RESEARCH ARTICLE

# Movement of forest-dependent dung beetles through riparian buffers in Bornean oil palm plantations

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## Abstract

1. Fragmentation of tropical forests is increasing globally, with negative impacts for biodiversity. In Southeast Asia, expansion of oil palm agriculture has caused widespread deforestation, forest degradation and fragmentation.

2. Persistence of forest-dependent species within these fragmented landscapes is likely to depend on the capacity of individuals to move between forest patches. In oil palm landscapes, riparian buffers along streams and rivers are potential movement corridors, but their use by moving animals is poorly studied.

3. We examined how six dung beetle species traversed riparian buffers connected to a continuous forest reserve area within an oil palm plantation in Sabah, Malaysian Borneo. We used a mark–release–recapture study and a new Bayesian Joint Species Movement Modelling (JSMM) approach, extended to a continuous capture process model.

4. Dung beetle species were fairly generalist in their habitat use, but two species showed a statistically supported preference for riparian buffer forest over oil palm, and one species showed a strong preference for forest reserve over riparian buffer, indicating the importance of forested areas within oil palm landscapes for some species.

5. A land-use change simulation indicated that the loss of riparian buffers in oil palm will result in reduced movement by forest-dependent species.

6. *Synthesis and applications*. Our results provide evidence for the use of riparian buffers in oil palm plantations for forest-dependent dung beetle species, strengthening the case for their retention, restoration and re-establishment. Furthermore,

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our study demonstrates the wider applicability of the Joint Species Movement Modelling (JSMM) framework to assess movement behaviour of species in fragmented landscapes, a vital tool for future forest and landscape management and conservation prioritisation exercises.

## 1 | INTRODUCTION

Threats to tropical forest biodiversity are unprecedented due to the unparalleled rates of forest degradation, fragmentation and conversion to agriculture (Barlow et al., 2016; Hansen et al., 2013; Newbold et al., 2014; Phalan et al., 2013). Southeast Asia has some of the highest rates of forest loss, with only ~19% of its intact forests remaining (Achard et al., 2014; Estoque et al., 2019; Lewis et al., 2015; Sodhi et al., 2010). The rapid expansion of oil palm (*Elaeis guineensis* Jacq.) has made the region the world's primary source for vegetable oil (Fitzherbert et al., 2008; Gaveau et al., 2014; Turner et al., 2008). Although biodiversity loss in oil palm plantations is well documented (Meijaard et al., 2020; Meijaard et al., 2018), oil palm is now an integral part of the economies of Southeast Asian countries accounting for 3.82% of the gross domestic product in Malaysia alone (~$896 million per year; Mahidin, 2018). Therefore, it is important to understand how best to manage and design the increasingly common mosaic landscapes that incorporate both natural forest and oil palm agriculture, in order to support the remaining biodiversity of the region.

Remaining forest patches within mosaic oil palm landscapes are often found in the form of strips of natural or restored vegetation by the side of waterways known as riparian buffers (also called riparian reserves or riparian strips; Luke et al., 2019). These riverine forest areas are primarily set aside to reduce run-off into streams (Sweeney et al., 2004) but can also improve water quality (Mayer et al., 2007) and benefit aquatic and forest-dependent terrestrial fauna (Gray et al., 2014, 2019b; Marczak et al., 2010; Ricketts, 2004). In addition, riparian buffers have the potential to serve as movement corridors between forest fragments and continuous forest (Beier & Noss, 1998; Tewksbury et al., 2002). The importance of riparian buffers in oil palm landscapes has recently resulted in their addition as a requirement for Roundtable on Sustainable Palm Oil (RSPO) certification (Barclay et al., 2017; Lucey et al., 2017). The requirement stipulates a minimum forest buffer of 5 to >200 m on each side of the river, with the minimum buffer width depending on river width, buffer placement and perceived use (Barclay et al., 2017; Lucey et al., 2017). However, the legal minimum width varies across countries; in Sabah, Malaysia it is 20 m on each side of rivers >3 m (Sabah Water Resources Enactment, 1998), but can be increased where the buffers are thought to represent important corridors for wildlife (Environment Protection Enactment, 2002).

As forest patches within oil palm landscapes become increasingly fragmented and isolated, the persistence of species within forest patches may become critically dependent on the connectivity between fragments (Ewers & Didham, 2006; Hanski, 1999; Lucey & Hill, 2012). Therefore, understanding how animal species move through the landscape separating fragments has become a key consideration in conservation and management strategies for human-modified landscapes (Doherty et al., 2021; Gray et al., 2019b). Movement ability within a fragmented landscape can be influenced by a species' behavioural responses to habitat boundaries (Jain et al., 2020; Kallioniemi et al., 2014; Lucey & Hill, 2012), the physical costs of movement (Bonte et al., 2012) and the permeability of the matrix (Ewers & Didham, 2006; Scriven et al., 2017). Furthermore, species-specific life-history traits can impact movement (Ovaskainen et al., 2019). Species most vulnerable to fragmentation are forest-dependent taxa (i.e. those that need forest to support viable populations). These species typically have restricted ranges and are reluctant to cross forest boundaries, resulting in small, isolated populations which can suffer local extinctions with little prospect of recolonisation (Scriven et al., 2015; Sodhi et al., 2010). However, despite the importance of connectivity of fragments for conservation planning, relatively few studies have investigated the movement behaviour of tropical forest-associated taxa (Bouchard & Brooks, 2004; Brouwers & Newton, 2009; Gray et al., 2019b; Khazan, 2014; Lucey & Hill, 2012; Scriven et al., 2017).

Here, we examine the movement behaviour of forest-associated dung beetles (Scarabaeidae: Scarabaeinae) in riparian buffers within oil palm landscapes in Sabah, Malaysian Borneo. Tropical dung beetles are good indicators of habitat disturbance (e.g. Davis et al., 2001; Gardner et al., 2008; Nichols & Gardner, 2011), and there have been several studies on their movement in tropical agricultural landscapes (Arellano et al., 2008; Cultid-Medina et al., 2015; Gray et al., 2016; da Silva & Hernández, 2015). 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 has documented limited 'spillover' of dung beetles across riparian buffer

boundaries into oil palm, but did not document or measure movement directly (Gray et al., 2016).

We used mark–release–recapture (MRR) methods, a common technique for the study of insect movement (Gray et al., 2019b; Hanski, 1999; Lewis et al., 1997; Slade et al., 2013) and the newly developed Joint Species Movement Modelling approach (JSMM—Ovaskainen et al., 2019). JSMM allows both species- and community-level movement parameters to be estimated simultaneously. Here, we extend the framework to account for a continuous capture process and to model different land-use change scenarios. We used these methods to ask how riparian buffers influence the movement of dung beetles within oil palm landscapes. In particular, we test the following hypotheses: (a) Dung beetles are more likely to prefer moving in riparian buffers than in oil palm plantations, and to prefer moving in continuous forest reserve to riparian forest buffers. (b) Movement ability and the rates at which dung beetles cross habitat boundaries will differ among species. (c) Conversion of forest to oil palm will limit the ability of dung beetles to move within fragmented landscapes, reducing the number of individuals captured in oil palm.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

Our three sites were situated within the Stability of Altered Forest Ecosystems (SAFE) Project landscape in south-eastern Sabah, Malaysia (4.72°N, 117.60°E; Ewers et al., 2011; Figure 1a). At each site there was a forested riparian buffer embedded within an oil palm matrix, which was connected to a larger area (2,200 ha) of continuous forest reserve consisting of lowland dipterocarp rainforest. The forest reserve is part of a >1 million ha area of protected forest (Ewers et al., 2011). The palms within each oil palm matrix surrounding the riparian buffers were approximately the same age (~8 years). Selection of the three focal sites (RR03, RR10 and RR18) was made to ensure an approximate standard configuration and structure of the landscape. Riparian buffer forest was composed of remnant old-growth and secondary forest. The forest within each site had tall trees (some >40 m), high canopy cover and similar mean riparian forest widths (48, 58 and 41 m in RR03, RR10 and RR18 respectively; Gray et al., 2019b; Williamson et al., 2020). Minor variations were inevitably found among sites in the precise configuration of landscape elements (Figure 1b–d). Fieldwork took place between November 2016 and April 2017.

### 2.2 | Species selection

Six dung beetle species were selected based on a previous study (Gray et al., 2016) to span a range of body sizes (~1–5 cm), include species representing the two main dung burial modes (tunnellers and rollers), and both diurnal and nocturnal species (Table 1). All six species were chosen as they occur commonly in forest habitat and have been observed in oil palm plantations at much lower abundances (Gray et al., 2016). In addition, the six species had high abundance in previous studies indicating they were effective candidates for a MRR study. As only the males of *Catharsius renaudpauliani* (Ochi & Kon, 1996) and *Catharsius dayacus* (Lansberge, 1886) 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 buffers in this study area (Gray et al., 2016), and we assume that the majority of individuals were of this species.

### 2.3 | Dung beetle movement

At 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 (Figure 1b–d; Gray et al., 2016; Larsen & Forsyth, 2005; da Silva & Hernández, 2015). Six traps were placed in the oil palm matrix, seven or eight in the riparian buffer and four in the forest reserve. One trap was removed from RR10 as it could not be successfully established. 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 25 g of human faeces, wrapped in muslin and suspended 5 cm above the funnel (Parrett et al., 2019). 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 (Parrett et al., 2019).

Traps were checked and re-baited every second day for a period of 14 days and all individuals of the focal dung beetle species marked. 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 0.8 mm). Pilot studies showed that marks on the beetles lasted for at least 14 days, and previous studies have shown no effect on beetle longevity (Bates et al., 2006). Each individual of the focal species was given a unique code using a series of dots on the elytra (Arellano et al., 2008; Larsen & Forsyth, 2005; Noriega & Acosta, 2011). After marking, the traps were closed and bait removed to allow the beetles 24 hr to disperse before the bait was replaced the following day. Both newly marked and recaptured beetles were recorded and released into the vegetation at the point of capture. Similar MRR methods have been used previously to assess dung beetle movement (Arellano et al., 2008; Cultid-Medina et al., 2015; da Silva & Hernández, 2015).

### 2.4 | Data and statistical analysis

All statistical analysis was conducted in R (Version 4.0.3 - R Development Core Team, 2021). We applied the JSMM framework of Ovaskainen et al. (2019) to analyse the capture–recapture datasets over the three focal sites (Figure 1b–d). As the process model
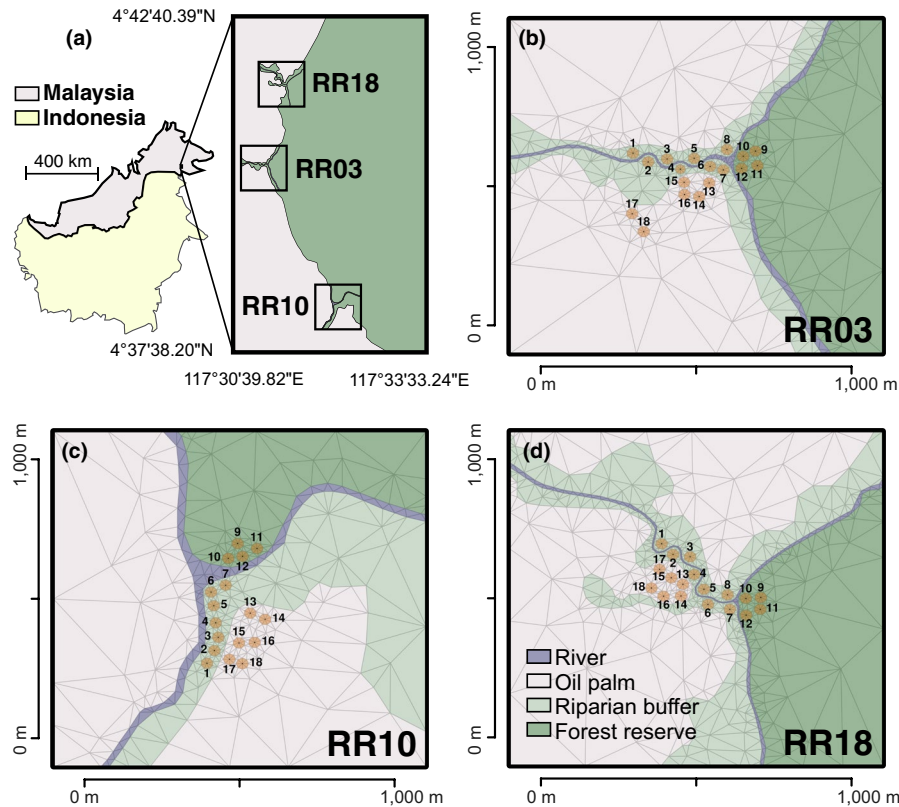
**FIGURE 1** (a) The left panel highlights the location of the study area in Sabah, Northern Borneo. The right panel displays a map of the riparian sites used in this study. (b, c and d) are maps of the three study sites RR03, RR10 and RR18, respectively, showing the position of the dung-baited pitfall traps (orange circles with radius of 20 m). The landscape is characterised by Riparian Buffer (light green), Forest Reserve (dark green), Oil Palm (beige) and River (blue) habitats. The triangulation shown in the panels was used to implement the Joint Species Distribution Modelling. Mapped distances between traps (numbered 1–18 at each site) are scaled to represent actual distances in the field, with a minimum of 50 m between traps. Traps were checked and re-baited every second day for a period of 14 days and individuals of the focal dung beetle species marked. One trap (number 8) is missing from the RR10 site

**TABLE 1** Table of species with their taxonomic authority and traits. Dung burial mode and temporal activity are from Gray et al. (2016). Species ID represents the code used in the Joint Species Movement Modelling analysis

| Species ID ($s$) | Species | Taxonomic authority | Dung burial mode | Temporal activity |
|---|---|---|---|---|
| 1 | *Catharsius* spp. | — | Tunneller | Nocturnal |
| 2 | *Onthophagus mulleri* | Lansberge, 1883 | Tunneller | Diurnal |
| 3 | *Onthophagus obscurior* | Boucomont, 1914 | Tunneller | Diurnal |
| 4 | *Proagoderus watanabei* | Ochi & Kon, 2002 | Tunneller | Diurnal |
| 5 | *Paragymnopleurus sparsus* | Sharp, 1875 | Roller | Diurnal |
| 6 | *Sisyphus thoracicus* | Sharp, 1875 | Roller | Diurnal |

we assumed the movement model of Ovaskainen (2004), that is, spatially explicit diffusion supplemented with mortality and habitat selection at edges between habitat types. For each species $s$ (Table 1), we denoted the diffusion coefficient by $D_s$ (unit $m^2$/day; measuring the movement rate) and the mortality rate by $m_s$ (unit/day). As the data were not sufficient to estimate these parameters separately for each habitat type, we assumed them to be constant over the entire study area. We set the habitat selection parameter to riparian buffers as $k_s^{RB} = 1$, and thus measured habitat selection for the oil palm ($k_s^{OP}$) and forest reserve ($k_s^{FR}$) habitats relative to

the riparian buffers. For the model, we set the river as part of the riparian buffer habitat.

The JSMM model of Ovaskainen et al. (2019) assumed an instantaneous capture process that mimics a researcher visiting a particular site and attempting to capture the marked individuals during a short time period. The present data originated from baited traps that captured individuals continuously over the 24-hr period for which the traps were kept active, and thus the assumption of instantaneous capture would be a poor approximation. We extended the model of Ovaskainen et al. (2019) by implementing the alternative

observation model of a continuous capture process, where the active traps capture individuals at the species-specific rate $q_s$ within a distance of 20 m from the centre of the trap (see Appendices S2 and S3 for details on the implementation). As traps were spaced a minimum of 50 m apart, a radius of 20 m was chosen to represent the circular area surrounding a trap that was distinct to that trap.

We combined the movement and observation parameters of each species $s$ to the vector:

$$\Theta_s = \left( \log\left(k_s^{RB}\right), \log\left(k_s^{FR}\right), \log\left(k_s^{OP}\right), \log\left(m_s\right), \log\left(D_s\right), \log\left(q_s\right) \right),$$

where the parameters were log-transformed to enable a multivariate normal model for $\Theta_s$ (Ovaskainen et al., 2019). We fitted the model with Bayesian inference, computing the likelihood of observing the movement data jointly over the three study sites. We assumed the same prior distribution as Ovaskainen et al. (2019) and followed their Markov chain Monte Carlo (MCMC) method to sample the posterior distribution. We performed 43,000 iterations with a burn-in period of 3,000 iterations and set a thinning of 10. All the model analyses were performed over saved samples every 10 iterations, to produce 4,000 posterior samples (See Appendix S3 for details about the parameter estimates and convergence diagnostics).

We evaluated model fit by generating posterior predictive data, where we released individuals in the same locations and at the same times as they were first observed in the real data, and assumed the same spatio-temporal variance in capture effort as in the real data. We compared the posterior predictive data to the real data in terms of the distribution of days from first to last capture and in terms of the distribution of the total distance moved.

To assess the influence of the habitat composition on dung beetle movement, we generated posterior predictive data for an artificial landscape RR18* (Figure 2a), which represents a modified version of the actual study site RR18 (Figure 1d). In landscape RR18*, the riparian buffer surrounding the traps was removed entirely and replaced with oil palm habitat. We simulated the release of 100 dung beetles from the trap locations in the continuous forest reserve within landscape RR18* and within the study RR18 site. We repeated the process with 100 simulated datasets. The posterior predictive data were compared between the RR18 movements and the movements in landscape RR18* (Figure 2a). We compared the proportional number of individuals caught in the two habitats in landscape RR18* (oil palm and forest reserve) with the three habitats in RR18 (oil palm, riparian buffer and forest reserve).

## 3 | RESULTS

We marked a total of 8,646 beetles, of which 355 were recaptured, giving an overall recapture frequency across all three sites and all species of 4.11% (Appendix S1: Table 1). *Onthophagus mulleri* (Lansberge, 1883) had the highest recapture frequency (6.19%) and *Proagoderus watanabei* (Ochi & Kon, 2002) the lowest (3.03%). Of the recaptures, 29% involved individuals caught in the trap from

which they had been released. Of recaptured individuals, 10% of dung beetles were recaptured within 24 hr of release, and the remainder after multiple days (2 to 12 days). Dung beetle movements varied among and within species (Figures 3 and 4), and were not obviously linked to interspecific differences in size or dung burial mode (Table 1), with small beetles such as *Sisyphus thoracicus* (Sharp, 1875) and *Onthophagus obscurior* (Boucomont, 1914) moving as far as the larger beetles. For the empirical data, the mean observed movement distance was 102.1 ± SE 5.27 m/day, with a maximum observed movement distance of 220 m/day (Appendix S1: Table 2). All species were found to move at least 100 m along the buffer, and three species moved 350 m (the largest distance within the study design). Individuals from each species captured in the forest showed movement to the furthest point along the riparian buffer, although this showed no distinct pattern, varying by species and site (Figure 4).

### 3.1 | Joint species movement modelling

Based on a visual inspection of the trace plots (Appendix S3), the MCMC sampling scheme showed satisfactory convergence, and the posterior predictive data matched generally well with the real data (Figure 5). However, it predicted fewer very long or very short movement distances (and hence more intermediate movement distances) than observed in the real data (Figure 5b; Appendix S4: Table 8). This indicates that there is some level of heterogeneity within and/or among individuals in their movement rates that is not captured by the movement model where the diffusion parameter is assumed to be species- rather than individual specific, and where it is assumed to remain constant over space and time.

Our results indicate variation among dung beetle species in their preference for difference habitats, their mortality rates, their movement ability and their capture probability (Figure 6; Appendix S3: Table 1). Four of the six species showed no preference for riparian buffers over oil palm habitats (Figure 6a), with only *O. mulleri* and *S. thoracicus* showing a significant preference for riparian buffer habitat, and *Catharsius* spp. and *P. sparsus* showing a slight preference for oil palm habitat (Figure 6a). Only *S. thoracicus* showed a significant preference for forest reserve over riparian buffer, although *P. watanabei*, *Catharsius* spp. and *O. mulleri* also showed a slight preference for forest reserves (Figure 6b). The estimated mortality rates were high and consistent across species, corresponding to an average life span of *c.* 5 days across species (expected life span = 1/mortality rate), and are more likely to reflect the individuals becoming inactive or leaving the study area, or the marks rubbing off the elytra, than actual mortality (Figure 6c). Species showed similar movement rates, except *P. sparsus* which had a lower movement rate than the other species (Figure 6d). This species also had a much lower capture rate than the other species (Figure 6f).

The simulation of land-use change demonstrated similar patterns in dung beetle preference for different habitats (Figure 2b). *S. thoracicus* showed a lower capture rate in the non-release habitat following the removal of the riparian buffer, which result is in line
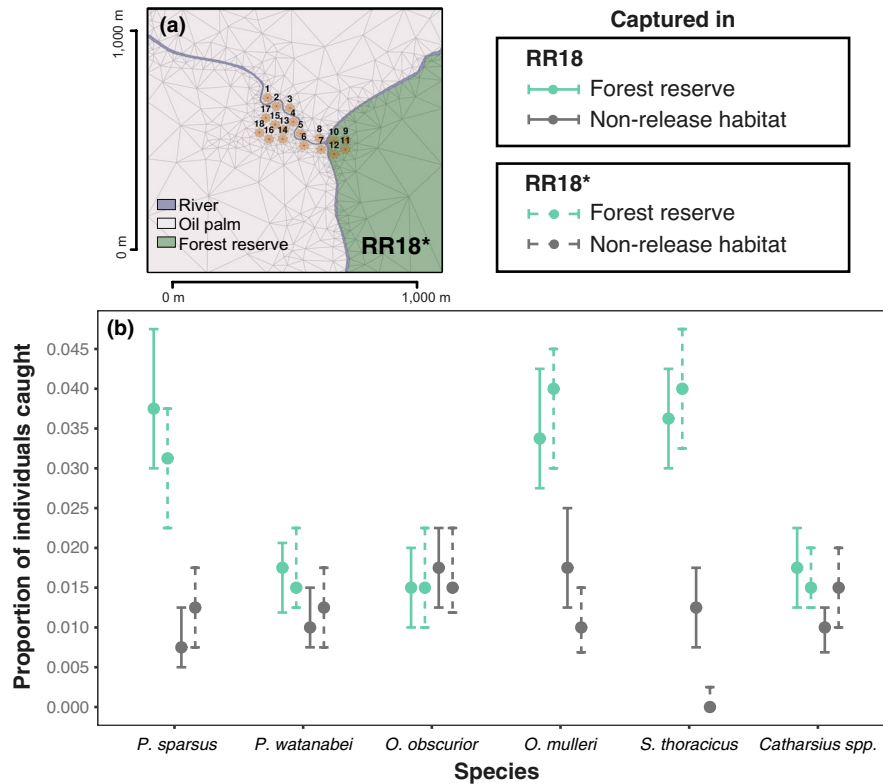
**FIGURE 2** Effect of simulated land use change (removal of riparian buffer) on the proportion of individuals caught in each habitat. (a) Shows an artificial landscape RR18* that was modified from the actual RR18 site (Figure 1d) by replacing the riparian buffer with oil palm plantation habitat. For this simulation, on the first day, 100 dung beetles were released for each species from each trap in the forest reserve (9,10,11,12) of RR18 and RR18*, and then their next capture location determined. The process was repeated to generate 100 datasets that assumed the same capture–recapture design as in the field study. The parameters for each dataset were sampled from the posterior. (b) The panel shows the proportion of individuals of each species whose last capture location was the forest reserve—same as the release (green lines), and those whose last capture location was different to the release habitat (i.e. within oil palm in RR18* or within oil palm or riparian buffer in RR18; grey lines). Points represent the posterior median and the bars the 95% credible interval. Solid and dashed lines represent the sites RR18 and RR18* respectively

with the species preference for riparian buffer over oil palm habitat (Figure 6a). Similarly, *O. mulleri* showed a lower median capture rate in the non-release habitat (Figure 2b). Only *Catharsius* spp., showed a higher median capture rate in the non-released habitat following the removal of riparian buffer but this difference was not significant (Figure 2b). None of the species displayed differences in their capture rates in the forest reserve following the simulated removal of the riparian buffer, indicating a preference for remaining in forested habitat (Figure 2b).

## 4 | DISCUSSION

Habitat boundaries are often barriers to the dispersal and movement behaviour of insects (Jain et al., 2020), especially for forest-dependent species (Gray et al., 2016, 2019b; 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 functionally important insects, dung beetles, in riparian forest buffer adjacent to an oil palm matrix.

Low recapture rates were similar to previous studies on dung beetles (5% in Mexico - Arellano et al., 2008; 18% in Colombia—Cultid-Medina et al., 2015; 3% in Brazil—da Silva & Hernández, 2015) and on other invertebrates in matrix landscapes in Sabah, Malaysia (31.6% for butterflies—Scriven et al., 2017; 33.7% for moths—Gray et al., 2019b). These low recapture rates (due to dung beetles becoming inactive, leaving the area, or because the marks rubbed off the elytra) may lead to underestimates of movement or recapture rates over longer time periods, despite species being recaptured up to 12 days later. Movement showed interspecific variation and although mean distances moved were normally less than 50 m in 24 hr, our results showed that dung beetles can move much greater maximum distances in a day: typically >100 m and up to 220 m within 24 hr (Figure 4; Appendix S1). Therefore, previous standards for dung beetle trapping which assumed daily movement distances of <100 m and so considered traps spaced 50 m apart as independent (Larsen & Forsyth, 2005), are probably not sufficient for Southeast Asian dung beetles. We recommend that traps be spaced 150–200 m apart to assure independence between traps in future studies. Similar recommendations have been suggested following studies on South American forest dung beetles showing movements
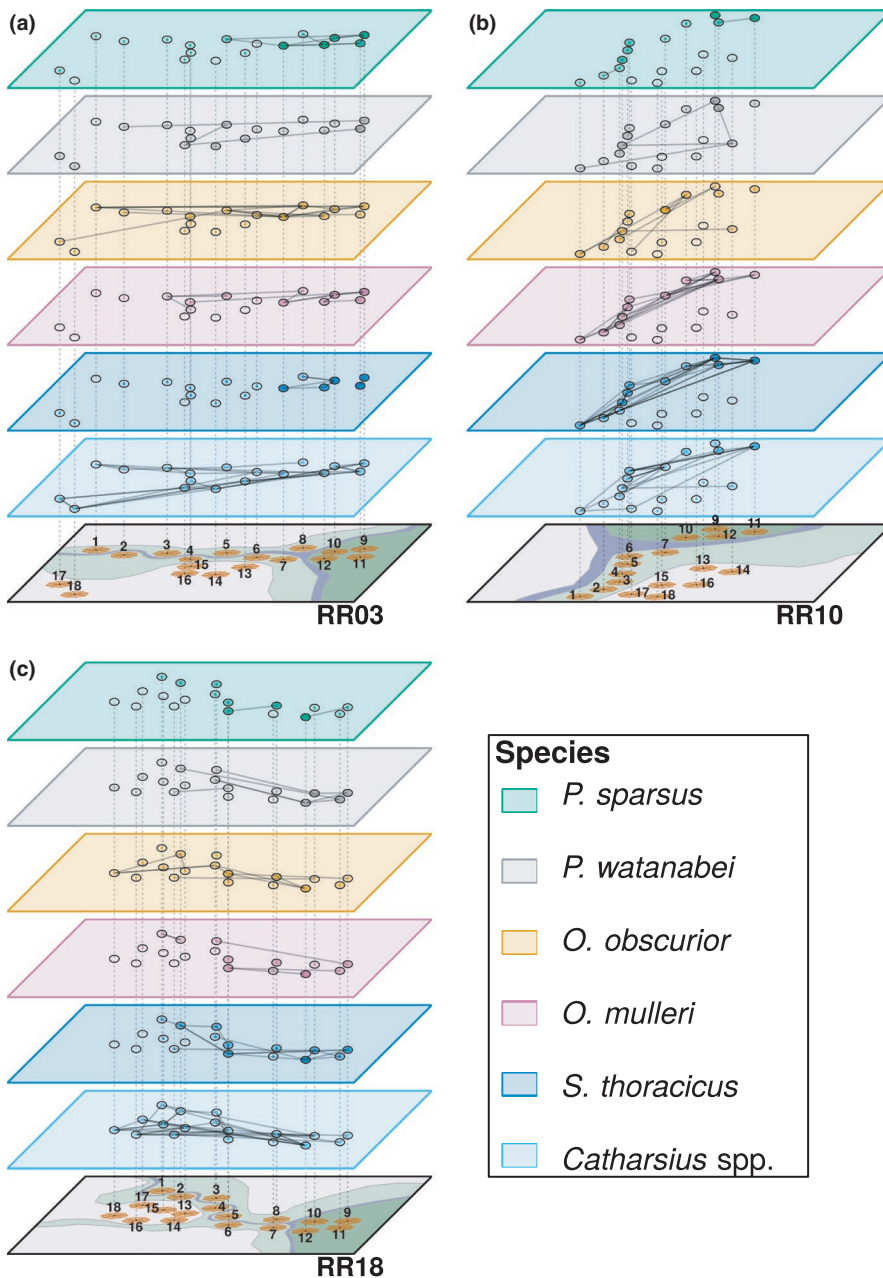
**FIGURE 3** Focal dung beetle movement trajectories for the three study sites (a) RR03, (b) RR10 and (c) RR18. Lines represent movement between a trap the dung beetle was released from and recaptured in. The intensity of the colour of each dot represents the proportion of captures that occurred in the corresponding dung-baited pitfall trap during the empirical study. Numbers indicate trap number at the site

between 20 and 500 m, depending on species and habitat (Arellano et al., 2008; Cultid-Medina et al., 2015; Noriega & Acosta, 2011; da Silva & Hernández, 2015).

Our results indicate that some dung beetle species move freely between forest areas and oil palm, while others demonstrate strong specificity to forested areas. Riparian buffers did not display a constraint on movement, with no obvious distance decay; however, there were no species- or site-specific patterns in the movement of beetles from the forest down the riparian buffer. The focal species in our study were chosen to represent a range of sizes and functional groups of dung beetles found in the area and so the patterns we see likely represent the movement patterns of dung beetles within this region. Our findings highlight the significance of set-aside forest areas within oil palm landscapes and support the growing evidence base that contiguous riparian forest buffers are important

for maintaining biodiversity for a wide range of invertebrate taxa (Barlow et al., 2010; Gray et al., 2016, 2019b; Luke et al., 2017; Scriven et al., 2017; Williamson et al., 2020).

## 4.1 | Habitat preference of dung beetle species

Dung beetle recaptures largely consisted of within-habitat movements within riparian buffers and continuous forest. Individual species differed in habitat specificity. Two species (*S. thoracicus* and *O. mulleri*) showed high and medium specificity, respectively, to both forest reserve and riparian buffer strips, and rarely crossed into the oil palm matrix. Rollers, such as *S. thoracicus*, can be particularly affected by forest conversion to oil palm, and are rarely found in oil palm plantations (Gray et al., 2016). Previous studies have shown

changes in community composition of dung beetle communities between forest, riparian buffers and oil palm (Gray et al., 2014), and weak spillover effects from riparian buffers for forest-dependent dung beetles (Gray et al., 2016). Preferential use of forest over oil palm may be because higher mammal abundance in forested areas increases dung availability (Barlow et al., 2010; Deere et al., 2018).

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 (Birkett et al., 2017; Roslin et al., 2009; Williamson et al., 2020). Edge effects
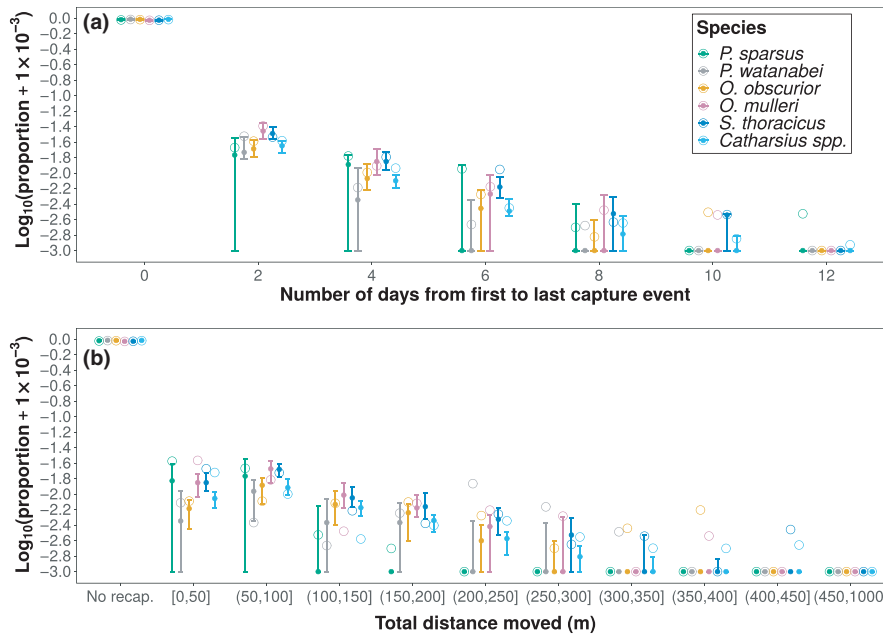
**FIGURE 5** JSMM model fit against the data used for parametrisation, showing (a) the proportion of individuals as a function of the number of days from first to last capture event, and (b) the proportion of individuals as a function of the total distance (m) moved across the three sites. The model consisted of generating 100 datasets that mimic the capture–recapture design in the field study. Each individual was released at exactly the same time and location as in the empirical data. Points and error bars represent the median and 95% credible interval respectively. The proportion of captured individuals used for parametrisation is represented by open points. The label 'Not recaptured' corresponds to the proportion of individuals that were never seen again after their first capture and release. JSMM, Joint Species Movement Modelling
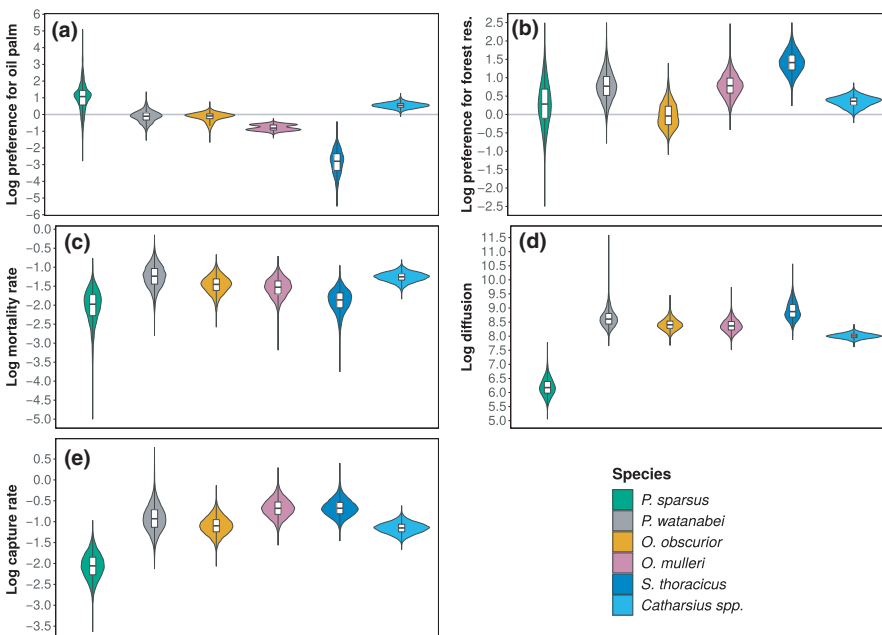


**FIGURE 6** Violin plots (95% credible intervals and posterior median) of the JSMM model parameters: (a) $k^{OP}$ (preference for oil palm habitat), (b) $k^{FR}$ (preference for forest reserve habitat), (c) $m$ (mortality rate), (d) $D$ (diffusion) and (e) $q$ (capture rate). Horizontal grey lines on a, b panels represent the set value in the model for the $k^{RB}$ (riparian buffer preference). All values are expressed in log form. For details about the corresponding estimated parameter values, see Appendix S3: Table 1. JSMM, Joint Species Movement Modelling

from increased temperatures and drought can extend up to 300 m into forests adjacent to oil palm plantations (Nunes et al., 2021), affecting mammal and insect communities. Dung beetle diversity has been found to decrease with increasing edge effects and temperature changes in riparian buffers up to around 80 m in buffer width (Williamson et al., 2020). These edge effects in both patches and

linear forest fragments are likely to impact the movement of forest-dependent dung beetles and need further investigation. The riparian buffer widths in our study were relatively large (40–60 m) and so structurally similar to forest reserves in the area. Smaller buffer widths would be hotter and drier which may result in them being less used as movement corridors (Williamson et al., 2020). Further

studies investigating how buffer width and forest quality affect movement across larger spatial and temporal scales are needed.

Microclimate changes between oil palm and riparian reserves are extreme, particularly during the day (Jucker et al., 2018; Williamson et al., 2020). As all the species studied, except *Catharsius* spp., are diurnal (Appendix S1: Table 1), lower thermal tolerances may limit the opportunity for dung beetles to penetrate the boundary during the day. In fact, riparian buffers act as microclimate refugia for many dung beetle species (Williamson et al., 2020). Interestingly, while *Catharsius* spp. showed a slight preference for forest over riparian reserve, it also showed a slight preference for moving through oil palm over riparian reserve. This suggests that this species does not rely on riparian buffers to move through the oil palm matrix. Previous studies have also found *Catharsius* spp. to be a disturbed habitat specialist, occurring in large numbers in oil palm plantations (Gray et al., 2014, 2016; Slade et al., 2014). As this species is nocturnal this may explain why they can utilise the oil palm areas, being active at night when temperatures are cooler.

## 4.2 | Effects of land-use change on dung beetle movement

Results of the land-use change simulations were highly consistent with that of the JSMM model, demonstrating the importance of forested areas within the oil palm matrix for dung beetle movement. Dung beetles that had a preference for forested habitat (riparian buffer or forest reserve) showed a reduction in their movement through oil palm following the removal of the riparian buffer, emphasising the importance of maintaining these buffer forests as habitats, avoiding further degradation and promoting their restoration, to ensure the persistence of functionally important, forest-dependent species. The effect of forest fragmentation and the expansion of agriculture as barriers to the movement of invertebrate and vertebrate taxa in human-modified landscapes has been highlighted in recent years (Ancrenaz et al., 2021; Gray et al., 2019b; Scriven et al., 2017; Seaman et al., 2019). This study adds to this growing body of evidence that supports the need for increased connectivity between forest fragments through corridors such as riparian buffers (Ancrenaz et al., 2021; Gray et al., 2019b; Mitchell et al., 2018; Mullin et al., 2020). While our study provides some of the first evidence that strips of linear forest do aid the movement of invertebrates at small spatial scales, our study would need to be extended to a larger landscape scale of inter-connecting forest patches to enable us to examine long distance movement patterns and gene flow across the landscape. Such studies will be crucial if we are to establish the effectiveness of corridors to promote connectivity across fragmented landscapes, and to optimise future land use planning.

## 4.3 | Implications for land management and future research

Our study provides the first evidence that riparian forest buffers may aid in the movement of forest-dependent dung beetle species supporting their retention and restoration in oil palm forest matrices. The buffer widths in our study were greater than those legally required in Sabah (20 m - Sabah Water Resources Enactment, 1998) and our results suggest these wider buffers are important for dung beetle movement as well as diversity (Gray et al., 2014; Williamson et al., 2020) of dung beetles in these landscapes. However, further research on the trade-offs of wider buffers for biodiversity versus the effects on oil palm yield is needed; this is a multi-faceted question which will likely vary depending on the local and landscape context (Bicknell et al., 2021; Luke et al., 2019).

Standardising the regulation of riparian buffer width across countries and regions and in different contexts, through certification schemes such as Roundtable for Sustainable Palm Oil (RSPO), is helping to highlight the importance of riparian buffers as habitats and potential corridors (Cole et al., 2020; Luke et al., 2019). Our study emphasises the need to prioritise riparian buffer forest fragments connected to contiguous forest as set-aside and suggests that restoration of buffers has the potential to act as habitat refugia and movement corridors. The importance of habitat connectivity at landscape scales is still vastly understudied despite being critical to informing land use and conservation planning (Hilty et al., 2020). The movement of animals at both local and landscape scales is likely to rely on the quality, width, length and microclimate of the corridors (Mullin et al., 2020; Seaman et al., 2019; Williamson et al., 2020) and determining how these factors interact to enable ecological connectivity in human-modified landscapes is crucial to inform landscape-level conservation strategies that are resilient to future land-use and climate change.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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## SUPPORTING INFORMATION

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