Riparian reserves in oil palm plantations may provide movement corridors for invertebrates

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ABSTRACT

Tropical forests are becoming increasingly fragmented through conversion to agriculture, with negative consequences for biodiversity. Movement of individuals among the remaining fragments may be critical to allow populations of forest-dependent taxa to persist. In SE Asia, conversion of forests to oil palm plantations is a particular threat. Many oil palm dominated landscapes retain forested riparian reserves along streams and rivers, but the extent to which these riparian reserves are used for movement, relative to the oil palm matrix, is poorly understood. We used mark-release-recapture methods to investigate the movement of moths and dung beetles in riparian reserves connected to a continuous forest area within oil palm in Sabah, Malaysian Borneo. Both moths and dung beetles moved more frequently through riparian reserves, orienting towards riparian forest rather than towards continuous forest or into oil palm. Only two dung beetle species were found to move regularly from forest and riparian reserves into oil palm. Neither moths nor dung beetles moved further per day within riparian reserves than within oil palm, and distances moved did not differ among species. Movement rates differed significantly among dung beetle species, but did not differ significantly between habitats. Movement behaviours were not clearly associated with life history traits of individual species, with the exception of body area, with smaller-bodied species moving at higher rates. Overall, our results suggest that riparian reserves may provide valuable movement corridors through oil palm plantations, strengthening the case for their retention and re-establishment.

Key Words: Borneo; dispersal; Dung Beetles; Moths; Tropical Forest; Malaysia

TROPICAL FORESTS ARE INCREASINGLY BEING DEGRADED, FRAGMENTED AND CONVERTED TO AGRICULTURE, WITH DETRIMENTAL EFFECTS ON BIODIVERSITY (GARDNER *ET AL.* 2009, BARLOW *ET AL.* 2010, HANSEN *ET AL.* 2013, HADDAD *ET AL.* 2015). South East Asian forests have been particularly affected, with the Indo-Malayan biodiversity hotspot experiencing pronounced biodiversity loss (Myers *et al.* 2000, Sodhi *et al.* 2004, Sodhi *et al.* 2010, Gibson *et al.* 2011, Ewers *et al.* 2015, Lewis *et al.* 2015). A major threat is the rapid expansion of areas planted with oil palm (*Elaeis guineensis* Jacq.) (Fitzherbert *et al.* 2008, Gaveau *et al.* 2014), which is now the world's primary source of vegetable oil and fat (Turner *et al.* 2008). Despite marked reductions in biodiversity in oil palm plantations (Fitzherbert *et al.* 2008, Edwards *et al.* 2014), oil palm is now a vital part of the economies of Southeast Asia, accounting for more than 5% of the gross national income in Malaysia alone (Basiron 2007, Koh & Wilcove 2007, Lucey & Hill 2012). As mosaic landscapes that incorporate both natural forest and oil palm agriculture become increasingly common, it is important to understand how best to manage and design these landscapes to support their remaining biodiversity.

Frequent features of mosaic oil palm landscapes are riparian reserves (also called buffer zones or riparian strips) (Barlow *et al.* 2010, Gray *et al.* 2014). These are linear areas of riverine forest, set aside by oil palm companies primarily to reduce run-off into streams (Sweeney *et al.* 2004). Riparian reserves improve water quality (Mayer *et al.* 2007) and benefit aquatic and forest-dependent terrestrial fauna (Ricketts 2004, Marczak *et al.* 2010, Lucey & Hill 2012). They may also serve as movement corridors linking fragments to continuous forest (Beier & Noss 1998, Tewksbury *et al.* 2002). Recently, riparian reserves have also been added as a requirement for Roundtable on Sustainable Palm Oil (RSPO) certification, with a minimum forest buffer of

30 to 100 m depending on river width, reserve placement, and perceived use (Barclay *et al.* 2017, Lucey *et al.* 2017).

As rainforest habitats become increasingly fragmented and isolated, connectivity between forest fragments may become critical to allow populations to persist (Hanski 1999, Ewers & Didham 2006, Lucey & Hill 2012). Understanding the movement ability of flora and fauna is therefore a key consideration in conservation and management strategies in human-modified landscapes. Movement ability is influenced by the behavioural responses of different species to habitat boundaries (Lucey & Hill 2012, Kallioniemi *et al.* 2014), the physical costs of movement (Bonte *et al.* 2012), and the permeability of the matrix (Ewers & Didham 2006, Scriven *et al.* 2017). Forest dependent-taxa (i.e. those that need forest to support viable populations) are the most vulnerable to fragmentation, as their restricted ranges and reluctance to cross forest to non-forest boundaries results in small, isolated populations which suffer local extinctions with little prospect of recolonization (Sodhi *et al.* 2010, Scriven *et al.* 2015). However, only a few studies have investigated the movement behaviour of tropical forest-associated taxa (Bouchard & Brooks 2004, Brouwers & Newton 2009, Lucey & Hill 2012, Khazan 2014, Scriven *et al.* 2017).

Here, we examine the movement behaviour of forest-associated moths and dung beetles in riparian reserves within oil palm landscapes in Sabah, Malaysian Borneo. Moths are a species-rich and functionally important taxon in tropical forests, acting as pollinators, herbivores, and prey for a variety of taxa (Kitching *et al.* 2000, Summerville *et al.* 2004, Slade *et al.* 2013). Tropical forest moths are relatively understudied in terms of dispersal and movement; studies in temperate agricultural landscapes show that habitat connectivity is critical for their movement (Merckx *et al.* 2010, Slade *et al.* 2013). Tropical dung beetles are good indicators of habitat disturbance (Davis *et al.* 2001, Gardner *et al.* 2008, Nichols & Gardner 2011), and there have

been several studies on their movement in topical agricultural landscapes (Arellano *et al.* 2008, Cultid-Medina *et al.* 2015, da Silva & Hernández 2015, Gray *et al.* 2016). Forest-associated species in southern Mexico were found to move through highly fragmented deciduous forest landscapes, provided there were corridors to connect the fragments (Arellano *et al.* 2008), while dung beetles in Andean agricultural landscapes showed interspecific differences in movement patterns and movement distances, associated with wing loading and habitat preferences (Cultid-Medina *et al.* 2015). Within oil palm dominated landscapes, there has been only one study which investigated 'spillover' of dung beetles across riparian reserve boundaries into oil palm, but did not document or measure movement directly (Gray *et al.* 2016).

We used mark-release-recapture methods, a common technique for the study of movement (Hanski 1999), to answer four questions. First, we asked whether forest-associated moths and dung beetles were more likely to move through riparian reserves and towards continuous forest than into or through oil palm. Second, we assessed whether individual moth and dung beetle species moved longer distances within riparian reserves than within oil palm. Third, we tested whether species moved at higher rates through riparian reserves than through the oil palm matrix. Finally, for dung beetles, we asked whether movement distances, rates, or orientation were associated with the life history traits of individual species.

METHOD

STUDY SITES – Sites were situated within the Stability of Altered Forest Ecosystems (SAFE) project landscape in South Eastern Sabah, Malaysia (4°38” N to 4°41” N, 117°31” E; Ewers *et al*. 2011; Fig. 1A). We selected three focal sites where a riparian forest reserve, embedded within an oil palm matrix, was connected to a large block of continuous virgin jungle reserve (VJR) of lowland dipterocarp rainforest. Fieldwork took place between November 2016 and April 2017, during the “wetter” part of the year (Walsh *et al.* 2013).

SPECIES SELECTION – Pilot studies identified five forest-associated moth taxa which could be trapped in sufficient numbers for a focused study: *Erebus ephesperis* Hübner, *Erebus camprimulgus* Fabricius, *Ischyja* spp., *Erebus gemmans* Guenée and *Hypoprya* spp. Guenée (Holloway 2005). Multiple *Ischyja* and *Hypoprya* species were present in our samples; living individuals could not always be identified reliably to species in the field, so individuals within each of these genera were pooled for analyses. Seven dung beetle species were selected based on previous work (Gray *et al.* 2016) to span a range of body sizes and include taxa representing the two main dung burial modes (tunnellers and rollers), and both diurnal and nocturnal species (Table S1). As only the males of *Catharsius renaudpauliani* and *Catharsius dayacus* could be distinguished reliably to species level in the field, these two species were pooled for the analysis. However, *Catharsius renaudpauliani* is the more abundant *Catharsius* species in riparian reserves at this site (Gray *et al.* 2016), and we suspect that the majority of individuals were of this species.

MOTH MOVEMENT – In each of the three study sites we established a network of baited traps, spaced by a minimum of 50 m, with a single central release point (without a trap) (Fig. 1B; individual site diagrams in Fig. S1). Six traps were placed within oil palm, six traps in the riparian reserve, and four traps in the continuous forest (VJR). We used Bugdorm© Pop-up Butterfly Bait Traps with 10 cm cone openings, baited with fermented banana and suspended so that the base was at least 1 m above the ground. During each round of sampling, traps were set on day 1 and allowed to accumulate moths for 24 hours. On day 2, individuals of the focal moths were removed from the trap sequentially and marked on the wing with a unique number using a black Sharpie™ permanent marker (Betzholtz 2002, Truxa & Fiedler 2012). Moths were transported in a ventilated, sealed container to the release point, where they were released into dense vegetation while inactive. Data on species, trap of capture, release date, and recapture data were recorded for each individual. Baits were replaced each day and any moths from non-focal species were removed from the traps without marking. On day 3, the abundance of focal moths in the traps was recorded, any new moths were marked and released from the release point, and any recaptures were recorded. The protocol for day 3 was repeated for 8 to 14 days until a minimum of 60 recapture events (across all focal taxa) had been accumulated at each site.

DUNG BEETLE MOVEMENT – In each site 17-18 live-capture baited pitfall traps were set, spaced a minimum of 50 m apart, following standard methods for dung beetle sampling (Fig. 1B; Larsen & Forsyth 2005, da Silva & Hernández 2015, Gray *et al*. 2016; individual site diagrams in Fig. S1). Six traps were placed in the oil palm matrix, seven or eight in the riparian reserve, and four in the continuous forest (VJR). Each trap consisted of a 1.5 L plastic bottle with its top removed and inverted to form a funnel (~92 mm diameter). Traps were baited with 25g of human faeces,

wrapped in muslin and suspended 5 cm above the funnel (Larsen *et al.* 2006, Slade *et al.* 2011, Marsh *et al.* 2013, Gray *et al.* 2014). Small holes were made in the base of the trap to allow rainwater to drain, and a handful of leaves was placed in the bottom to provide shelter for trapped beetles. A Styrofoam plate protected the trap from rain. Two pen types were used to mark beetles (Mitsubishi Uni Paint Marker PX-21 Fine Bullet Tip in Orange/Green/Pink, and Artline 999XF Silver Metallic Bullet Tip Marker 0.8mm). Pilot studies showed that marks on the beetles lasted for at least 7 days, and previous studies have shown no effect on beetle longevity (Bates *et al.* 2006). Each individual of the focal species was identified to species and given a unique code using a series of dots on the elytra (Larsen & Forsyth 2005, Arellano *et al.* 2008). Individuals of some species were also sexed. Traps were checked and re-baited every second day for a period of 14 days and the focal dung beetle individuals marked. After marking, the traps were closed, and bait removed to allow the beetles 24 hours to disperse before the bait was replaced the following day. Both newly-marked and recaptured beetles were recorded and released at the point of capture.

DATA ANALYSIS – Using a generalised linear model (GLM), with a quasipoisson error distribution to account for over-dispersed count data, we tested three aspects of moth movement: (1) how the number of recaptures of individuals changed with distance from the release point; (2) whether moths were recaptured more frequently in riparian forest than oil palm or continuous forest; (3) whether moths were using the reserves as corridors and so orienting to move through riparian forest towards continuous forest, as opposed to orienting towards riparian forest or into oil palm. The response variable was frequency of recapture in each trap (referred to subsequently as ‘movement frequency’) and the explanatory variables were the distance of the trap from the

release point, the habitat of recapture (riparian forest, continuous forest, oil palm), the orientation of movement (towards continuous forest, towards riparian, or into oil palm), genus/species, and all two-way interactions.

For dung beetles, we used a Chi-squared test of evenness to assess whether the distribution of movement frequencies across the three habitats differed significantly from random. We then used two GLMs with quasipoisson error distribution to test (1) whether within-habitat movement frequency was higher than between-habitat movement frequency; (2) whether dung beetles were using the reserves as corridors and so orienting to move through riparian forest towards continuous forest, versus towards riparian forest or oil palm. The response variable for these models was movement frequency and the explanatory variables were 'movement type' (within or between habitats) and genus/species for analysis (1), and movement orientation (towards continuous forest, towards riparian forest, or into oil palm) and genus/species for the analysis (2). All two-way interactions were also tested.

To assess whether individual moth and dung beetle species moved longer distances within riparian reserves than within oil palm we used a set of linear models (LM) with Gaussian error structure. Movement distance was standardised for each individual by dividing the absolute distance travelled by the number of days taken to travel that distance, a value we refer to as 'movement distance' (m/day). The explanatory variables in each test were habitat (riparian or oil palm), taxon, and their interaction.

Since movement distance is expected to increase with time, we calculated a measure of what we refer to as 'movement rate', dividing the number of recaptures of each taxon at each trap by the mean number of days between release and recapture for that taxon at that trap. To examine whether moths and dung beetles moved at higher rates through riparian corridors than

the oil palm matrix we used linear models with Gaussian error structure. The explanatory variables were habitat (riparian or oil palm), genus/species, and their interactions. However, for dung beetles, a subset of the data containing only within-habitat movements was used in this model to restrict the movements to each habitat type. To compare movement rates of male and female moths across all habitats a Mann-Whitney U test was used.

Finally, linear models with either Gaussian or Poisson error distributions (as appropriate, based on the nature of the response variable and model criticism) were used to examine the effect of dung beetle life history traits (dung burial mode, temporal activity, body area, wing loading) on orientation of movement, movement distance, and movement rate. Trait data were taken from Raine (2013), and additional data for *O. mulleri* from work by Dr. Jonathan Parrett (unpublished data). Body area (mm^2) was calculated by multiplying the body length of the beetle by the width of the thorax. Wing loading was subsequently calculated by dividing the wing area (mm^2) by the body area (mm^2). All statistical analyses were carried out in R (R Development Core R-Development-Core-Team 2017).

RESULTS

We marked a total of 1074 moths of which 404 were recaptured, giving an overall recapture frequency across all three sites and all species of 38% (Table S2). *Hypoprya* spp. had the highest recapture frequency (90%) and *Ischyja* spp. the lowest (30%; Table S2). We marked a total of 8689 beetles, of which 425 were recaptured, giving an overall recapture frequency across all three sites and all species of 4.9% (Table S3). *Onthophagus mulleri* had the highest recapture frequency (7.8%) and *Catharsius* spp. the lowest (3.7%). 29% of recaptures involved individuals

caught in the trap they had been released from. Of recaptured individuals, 37% of moths and 10% of dung beetles were recaptured within 24 hours of release, and the remainder after multiple days (2 to 12 days).

MOVEMENT ORIENTATION – Distance from release point showed no interaction with moth movement orientation (P = 0.338). However, moths were recaptured less frequently at further distances from the release point (Table 1A, Fig. 2A). Habitat had a significant effect on movement frequency (Table 1A; Fig. 2B): moths were recaptured more frequently in riparian forest (GLM coefficient for riparian = –0.555, SE = 0.242, t_{63} = –2.30, P < 0.05; Fig. 2B) and continuous forest (GLM coefficient for continuous forest = –0.771, SE = 0.281, t_{63} = –2.74, P < 0.01; Fig. 2B) than in oil palm. Moreover, orientation significantly affected movement frequency, but was species dependent (Table 1A; 2C). Overall, moths had a greater tendency to orient towards riparian forests away from continuous forest than towards oil palm or towards continuous forest (GLM coefficient for riparian = 0.784, SE = 0.254, t_{63} = 3.01, P < 0.01; Fig. 2C).

TABLE 1. Minimum adequate models testing multiple fixed effects on moth (A) and dung beetle (B) movement frequency. All two-way interactions were tested, with non-significant interactions and effects dropped based on AIC scores. * denotes P < 0.05 to 95% CI

Fixed Effects	numDF	denDF	*F*-value	*P* > F
(A) *Moths*				
Distance	1	78	156.5	< 0.001

Habitat	2	76	17.2	< 0.001
Orientation	1	75	26.1	< 0.001
Taxon	4	71	18.9	< 0.001
Taxon x Orientation	8	63	6.02	< 0.001
(B) *Dung Beetles* – Model 1				
Movement Type	1	87	28.9	< 0.001
Taxon	5	82	5.98	< 0.001
(B) *Dung Beetles* – Model 2				
Orientation	2	49	5.60	0.006*
Taxon	5	44	3.52	0.009*

Dung beetles showed non-random orientation of movement (χ^2 = 77.0, df = 10, N = 424, P < 0.001; Fig. 2C). Taxa did not differ significantly in movement type (within or between habitats) or movement orientation, but did differ significantly in terms of movement frequency (Table 1B; Fig. 3). Movement type had a significant effect on movement frequency (Table 1B): within-habitat movements were more frequent than between-habitat movements (GLM coefficient for within movement = 0.858, SE = 0.164, t_{82} = 5.24, P < 0.001; Fig. 2D). Movement orientation also had a significant effect on movement frequency (Table 1B), with dung beetles tending to orient towards riparian forest rather than towards continuous forest (GLM coefficient for riparian orientation = 0.611, SE = 0.252, t_{44} = 2.43, P < 0.001) and showing a marginal tendency to orient towards riparian forest than towards oil palm (GLM coefficient for riparian orientation = 0.911, SE = 0.459, t_{44} = 1.98, P = 0.054; Fig. 2D & Fig. 3).

MOVEMENT DISTANCE AND RATE – Moths on average moved 95.1 m/day, with a maximum movement distance of 200 m/day. Movement distances did not differ significantly for moths recaptured in riparian areas and those recaptured in oil palm (LM coefficient for habitat = –2.62, SE = 7.55, t_{364} = –0.346, P = 0.729; Fig. 4A). Moreover, movement rates did not differ significantly for moths recaptured in riparian habitat (mean 1.95 recaptures per day) versus in oil palm (mean 1.58 recaptures per day; LM coefficient for habitat = 0.350, SE = 0.366, t_{85} = 0.956, P = 0.342). There were no significant differences among moth taxa in their movement distances (Table 2A; Fig. 4A; Table S5), or movement rates (Table 2B; Fig. 4B). However, female *Erebus camprimulgus* had significantly higher movement rates than males, with 2.19 and 0.84 recaptures per day, respectively (W = 154, df = 27, P < 0.05).

TABLE 2. Minimum adequate models testing the effects of habitat and genus/species on movement distance and movement rate of moths and dung beetles. All two-way interactions were tested, with non-significant interactions dropped based on AIC scores. * denotes P < 0.05 to 95% CI.

Fixed Effects	numDF	denDF	*F*-value	*P* > F
(A) *Moths* - Distance				
Habitat	2	375	19.0	< 0.001*
Taxon	4	371	1.96	0.101
Habitat x Taxon	7	364	3.15	0.003*
(B) *Moths* - Rate				
Habitat	2	89	2.45	0.092

Taxon	4	85	1.52	0.203
(C) *Dung Beetles* - Distance				
Habitat	2	254	9.43	< 0.001*
Taxon	5	249	0.934	0.460
(D) *Dung Beetles* - Rate				
Habitat	2	33	0.123	0.894
Taxon	5	28	4.02	0.007*

Dung beetles moved 102.1 m/day on average, with a maximum movement distance of 220 m/day. Collectively, dung beetles did not move significantly further per day within riparian reserves than within oil palm (LM coefficient for riparian = 0.073, SE = 5.25, t_{249} = 0.014, P = 0.989) and the movement rates of dung beetles within riparian forest were not significantly different to those within oil palm or within continuous forest (Table 2D). Dung beetle species did not differ significantly in their movement distance within habitats (Table 2C; Fig 3 & 4C; Table S6). In contrast, movement rates differed significantly among species (Table 2D), with *Catharsius* sp. and *S. thoracicus* displaying the highest mean movement rates, 4.16 and 3.73 recaptures per day, respectively (Fig. 4D).

LIFE HISTORY TRAITS AND MOVEMENT – Dung beetle orientation of movement, movement distance, and movement rate were not significantly affected by life history traits (dung burial mode, temporal activity, body area, wing loading; Table S7). However, body area had a significant effect on movement rate, with smaller species moving at higher rates ($F_{1,47}$ = 4.33, P < 0.05; Fig. 5).

DISCUSSION

Previous studies on the dispersal and movement behaviour of insects have shown that habitat boundaries are often barriers for forest-dependent species (Gray *et al.* 2016, Scriven *et al.* 2017), suggesting that agricultural habitats bordering forest habitats may limit movement (Arellano *et al.* 2008, Merckx *et al.* 2010, Slade *et al.* 2013). Our data provide new information on the movement behaviour of insects in riparian forest corridors adjacent to an oil palm matrix for two functionally-important invertebrate groups, dung beetles and moths.

Overall, our results indicate that movement by both moth and dung beetle species in this study responded strongly to habitat type and boundaries. Both moths and dung beetles preferentially used riparian reserves to move, showing directionality of movement towards riparian forest rather than towards continuous forests or into oil palm. Only two dung beetle species, *Catharsius* spp. and *O. obscurior,* moved regularly from forest and riparian reserves into the oil palm.

MOVEMENT ORIENTATION – Moths movements were affected by habitat type and boundaries, with more frequent movements through riparian forest than into oil palm and a preference to move towards riparian forest rather than towards continuous forest or into oil palm. This supports previous studies in temperate regions showing that moths are often restricted by habitat boundaries (Betzholtz 2002, Slade *et al.* 2013). The moth species investigated are relatively specialised in terms of larval host plants and feed primarily on forest vines, shrubs and trees (Holloway 2005). The absence of these resources within plantations, along with a contrasting

vegetation structure characterised by a more open canopy, may have discouraged movement into adjacent oil palm (Barlow *et al.* 2010). Since traps were placed relatively close to the riparian reserve (between 50 – 150 m), movements of some individuals into the oil palm may represent a 'spillover effect', as has been documented for butterflies in forest-oil palm matrices (Lucey & Hill 2012, Scriven *et al.* 2017). Furthermore, plantations likely provide feeding opportunities for adult moths in the form of abundant oil palm fruits.

Dung beetle recaptures largely involved within-habitat movements within riparian reserves and continuous forest. Our results suggest that dung beetles show strong habitat specificity, consistent with a recent study showing weak spillover effects for forest-dependent dung beetles (Gray *et al.* 2016). However, our data do not reveal whether the reserves act as movement corridors between forest patches, or as habitat patches in their own right. Dung beetles may preferentially use riparian reserves because higher mammal abundance increases dung availability (Barlow *et al.* 2010). Alternatively, habitat boundaries may act as barriers to dung beetle movement (Gray *et al.* 2016), for example if beetles perceive structural changes to the vegetation that might increase exposure to predators (Barlow *et al.* 2010), or if beetles have differences in thermal tolerance that act as a filter between habitat microclimates (Roslin *et al.* 2009, Slade & Roslin 2016, Birkett *et al.* 2017). Microclimate changes between oil palm and riparian reserves are extreme, particularly during the day (Hardwick *et al.* 2015). As all species studied, except *Catharsius* spp., are diurnal (Table S1), lower thermal tolerances will limit the opportunity for dung beetles to penetrate the boundary during the day. As *Catharsius* spp. are nocturnal this may also explain their more frequent movements into the oil palm matrix (Fig. 3).

MOVEMENT DISTANCE AND RATE – For the moth species we studied, movement distances and rates differed little between riparian forest and oil palm, or between species. The absence of interspecific differences in movement may reflect the fact that all species investigated had similar body sizes and are forest-associated; similar affinities for habitat type have been shown to correlate with similar movement distances (Franzén & Nilsson 2012, Slade *et al.* 2013), while body size is a strong predictor of mobility across species in Lepidoptera (Stevens *et al.* 2010, Kuussaari *et al.* 2014). For the one species where sexes were distinguished in the field, female moths moved greater distances and at greater rates than males. This could reflect underlying differences in flight capacities (but see Margaritopoulos *et al.* 2012), or might reflect differences between sexes in foraging activity and mating behaviour.

Interestingly, we found that collectively dung beetles did not move further or more quickly in riparian reserves than in oil palm. Relatively similar movement distances and rates by the different species in their preferred habitats may explain this effect. Consistent with previous studies (da Silva & Hernández 2015), we found species-specific differences in movement rates, but these differences were not explained by the traits investigated (Table S7). For example, both the smallest (*Sisyphus*) and largest (*Catharsius*) beetle species moved large distances, suggesting that other traits, such as thermo-tolerance, may be important to this group of insect's movement ability and choices. Experiments to connect thermo-tolerance traits to the movement behaviour of dung beetles would be of interest.

LIFE HISTORY TRAITS AND SOURCE-SINK HABITAT – None of the movement metrics we measured were influenced by life history traits, except for the effect of body area on movement rate (Fig. 5). In contrast, da Silva & Hernández (2015), found that both movement distance and

rate correlated positively with dung beetle body size and wing loading, and Slade *et al*. (2013), found that wing size correlated positively with movement distance in temperate moths. These differences may be because our study focused on movement at a relatively small spatial scale (~500 m), whereas da Silva & Hernández (2015) investigated movement distances up to 900 m. Alternatively, the relatively small pool of species investigated, with few species per functional group, may have limited our ability to detect correlations between life history traits and movement metrics. The higher movement rates of smaller species may be because they require less energy to move faster and are less thermally limited than larger species. The exception of *Catharsius* may reflect their activity at night, when thermal limitations are likely to have less impact on movement rates.

IMPLICATIONS FOR LANDSCAPE MANAGEMENT – Our results suggest that the moth species we studied appear to be restricted to fragmented riparian reserves within oil palm landscapes much like the butterflies previously studied in similar forest patches (Scriven *et al.* 2017). Similarly, several dung beetle species were unable to penetrate the oil palm matrix and preferentially used the riparian reserves to move within the matrix landscape. Our findings highlight the significance of set-aside forest areas within oil palm landscapes for habitat and support the growing evidence base that contiguous riparian forest reserves are important for maintaining biodiversity for many invertebrate taxa (Barlow *et al.* 2010, Gray *et al.* 2016, Luke *et al.* 2017, Scriven *et al.* 2017).

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Data Availability: The data used in this study are archived at the Dryad Digital Repository (DOI will be added following acceptance) and are available on Zenodo through the SAFE project website (www.safeproject.net, Dataset ID: to be added following acceptance).

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FIGURE LEGENDS

FIGURE 1. (A) The upper panel highlights the location of the study area in Sabah, Northern Borneo. The lower panel displays a map of riparian reserve sites used in this study. The map is adapted from Gray *et al.* (2014). Black clumps represent the riparian sampling sites labelled RR18, RR3 and RR10 from top to bottom. The dotted black line shows the SAFE project experimental boundary. The solid grey shaded area in the top panel is the remaining logged

forest, blue lines indicate rivers, and the white area indicates the matrix of oil palm plantations. (B) Schematic representation of the general sampling design in each riparian reserve for the mark-release-recapture study for moths (top) and dung beetles (bottom). Black crosses indicate trapping points which were spaced by at least 50 m. The red star in the moth panel indicates the release point of marked moths.

FIGURE 2. Movement orientations for moths and dung beetles. (A) Moth recapture frequency at different distances from the release point. Symbols indicate species. The dotted line indicates the release point of the moths following marking, with negative values of 'Distance from release point' corresponding to movements towards the continuous forest and into oil palm, and positive values indicating movements away from the forest and into oil palm. (B) Frequency of moth movement orientations. (C) Frequency of dung beetle movement orientations. R = riparian forest, F = continuous forest (VJR), OP = oil palm matrix. Bars are shaded based on species.

FIGURE 3. Dung beetle movement networks for the three rivers (A) RR3, (B) RR10 and (C) RR18. Circles with numbers indicate pitfall traps and shading indicates habitat: dark grey = riparian forest, medium grey = continuous forest (VJR), light grey = oil palm matrix. Distances between traps are scaled to represent actual distances in the field, with a minimum of 50 m between traps. The colour of each arrow indicates the dung beetle species and its direction indicates direction of movement. Width of arrow indicates the frequency of movement with the smallest width indicating 1 movement and the widest indicating 4 movements. Dung beetles returning to the trap from which they were released are excluded.

FIGURE 4. Mean movement distance over 24 hours and mean movement rates for moths (A) and (C), and dung beetles (B) and (D). Error bars show 95% CI. Dung beetle species are ordered from left to right in increasing body area (mm^2).

FIGURE 5. Relationship between mean body area and mean movement rate for dung beetle species. Symbols represent different species. The line represents a linear model with the shaded area representing standard error either side of the line ($P < 0.05$).

FIGURES

Figure 1

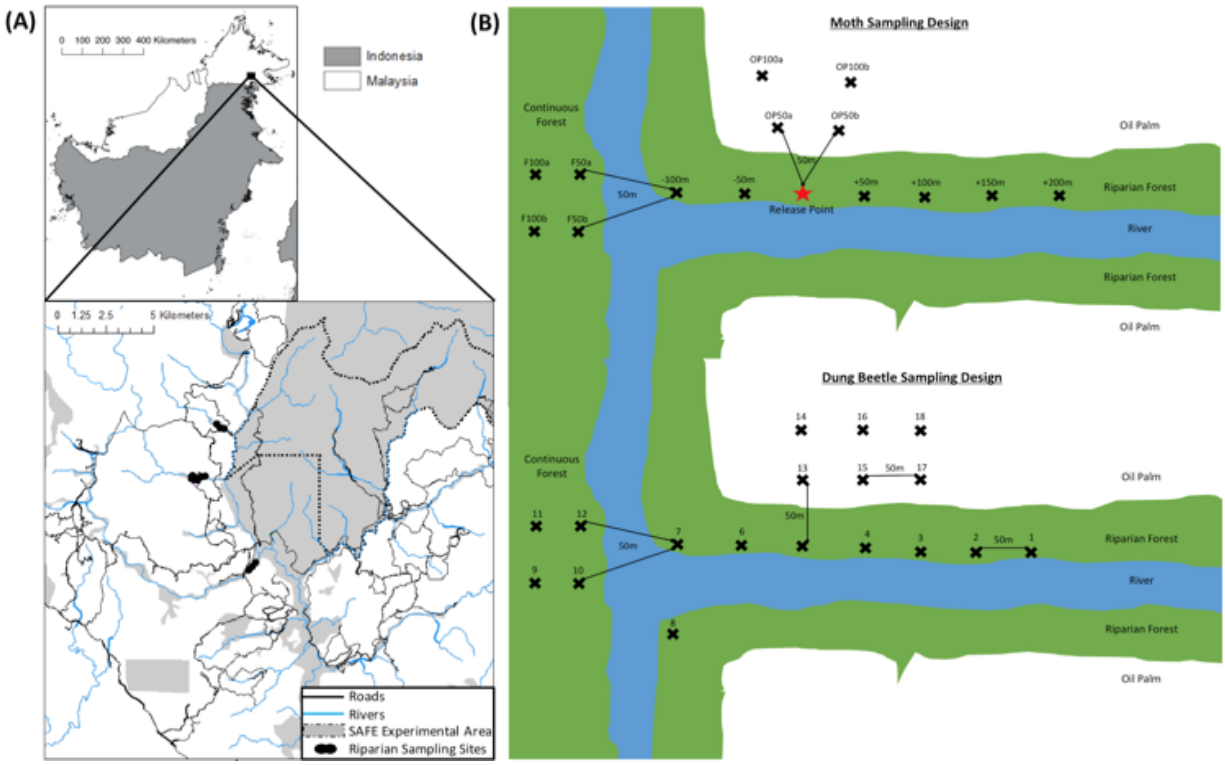


Figure 2

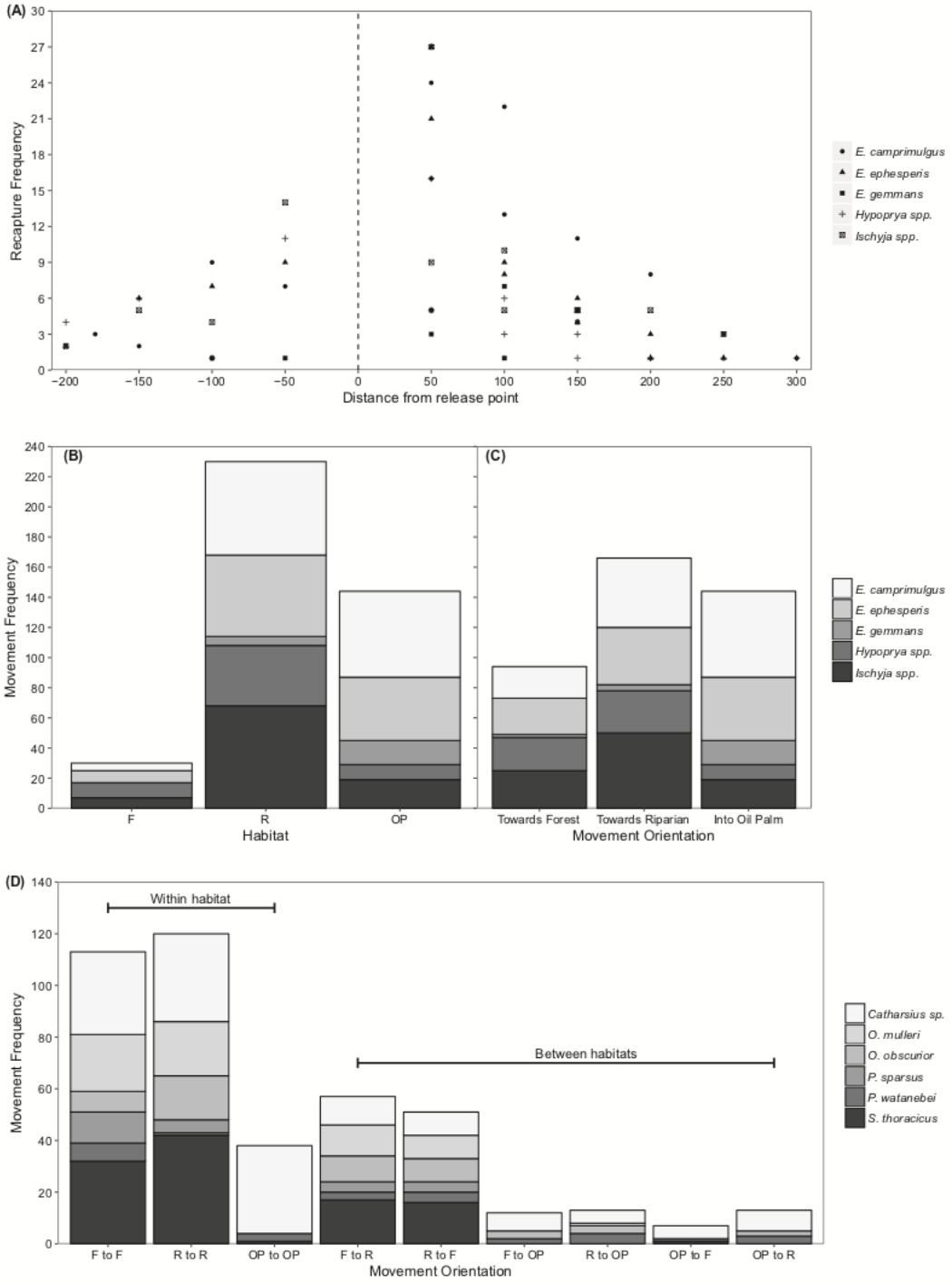

(A)
Recapture Frequency
Distance from release point
E. camprimulgus
E. ephesperis
E. gemmans
Hypoprya spp.
Ischyja spp.
(B)
(C)
Movement Frequency
F
R
OP
Habitat
Towards Forest
Towards Riparian
Into Oil Palm
Movement Orientation
(D)
Within habitat
Between habitats
Movement Frequency
F to F
R to R
OP to OP
F to R
R to F
F to OP
R to OP
OP to F
OP to R
Movement Orientation
Catharsius sp.
O. mulleri
O. obscurior
P. sparsus
P. watanebei
S. thoracicus

Figure 3

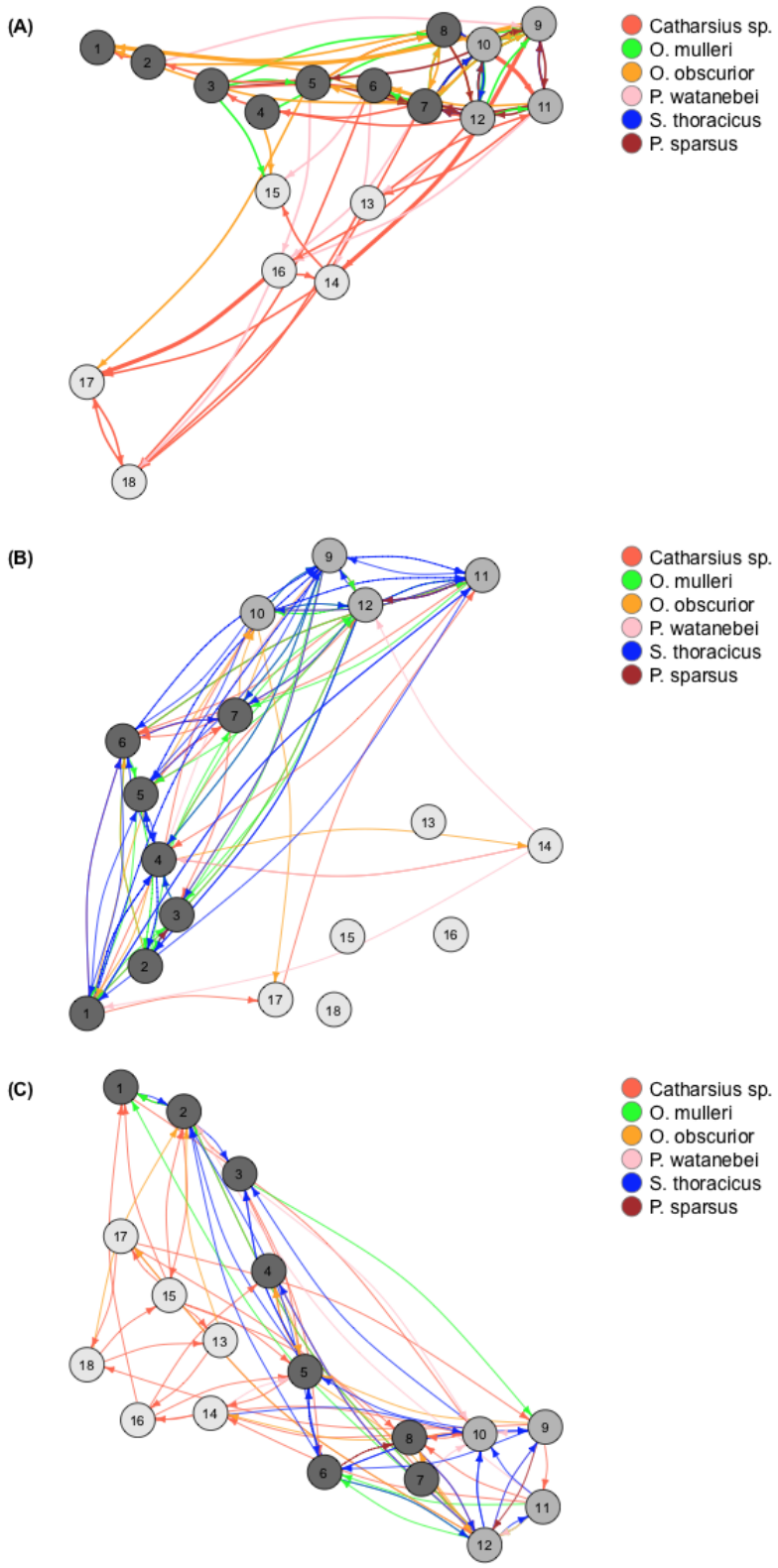

(A)
(B)
(C)
Catharsius sp.
O. mulleri
O. obscurior
P. watanebei
S. thoracicus
P. sparsus

Figure 4

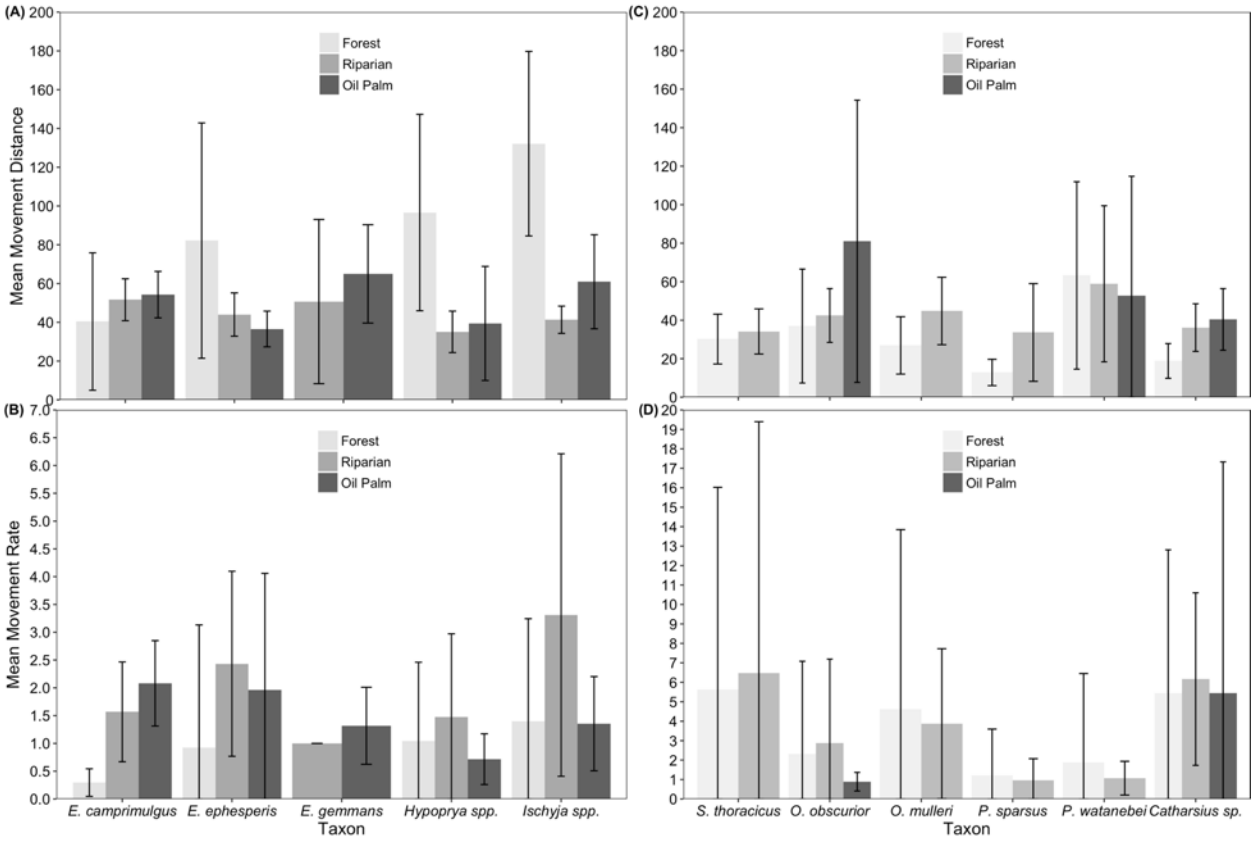
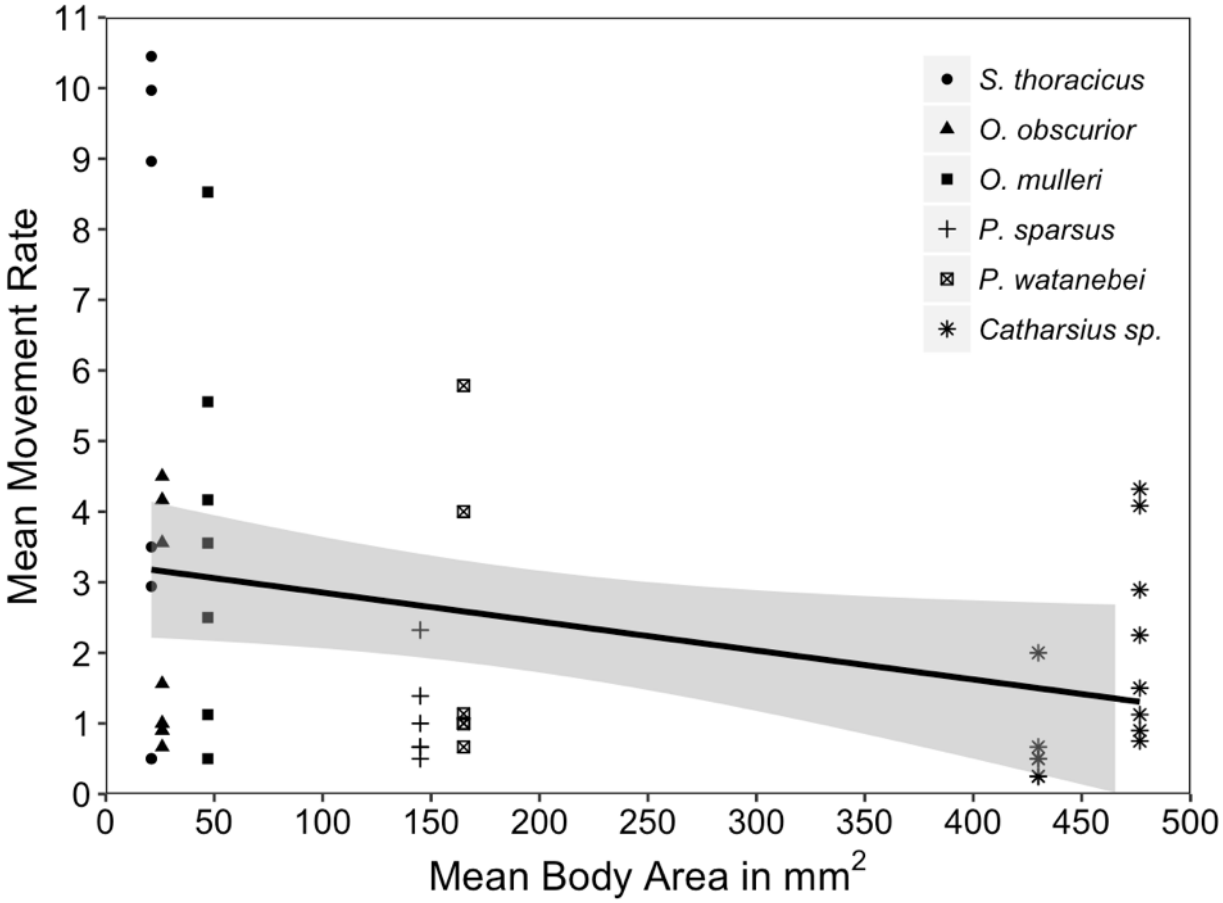

(A)
(B)
(C)
(D)
Forest
Riparian
Oil Palm
Mean Movement Distance
Mean Movement Rate
E. camprimulgus
E. ephesperis
E. gemmans
Hypoprya spp.
Ischyja spp.
S. thoracicus
O. obscurior
O. mulleri
P. sparsus
P. watanebei
Catharsius sp.
Taxon

Figure 5


Mean Movement Rate
Mean Body Area in mm^2
S. thoracicus
O. obscurior
O. mulleri
P. sparsus
P. watanebei
Catharsius sp.
0
1
2
3
4
5
6
7
8
9
10
11
0
50
100
150
200
250
300
350
400
450
500