dung removal in the fragmentation analysis. Dung beetle responses to habitat disturbance show a general pattern over a large geographical range. Using taxa that can provide quantifiable community and functional data for habitat quality assessment can yield interesting insights to what aspects of the species community are important in linking biodiversity with ecosystem functions.

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SUPPLEMENTARY MATERIAL

S1. Description of study sites in Sri Lanka, Malaysia, and Singapore.

Study cited	Study sites	Coordinates	Elevation (m)	Climate characteristics	Vegetation characteristics	Habitat types	No. sites	Time period of study conducted
Kudavigdanage (2011)	**Sri Lanka**							
	Sinharaja	6°21–6°26'N, 80°21'–80°34'E	300–1170	Annual rainfall ranging 3,750–5,000 mm; monthly temperature ranges from 18–27°C	Lowland tropical rainforests	Primary forests (PF), selectively logged forests (OSLF), tea plantations (TEA), and home gardens (HG)	12 sites	Jan.2008 – Jan.2010
	Kanneliya	6°11'N, 80°25'E	60–425					
	Kottawa-Kombala	6°5'N, 80°18'E	10–260					
Qie (2011)	**Malaysia** Lake Kenyir, Terengganu	5°00'N, 102°48'E	145	Northeast monsoon from Nov–Mar and hot and dry season from May–Oct; annual precipitation varying between 2,700–4,000 mm	Lowland tropical dipterocarp forests; forests selectively logged before creation of dam	Forested islands of varying sizes (2.5–383.3 ha for islands) along with mainland sites, with historical selective logging	11 islands and 3 mainland sites	Jun.2008 – Oct.2009
Lee et al. (2009)	**Malaysia**							
	Belumut, Johor	2°01'N, 103°31'E	<200	High mean annual temperatures (30°C); high average daily humidity 90%; mean annual rainfall over 2000 mm, exceeds 100 mm even in driest months; main wet season Nov–Jan, less rainfall in Jun–Jul	Lowland tropical dipterocarp forests	Old growth dipterocarp forests (PCF)		Sep.2007 – Mar.2008
	Bekok, Johor	2°17'N, 103°08'E	<200		Lowland tropical dipterocarp forests	Old growth Dipterocarp forests (PCF)		Sep.2007 – Mar.2008
	Singapore							
	Forest fragments	1°38'N, 103°40'E	<200		Lowland tropical dipterocarp forests	Tall secondary forest with fragments of old growth (PSF), young secondary forests (YSF), disturbed forests (HDF)	5 sites	Sep.2007 – Mar.2008

S2. Description of sampling methods carried out in individual studies.

Study cited	No. transects	Trap interval (m)	No. traps per transect	No. sampling cycles	Type of dung used as trap bait
Kudavigdanage (2011)	5	50–100	5	3	human
Qie (2011)	2–6 (depending on island size)	30–50	3–5 (depending on island size)	2	cattle
Lee et al. (2009)	2–6 (depending on habitat size)	30	5	3	cattle

S3. List of dung beetle species included in this study by the authors EK, JL, and LQ, and their guild classification (D = dweller; R = roller; T = tunneller). For clarity, unidentified morpho-species were coded with reference to the repective study (e.g., *Aphodius* sp. JL1 corresponds to *Aphodius* sp. 1 in JL's study). * indicates potentially new species that closely resemble the given species.

Species	Study			Guild
	EK	JL	LQ	
Aphodius sp. JL1		Yes		D
Aphodius sp. EK1	Yes			D
Aphodius sp. EK3	Yes			D
Apohodius sp. EK2	Yes			D
Caccobius unicornis Fabricius, 1798		Yes	Yes	T
Catharsius molossus Linnaeus, 1758	Yes	Yes	Yes	T
Copris agnus Sharp, 1875		Yes		T
Copris doriae Harold, 1877		Yes	Yes	T
Copris haroldi Lansberge, 1886		Yes	Yes	T
Copris ramosiceps Gillet, 1921		Yes		T
Copris signatus Walker, 1858	Yes			T
Copris sodalis Walker, 1858	Yes			T
Drepanocerus setosus Wiedemann, 1823	Yes			D
Gymnopleurus melanarius Harold, 1867	Yes			R
Liatongus femoratus Illiger, 1800			Yes	T
Ochicanthon nonpatterned		Yes		R
Ochicanthon peninsularis Krikken & Huijbregts, 2007		Yes	Yes	R
Oniticellus tessellatus Harold, 1879			Yes	D
Onthophagus sp. EK1	Yes			T
*Onthophagus *amphinasus* 3	Yes			T
*Onthophagus *refulgens* r	Yes			T
*Onthophagus *solidus*	Yes			T
Onthophagus angustatus Boucomont, 1914		Yes	Yes	T
Onthophagus aphodiodes Lansberge, 1883		Yes	Yes	T
Onthophagus babirussa 1		Yes	Yes	T
Onthophagus babirussa 2			Yes	T
Onthophagus babirussa 3		Yes	Yes	T
Onthophagus bifaciatus Fabricius 1781	Yes			T
Onthophagus castetsi near	Yes			T
Onthophagus centricornis Fabricius, 1798	Yes			T
Onthophagus cervicapra Boucomont, 1914		Yes		T
Onthophagus cervus Fabricius, 1798	Yes			T
Onthophagus congerro			Yes	T
Onthophagus crassicollis Boucomont, 1913		Yes		T
Onthophagus cryptogenus Boucomont, 1914	Yes			T
Onthophagus dama Fabricius, 1798	Yes			T
Onthophagus deflexicollis Lansberge, 1883		Yes		T
Onthophagus deliensis Lansberge, 1885		Yes		T
Onthophagus favrei Boucomont, 1914	Yes			T
Onthophagus hairy 1		Yes		T
Onthophagus hairy 2			Yes	T
Onthophagus hairy 3		Yes		T
Onthophagus hairy 4		Yes		T
Onthophagus javanus 2		Yes		T
Onthophagus javanus 3		Yes	Yes	T
Onthophagus javanus 4		Yes		T
Onthophagus laevis Harold, 1880		Yes	Yes	T
Onthophagus martialis Boucomont, 1914	Yes			T
Onthophagus mentaweiensis 1		Yes		T
Onthophagus mentaweiensis 2		Yes		T
Onthophagus miltaris Boucomont, 1914	Yes			T
Onthophagus negligens Walker, 1858	Yes			T
Onthophagus oculatus Arrow, 1931	Yes			T

S3. Cont'd.

Species	Study			Guild
	EK	JL	LQ	
Onthophagus orientalis 1			Yes	T
Onthophagus pacificus 1			Yes	T
Onthophagus pacificus 3		Yes		T
Onthophagus pacificus 4		Yes		T
Onthophagus pedator Sharp, 1875		Yes		T
Onthophagus pygmaeus Schaller, 1783	Yes			T
Onthophagus refulgens Arrow, 1931??	Yes			T
Onthophagus rorarius Harold, 1877		Yes	Yes	T
Onthophagus rudis Sharp, 1875		Yes	Yes	T
Onthophagus rugicollis Harold, 1880		Yes		T
Onthophagus rutilans Sharp, 1875		Yes	Yes	T
Onthophagus semicupreus Harold, 1877		Yes		T
Onthophagus semifex Krikken & Huijbregts, 2008		Yes	Yes	T
Onthophagus sideki Krikken & Huijbregts, 1987		Yes		T
Onthophagus sp. EK112	Yes			T
Onthophagus sp. EK24	Yes			T
Onthophagus sp. EK54	Yes			T
Onthophagus sp. JL18		Yes		T
Onthophagus sp. JL19		Yes		T
Onthophagus sp. JL20		Yes		T
Onthophagus sp. LQ9			Yes	T
Onthophagus spinifex Fabricius, 1881	Yes			T
Onthophagus taprobanus Arrow, 1931	Yes			T
Onthophagus turbatus Walker, 1858	Yes			T
Onthophagus uenoi Ochi, 1995		Yes		T
Onthophagus unifasciatus Schaller, 1783	Yes			T
Onthophagus vulpes Harold, 1877		Yes	Yes	T
Panelus setosus Arrow, 1931	Yes			R
Panelus sp. LQ1			Yes	R
Paragymnopleurus maurus Sharp, 1875		Yes	Yes	R
Sisyphus hirtus Wiedemann, 1823	Yes			R
Sisyphus thoracicus Sharp, 1875		Yes	Yes	R
Yvescambefortius sarawacus Gillet, 1926		Yes	Yes	T