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

Ross E. J. Gray[1 2], Eleanor M. Slade[2*] and Owen T. Lewis[2]

[1] Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK.

[2] Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

[*] Corresponding author: eleanor.slade@zoo.ox.ac.uk

ABSTRACT (250)

Tropical forests are increasingly fragmented by conversion to agriculture, with negative consequences for rainforest biodiversity. Dispersal of individuals among the remaining fragments may be critical to allow populations of forest-dependent to persist. In SE Asia, conversion of forests to oil palm agriculture is a particular threat. Many oil-palm dominated landscapes retain forested riparian reserves along streams and rivers, providing potential dispersal corridors to link forest fragments. However the extent to which these riparian reserves are used for dispersal, relative to the oil palm matrix, is poorly understood. We used mark-release-recapture methods to investigate the dispersal behaviour of forest-dependent moths and dung beetles in riparian reserves within oil palm dominated landscapes in Sabah, Malaysian Borneo. We found that moth dispersal was largely unaffected by habitat type and by habitat boundaries, although dispersal distances were significantly higher within riparian reserves than elsewhere. In contrast, dung beetle dispersal responded strongly to habitat type and boundaries. Dung beetles preferentially used riparian reserves to move in and out of forest, and only two dung beetle taxa, *Catharsius* sp. and *O. obscurior,* were found to disperse from forest and riparian reserves into oil palm. Dispersal behaviours were not clearly associated with the life history traits of individual species. Our results suggest that, even if riparian reserves are unable to support viable populations of forest-dependent invertebrate species, they may provide valuable dispersal corridors through oil palm plantations, strengthening the case for their retention and re-establishment.

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

INTRODUCTION

TROPICAL FORESTS ARE INCREASINGLY BEING DEGRADED, FRAGMENTED AND CONVERTED TO AGRICULTURE, WITH SEVERE DETRIMENTAL EFFECTS ON BIODIVERSITY (Gardner *et al*. 2009, Hansen *et al*. 2013, Haddad *et al*. 2015, Barlow *et al*. 2016). 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 particular 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*. 2011), oil-palm is now a vital part of the economies of Southeast Asian, accounting for more than 5% of the gross national income in Malaysia alone (Basiron 2007, Koh &Wilcove 2007, Lucey & Hill 2012). Mosaic landscapes that incorporate both natural forest and oil palm agriculture will inevitably become the norm, and we need to understand how best to manage and design these landscapes to conserve the remaining biodiversity within them.

Common 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 to reduce run-off into streams (Sweeney *et al*. 2004), improve water quality (Mayer *et al*. 2007), and benefit aquatic and forest-dependent terrestrial fauna (Ricketts 2004, Marczak *et al*. 2010, Lucey & Hill 2012). Riparian reserves may also act as movement corridors between larger fragments and continuous forest (Beier & Noss 1998, Tewksbury *et al*. 2002). Recently, riparian reserves have also been added as a requirement for RSPO (Roundtable on Sustainable Palm Oil) 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 dispersal ability of flora and fauna is therefore a key consideration in conservation strategies. Dispersal 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). To develop effective conservation strategies, there is a pressing need to determine the dispersal potential and behaviour of forest-dependent species within fragmented landscapes (Scriven *et al*. 2017). However, only a few studies have investigated the dispersal behaviour of tropical forest-dependent taxa (Bouchard & Brooks 2004, Brouwers & Newton 2009, Lucey & Hill 2012, Khazan 2014, Scriven *et al*. 2017).

Here, we examine the dispersal behaviour of forest-dependent moths and dung beetles in riparian reserves within oil-palm landscapes in Sabah, Malaysian Borneo. Moths are an extremely 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, but studies in temperate agricultural landscapes show that habitat connectivity is critical for their dispersal

(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 their dispersal is relatively well studied in comparison to moths (Gray *et al*. 2016, Arellano, León-Cortés & Ovaskainen 2008, Cultid-Medina *et al*. 2015, Larsen & Forsyth 2005, 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, León-Cortés & Ovaskainen 2008), while dung beetles in Andean agricultural landscapes showed interspecific differences in movement patterns and movement distances, which were associated with wing loading and habitat preferences (Cultid-Medina *et al*. 2015). Within oil-palm dominated landscapes, we are aware of only one study which investigated 'spillover' of beetles across riparian reserve boundaries into oil palm, but did not document or measure dispersal directly (Gray *et al*. 2016).

We used mark-release-recapture methods, a common technique for the study of dispersal (Hanski *et al*. 2000), to answer four questions. First, we asked whether forest-dependent 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 forest-associated moth and dung beetle species moved longer distances within riparian reserves than within oil palm. Third, we tested whether forest-dependent species moved at higher rates through riparian corridors than through the oil palm matrix. Finally, for dung beetles, we asked whether dispersal 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 corridor, embedded within an oil palm matrix, was connected to a much larger block of lowland dipterocarp rainforest. Fieldwork took place between November 2016 and April 2017.

SPECIES SELECTION – Pilot studies identified five forest-associated moth taxa: *Erebus ephesperis* Hübner, *Erebus camprimulgus* Fabricius, *Ischyja* spp., *Erebus gemmans* Guenée and *Hypoprya sp*. Guenée (Holloway, 2005). Multiple *Ischyja* species were present in our samples; living individuals could not be identified reliably to species in the field, so individuals from this genus 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 *Catharsius renaudpauliani* and *C. dayacus* males could not be distinguished in the field, these two species were pooled for analysis. Previous studies have shown that most *Catharsius* individuals caught in riparian reserves are *C. renaudpauliani* (Gray *et al*. 2016)

MOTH DISPERSAL – In each site we established a network of baited traps, spaced by a minimum of 50 m, along with a single central release point (without a trap) (**Fig. 1b**). Six traps were placed within oil palm, six traps in the riparian corridor, and four traps in continuous forest. 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 wings

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. Data on species, trap identity, capture date, and release date 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 species) was recorded at each site.

DUNG BEETLE DISPERSAL – In each site a network of 17-18 live-capture baited pitfall traps was set up, spaced a minimum of 50 m apart, corresponding to standard methods in dung beetle sampling (**Fig. 1b**; Larsen & Forsyth 2005, da Silva & Hernández 2015, Gray *et al*. 2016). Six traps were placed in the oil palm matrix, seven or eight in the riparian corridor, and four in the continuous forest. Each trap consisted of a 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 (Davis *et al*. 2001, Larsen *et al*. 2006, Marsh *et al*. 2013, Gray *et al*. 2014). Small holes were made in the base of the trap to allow rain to drain out, and a handful of leaves was placed in the bottom to provide shelter to trapped beetles. A Styrofoam plate protected the trap from rain. Two pens 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 over 1 week, and previous studies have shown no effect on beetle longevity (Bates & Sadler 2004). Each individual of the focal species was identified to species and given a unique code by marking a series of dots of the elytra (Fig. S1; Larsen & Forsyth 2005, Arellano *et al*., 2008).

Some species were also sexed in the process of recording. 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 – A Chi-squared test was used to initially examine whether movement by moths and dung beetles was different to that of homogenous movement orientation in the landscape. We then set out to test our four hypotheses. Chi-squared tests and generalized linear models to examine whether moths and dung beetles oriented to move through riparian forest or towards continuous forest rather than into or along oil palm. Mann-Whitney U tests were used to compare dung beetle dispersal frequency within and between habitats and to compare dispersal rates of male and female moths. The majority of recaptures represented individuals captured 24 hours after release. Individuals recaptured after multiple days were accounted for by calculating a measure of dispersal rate by dividing the frequency of dispersal by the average number of days between marking and recapture. Generalized linear models were used to examine the effect of habitat and species on distance dispersed and dispersal rates for both moth and dung beetles. Similarly, generalized linear models were used to examine the effect of dung beetle life history traits on dispersal distance, dispersal rate, and orientation of movement. Finally, to assess the extent to which forest habitats act as sink habitats, a GLM with quasipoisson error distribution was used to assess the abundance of (unmarked) focal moths trapped in relation to distance from continuous forest. All statistical analyses were carried out in R (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%. *Hypoprya* sp. had the highest recapture frequency (90%) and *Ischyja* sp. the lowest (30%). The frequency of recapture decreased significantly with distance from the release point (Slope = –0.013, se = 0.002, $t_{47} = -7.40$, $P < 0.05$). 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%. *Onthophagus mulleri* had the highest recapture frequency (7.8%) and *Catharsius* sp. the lowest (3.7%). 29% of the recaptures involved individuals caught in the same trap they had been released from.

DISPERSAL ORIENTATION – Moth orientation was significantly different from that expected under random movement ($\chi^2 = 43.14$, df = 8, $P < 0.05$). However, there was no evidence that moths had a greater tendency to move along riparian reserves towards continuous forest rather than moving into or through oil palm, at either small or larger spatial scales (Full distance: $\chi^2 = 30$, df = 28, $P = 0.363$; First 100m: $\chi^2 = 10$, df = 8, $P = 0.265$; **Fig. a**). Dung beetles showed non-random orientation of movement ($\chi^2 = 139$, df = 40, $P < 0.05$; **Fig. 3**). Within-habitat movements were more frequent than between-habitat movements (W = 652, $P < 0.05$), and dung beetles moved more often within riparian reserves and towards continuous forest than into or through oil palm (slope = 27.567, se = 12.05, $t_{14} = 2.29$, $P < 0.05$; **Fig. 2b & 3**).

DISPERSAL DISTANCE AND RATE – The mean dispersal distance of moths was not significantly different between riparian reserves and oil palm ($P = 0.59$). However, dispersal distances were significantly higher within riparian reserves than elsewhere (slope = 1.14, se = 0.475, $t_{85} = 2.41$, $P < 0.05$). There were no significant differences among moth taxa in their dispersal distances (df = 4, dev = 19616, res.df = 374, res.dev = 947371, $P = 0.102$; **Fig. 4a**), or dispersal rates (df = 4, dev = 15.04, res.df = 85, res.dev = 213.33, $P = 0.2$; **Fig. 4b**). However, sex appeared to have a

significant effect on dispersal rate with female *Erebus camprimulgus* and male *Erebus camprimulgus* displaying the highest and lowest mean dispersal rates respectively (2.19 and 0.84, W = 154, $P < 0.05$).

Dung beetles did not disperse further in riparian reserves than in oil palm (slope = 10.59, se = 13.32, $t_{247} = 0.795$, $P = 0.427$). Dung beetle species showed no difference in their dispersal distance within habitats (df = 5, dev = 39043, res.df = 251, res.dev = 1067181, $P = 0.102$), but between habitats *P. sparsus* showed a significantly lower mean dispersal distance than all other species, resulting in 'species' having an overall significant effect on dispersal distance (df = 4, dev = 116215, res.df = 274, res.dev = 3201283, $P < 0.05$; **Fig. 3 & 4c**). Overall dispersal rates did not differ between habitats, indicating species were equally likely to move through riparian reserves as they were through oil palm (df = 2, dev = 0.832, res.df = 33, res.dev = 177.12, $P = 0.893$). However, dispersal rate differed significantly among species (df = 5, dev = 135.4, res.df = 36, res.dev = 265.8, $P < 0.05$), with *Catharsius* sp. and *S. thoracicus* displaying the highest mean dispersal rates (4.16 and 3.73 respectively; **Fig. 4d**).

LIFE HISTORY TRAITS AND SOURCE-SINK HABITAT – Dung beetle dispersal distance, dispersal rate, and orientation of movement were not significantly affected by life history traits (dung burial mode, temporal activity, body area, wing loading).

DISCUSSION

Previous studies on the dispersal behaviour of insects have shown that habitat boundaries are often barriers to dispersal for forest-dependent species (Gray *et al*. 2016, Scriven *et al.* 2017), suggesting that agricultural habitats bordering forest habitats may limit dispersal (Merckx *et al*. 2010, Arellano, León-Cortés & Ovaskainen 2008, Slade *et al*. 2013). Our data provide new

information on the dispersal behaviour of insects in riparian forest corridors adjacent to an oil palm matrix for two functionally-important invertebrate taxa, dung beetles and moths.

Overall, our results indicate that moth dispersal is largely unaffected by habitat type and by habitat boundaries, whereas dung beetle dispersal responded strongly to habitat type and boundaries. Dung beetles preferentially used riparian reserves to move in and out of forest. Only two taxa, *Catharsius* sp. and *O. obscurior,* dispersed from forest and riparian reserves into the oil palm.

DISPERSAL ORIENTATION – Moths moved equally frequently across habitat boundaries and through oil palm as they did through riparian forest. This contrasts with previous studies in temperate regions showing that moths are often reluctant to cross habitat boundaries (Betzholtz 2002, Slade *et al*., 2013). The relative structural similarity of oil palm to forest may facilitate boundary-crossing behaviour. Mature oil pam plantations are likely to provide more shelter than the agricultural landscapes investigated in other studies, and the perceived boundary between the habitats may be less pronounced. Alternatively, the moth species investigated may be forest-specialists as immature stages only: they are relatively specialised in terms of larval host plants, feeding on forest vines, shrubs and trees (Holloway, 2005). These plants are absent from oil palm plantations, where the palms themselves are the only woody plants. However, plantations may provide feeding opportunities for adult moths, in the form of abundant oil palm fruits. As traps were placed relatively near the riparian reserve, a 'spillover effect' may operate, something that has been documented for butterflies in forest-oil palm matrices (Lucey & Hill 2012, Scriven *et al*. 2017).

Dung beetles showed higher within-habitat movement and dispersed more within riparian reserves and towards forest than into or through oil palm. This is consistent with a recent study

showing week spillover effects for forest-dependent dung beetles (Gray *et al*. 2016). Dung beetles may preferentially use riparian reserves because higher mammal abundances increase dung availability (Barlow *et al*. 2010). Alternatively, habitat boundaries may act as barriers to dung beetle dispersal (Gray *et al*. 2016), for example if beetles perceive changes in microclimate or structural changes to the vegetation that might increase exposure to predators (Barlow *et al*. 2010).

DISPERSAL DISTANCE AND RATE – Moths dispersal distances and rates differed little between riparian forest and oil palm, or between species. The absence of interspecific differences in dispersal may reflect the fact that all species investigated had similar body sizes and are forest-specialists; similar affinities for habitat type have been shown to correlate with similar dispersal 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, Kuuassari *et al*., 2014).

Interestingly, we found that on average dung beetles did not disperse further or quicker in riparian reserves than in oil palm, despite showing a preference for movement within the habitat. This may be because dung beetle dispersal distance and rate is not influenced by environmental factors but rather by food or mate availability. There were, however, significant differences between species in both mean dispersal distance and mean dispersal rate, a pattern that has been seen in dispersal studies in South America (Cultid-Medina *et al*. 2015, da Silva & Hernández 2015). The species-specific differences suggest that ecological traits may contribute to the dispersal ability and behaviour of dung beetles (da Silva & Hernández 2015). The lower dispersal distances and rates of *P. sparsus* were most likely due to the fact it is a large roller: this functional group has been shown to be particularly sensitive to oil palm conversion and changes in temperature (Edwards *et al.* 2013, Gray *et al*. 2014).

LIFE HISTORY TRAITS AND SOURCE-SINK HABITAT – None of the dispersal metrics we measured were influenced by life history traits. In contrast, da Silva & Hernández (2015) found that dispersal 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 dispersal distance in temperate moths. The relatively small number of species included means that the power to detect such effects was limited in our study.

The abundance of unmarked moths captured did not decrease significantly with distance from continuous habitats, suggesting that riparian corridors are habitats in their own right for moths, rather than being sink habitats dependent on dispersal from nearby continuous forest (Tscharntke, Rand & Bianchi 2005).

IMPLICATIONS FOR LANDSCAPE MANAGEMENT – Our results suggest that the moth species we studied appear to be resilient to forest fragmentation, and may be able to survive in, or at least disperse through, oil palm mosaic landscapes. For these moths, oil palm may be less of a barrier than it is for butterflies (Scriven *et al*. 2017). In contrast, for dung beetles, we found that for several species they were unable to penetrate the oil palm matrix and preferentially used the riparian reserves to move within the matrix landscape and between forests. Our findings have implications for setaside forest within oil palm landscapes and support the growing evidence base that contiguous riparian forest corridors are essential for maintaining biodiversity for many invertebrate taxa (Barlow *et al*., 2010, Gray *et al*. 2016, Luke *et al*. 2017, Scriven *et al*. 2017).

LITERATURE CITED

ANDRESEN, E., 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography,* 26(1), pp. 87-97.

ARELLANO, L., LEÓN-CORTÉS, J.L. and OVASKAINEN, O., 2008. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (Canthon cyanellus cyanellus) in Southern Mexico. *Landscape Ecology,* 23(1), pp. 69-78.

BARLOW, J., LOUZADA, J., PARRY, L., HERNANDEZ, M., HAWES, J., PERES, C., VAZ-DE-MELLO, F. and GARDNER, T., 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. *Journal of Applied Ecology,* 47(5), pp. 1158-1158.

BARLOW, J., LENNOX, G.D., FERREIRA, J., BERENGUER, E., LEES, A.C., NALLY, R.M., THOMSON, J.R., FERRAZ, S.F.D.B., LOUZADA, J., OLIVEIRA, V.H.F., PARRY, L., RIBEIRO DE, C.S., VIEIRA, I.C.G., ARAGÃO, L.E.O.C., BEGOTTI, R.A., BRAGA, R.F., CARDOSO, T.M., JR, R.C.D.O., SOUZA JR, C.M., MOURA, N.G., NUNES, S.S., SIQUEIRA, J.V., PARDINI, R., SILVEIRA, J.M., VAZ-DE-MELLO, F.Z., VEIGA, R.C.S., VENTURIERI, A. and GARDNER, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature,* 535(7610), pp. 144-147.

BASIRON, Y., 2007. Palm oil production through sustainable plantations. *European Journal of Lipid Science and Technology,* 109(4), pp. 289-295.

BATES, A. and SADLER, J., 2004. A long-lasting method for marking beetles (Coleoptera), which does not enhance mortality. *Entomological news,* 115(1), pp. 49-51.

BEIER, P. and NOSS, R.F., 1998. Do habitat corridors provide connectivity? *Conservation Biology,* 12(6), pp. 1241-1252.

BETZHOLTZ, P., 2002. Population structure and movement patterns within an isolated and endangered population of the moth Dysauxes ancilla L.(Lepidoptera, Ctenuchidae): implications for conservation. *Journal of Insect Conservation,* 6(1), pp. 57-66.

BONTE, D., VAN DYCK, H., BULLOCK, J.M., COULON, A., DELGADO, M., GIBBS, M., LEHOUCK, V., MATTHYSEN, E., MUSTIN, K. and SAASTAMOINEN, M., 2012. Costs of dispersal. *Biological Reviews,* 87(2), pp. 290-312.

BOUCHARD, P. and BROOKS, D., 2004. Effect of vagility potential on dispersal and speciation in rainforest insects. *Journal of Evolutionary Biology,* 17(5), pp. 994-1006.

BROUWERS, N.C. and NEWTON, A.C., 2009. Movement rates of woodland invertebrates: a systematic review of empirical evidence. *Insect Conservation and Diversity,* 2(1), pp. 10-22.

BRYAN, J.E., SHEARMAN, P.L., ASNER, G.P., KNAPP, D.E., AORO, G. and LOKES, B., 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PloS one,* 8(7), pp. e69679.

CHEN, I.C., HILL, J.K., OHLEMULLER, R., ROY, D.B. and THOMAS, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science (New York, N.Y.),* 333(6045), pp. 1024-1026.

CULTID-MEDINA, C.A., MARTÍNEZ-QUINTERO, B.G., ESCOBAR, F. and DE ULLOA, P.C., 2015. Movement and population size of two dung beetle species in an Andean agricultural landscape dominated by sun-grown coffee. *Journal of Insect Conservation,* 19(4), pp. 617-626.

DA SILVA, P.G. and HERNÁNDEZ, M.I.M., 2015. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PloS one,* 10(5), pp. e0126112.

DAVIS, A.J., HOLLOWAY, J.D., HUIJBREGTS, H., KRIKKEN, J., KIRK-SPRIGGS, A.H. and SUTTON, S.L., 2001. Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology,* 38(3), pp. 593-616.

DEVICTOR, V., VAN SWAAY, C., BRERETON, T., CHAMBERLAIN, D., HELIÖLÄ, J., HERRANDO, S., JULLIARD, R., KUUSSAARI, M., LINDSTRÖM, Å. and ROY, D.B., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change,* 2(2), pp. 121-124.

DUMBRELL, A.J. and HILL, J.K., 2005. Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: Implications for sampling. *Biological Conservation,* 125(1), pp. 123-131.

EDWARDS, F., EDWARDS, D., LARSEN, T., HSU, W., BENEDICK, S., CHUNG, A., VUN KHEN, C., WILCOVE, D. and HAMER, K., 2014. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation,* 17(2), pp. 163-173.

EDWARDS, D.P., LARSEN, T.H., DOCHERTY, T.D., ANSELL, F.A., HSU, W.W., DERHE, M.A., HAMER, K.C. and WILCOVE, D.S., 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings Biological Sciences,* 278(1702), pp. 82-90.

EWERS, R.M. and DIDHAM, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological reviews,* 81(1), pp. 117-142.

EWERS, R.M., DIDHAM, R.K., FAHRIG, L., FERRAZ, G., HECTOR, A., HOLT, R.D., KAPOS, V., REYNOLDS, G., SINUN, W., SNADDON, J.L. and TURNER, E.C., 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical transactions of the Royal Society of London.Series B, Biological sciences,* 366(1582), pp. 3292-3302.

EWERS, R.M., BOYLE, M.J.W., GLEAVE, R.A., PLOWMAN, N.S., BENEDICK, S., BERNARD, H., BISHOP, T.R., BAKHTIAR, E.Y., CHEY, V.K., CHUNG, A.Y.C., DAVIES, R.G., EDWARDS, D.P., EGGLETON, P., FAYLE, T.M., HARDWICK, S.R., HOMATHEVI, R., KITCHING, R.L., KHOO, M.S., LUKE, S.H., MARCH, J.J., NILUS, R., PFEIFER, M., RAO, S.V., SHARP, A.C., SNADDON, J.L., STORK, N.E., STRUEBIG, M.J., WEARN, O.R., YUSAH, K.M. and TURNER, E.C., 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications,* 6, pp. 6836.

FITZHERBERT, E.B., STRUEBIG, M.J., MOREL, A., DANIELSEN, F., BRÜHL, C.A., DONALD, P.F. and PHALAN, B., 2008. How will oil palm expansion affect biodiversity? *Trends in ecology & evolution,* 23(10), pp. 538-545.

FRANZÉN, M. and NILSSON, S.G., 2012. Climate-dependent dispersal rates in metapopulations of burnet moths. *Journal of Insect Conservation,* 16(6), pp. 941-947.

GARDNER, T.A., BARLOW, J., ARAUJO, I.S., ÁVILA-PIRES, T.C., BONALDO, A.B., COSTA, J.E., ESPOSITO, M.C., FERREIRA, L.V., HAWES, J. and HERNANDEZ, M.I., 2008. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters,* 11(2), pp. 139-150.

GARDNER, T.A., BARLOW, J., CHAZDON, R., EWERS, R.M., HARVEY, C.A., PERES, C.A. and SODHI, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters,* 12(6), pp. 561-582.

GAVEAU, D.L., SLOAN, S., MOLIDENA, E., YAEN, H., SHEIL, D., ABRAM, N.K., ANCRENAZ, M., NASI, R., QUINONES, M. and WIELAARD, N., 2014. Four decades of forest persistence, clearance and logging on Borneo. *PloS one,* 9(7), pp. e101654.

GIBSON, L., LEE, T.M., KOH, L.P., BROOK, B.W., GARDNER, T.A., BARLOW, J., PERES, C.A., BRADSHAW, C.J., LAURANCE, W.F. and LOVEJOY, T.E., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature,* 478(7369), pp. 378-381.

GRAY, C., SIMMONS, B., FAYLE, T., MANN, D.J. and SLADE, E.M., 2016. Are riparian forest reserves sources of invertebrate biodiversity spillover and associated ecosystem functions in oil palm landscapes? *Biological Conservation,* 194, pp. 176-183.

GRAY, C.L., SLADE, E.M., MANN, D.J. and LEWIS, O.T., 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecology and evolution,* 4(7), pp. 1049-1060.

HADDAD, N.M., BRUDVIG, L.A., CLOBERT, J., DAVIES, K.F., GONZALEZ, A., HOLT, R.D., LOVEJOY, T.E., SEXTON, J.O., AUSTIN, M.P. and COLLINS, C.D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances,* 1(2), pp. e1500052.

HANSEN, M.C., POTAPOV, P.V., MOORE, R., HANCHER, M., TURUBANOVA, S.A., TYUKAVINA, A., THAU, D., STEHMAN, S.V., GOETZ, S.J., LOVELAND, T.R., KOMMAREDDY, A., EGOROV, A., CHINI, L., JUSTICE, C.O. and TOWNSHEND,

J.R., 2013. High-resolution global maps of 21st-century forest cover change. *Science (New York, N.Y.),* 342(6160), pp. 850-853.

HANSKI, I., 1999. *Metapopulation ecology.* Oxford University Press.

HOLLOWAY, J.D., 2015. *The Moths of Borneo, Parts 15 & 16*. Southdene Sdn Bhd, Kuala Lumpur.

KALLIONIEMI, E., ZANNESE, A., TINKER, J.E. and FRANCO, A., 2014. Inter-and intra-specific differences in butterfly behaviour at boundaries. *Insect conservation and diversity,* 7(3), pp. 232-240.

KHAZAN, E.S., 2014. Tests of biological corridor efficacy for conservation of a Neotropical giant damselfly. *Biological Conservation,* 177, pp. 117-125.

KITCHING, R., ORR, A., THALIB, L., MITCHELL, H., HOPKINS, M.S. and GRAHAM, A.W., 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology,* 37(2), pp. 284-297.

KOH, L.P. and WILCOVE, D.S., 2007. Cashing in palm oil for conservation. *Nature,* 448(7157), pp. 993-994.

KUUSSAARI, M., SAARINEN, M., KORPELA, E., PÖYRY, J. and HYVÖNEN, T., 2014. Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. *Ecology and Evolution,* 4(19), pp. 3800-3811.

LABRIÈRE, N., LAUMONIER, Y., LOCATELLI, B., VIEILLEDENT, G. and COMPTOUR, M., 2015. Ecosystem services and biodiversity in a rapidly transforming landscape in northern Borneo. *PloS one,* 10(10), pp. e0140423.

LARSEN, T.H. and FORSYTH, A., 2005. Trap Spacing and Transect Design for Dung Beetle Biodiversity Studies1. *Biotropica,* 37(2), pp. 322-325.

LARSEN, T.H., LOPERA, A. and FORSYTH, A., 2006. Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin,* 60(4), pp. 315-324.

LEWIS, S.L., EDWARDS, D.P. and GALBRAITH, D., 2015. Increasing human dominance of tropical forests. *Science (New York, N.Y.),* 349(6250), pp. 827-832.

LUCEY, J.M. and HILL, J.K., 2012. Spillover of insects from rain forest into adjacent oil palm plantations. *Biotropica,* 44(3), pp. 368-377.

LUKE, S.H., DOW, R.A., BUTLER, S., VUN KHEN, C., ALDRIDGE, D.C., FOSTER, W.A. and TURNER, E.C., 2017. The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo. *Freshwater Biology,* 62(3), pp. 491-506.

MARCZAK, L.B., SAKAMAKI, T., TURVEY, S.L., DEGUISE, I., WOOD, S.L. and RICHARDSON, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecological Applications,* 20(1), pp. 126-134.

MARGARITOPOULOS, J.T., VOUDOURIS, C.C., OLIVARES, J., SAUPHANOR, B., MAMURIS, Z., TSITSIPIS, J.A. and FRANCK, P., 2012. Dispersal ability in codling moth: Mark–release–recapture experiments and kinship analysis. *Agricultural and Forest Entomology,* 14(4), pp. 399-407.

MARSH, C.J., LOUZADA, J., BEIROZ, W. and EWERS, R.M., 2013. Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). *PLoS One,* 8(8), pp. e73147.

MAYER, P.M., REYNOLDS, S.K., MCCUTCHEN, M.D. and CANFIELD, T.J., 2007. Meta-analysis of nitrogen removal in riparian buffers. *Journal of environmental quality,* 36(4), pp. 1172-1180.

MERCKX, T., FEBER, R.E., MCLAUGHLAN, C., BOURN, N.A., PARSONS, M.S., TOWNSEND, M.C., RIORDAN, P. and MACDONALD, D.W., 2010. Shelter benefits less mobile moth species: the field-scale effect of hedgerow trees. *Agriculture, Ecosystems & Environment,* 138(3), pp. 147-151.

MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A. and KENT, J., 2000. Biodiversity hotspots for conservation priorities. *Nature,* 403(6772), pp. 853-858.

NICHOLS, E.S. and GARDNER, T.A., 2011. Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: L.W. SIMMONS and T.J. RIDSDILL-SMITH, eds, *Ecology and evolution of dung beetles.* Chichester, U.K.: John Wiley & Sons, Ltd., pp. 267-291.

NICHOLS, E., SPECTOR, S., LOUZADA, J., LARSEN, T., AMEZQUITA, S., FAVILA, M. and NETWORK, T.S.R., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation,* 141(6), pp. 1461-1474.

R DEVELOPMENT CORE TEAM., 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

REYNOLDS, G., PAYNE, J., SINUN, W., MOSIGIL, G. and WALSH, R.P., 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on

the Danum Valley region. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences,* 366(1582), pp. 3168-3176.

RICKETTS, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology,* 18(5), pp. 1262-1271.

ROSLIN, T., AVOMAA, T., LEONARD, M., LUOTO, M. and OVASKAINEN, O., 2009. Some like it hot: microclimatic variation affects the abundance and movements of a critically endangered dung beetle. *Insect Conservation and Diversity,* 2(3), pp. 232-241.

SCRIVEN, S.A., BEALE, C.M., BENEDICK, S. and HILL, J.K., 2017. Barriers to dispersal of rain forest butterflies in tropical agricultural landscapes. *Biotropica,* 49(2), pp. 206-216.

SCRIVEN, S.A., HODGSON, J.A., MCCLEAN, C.J. and HILL, J.K., 2015. Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change. *Biological Conservation,* 184, pp. 414-423.

SLADE, E.M., MERCKX, T., RIUTTA, T., BEBBER, D.P., REDHEAD, D., RIORDAN, P. and MACDONALD, D.W., 2013. Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology,* 94(7), pp. 1519-1530.

SODHI, N.S., KOH, L.P., BROOK, B.W. and NG, P.K., 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution,* 19(12), pp. 654-660.

SODHI, N.S., KOH, L.P., CLEMENTS, R., WANGER, T.C., HILL, J.K., HAMER, K.C., CLOUGH, Y., TSCHARNTKE, T., POSA, M.R.C. and LEE, T.M., 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation,* 143(10), pp. 2375-2384.

STEVENS, V.M., TURLURE, C., BAGUETTE, M.A. (2010). Meta-analysis of dispersal in butterflies. *Biol. Rev. Camb. Philos. Soc.* 85, 625-42.

SUMMERVILLE, K.S., RITTER, L.M. and CRIST, T.O., 2004. Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation,* 116(1), pp. 9-18.

SWEENEY, B.W., BOTT, T.L., JACKSON, J.K., KAPLAN, L.A., NEWBOLD, J.D., STANDLEY, L.J., HESSION, W.C. and HORWITZ, R.J., 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences of the United States of America,* 101(39), pp. 14132-14137.

TEWKSBURY, J.J., LEVEY, D.J., HADDAD, N.M., SARGENT, S., ORROCK, J.L., WELDON, A., DANIELSON, B.J., BRINKERHOFF, J., DAMSCHEN, E.I. and TOWNSEND, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America,* 99(20), pp. 12923-12926.

TRUXA, C. and FIEDLER, K., 2012. Attraction to light-from how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology,* 109(1), pp. 77.

TSCHARNTKE, T., RAND, T.A. and BIANCHI, F.J., 2005. The landscape context of trophic interactions: insect spillover across the crop—noncrop interface, *Annales Zoologici Fennici*, 43: pp. 421-432.

TURNER, E.C., SNADDON, J.L., FAYLE, T.M. and FOSTER, W.A., 2008. Oil palm research in context: identifying the need for biodiversity assessment. *PLoS One,* 3(2), pp. e1572.

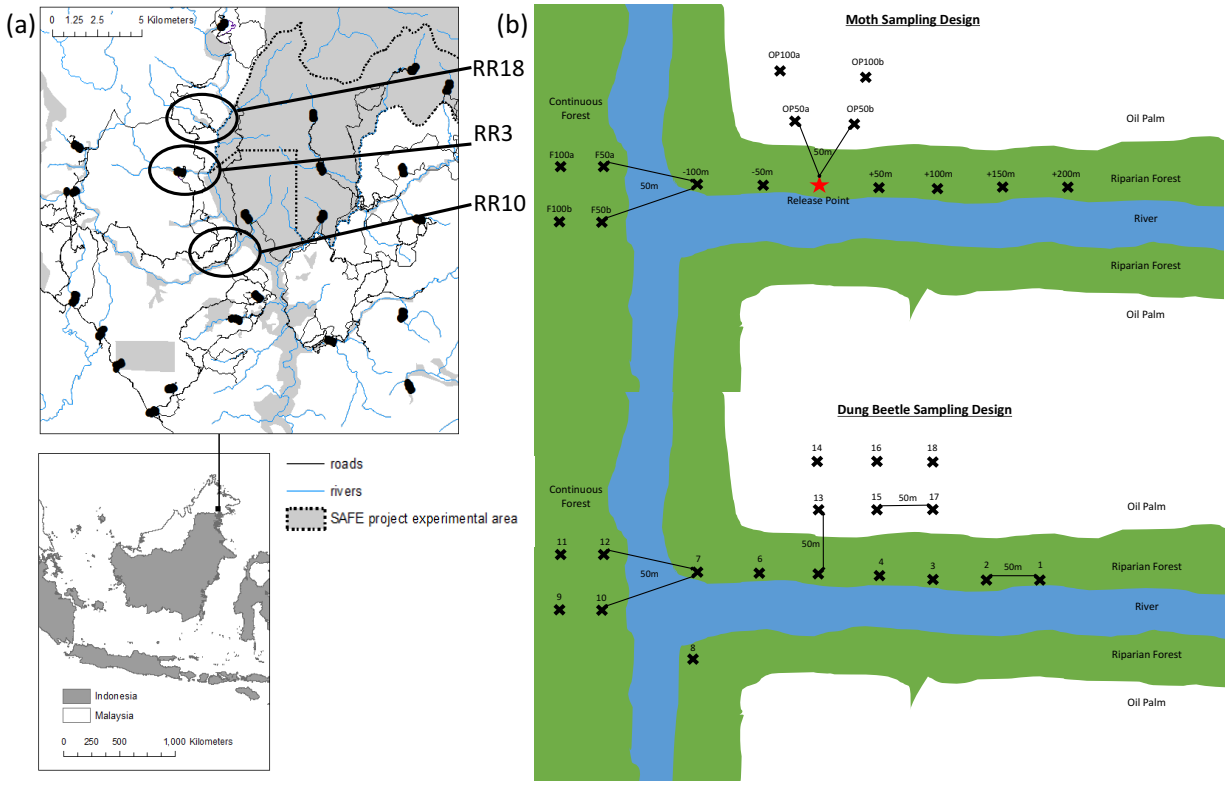

FIGURE 1. a) Map of riparian reserve sites (labelled RR3, RR10 and RR18) used in this study. Maps are adapted with permission from Gray *et al*. (2014). The dotted black line shows the SAFE project experimental boundary. The solid grey shaded area in the top panel is the remaining logged forest, blue lines indicate of rivers, and the white area indicates the matrix of oil palm plantations. The lower panel highlights the location of the study area in Sabah, Northern Borneo. 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.

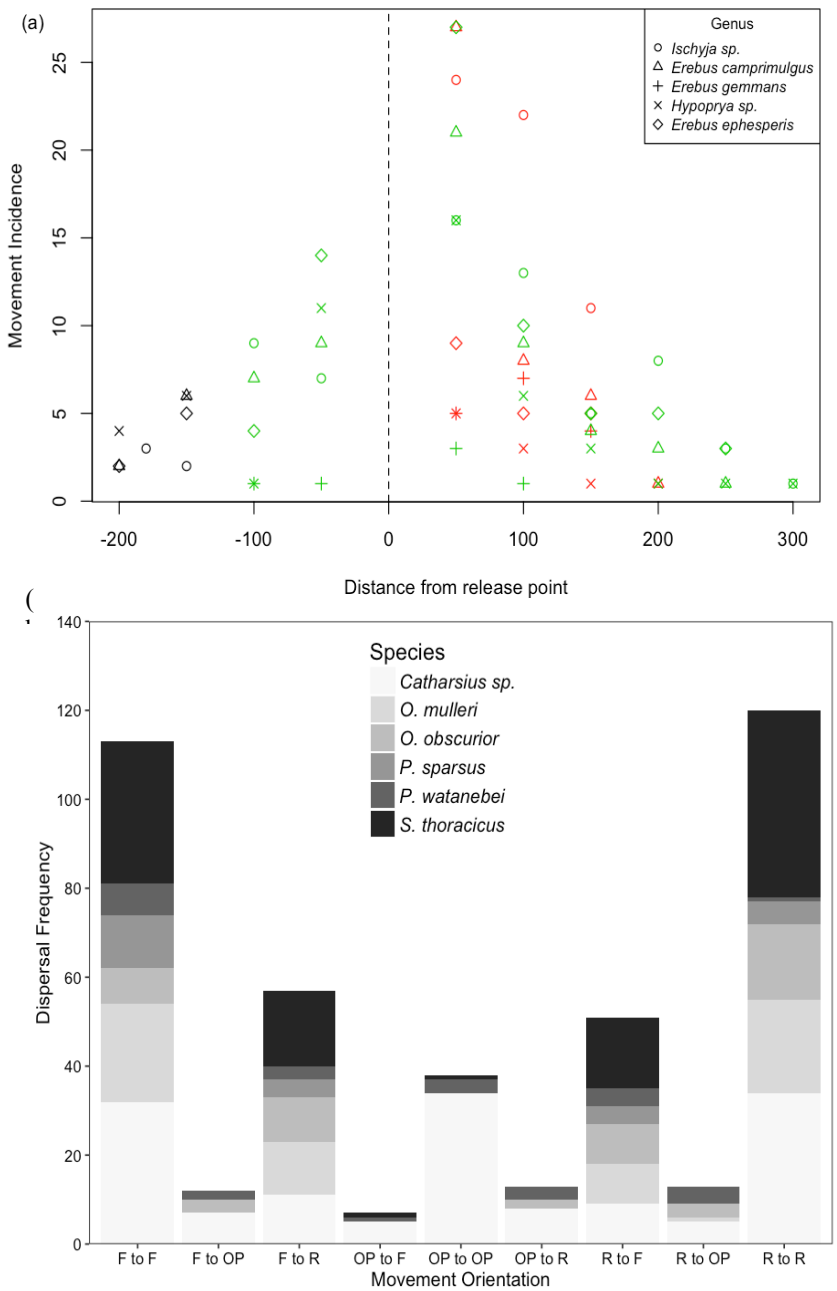

FIGURE 2. Dispersal orientations for moths and dung beetles across the three sites. a) Moth frequency of recapture at different distances from the release point. Colours indicates habitat (green is riparian forest, red is oil palm and black is continuous forest). Symbols indicate species. The dotted line indicates the release point of the moths following marking, with negative values of 'Distance from release point' corresponding to movements towards the forest, and positive values indicating movements away from the forest. b) Frequency of dung beetle dispersal orientations. R = riparian forest, F = continuous forest and OP = oil palm matrix. Bars are proportional and shaded based on species.

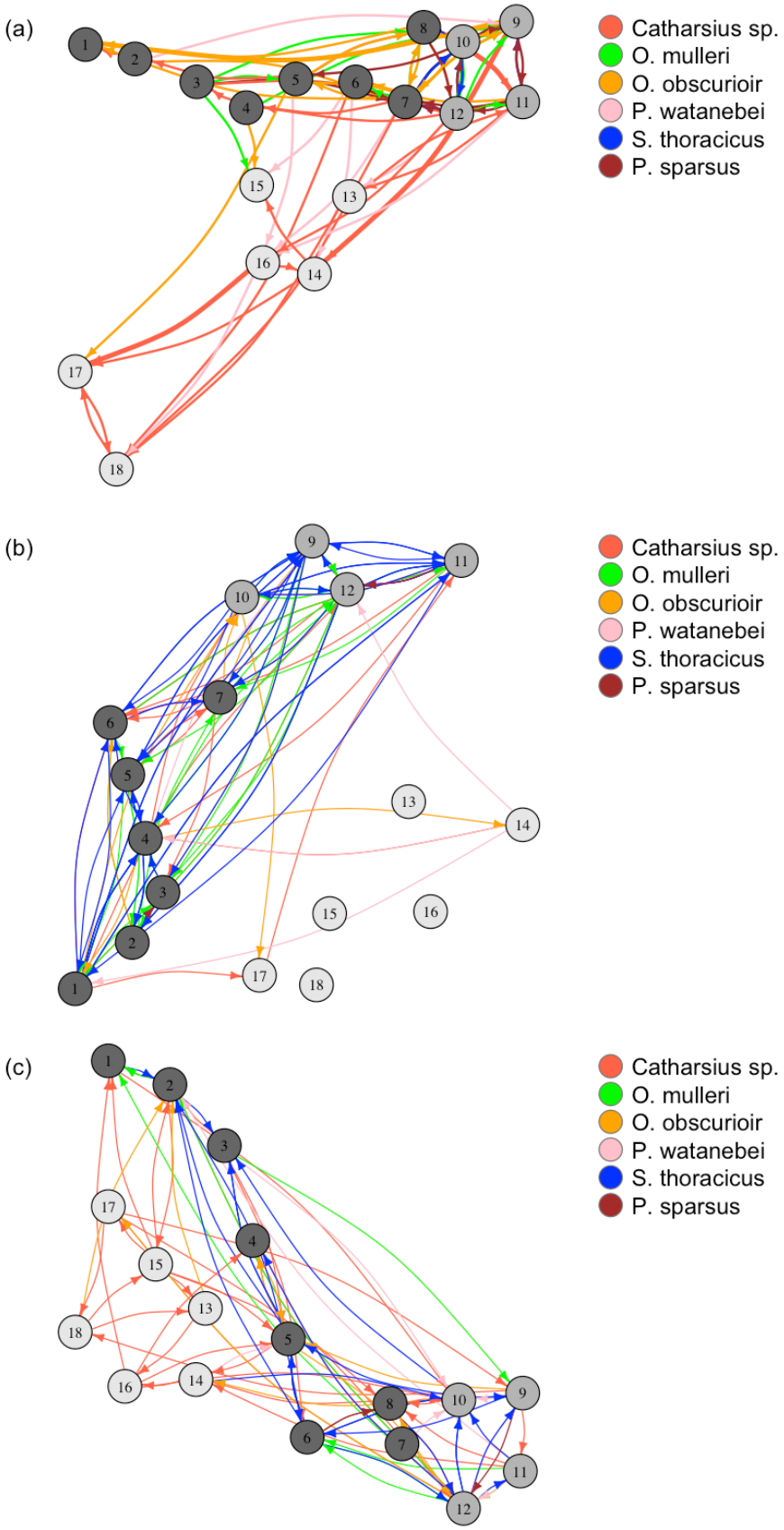
(a)
(b)
(c)
Catharsius sp.
O. mulleri
O. obscurioir
P. watanebei
S. thoracicus
P. sparsus

FIGURE 3. Dung beetle dispersal 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, light grey = oil palm matrix. Distances between traps are scaled to represent actual distances in the field. The colour of each arrow indicates the dung beetle species and its direction indicates direction of dispersal. Width of arrow indicates the frequency of dispersal with the smallest width indicating 1 dispersal incidence and the widest indicating 4 dispersal incidences. Dung beetles that returned to the trap they were released from are excluded.

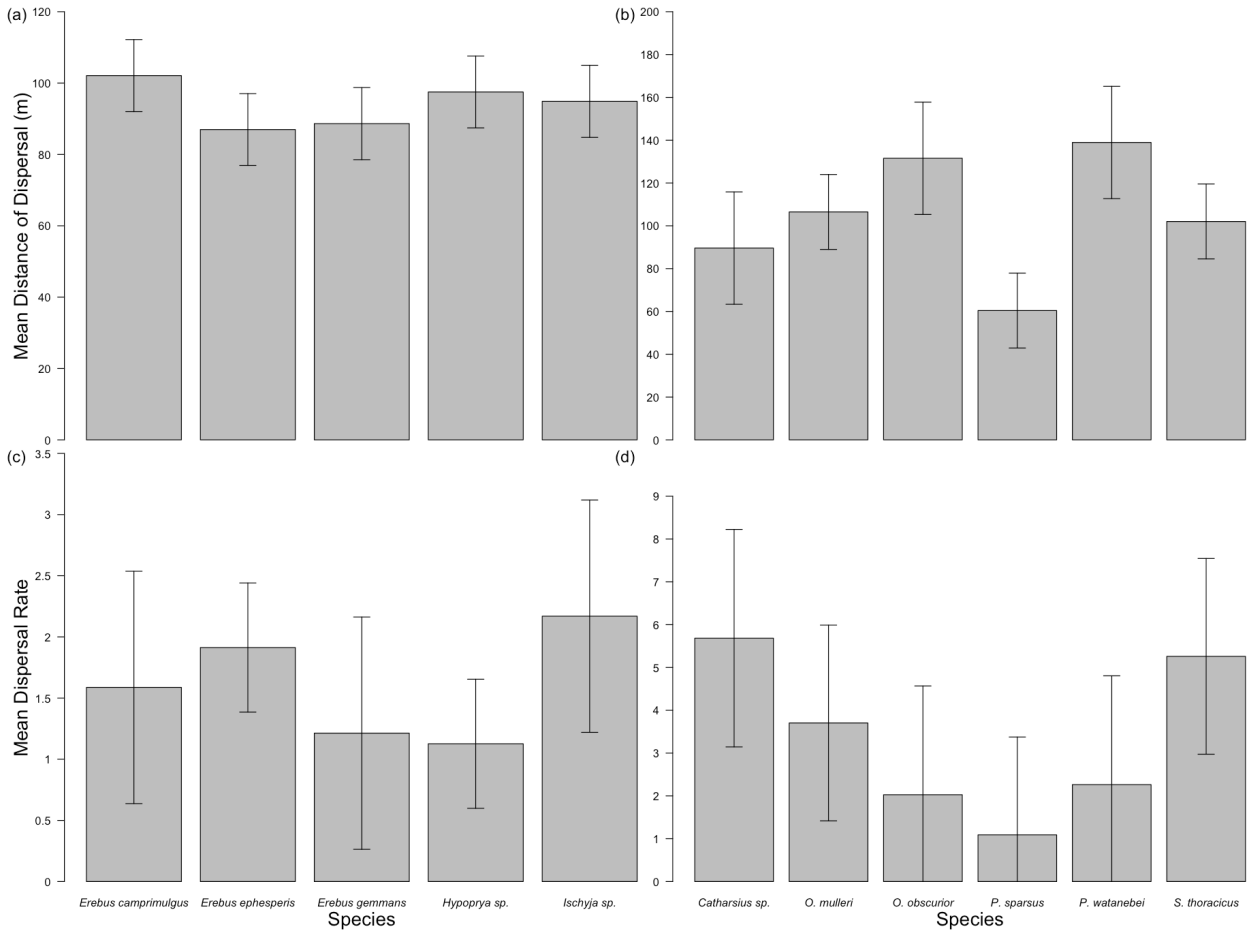

FIGURE 4. Bar graphs showing the mean dispersal distance and rates for moths a) and c) and dung beetles b) and d). Error bars show 95% CI.