



Trap type affects dung beetle taxonomic and functional diversity in Bornean tropical forests

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Abstract Baited pitfall traps (BPTs) and flight intercept traps (FITs) are the most common methods employed for sampling dung beetle communities. These methods vary in their efficacy and are affected by factors such as the bait types used and the dispersal abilities of different dung beetle species. We present the first quantitative comparison of the community composition, taxonomic and functional diversity of dung beetles caught in human dung BPTs and FITs in Bornean tropical forests. Functional diversity metrics were calculated based on the three functional traits of nesting method, body length, and diel activity. We show that BPTs and FITs captured complementary communities with different functional traits, and that BPTs captured more functionally diverse communities. We therefore recommend using a combination of both BPTs and FITs for studies assessing the composition of dung beetles across habitat types. Our results also highlight that it is important to consider how trap type affects the trait composition of communities when relating dung beetle communities and functional traits to ecological functioning. We suggest modifications to FITs based on the design of harp traps to increase their effectiveness in capturing larger-bodied beetles.

Key words: biodiversity survey, Scarabaeidae, functional traits, Southeast Asia, sampling method.

INTRODUCTION

Dung beetles (Coleoptera: Scarabaeidae) are a model taxon for biodiversity research as they respond rapidly to environmental change and can be sampled cost-effectively (Nichols & Gardner 2011). While the majority of dung beetle species feed and breed exclusively on dung, some species utilise carrion, rotting fruit, fungi and decaying plant matter as alternative resources (Hill 1996; Halffter & Halffter 2009). As such, dung beetles contribute to a series of beneficial ecosystem functions and services to tropical rainforests, such as dung removal, nutrient cycling, soil aeration and secondary seed dispersal (Nichols *et al.* 2008).

Various methods have been employed to sample dung beetles, ranging from baited sampling methods, such as baited pitfall traps (Newton & Peck 1975) and bait pads (Davis *et al.* 1988), to non-baited methods, such as flight intercept traps (Hammond 1990) and pan traps (Sha'ari & Arumugam 2019). Among these, baited pitfall traps (BPTs) (Fig. S1a),

often using mammalian dung, are most extensively employed and take advantage of odour cues which the dung beetles use when searching for food (Frank *et al.* 2018). In the tropical forests of Southeast Asia, human dung BPTs are most commonly used (e.g. Kahono & Ubaidillah 2003; Slade *et al.* 2007; Dwi-badra *et al.* 2008; Gray *et al.* 2014), while in the Neotropics, BPTs are most often baited with human or howler monkey dung (e.g. Andrade *et al.* 2011; Feer 2013; Macedo *et al.* 2020), cattle dung (e.g. Correa *et al.* 2020; Macedo *et al.* 2020), pig dung (e.g. Carvalho *et al.* 2018) or a combination of human and pig dung (e.g. Marsh *et al.* 2013; França *et al.* 2018; Carvalho *et al.* 2020). BPTs are usually comprised of a rain cover with the bait of choice suspended over a container, which is buried flush with the ground and half-filled with a water, salt and detergent solution to drown attracted insects (Newton & Peck 1975). The traps can be modified to contain leaves and soil rather than water to capture the beetles alive (e.g. Gray *et al.* 2017b; Parrett *et al.* 2019). BPTs are quick to set up and capture large numbers of individuals within two to four trapping days (Spector 2006). However, the trapping efficacies

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and species caught depend on bait types, size and proportion of bait (Marsh *et al.* 2013; Raine *et al.* 2019), and the dispersal abilities of different species, which affects the potential sampling area of each trap (Larsen & Forsyth 2005; Silva & Hernández 2015). Due to vertical stratification of dung beetle communities in the forest canopy, the height of BPTs could also influence captured communities (Davis *et al.* 1997; Tregidgo *et al.* 2010; Abdul Rahman *et al.* 2021).

Flight intercept traps (FITs) (Fig. S1b) are also commonly used for dung beetle sampling, and occasionally used alongside BPTs (e.g. Hill 1996; Davis *et al.* 2001; Filgueiras *et al.* 2011; Feer 2013; Silva *et al.* 2020). FITs consist of a fine dark-coloured mesh or clear plexiglass intercept, usually 1–2 m high and strung between two trees or poles, beneath which a series of trays filled with a solution of water, salt and detergent are placed, to capture the insects as they hit the intercept and fall below (Hammond 1990; Chey & Chung 2002). FITs target flying individuals regardless of their bait preferences and thus may sample different dung beetle assemblages from baited pitfall traps (Davis 2000; Davis *et al.* 2000; Andrade *et al.* 2011; Puker *et al.* 2020). However, FITs are logistically more difficult to set up, take a longer time to collect representative samples than BPTs (Milhomem *et al.* 2003; Andrade *et al.* 2011), and flightless species or species with lower flight frequencies are less likely to be captured (Davis *et al.* 2001).

To our knowledge, only one study (in the Neotropics) has quantitatively compared the sampling efficacies of both trapping methods, in terms of taxonomic diversity and community composition (Andrade *et al.* 2011). Such quantitative comparisons have not been conducted for Southeast Asia, where past studies that used both trapping methods only comprised a small number of traps (e.g. six FITs in Davis 2000; five FITs in Davis *et al.* 2001). There are also no studies that compare functional diversity metrics among different trapping methods. Comparing functional diversity metrics provides insights into whether there are functional differences in the communities captured and if certain trapping methods are more effective in capturing more functionally diverse communities. This is especially important for studies that assess the relationship between biodiversity and ecosystem functioning, and how communities respond to environmental change (see Raine & Slade 2019).

Here, we present the first quantitative comparison for Southeast Asia of the community composition, taxonomic and functional diversity of dung beetles caught in human dung-baited pitfall traps and FITs. Large-bodied dung beetle species are of particular importance for ecosystem functioning (Slade *et al.*

2007) but rarely caught in FITs (Davis *et al.* 2001; Chung 2004; Gray *et al.* 2017a), despite their high movement rates and ability to move large distances (Gray *et al.* 2017b). We therefore also document the incidental captures of *Catharsius* species caught in harp traps (Tidemann & Woodside 1978) (Fig. S1c) during a study on the insectivorous bats of the area (Hemprich-Bennett *et al.* 2020) and suggest that a modified FIT could present a potential way of capturing large beetles passively.

Specifically, we test the following hypotheses:

1. Across different habitat types, the community composition, taxonomic and functional diversity of dung beetles will differ between BPTs and FITs.
2. For the large-bodied species, we expect FITs to sample fewer individuals than BPTs, but that harp traps might provide an alternative for capturing these larger species.

METHODS

The BPT and FIT data were collated from previous published (Slade *et al.* 2007, 2011; Gray *et al.* 2014, 2017a) and unpublished studies (Slade, Bush, *et al.* 2019; Slade, Milne, *et al.* 2019; Slade *et al.* 2020) conducted between November 2005 and October 2018. The harp trap data were collected during a bat-trapping campaign in 2017 (Hemprich-Bennett *et al.* 2020).

Study sites

Trapping was carried out within and around the Yayasan Sabah Forest Management Area in Sabah (Malaysian Borneo; 4°58'N, 117°E). Study sites were situated within the Stability of Forest Ecosystems (SAFE) project site, Danum Valley Conservation Area, Maliau Basin Conservation Area, and two timber concessions surrounding Danum Valley: Ulu Segama Forest Reserve and Malua Forest Reserve (Fig. S2). The SAFE project is a large-scale forest fragmentation experiment that consists of low- and high-intensity logged lowland dipterocarp forest, and oil palm plantation (Ewers *et al.* 2011). Sampling was conducted in the old-growth forest of Danum Valley and Maliau Basin; selectively logged forest in SAFE, Ulu Segama Forest Reserve, and Malua Forest Reserve, and riparian forest embedded in oil palm within the SAFE landscape (Table 1; see Gray *et al.* 2014, 2017a; Slade *et al.* 2007, 2011; Hemprich-Bennett *et al.* 2020 for further details on sampling periods and methods).

Dung beetle sampling

BPTs were baited with 25 g of human dung. Each BPT consisted of a rain cover and a plastic cup (top diameter = 8 cm, bottom diameter = 5.5 cm and depth = 12.5 cm) half-filled with water, salt and detergent solution, and

Table 1. Sampling period, number of sites, number of traps, and trap nights for BPT (human dung-baited pitfall trap), FIT (flight intercept trap), and harp trap surveys in each locality

Locality	Trapping Method											
	Sampling period	BPT			FIT			Harp				
		Sites (#)	Traps (#)	Trap nights (#)	Sampling period	Sites (#)	Traps (#)	Trap nights (#)	Sampling period	Sites (#)	Traps (#)	Trap nights (#)
Old-growth forest												
Danum Valley	Nov 2005	2	10	20	Feb – Apr 2005	2	10	60	2017	1	6	60
Maliau Basin	Feb–Mar 2011; Jan–Feb 2015	3	54	108	-	-	-	-	2017	1	6	60
Logged forest												
Ulu Segama Forest Reserve	Nov 2005	2	10	20	Feb–Apr 2005	2	10	60	-	-	-	-
Malua Forest Reserve	Nov 2005	2	10	20	Feb–Apr 2005	2	10	60	-	-	-	-
SAFE forests	Feb–Mar 2011; Jan–Feb 2015; Jul–Oct 2018	13	408	816	Oct–Nov 2012	4	4	24	2017	3	6	180
Riparian reserve												
SAFE riparian reserves	Oct–Nov 2012	23	112	224	Oct–Nov 2012	4	12	72	-	-	-	-
Total	-	46	604	1208	-	14	46	276	-	5	18	300

buried flush with the ground. In old-growth and logged forests, 492 BPTs were set along transects at 22 sites, spaced 125–175 m apart [in SAFE sites, the traps followed the second-order fractal points of each site (see Ewers *et al.* 2011); Slade *et al.* 2011]. There were 23 sites in riparian reserves, each with five traps set in a grid with 50 m between traps (Gray *et al.* 2017a). All traps were left in the field for 48 h before collection (Slade *et al.* 2011; Gray *et al.* 2014). In total, 604 BPTs were set, resulting in 1208 trap nights.

Each FIT consisted of a black nylon mesh (mesh size = 0.5 cm and dimensions = 1.5 m × 2 m), and ten collection trays (length = 30 cm, width = 20 cm and depth = 10 cm) placed on the ground on each side of the net and filled with a water, salt and detergent solution. All FITs were protected by a rain cover. In old-growth sites in Danum Valley ($n = 2$) and logged forest sites in Ulu Segama and Malua Forest Reserves ($n = 4$), five FITs were placed 250 m apart along a transect. Tray contents were collected after 48 h, with three temporal replicates in three different months. In SAFE logged forest and riparian reserve sites ($n = 8$), FITs were placed at four set distances from the logged forests (i.e. logged forest: 0 m; Riparian reserve: 200 m, 500 m, 1 km; Gray *et al.* 2017a). Tray contents were collected separately for each side of the FIT every 48 h for 6 days. In total, 46 FITs were set, resulting in 276 trap nights. A summary on the sampling period, number of sites and number of traps for the BPT and FIT surveys in each locality is provided in Table 1.

Harp traps are used by bat researchers when studying forest-interior bats in the palaeotropics (Struebig *et al.* 2013; Voigt & Kingston 2016). While harp traps have not been used to sample dung beetles intentionally, they are essentially large FITs. The traps are made up of a metal frame on legs, with parallel rows of fishing line extending from the top of the trap (about 350 cm high) to

approximately 50 cm off the floor, where a collection bag hangs. Animals flying into the strings of the trap are interrupted in a similar manner to that of flight intercept traps. In 2017, harp traps were erected along bat flyways at five sites within SAFE, Danum Valley and Maliau Basin. These flyways are linear features in the landscape, such as streams and human paths, that bats use as commuting routes due to their lower level of obstructions compared with dense forests. Each site had six harp traps that were each left out for ten nights, resulting in a total trapping effort of 60 trap nights per site (Hemprich-Bennett *et al.* 2020). At Danum Valley and Maliau Basin, harp traps were erected at 60 unique trapping positions, whilst at SAFE, the traps were erected twice at 30 trapping positions, with the second deployment occurring 56 nights after the first (see Table 1 for sampling period and trapping methods used in each habitat type).

Individuals collected from the BPTs and FITs were stored in 90% alcohol and identified using Balthasar (1963), Boucomont (1914), publications describing Bornean Scarabaeinae (e.g. Ochi *et al.* 1996), and the reference collections at the Oxford University Museum of Natural History. Specimens that could not be identified to species were assigned morphospecies numbers. In Sabah, the genus *Catharsius* consists of two species *C. dayacus* and *C. renaud-pauliani*. However, females of the two species are difficult to separate, especially in live specimens. Therefore, abundance comparisons of *Catharsius* found among trap types, including the harp traps, are made at the genus level.

Data analysis

The climate in Sabah's lowland forests is relatively aseasonal (Marsh & Greer, 1992), and the majority of BPT and FIT surveys were conducted during the northern monsoon

period in Borneo (September to February). As the trapping duration of each trap type was different, all analyses were performed based on samples collected after two trap nights (i.e. 48 h) from each BPT and FIT. We calculated the sampling completeness of dung beetle communities captured in BPTs and FITs in each habitat type using *iNext* (Hsieh *et al.* 2019). We plotted the mean abundance of each species captured in BPTs and FITs on to a scatterplot to visualise the difference in species found between the two trapping methods.

To test our first hypothesis that taxonomic diversity and dung beetle community composition is significantly different between trap types and habitat types, we first visualised the community composition of each trap type and habitat type (old-growth forest, logged forest and riparian reserve) using non-metric multidimensional scaling (NMDS) with a Chao index (Chao *et al.* 2005) using *vegan* (Oksanen *et al.* 2019). We selected the number of ordination dimensions (k) according to the generated stress values that were equal to or below 0.2 (Clarke 1993). We used the *manyglm* function in *mvabund* (Wang *et al.* 2012) to test for significant differences in dung beetle communities, with the community matrix as a response variable and trap type, habitat type, and their interaction as explanatory variables. Our models were fitted with a negative binomial error distribution and simplified using backward deletion ($P > 0.05$). The significance of explanatory variables was determined using likelihood ratio tests and resampled P -values that were calculated via 999 PIT-trap iterations (Warton *et al.* 2017).

To test for significant differences in taxonomic diversity between trap types and habitat types, we calculated three taxonomic metrics for each BPT and FIT. The taxonomic metrics were as follows: (1) total abundance; (2) species richness; and (3) Shannon's diversity. We built generalised linear mixed effects models (GLMM) using a negative binomial error distribution for total abundance and Poisson error distribution for species richness, and linear mixed effects models (LME) for Shannon's diversity. GLMM and LME models were built using *lme4* (Bates *et al.* 2015) and included trap type, habitat type and their interaction as fixed effects, and site (i.e. each unique site within each locality; see Table S1) as a random effect.

To test that the functional diversity of communities between trap types and habitat types would be significantly different, we calculated three functional metrics for each BPT and FIT: (1) Functional richness (FRic), which is the amount of functional space filled by species in a community; (2) Functional evenness (FEve), which represents the evenness of abundance distributions in a functional space (between 0 and 1, with 1 representing high FEve) and; (3) Functional dispersion (FDis), which is a distance-based metric that indicates functional dissimilarity in the functional trait space (Mason *et al.* 2005; Laliberté & Legendre 2010). Functional diversity metrics were calculated using FD (Laliberté & Legendre 2010) and were based on three functional traits: (1) nesting method (tunnellers, rollers and dwellers); (2) body length (small: <10 mm; medium: 10–20 mm; and large: >20 mm); and (3) diel activity (diurnal, nocturnal) (see Slade *et al.* 2007, 2011; Gray *et al.* 2014). We transformed these categorical traits into continuous variables by calculating Gower's distance and running a

principal coordinates analysis (PCoA). We used the first four PCoA axes to calculate our four functional metrics (Villéger *et al.* 2008).

We then built LME models with each functional metric as a response variable to test for significant differences between trap types and habitat types. Data on the three functional traits of nesting method, body size and diel activity were also visualised on the NMDS plot. LME models were built using *lme4* (Bates *et al.* 2015) and included trap type, habitat type and their interaction as fixed effects, and site as a random effect. All models were simplified using backward deletion ($P > 0.05$). The significance of fixed effects (including Habitat \times Trap) for GLMM models was tested with Type II Wald Chi-square tests using the *Anova* function in *car* (Fox & Weisberg 2019), while the significance of fixed effects for LME models was tested with Type II tests via Satterthwaite's degrees of freedom method in *lmerTest* (Kuznetsova *et al.* 2017). For all models, we obtained the least-squares means using *emmeans* (Lenth 2021) and plotted them to visualise differences in the response variables among trap and habitat types.

To account for the unbalanced number of samples across trap and habitat types, we generated five randomised data sets, where each data set is comprised of 50 randomly selected samples (with replacement) from each trap and habitat type. We then perform the above analyses on the community composition, taxonomic diversity and observed functional diversity for each randomised dataset and compared the results with the original dataset.

To determine whether there were more taxonomically and functionally similar communities than expected by chance in different trap and habitat types, we compared the standardised effect sizes (SES) of species richness, Shannon's diversity and the three functional metrics. SES was defined as follows: $[(observed - mean\ expected)/standard\ deviation\ of\ expected]$. We calculated expected species richness and Shannon's diversity from 999 bootstrap replications using *iNext* (Hsieh *et al.* 2019). We calculated expected functional metrics from 999 random communities generated from observed communities of each trap, and we used an independent swap algorithm in *picante* (Kembel *et al.* 2010) to maintain patterns of species richness. We then performed one-sample t-tests to determine whether each metrics' SES was significantly different from zero.

To address our second hypothesis, we compared the abundance of *Catharsius* species captured among BPTs, FITs and harp traps across all habitat types using a generalised linear model (GLM). As the trapping duration of each trap type was different, we included the number of trapping days as a fixed effect in our GLM. We then obtained and visualised the least-squares means of the abundance of captured *Catharsius* species in each trap type using *emmeans* (Lenth 2021). All statistical analyses were carried out in R version 4.1 (R Core Team 2021).

RESULTS

In total, 66,717 individuals and 128 dung beetle species were collected, of which 96 species were found in BPTs and 99 species in FITs (Table S1).

Sampling completeness was >99% for dung beetle communities captured in both BPTs and FITs across all habitat types (Fig. S3). We found similar trends in the community composition, taxonomic diversity and observed functional diversity between the original and randomised data sets (Figs. S5–S11), indicating that difference in sample sizes was not driving any differences found. Hence, we report the following results from our analyses of the original data set.

In line with our first hypothesis, NMDS ordination plots (non-metric fit $R^2 = 0.973$, linear fit $R^2 = 0.853$ and stress = 0.164 with $k = 3$) showed that communities attracted to BPTs and FITs across all habitat types were generally distinct from each other, except for logged forests where communities were slightly overlapping. Species that were rollers, medium to large in body size or nocturnal were more associated with BPTs, while FITs captured mostly small diurnal tunnellers and dwellers (Figs 1–2). There was a significant interaction between habitat and trap type on dung beetle communities (Habitat \times Trap: $\chi^2_{2,736} = 587.7$, $P = 0.001$), where the NMDS plots show some overlap of dung beetle communities between trap types placed in logged forests (Fig. 1).

We found a significant interaction between habitat and trap type on species abundance, richness and diversity (Habitat \times Trap: abundance: $\chi^2_{2,454.37} = 97.3$, $P < 0.001$; richness: $\chi^2_{2,675.82} = 75.4$, $P < 0.001$; diversity: $F_{2,425.4} = 9.6$, $P < 0.001$). BPTs had a higher abundance in old-growth and

logged forests, and FITs had a higher abundance, richness and diversity in riparian reserves (Figs 3a–c, S4a–c). We found that observed species richness and diversity were similar to expected. For functional diversity, we found a significant interaction between trap and habitat type on observed FRic (Habitat \times Trap: $F_{2,260.1} = 23.6$, $P < 0.001$) and observed FDis (Habitat \times Trap: $F_{2,426.9} = 4.5$, $P = 0.01$), and a significant difference in observed FEve between trap types ($F_{1,156.9} = 103.3$, $P < 0.001$). BPTs had higher observed FRic in old-growth and logged forests (Figs 3d, S4d), and higher observed FEve and FDis across all habitat types (Figs 3e–f, S4E–F). Observed FRic, FEve and FDis were lower than expected for FITs across all habitat types (Fig. S12).

The abundance of *Catharsius* species significantly differed among BPTs, FITs and harp traps, where BPTs had the highest abundance ($\chi^2_{2,949} = 5809$, $P < 0.001$, Fig. 4). There was no significant difference in the abundance of *Catharsius* species between FITs and harp traps (Fig. 4 inset).

DISCUSSION

Our study presents the first quantitative comparison of community composition, taxonomic and functional diversity of dung beetles of Southeast Asia captured using two commonly employed trapping methods (BPTs and FITs). Previous studies in Bornean tropical forests had demonstrated qualitatively

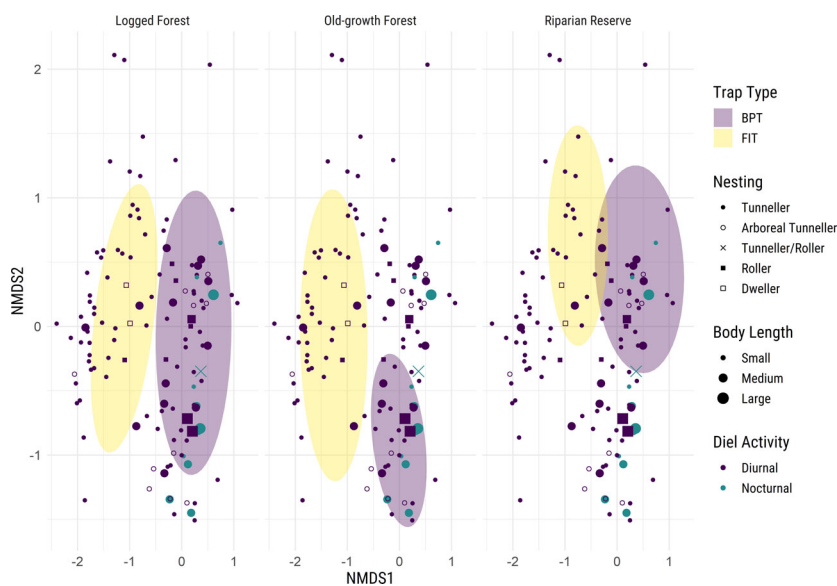


Fig. 1. First two axes from non-metric multidimensional scaling (NMDS) representing dung beetle assemblages attracted to human dung-baited pitfall traps (BPT) and flight intercept traps (FIT) across three habitat types (old-growth forest, logged forest and riparian forest). Dung beetle species are classified by nesting method, body length and diel activity. Each point represents a dung beetle species. Trap types are represented as 95% confidence interval ellipses. 3D plots of the first three axes can be viewed in Supporting Information 2.

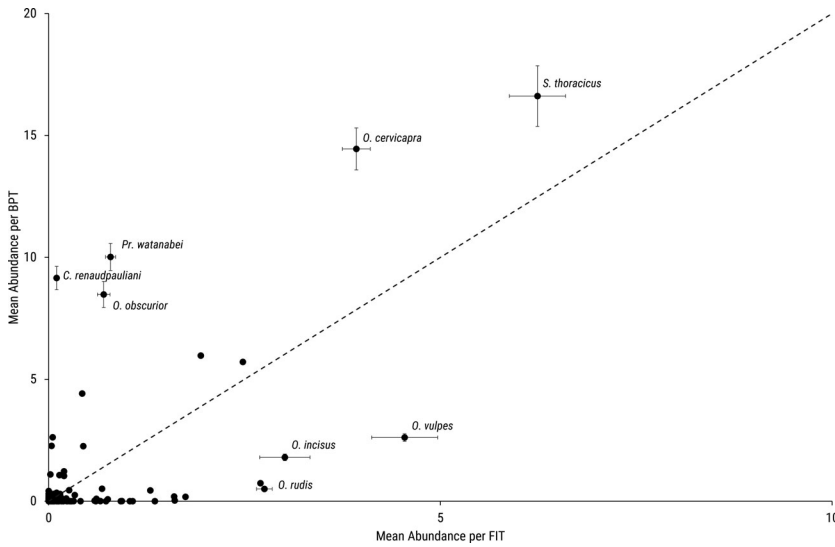


Fig. 2. Mean abundance of each species captured in human dung-baited pitfall traps (BPTs) and flight intercept traps (FITs). Species that fall on the dotted diagonal line are equally represented in both BPTs and FITs. The five most abundant species captured in BPTs and FITs are annotated, and standard error bars are shown.

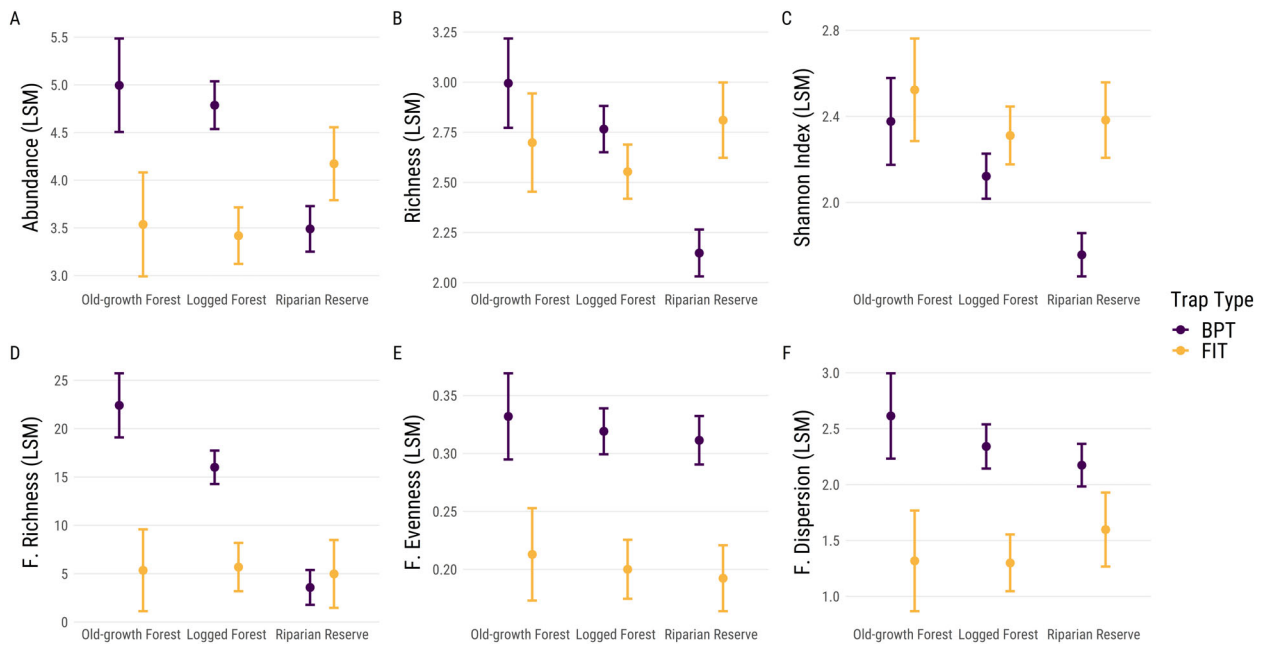


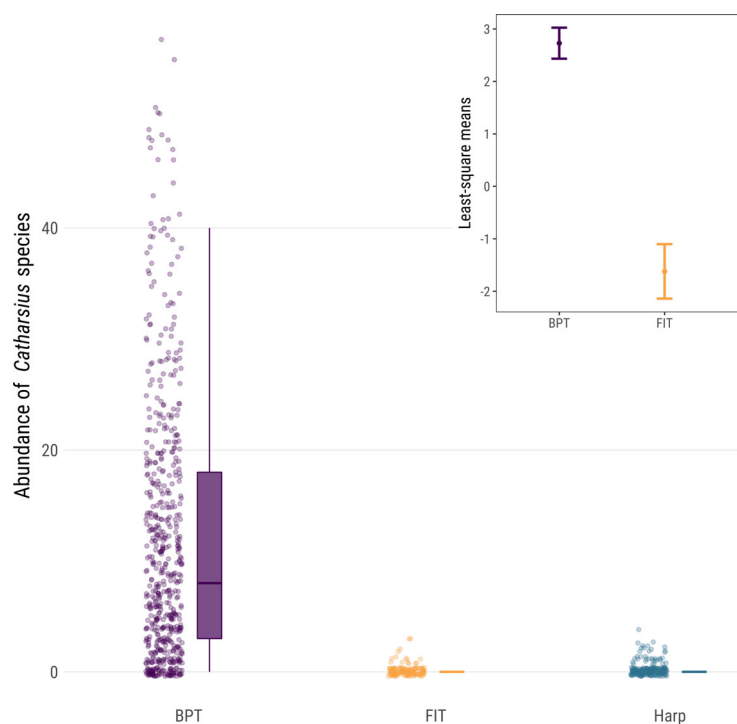
Fig. 3. Least-square means of taxonomic and functional metrics for dung beetle communities among trap (BPT: human dung-baited pitfall traps and FIT: flight intercept traps) and habitat types. Taxonomic metrics: (a) total abundance, (b) species richness, and (c) Shannon diversity. Functional metrics: (d) functional richness, (e) functional evenness, and (f) functional dispersion.

that BPTs and FITs captured complementary aspects of the dung beetle community (e.g. Davis 2000; Davis *et al.* 2001). Our quantitative analyses showed a clear difference in dung beetle communities captured between BPTs and FITs across all habitat types. Furthermore, FITs had more taxonomically diverse communities than BPTs, especially in riparian reserves, as they captured species regardless of their bait preferences, which is consistent with similar trapping comparison studies in the

Neotropics (e.g. Hyvärinen *et al.* 2006; Andrade *et al.* 2011).

Importantly, our results indicated that a wider range of functional groups, including large nocturnal tunnellers and medium to large diurnal rollers, were captured in BPTs. Correspondingly, we found that communities captured in BPTs were significantly more functionally diverse than FITs, in terms of functional richness, evenness and dispersion. Notably, BPTs are more effective at sampling the

Fig. 4. Boxplot and raincloud plot showing abundance of *Catharsius* species captured in human dung-baited pitfall traps (BPT), flight intercept traps (FITs) and harp traps. Each point in the raincloud plot represents the number of *Catharsius* individuals caught in an individual trap. Inset: Least-square means of *Catharsius* species abundance between trap types.



functional group of large, nocturnal tunnellers. This group is particularly important for ecosystem functioning, being responsible for large amounts of dung removal in both forest and oil palm (Slade *et al.* 2007, 2011; Gray *et al.* 2014). Thus, as BPTs can be used to assess communities specifically associated with particular dung types, we suggest the use of BPTs over FITs in Southeast Asian landscapes for studies linking dung beetle functional groups to the ecosystem functions associated with dung removal and burial.

However, for biodiversity surveys assessing the composition of dung beetle species across multiple habitat types (e.g. Rapid Assessment Program surveys like Alonso & Larsen 2013), a combination of baited BPTs and FITs is recommended to ensure the whole community is sampled. While BPTs are useful when answering questions about the coprophagic component of a community, they do not capture the full range of dung beetle species present in an area. Our study showed that FITs captured several small diurnal tunneller species that were rarely or never found in BPTs (Table S1). While we are uncertain of the dietary preferences of species found exclusively in FITs, this assemblage may include carrion, fruit or fungi-feeding species that are rarely found in BPTs unless baited with non-dung baits (e.g. Edwards *et al.* 2013) or specialists on non-primate dung. For example, *Anoctus*, *Cyobius* and *Haroldius* species were caught almost exclusively in FITs and are suspected to be myrmecophilous/termitophilous beetles rather than dung feeders (see Krikken & Huijbregts 2006).

In addition, we found that observed functional diversity metrics of FIT communities were lower than expected, indicating that these communities may have higher functional diversity. As our functional metrics were only based on three categorical functional traits, including additional quantitative morphological traits that correspond directly to ecosystem functioning (e.g. hind leg size and eye size; see Raine *et al.* 2018) and qualitative traits, such as dietary preferences, could provide more insights into the functional differences observed.

The lack of funding and support for taxonomy and natural history has been identified as a major impediment to the study and conservation of insects (Cardoso *et al.* 2011; Travis 2020). This is particularly true in Southeast Asia, where the natural history of Bornean dung beetles is very poorly known, and their taxonomy is still in flux. As Table S1 highlights, many species in the genus *Onthophagus* are still undescribed, and most of these undescribed species are from FITs. As these species are rarely caught in BPTs, we suspect that many of these species could be non-primate dung specialists or feed on resources other than dung. Further research into the taxonomy and natural history of dung beetles in this region is critical if we are to be able to understand and predict how they interact with, and respond to changes in, their environment.

Our results show that it is possible to incidentally capture *Catharsius* species when using harp traps in a Southeast Asian rainforest. The abundance of *Catharsius* species is likely too low for unmodified harp traps

to be an effective technique for capturing them, and they would 'incidentally' capture large numbers of bats (1021 over the course of the study period in this case). However, the capture of these large beetles in the harp traps suggests that larger dung beetles could perhaps be captured using modified FITs. One modification would be to extend the FITs higher from the ground. However, larger beetles were also found to be missing from FITs set across a vertical stratification gradient from ground to 12 m in Sabah's forest (Chung 2004), and most dung beetle species in Sabah do not appear to be attracted to BPTs more than 5 m from the ground (Davis *et al.* 1997). Thus, the height of the FIT is unlikely to be the primary cause for the low numbers caught. Instead, it may be that the large beetles are bouncing off the FITs and not being caught in the relatively small and shallow traps underneath. There are also anecdotal reports of large dung beetles such as *Oryctes rhinoceros* and *Catharsius renaudpaulinani* captured in mist nets (J. Hightower, *pers comm*, 2021).

Additional modifications such as extending the width and depth of trays underneath the FIT, or including collection bags, similar to those used in the harp traps and mist nets, may increase captures. It may also be that the black mesh commonly used in FITs is detected by the beetles, or that it is not enough to stop them flying when they hit it. Other intercept materials, such as plexiglass used in window-pane traps (Lamarre *et al.* 2012) or strings used in harp traps and mist nets, should be investigated. Modified FITs may be useful to investigate the movement ecology of beetles. To date, the study of dung beetle movements has relied on BPTs that attract the beetles with the bait, thus distorting their movement patterns (e.g. Silva & Hernández 2015; Gray *et al.* 2017b). A modified FIT, that captures beetles alive (as the harp traps do), could be an effective method for future mark–release–recapture studies, allowing us to gain accurate information about how these functionally important insects move across the landscape.

In conclusion, our study confirms that BPTs and FITs capture different subsets of the dung beetle community in the tropical forests of Borneo, with corresponding differences in the functional traits of nesting method, body size, and diel activity. We recommend using a combination of baited BPTs and FITs for studies trying to assess the full assemblage of dung beetles across habitat types. However, for biodiversity–ecosystem functioning studies that relate dung beetle communities and functional traits to ecological functions (e.g. dung removal) or more specific studies on diet preferences, the use of BFTs that specifically capture beetles associated with dung will be more appropriate. To study the movement ecology of dung beetles, modifications to FITs based upon the design of harp traps may be useful.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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AUTHOR CONTRIBUTIONS

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(supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing-original draft (supporting); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo: <http://doi.org/10.5281/zenodo.3247492>; <http://doi.org/10.5281/zenodo.3247494>; <http://doi.org/10.5281/zenodo.3832076>; and <http://doi.org/10.5281/zenodo.5530159>.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Table S1 Number and species of dung beetles collected from dung-baited pitfall traps (BPT) and flight intercept traps (FIT) across three habitat types: old-growth forests (OG), logged forests (LF) and riparian reserves (RR).

Figure S1 Trapping methods analysed in this study: a) Baited pitfall traps; b) Flight intercept traps; c) Harp traps.

Figure S2 Map of study sites (Base map by Li Yuen Chiew).

Figure S3 Species accumulation curves for dung beetle communities captured in both BPTs and FITs across all habitat types.

Figure S4 Observed taxonomic and functional metrics for dung beetle communities attracted to BPT and FIT across all habitat types.

Figure S5 Non-metric multidimensional scaling (NMDS) representing dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S6 Least square means of total abundance of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S7 Least square means of species richness of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S8 Least square means of Shannon Index of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S9 Least square means of functional richness of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S10 Least square means of functional evenness of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S11 Least square means of functional dispersion of dung beetle communities attracted to BPT and FIT across all habitat types for original and randomised datasets (R1 to R5).

Figure S12 Mean standardised effect sizes (SES) of functional metrics: a) functional richness, b) functional evenness, and c) functional dispersion in each trap and habitat type.