

Are riparian forest reserves sources of invertebrate biodiversity spillover and associated ecosystem functions in oil palm landscapes?



C.L. Gray^{a,b,*}, B.I. Simmons^{c,1}, T.M. Fayle^{d,e,f}, D.J. Mann^g, E.M. Slade^{a,h}

^a Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

^b School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

^c Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

^d Institute of Entomology, Biology Centre of Academy of Sciences Czech Republic, Branišovská 31, 370 05, České Budějovice, Czech Republic

^e Forest Ecology and Conservation Group, Imperial College London, Silwood Park Campus, Buckhurst Road, Berkshire SL5 7PY, UK

^f Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, 88400 Kota Kinabalu, Sabah, Malaysia

^g Life Collections, Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK

^h Lancaster Environment Centre, LEC Building, Lancaster University, Bailrigg, Lancaster LA1 4YQ, UK

ARTICLE INFO

Article history:

Received 29 May 2015

Received in revised form 9 December 2015

Accepted 14 December 2015

Available online xxxx

Keywords:

Ecosystem function
Forest fragments
Tropical agriculture
Dung beetles
Ants
Borneo

ABSTRACT

The world's forested landscapes are increasingly fragmented. The effects of fragmentation on community composition have received more attention than the effects on ecological processes, particularly in the tropics. The extent to which populations from forest fragments move (spillover) into surrounding agricultural areas is of particular interest. This process can retain connectivity between populations and alter the rate of beneficial or detrimental ecological functions. We tested whether riparian forest fragments (riparian reserves), are sources of two functionally important invertebrate groups (dung beetles and scavenging ants) within oil palm plantations in Malaysia. We also assessed whether forest fragments enhance rates of associated ecosystem functions (dung and bait removal). We found that oil palm sites with and without adjacent riparian reserves had similar overall beetle and ant communities and functional rates. However, dung beetle species richness, abundance and diversity declined with distance from a riparian reserve, providing evidence for a weak spillover effect. In addition, dung beetle community metrics within a riparian reserve predicted corresponding values in adjacent oil palm areas. These relationships did not hold for dung removal, ant community metrics or bait removal. Taken together, our results indicate that although riparian reserves are an important habitat in their own right, under the conditions in which we sampled they have a limited role as sources of functionally important invertebrates. Crucially, our results suggest that contiguous habitat corridors are important for maintaining connectivity of invertebrate populations, as forest dependent species may not easily be able to disperse through the agricultural matrix.

© 2015 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Across the tropics, agricultural expansion and intensification are driving forest conversion and fragmentation (Gibbs et al., 2010). As forest fragments become an increasingly common feature of our landscapes, we need to understand which communities and functions they support, and how they interact with the surrounding landscape. Understanding the ecology of forest fragments is especially important in the species-rich tropics given the high productivity of these areas

and the negative impacts of human-dominated land uses on a wide range of tropical species (Newbold et al., 2014). Palm oil production is a major industry across the tropics, especially in Southeast Asia, and plantations are expanding in Africa and the Neotropics (Butler and Laurance, 2010; Wich et al., 2014). This expansion is of concern as the conversion of native habitats to oil palm causes declines in many taxa (Savilaakso et al., 2014) and ecosystem functions (Barnes et al., 2014b).

Although existing evidence suggests that forest fragments in oil palm do not conserve biodiversity as well as continuous forest areas, they can support more bird species (Edwards et al., 2010), dung beetle species (Gray et al., 2014) and ant species (Gray et al., 2015) than nearby oil palm areas. Forest fragments provide resources for vertebrates such as the common palm civet (Nakashima et al., 2013) and large (>300 ha) forest fragments in oil palm landscapes can support diverse bat assemblages (Struebig et al., 2008). However, the degree to which forest fragments act as sources for functionally important species in oil palm plantations is less well known.

* Corresponding author at: School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK.

E-mail addresses: claudiagray@gmail.com (C.L. Gray), benno.simmons@gmail.com (B.I. Simmons), tmfayle@gmail.com (T.M. Fayle), darren.mann@oum.ox.ac.uk (D.J. Mann), eleanor.slade@zoo.ox.ac.uk (E.M. Slade).

¹ These authors contributed the majority of the work and should be considered as joint first authors.

Spillover is the movement of individuals from a “source” or “target” habitat to a “recipient” or “non-target” habitat (Brudvig et al., 2009; Rand et al., 2006). The term spillover has been used to refer to the increase in fish densities around marine protected areas (Roberts et al., 2001), the movement of species from forest into neighbouring agroforestry plantations (Tscharnatke et al., 2011), and the flow of chemicals from areas of intense agriculture into less disturbed habitats (Didham et al., 2015). Here, we are concerned with the spillover, or movement, of biodiversity from forest fragments into areas planted with oil palm. The dispersal of individuals across an agricultural matrix can affect species' survival in habitat remnants (Ewers and Didham, 2006) and the delivery of valuable ecosystem services such as pollination or pest-control (e.g. Karp et al., 2013; Ricketts, 2004). In oil palm plantations, spillover of communities from forest has been documented for butterflies (Lucey and Hill, 2012), ants (Lucey et al., 2014) and orchid bees (Livingston et al., 2013). However, few studies have assessed how forest fragments influence ecological processes in oil palm; recent evidence suggests that forest has little effect on the activity of herbivorous pests (Gray and Lewis, 2014) or on oil palm yield (Edwards et al., 2014).

Here, we quantify the extent of spillover from riparian reserves (strips of forest protected alongside rivers) into surrounding oil palm plantations in Sabah, Malaysian Borneo. Riparian reserves are protected because they improve water quality and reduce flood risk (McDermott et al., 2010), but they also provide habitat for forest-dependent species (Marczak et al., 2010). In Sabah, 20 m of natural vegetation must be retained either side of any river more than 3 m in width (Sabah water resources enactment, 1998). We surveyed two key insect groups (dung beetles and ground-foraging scavenging ants) and the ecological processes they support (dung and animal necromass removal respectively). These two processes are important because they potentially impact soil properties and plant growth (Frouz and Jilkova, 2008; Nichols et al., 2008). If ants and dung beetles are moving from riparian reserves into adjacent oil palm, this may be because dung or animal necromass resources are not being used by the species able to persist permanently in the oil palm, and so the spillover effect could result in an increase in important ecological functions.

We addressed the following questions:

1. Does the diversity, species richness, abundance, community composition or function of dung beetles and scavenging ants differ between oil palm with and without an adjacent riparian reserve?

2. Does the biodiversity and ecosystem function of these taxa in oil palm change with increasing distance from the riparian reserve boundary?
3. Does the biodiversity and ecosystem function of these taxa in riparian reserves predict biodiversity and ecosystem function in adjacent oil palm?

2. Methods

2.1. Study sites

Study sites were located adjacent to rivers (5–10 m width) in South Eastern Sabah, Malaysian Borneo (117.5°N, 4.6°E). The landscape is a mosaic of twice-logged lowland dipterocarp rainforest, acacia, and oil palm plantations (planted between 1998 and 2011). The sites also form part of the Stability of Altered Forest Ecosystems project (see Ewers et al. (2011) and www.safeproject.net for further details).

We collected data from 14 sites adjacent to rivers: seven in areas of continuous oil palm and seven in areas of oil palm with a riparian reserve (Fig. 1). At each site, we set up a sampling grid of 12 points, consisting of four transects perpendicular to the river. Transects were 100 m apart, with sampling points at 0 m, 50 m and 100 m from the high water line. At sites with a riparian reserve, sampling points fell both within the riparian reserve and in the oil palm adjacent to it. Due to variation in the width of the riparian reserves (mean 49 m, standard deviation = 30 m, referring to forest width on one side of the river), the number of sampling points falling outside the riparian reserve varied slightly between sites. All sites were separated by at least 1.5 km, and all riparian reserve sites were at least 1 km from the nearest continuous logged forest boundary.

2.2. Data collection

Data on dung beetle communities and function were collected between February and July 2011 (12 sampling points at each of 14 sites, giving 168 sampling points in total). Data on ant communities and function were collected between April and July 2011 (nine of the 12 sampling points per site, across 13 sites, giving 117 sampling points in total). Logistical difficulties prevented us collecting ant data from one of the oil palm sites (top left in Fig. 1). The months during which

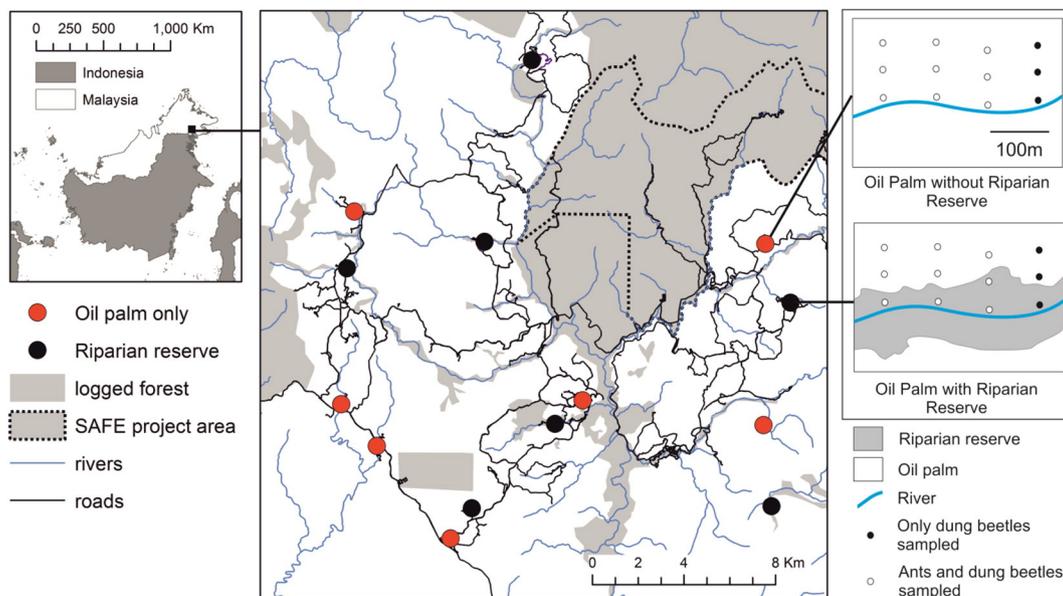


Fig. 1. Map of study sites within Sabah, Malaysian Borneo, and an example layout of sampling points at sites with a riparian reserve (black circles) and without a riparian reserve (red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sampling occurred fell in the slightly drier half of the year (Kumagai et al., 2005; Walsh and Newbery, 1999). The order in which sites were visited was randomised and transects were sampled sequentially to avoid confounding distance to river and time of day.

2.2.1. Dung beetle community structure and associated rates of dung removal

Dung beetles were collected using pitfall traps baited with 25 g of human dung. Dung removal rates were assessed using cattle dung because much larger quantities were required. Uniform pats of 700 g of cow dung were set out at each sampling point and collected after 24 h. Preliminary work in nearby forest sites in Sabah shows that large cattle dung baits attract a similar species composition to smaller human dung baits, with the exception of some carrion feeding species that are found in higher abundances in human dung (Slade et al., 2011, E. Slade and D.J. Mann, unpubl. data). To compare species composition data from pitfall traps with dung removal results, we therefore removed data on these carrion feeding species from the pitfall data. Dung removal experiments were carried out at least one month after pitfall traps were collected, to minimise interference. Further details of these methods are given by Gray et al. (2014).

Dung beetle specimens were stored in 90% alcohol and later identified to species level using Balthasar (1963); Boucomont (1914); publications describing Bornean Scarabaeinae (e.g. Ochi et al., 1996) and the reference collections at Oxford University Museum of Natural History (OUMNH). Species that could not be identified were given morphospecies numbers.

2.2.2. Ant community structure and associated rates of scavenging activity

At each sampling point we carried out a 30-minute observation of leaf litter ants to determine both community composition and rates of scavenging (bait removal). A bait card with 30 bait pellets of 4 different size classes was placed flush with the soil and the amount of bait removed was recorded. Baits were pellets made of crushed earthworm (average mass: 0.017 g, maximum diameter: 3 mm; Tropical Fish Food Earthworm Pellets: High Protein, ukfishfood.co.uk). To assess scavenger ant community composition, we collected specimens from all species entering the bait card. Full details of this method are given by Gray et al. (2015). Ant specimens were identified to species where possible using appropriate keys (Bolton, 1977; Eguchi, 2001; Fayle et al., 2014; Fisher, 2010), the online database AntWeb, and reference collections held in the University of Cambridge entomology collections and the Natural History Museum, London.

2.3. Analysis

For each sampling point we calculated the total abundance, raw species richness and diversity (Shannon index) of both dung beetles and ants, the dung mass removed by dung beetles and the bait mass removed by ants. All analyses were carried out using generalised linear mixed-effects models (GLMMs) in R version 3.0.2 (R Core Team, 2014) using the packages *vegan* 2.2-0 (Oksanen et al., 2013), *lme4* 1.1-7 (Bates et al., 2014) and *cluster* 1.15.3 (Maechler et al., 2013). Fixed terms were considered to be non-significant if the comparison of models with and without the term returned a *P*-value greater than or equal to 0.05. We used a Poisson error distribution (log link) where the response variable was abundance or species richness and a binomial error distribution (logit link) where the response variable was proportion of dung or number of bait pieces removed (Zuur et al., 2009). All other models used a Gaussian error distribution.

2.3.1. Does biodiversity or ecosystem function differ between areas of oil palm with and without an adjacent riparian reserve?

We tested whether biodiversity or functional metrics differed between sites with and without a riparian reserve (Question 1) using separate GLMMs for each biodiversity and functional response metric

calculated. From the riparian reserve sites, we only used data from points 50 or 100 m from the river that fell in oil palm (a total of $n = 39$ sampling points for ants and 52 for dung beetles, across seven sites; all points 0 m from the river fell inside the protected riparian forest). To maintain a balanced design, we also only used data from points 50 and 100 m away from the river at the oil palm sites ($n = 36$ sampling points for ants and 56 for dung beetles, across 6 and 7 sites respectively). The presence/absence of riparian reserve was included as a fixed effect and site as a random effect to account for spatial autocorrelation in the data. A similar preliminary analysis of the data on dung removal rates was presented in Gray et al. (2014).

Differences in community composition were visualised with detrended correspondence analyses. To test whether the presence of a riparian reserve influenced community composition we compared three groups of data: sampling points 50 or 100 m away from the river in oil palm sites without a riparian reserve (as above), sampling points from 50 m and 100 m in oil palm adjacent to a riparian reserve (as above), and sampling points at 0 m or 50 m from the river within the riparian reserves (24 sampling points in a riparian reserve for ants and 32 for dung beetles, across the 7 riparian reserve sites). We tested for significant differences in community composition using a permutational analysis of variance with 999 permutations and site as a grouping variable. Bonferroni corrections were applied to pairwise comparisons between the three habitat categories (riparian reserve, oil palm with riparian reserve, oil palm without riparian reserve).

2.3.2. Does biodiversity and ecosystem function vary with distance to the riparian reserve boundary?

We tested whether biodiversity metrics and function varied with distance to the riparian reserve boundary (Question 2) using only data from sampling points in oil palm adjacent to a riparian reserve. We calculated the distance from the nearest riparian reserve boundary in ArcMap version 10.1 (ESRI, 2012) (minimum = 1 m, maximum = 85 m), and used this as a fixed effect in separate GLMMs for each biodiversity or functional response metric. We specified site as a random factor with random slopes estimated for distance to riparian reserve boundary. As distance to riparian reserve boundary was confounded with distance to river, distance to river could also be driving observed relationships. If this was the case, we should also see a significant effect of distance to river at oil palm sites without a riparian reserve. For all response variables tested, we found no significant effect of distance to river in sites without a riparian reserve (Appendix A, Table A4).

2.3.3. Does the biodiversity and ecosystem function in riparian reserves predict biodiversity and ecosystem function in adjacent oil palm?

To test whether community metrics and function for sites in oil palm were predicted by those in adjacent riparian reserves (Question 3) we aggregated variables for each transect, by calculating the mean value of each response variable for a) the sampling points within the riparian reserve and b) the sampling points in the oil palm adjacent to the reserve. The mean value outside the riparian reserve was used as a response variable and the mean value inside the riparian reserve as a predictor, with site as a random factor.

3. Results

In total, we identified 3057 individuals from 36 species of dung beetle and observed 6194 individual ants from which we identified 58 (morpho) species. Full species lists are given in Appendix A: Tables A1 and A2.

3.1. Does biodiversity or ecosystem function differ between areas of oil palm with and without an adjacent riparian reserve?

The presence of a riparian reserve did not significantly affect any of the community or functional metrics for either dung beetles or ants in nearby oil palm (Table 1).

Table 1

Results of generalised linear mixed effects models testing whether the presence of a riparian reserve affects community and functional metrics of dung beetles and scavenging ants. χ^2 , df and *P* values are given for the comparison of a model with and without the factor describing presence of riparian reserve (two levels: present, absent) as a fixed effect.

Term	Dung beetles			Scavenging ants		
	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Species richness	0.51	1	0.472	0.34	1	0.561
Diversity	2.28	1	0.131	1.26	1	0.262
Abundance	1.15	1	0.284	0.95	1	0.329
Dung/bait removed	2.30	1	0.130	0.22	1	0.641

There were significant differences in community composition between habitat categories (ants: $F_{2,33} = 4.40, P < 0.001$, dung beetles: $F_{2,35} = 2.85, P < 0.001$, Fig. 2). The ant and dung beetle communities inside the riparian reserves were significantly different from those in oil palm adjacent to the riparian reserve (no overlap in 95% CI ellipse shown in Fig. 2; $F_{1,22} = 4.68, P = 0.003$; $F_{1,22} = 3.38, P = 0.006$ respectively), and those in oil palm sites without a riparian reserve (no overlap in 95% CI ellipse shown in Fig. 2; $F_{1,20} = 7.07, P = 0.003$; $F_{1,22} = 3.56, P = 0.003$ respectively). The ant and dung beetle communities in oil palm sites without a riparian reserve were not significantly different from those in oil palm adjacent to a riparian reserve (Fig. 2, $F_{1,24} = 1.74, P = 0.240$; $F_{1,26} = 1.56, P = 0.420$ respectively).

3.2. Does biodiversity and ecosystem function vary with distance to the riparian reserve boundary?

Dung beetle diversity, abundance and species richness declined with distance from a riparian reserve boundary (Table 2). However, for oil palm at all distances from a riparian reserve, abundance remained within the range of values (9 to 32 individuals per trap) for oil palm areas without a riparian reserve (Fig. 3a). Mean dung beetle diversity (Fig. 3b) and species richness (Fig. 3c) in oil palm adjacent to a riparian reserve declined by approximately 20% and 6% respectively with every 10 m from the riparian reserve boundary, but remained higher than the average values for oil palm sites without a riparian reserve up to 60 m away from a riparian reserve. There was no relationship between distance to the riparian reserve boundary and dung removal.

None of the ant community metrics varied significantly with distance to riparian reserve boundary, but ant scavenging activity

Table 2

Results of generalised linear mixed effects models testing whether the distance to a riparian reserve affects community and functional metrics of dung beetles and scavenging ants. χ^2 , df and *P* values are given for the comparison of the model with distance to riparian reserve boundary as a fixed effect against the null model.

Response	Dung beetles			Scavenging ants		
	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Species richness	4.08	1	0.044	0.13	1	0.717
Diversity	4.09	1	0.043	0.22	1	0.641
Abundance	4.26	1	0.039	0.48	1	0.488
Dung/bait removed	3.60	1	0.058	14.2	1	<0.001

increased by a small but significant amount (1 additional bait piece for every 20–25 m). However, this result was influenced by one outlier, a site at which the invasive ant, *Anoplolepis gracilipes* was particularly active (Table 2, Fig. A1).

3.3. Does the biodiversity and ecosystem function in riparian reserves predict biodiversity and ecosystem function in adjacent oil palm?

We found a significant positive relationship between all dung beetle community metrics in a riparian reserve and the corresponding adjacent oil palm adjacent (Table 3, Fig. 4). This relationship was not significant for dung removal, ant community metrics or bait removal by ants (Table 3).

4. Discussion

The movement of individuals from forest fragments into the surrounding agricultural area can promote species' survival by connecting populations (Ewers and Didham, 2006), and enhance the delivery of ecosystem services (Karp et al., 2013; Ricketts, 2004). As oil palm plantations are spreading rapidly across the biodiverse tropics, the dynamics of forest fragments in these landscapes is of increasing interest. We have shown that there is limited spillover of dung beetles, and no spillover of scavenging ants, from riparian reserves into adjacent oil palm. We also found little evidence that the presence of a riparian reserve affects the ecological processes supported by these groups.

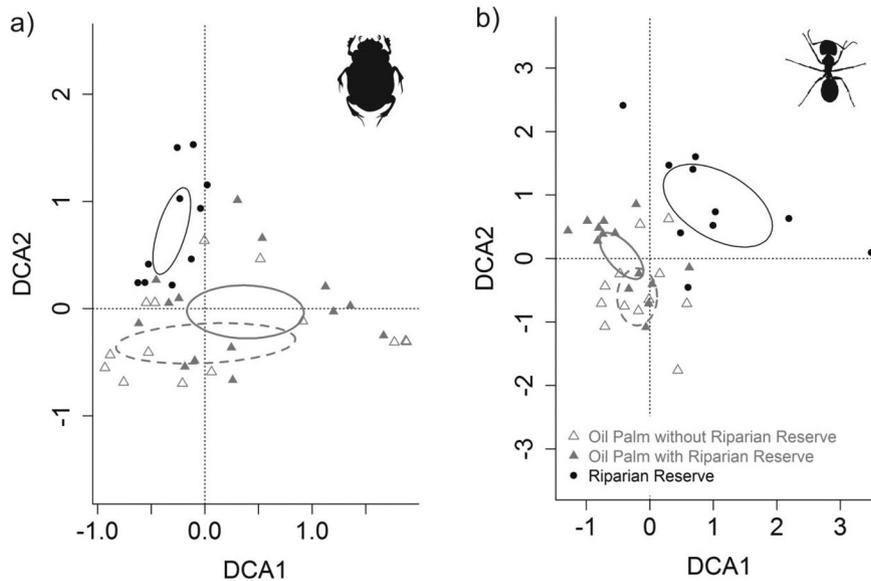


Fig. 2. The community composition of both ants and beetles in oil palm adjacent to a riparian reserve is not significantly different to that in oil palm without a riparian reserve but significantly different to the community within the reserve. Ellipses give 95% confidence intervals for the mean within a riparian reserve (black, solid), oil palm with a riparian reserve (grey, solid) and oil palm without a riparian reserve (grey, dashed).

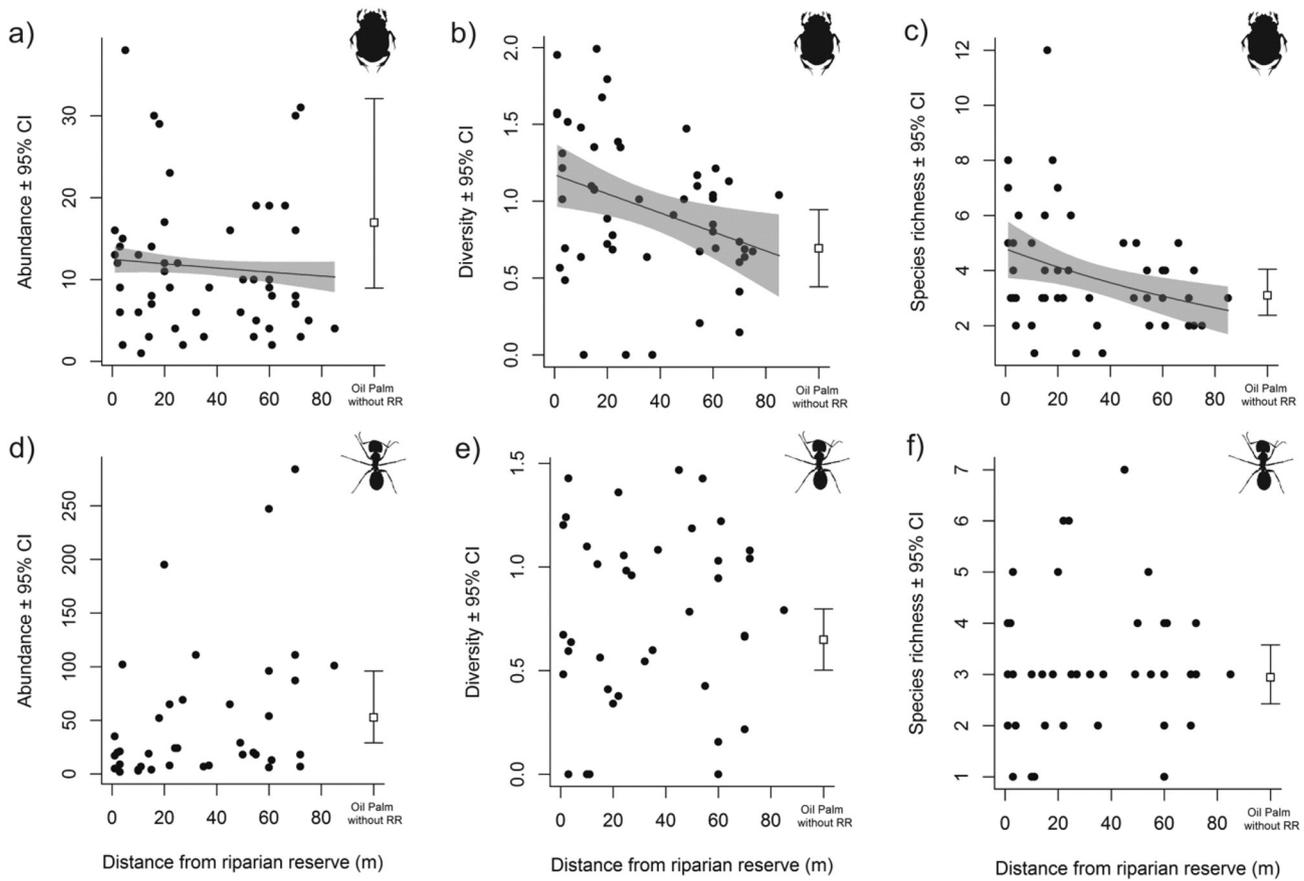


Fig. 3. Dung beetle abundance (a), diversity (b) and species richness (c) in oil palm plantation declined with distance from riparian reserve boundary. Ant abundance (d), diversity (e) and species richness (f) did not change with distance to riparian reserve (RR) boundary. Plots show means and 95% confidence intervals. Square points and error bars give the mean and 95% confidence intervals for corresponding metrics in oil palm sites without a riparian reserve.

4.1. Spillover of dung beetle and ant species

A small number of previous studies have looked at tropical dung beetle assemblages in agricultural areas at multiple distances from native forest. These report no spillover of dung beetles from large areas of Brazilian Atlantic forest into pasture/sugar cane (Filgueiras et al., 2015), and very limited (less than 100 m) spillover effects in areas of pasture adjacent to native forest in Nigeria (Barnes et al., 2014a). Similarly, we only found evidence for limited spillover of dung beetles from riparian reserves into adjacent oil palm. There were no overall significant differences in dung beetle community metrics at oil palm sites with and without a riparian reserve, but dung beetle diversity and species richness declined with increasing distance from a riparian reserve boundary. Such declines with distance to a source habitat are indicative of a spillover effect (Brudvig et al., 2009). We also found that dung beetle community metrics in the riparian reserve predicted corresponding values in the adjacent oil palm, further indicating an influence of the

riparian reserve community on the surrounding area. This relationship could occur because of similarities within sites (i.e. the dung beetles with a given riparian reserve and the adjacent oil palm are both remnants of the same original community and therefore may be more similar to each other than to other sites). However, specifying site as a grouping variable in the analysis accounts for some of this spatial autocorrelation, and within-site similarities do not explain the decline in abundance and diversity with increasing distance from the riparian reserve boundary. We therefore conclude that the relationship between community metrics within and adjacent to riparian reserves reinforces the conclusion that there is some, albeit limited, spillover of dung beetles from riparian reserves into the surrounding oil palm plantation.

We found no evidence that ant communities spillover from riparian reserves into the surrounding oil palm, despite this pattern appearing elsewhere (Lucey et al., 2014). There are several possible explanations for why our results differ to previous studies observing spillover of insects from forest fragments into agricultural areas. First, the forest fragments we studied are generally smaller and thinner. The riparian reserves we surveyed were on average only 100 m across (50 m on each side of the river) and a few kilometres long. These linear forest strips are exposed to extensive edge effects compared to the much larger, nonlinear fragments studied by others (e.g. 227 ha forest fragments in Ricketts et al., 2001, 6–500 ha in Lucey et al., 2014, and ~45,000 ha in Livingston et al., 2013). We might expect greater spillover effects from wider riparian reserves or those with more complex vegetation structure, because the source populations in larger fragments are bigger; this explanation has been suggested for the change in bee community composition and pollination rates in tropical agricultural areas seen with increasing size of nearby forest fragments (Brosi et al., 2008; Ricketts, 2004). The species richness/abundance of ants in oil palm has

Table 3

Results of linear models testing whether community and functional metrics of dung beetles and scavenging ants adjacent to a riparian reserve are predicted by corresponding values within the reserve. χ^2 , df and *P* values are given for the comparison of the model with values within the reserve as a fixed effect against the null model.

Response	Dung beetles			Scavenging ants		
	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Species richness	18.22	1	<0.001	0.07	1	0.793
Diversity	8.84	1	0.003	0.01	1	0.908
Abundance	15.81	1	<0.001	0.28	1	0.597
Dung/bait removed	1.20	1	0.274	1.25	1	0.262

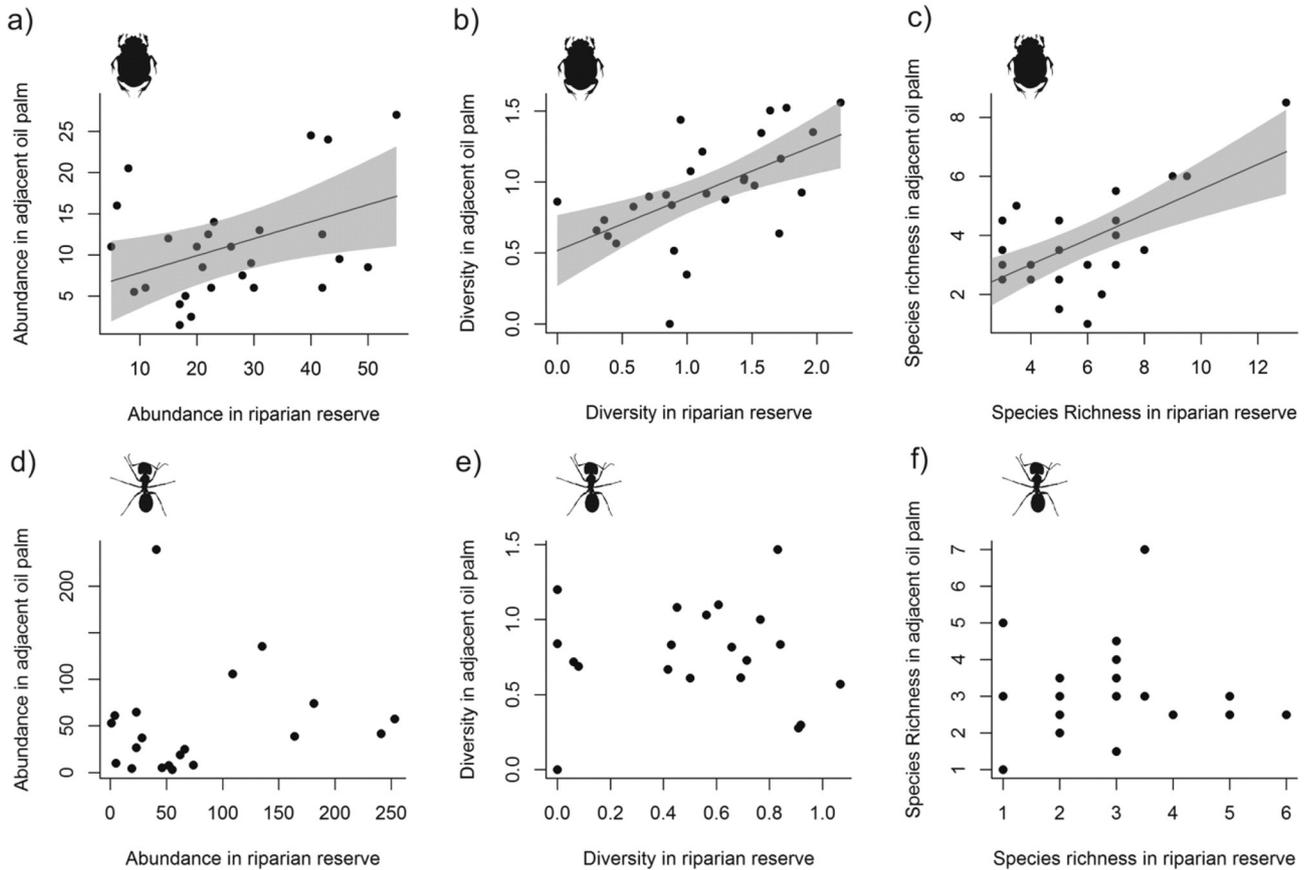


Fig. 4. For dung beetles, there was a positive correlation between dung beetle and (a) abundance, (b) diversity and (c) species richness in oil palm adjacent to a riparian reserve and inside the corresponding riparian reserve. For ants, no significant relationships were found (d, e, f).

also been observed to increase near larger forest fragments (Lucey et al., 2014). With only seven riparian reserve sites, we did not have much data to test this hypothesis, but we did not find any relationship between either reserve width or vegetation complexity and the extent of spillover for either ants or dung beetles (Appendix A Table A3). Riparian reserves may need to be much wider than those in our study landscape for greater spillover effects to be found.

Second, previous studies were carried out in mature oil palm (10–19 year old palms in Lucey et al., 2014; 10–25 year old palms in Livingston et al., 2013) and the sites we surveyed were much younger (0–13 years old). The lack of canopy cover in young plantations makes them much hotter and drier; these hostile conditions could prevent dispersal of invertebrates and, therefore, spillover of either ants or dung beetles from riparian reserves may be greater in mature areas of oil palm. Large areas of Southeast Asia are likely to undergo replanting in the near future (Snaddon et al., 2013), so the effect of oil palm age on matrix permeability deserves further study; large-scale replanting could have significant negative consequences for species of conservation concern.

Third, for ant communities the discrepancy between our findings and those of previous papers may be explained by differences in methodology. Different sampling approaches are likely to capture different genera or species, which may show different tendencies to move out of forest fragments into oil palm. In particular, Lucey et al. (2014) found spillover effects in ant communities using passive pitfall traps sampling both day and night. However, our baited platforms were only observed during the day. It is possible that diurnal species are less likely to show spillover effects as it is during the middle of the day that the microclimate in oil palm is most different from forest fragments; the temperature in oil palm is highest and the humidity is lowest (Luskin and Potts, 2011). Exploring the relationships between forest

species' daily activity patterns and their ability to penetrate into high-temperature matrix habitats might be a fruitful direction for future research.

It is also interesting that spillover effects vary between taxonomic groups and differences in social behaviour may provide some explanation. For example, Livingston et al. (2013) found that orchid bees travelled several kilometres into oil palm plantations. Orchid bees are predominantly solitary, and so may be less constrained by distance to the nest than foragers from social species such as ants. For social insects, spillover effects may be limited to the maximal foraging distance unless new colonies can establish in matrix habitats, and colony establishment is likely to be more constrained by environmental conditions. We therefore speculate that differences in sociality may explain the differences we observed between ants and dung beetles.

4.2. Spillover of ecosystem function

The activity of foraging ants and dung beetles removes organic material from the soil surface, moving and aerating the soil as well as contributing to soil fertility (Lach et al., 2010; Nichols et al., 2008). However, we found no evidence that proximity to a riparian reserve enhances the activity of dung beetles or ants in nearby oil palm. Indeed, our results suggest that proximity to a riparian reserve might even limit the scavenging activity of species found in oil palm and not in forest (such as the invasive yellow crazy ant, *A. gracilipes*).

It is possible that current micro-climatic conditions and dung/animal necromass availability are limiting spillover from riparian reserves into surrounding oil palm areas. As we observed some spillover of dung beetles, it is possible that the riparian habitat provides a reservoir of individuals that could move into the oil palm should dung availability increase. Although cattle were not grazed in our sampling area, many

oil palm plantations graze cattle under mature oil palm as an additional source of income. Dung beetle abundances, particularly those of the large, functionally important species are much higher in plantations where cattle are present (Slade et al., 2014). It is possible that a greater spillover effect might be observed if cattle were introduced. Furthermore, more mature oil palms might allow spillover of both beetles and ants (see above; Lucey et al., 2014), and hence proximity to riparian reserves in mature plantations might enhance the ecosystem functions underlying important services.

4.3. Implications for conservation policy

While we found some evidence of dung beetle spillover from riparian reserves into oil palm, overall our results suggest that in oil palm landscapes, the dispersal ability of forest-dependent invertebrates is very limited. Similarly, other studies have found that butterflies only move a few hundred metres from forest fragments into oil palm plantations (Lucey and Hill, 2012) and that Neotropical damselflies are unable to cross areas of pasture between forest fragments as narrow as 50–100 m (Khazan, 2014). For these invertebrates, the presence of vegetative corridors linking up forest fragments is likely to be crucial for conserving population connectivity across agricultural landscapes. If spillover does not enable population connectivity through non-forest areas, then connectivity of forest populations may only occur through forested corridors. The importance of habitat corridors is more commonly highlighted for vertebrates (e.g. De Lima and Gascon, 1999; Lees and Peres, 2008; Sekercioglu, 2009) but it may be that habitat corridors are even more important for invertebrate groups.

An important consideration is that corridors can have negative ecological effects, and these deserve further study for invertebrates and in oil palm landscapes. Habitat corridors have been observed to increase the colonisation rate of invasive species (Procheş et al., 2005). They can also act as ecological sinks, draining nearby source populations (Simberloff et al., 1992). This effect has been shown for hymenoptera in grassland corridors in temperate agricultural landscapes (Krewenka et al., 2011). More data is available for vertebrates, particularly birds, with some evidence that nesting success is lower in corridors than interior forest (Willson et al., 2001), although this is not always the case (Zuria et al., 2007). For some bird species mating success is also higher in habitat patches connected by corridors than in those without (Díaz et al., 2006). Our results indicate that two functionally important insect groups have a limited ability to disperse across oil palm landscapes, and therefore we suggest that habitat corridors may be very important for maintaining population connectivity of these groups; however, the possible negative effects of such habitat corridors should be a priority for future research.

5. Conclusions

Taken together, our results suggest that although there is some spillover of dung beetles from riparian reserves into oil palm plantations, this occurs over very short distances and is insufficient to cause strong differences between oil palm sites with and without a riparian reserve. The contrast between these results and those of previous studies of spillover effects from forest fragments in tropical agricultural landscapes may relate to differences in the size and location of the fragments, the taxonomic group studied or the age of the surrounding oil palm. It is possible that changes in the matrix surrounding the riparian forest fragments, such as increases in food resources or habitat complexity, may alter the permeability of the matrix and hence impact the degree of spillover. However, with current management approaches, our results strongly suggest that the ability of these invertebrate groups to cross the agricultural matrix is very limited, and that direct connectivity between remaining areas of forest may be crucial for gene-flow between forest dependent populations, the recolonisation of habitat patches and ultimately species' survival.

Author contributions

CLG designed the experiments, collected the data, identified specimens, carried out analyses and wrote the manuscript. BIS carried out analyses and wrote the manuscript. DJM identified specimens and commented on the manuscript. TMF and EMS designed the experiments and commented on the manuscript.

Data Access: All data and scripts used in this study are available at the Figshare account for Claudia Gray: <https://figshare.com/account/home#/projects/10644>.

Acknowledgments

We thank EPU Malaysia, Sabah Biodiversity Council and SEARRP for providing research permissions for field work in Sabah. The SAFE project coordinators (Ed Turner, Johnny Larenus and MinSheng Khoo), research assistants Max Gray and Joana Ferreira, as well as several members of the SAFE project field staff provided logistical support and helped with data collection. Bridget Gray helped with data entry and verification. The Hope Entomological Collections at the Oxford University Museum of Natural History provided resources for species' identification. CLG was supported by a NERC DTG studentship (NE/I528526/1) and TMF by Yayasan Sime Darby, the Czech Science Foundation (grant numbers 14-32302S, 16-09427S) and an Australian Research Council Discovery Grant (DP140101541). EMS was funded by a NERC HMTF grant (NE/K016261/1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.12.017>.

References

- Balthasar, V., 1963. *Monographie der Scarabaeidae und Aphodiidae der Palaearktischen und Orientalischen Region*. Verlag, Prague.
- Barnes, A.D., Emberson, R.M., Chapman, H.M., Krell, F.-T., Didham, R.K., 2014a. Matrix habitat restoration alters dung beetle species responses across tropical forest edges. *Biol. Conserv.* 170, 28–37. <http://dx.doi.org/10.1016/j.biocon.2013.12.006>.
- Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H., Brose, U., 2014b. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nat. Commun.* 5. <http://dx.doi.org/10.1038/ncomms6351>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. *lme4: linear mixed-effects models using Eigen and S4*. R package version 1, pp. 1–7.
- Bolton, B., 1977. The ant tribe Tetramorini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Oriental and Indo-Australian regions, and in Australia. *Bulletin of the British Museum (natural history)*. Entomol. Ser. 36.
- Boucomont, A., 1914. Les Coprophages de L'archipel Malais. *Ann. Soc. Entomol. Fr.* 83, 238–350.
- Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., Durán, G., 2008. The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* 45, 773–783. <http://dx.doi.org/10.1111/j.1365-2664.2007.01412.x>.
- Brudvig, L.A., Damschen, E.L., Tewksbury, J.J., Haddad, N.M., Levey, D.J., 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *PNAS* 106, 9328–9332. <http://dx.doi.org/10.1073/pnas.0809658106>.
- Butler, R., Laurance, W.F., 2010. Is oil palm the next emerging threat to the Amazon? *Trop. Conserv. Sci.* 2, 1–10.
- Core Team, R., 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- De Lima, M.G., Gascon, C., 1999. The conservation value of linear forest remnants in central Amazonia. *Biol. Conserv.* 91, 241–247.
- Díaz, I.A., Armesto, J.J., Willson, M.F., 2006. Mating success of the endemic *Des Murs' Wiretail* (*Sylviorthorhynchus desmursii*, Furnariidae) in fragmented Chilean rainforests. *Austral Ecol.* 31, 13–21. <http://dx.doi.org/10.1111/j.1442-9993.2006.01538.x>.
- Didham, R.K., Barker, G.M., Bartlam, S., Deakin, E.L., Denmead, L.H., Fisk, L.M., Peters, J.M.R., Tylmanakis, J.M., Wright, H.R., Schipper, L.A., 2015. Agricultural intensification exacerbates spillover effects on soil biogeochemistry in adjacent forest remnants. *PLoS ONE* 10, e0116474. <http://dx.doi.org/10.1371/journal.pone.0116474>.
- Edwards, F.A., Edwards, D.P., Sloan, S., Hamer, K.C., 2014. Sustainable management in crop monocultures: the impact of retaining forest on oil palm yield. *PLoS ONE* 9, e91695. <http://dx.doi.org/10.1371/journal.pone.0091695>.
- Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., Wilcove, D.S., 2010. *Wildlife-friendly oil palm plantations fail to protect biodiversity effectively*. *Conserv. Lett.* 3, 236–242.

- Eguchi, K., 2001. A revision of the Bornean species of the ant genus *Pheidole* (Insecta: Hymenoptera: Formicidae, Myrmicinae). *Tropics Monograph Series No. 2*.
- ESRI, 2012. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA, USA.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* 81, 117–142. <http://dx.doi.org/10.1017/S1464793105006949>.
- Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, A., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L., Turner, E.C., 2011. A large-scale forest fragmentation experiment: the stability of altered forest ecosystems project. *Philos. Trans. R. Soc. B* 366, 3292–3302. <http://dx.doi.org/10.1098/rstb.2011.0049>.
- Fayle, T.M., Yusah, K.M., Hashimoto, Y., 2014. Key to the ant genera of Borneo in English and Malay. <http://www.tomfayle.com/Ant%20key.htm>.
- Filgueiras, B.K.C., Tabarelli, M., Leal, I.R., Vaz-de-Mello, F.Z., Iannuzzi, L., 2015. Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects. *Ecol. Indic.* 55, 65–73. <http://dx.doi.org/10.1016/j.ecolind.2015.02.032>.
- Fisher, B., 2010. *Ant Course 2010 Guide to Genera*.
- Frouz, J., Jilkova, V., 2008. The effects of ants on soil properties and soil processes (Hymenoptera: Formicidae). *Myrmecol. News* 11, 191–199.
- Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *PNAS* 107, 16732–16737. <http://dx.doi.org/10.1073/pnas.0910275107>.
- Gray, C.L., Lewis, O.T., 2014. Do riparian forest fragments provide ecosystem services or disservices in surrounding oil palm plantations? *Basic Appl. Ecol.* 15, 693–700. <http://dx.doi.org/10.1016/j.baae.2014.09.009>.
- Gray, C.L., Lewis, O.T., Chung, A.Y.C., Fayle, T.M., 2015. Riparian reserves within oil palm plantations conserve logged forest leaf litter ant communities and maintain associated scavenging rates. *J. Appl. Ecol.* 52, 31–40. <http://dx.doi.org/10.1111/1365-2664.12371>.
- Gray, C.L., Slade, E.M., Mann, D.J., Lewis, O.T., 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecol. Evol.* 4, 1049–1060. <http://dx.doi.org/10.1002/ece3.1003>.
- Karp, D.S., Mendenhall, C.D., Sandi, R.F., Chaumont, N., Ehrlich, P.R., Hadly, E.A., Daily, G.C., 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecol. Lett.* 16, 1339–1347. <http://dx.doi.org/10.1111/ele.12173>.
- Khazan, E.S., 2014. Tests of biological corridor efficacy for conservation of a Neotropical giant damselfly. *Biol. Conserv.* 177, 117–125. <http://dx.doi.org/10.1016/j.biocon.2014.06.006>.
- Krewenka, K.M., Holzschuh, A., Tschamntke, T., Dormann, C.F., 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biol. Conserv.* 144, 1816–1825. <http://dx.doi.org/10.1016/j.biocon.2011.03.014>.
- Kumagai, T., Saitoh, T.M., Sato, Y., Takahashi, H., Manfroi, O.J., Morooka, T., Kuraji, K., Suzuki, M., Yasunari, T., Komatsu, H., 2005. Annual water balance and seasonality of evapotranspiration in a Bornean tropical rainforest. *Agric. For. Meteorol.* 128, 81–92. <http://dx.doi.org/10.1016/j.agrformet.2004.08.006>.
- Lach, L., Parr, C., Abbott, K., 2010. *Ant Ecology*. OUP Oxford.
- Lees, A.C., Peres, C.A., 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conserv. Biol.* 22, 439–449. <http://dx.doi.org/10.1111/j.1523-1739.2007.00870.x>.
- Livingston, G., Jha, S., Vega, A., Gilbert, L., 2013. Conservation value and permeability of Neotropical oil palm landscapes for orchid bees. *PLoS ONE* 8, e78523. <http://dx.doi.org/10.1371/journal.pone.0078523>.
- Lucey, J.M., Hill, J.K., 2012. Spillover of insects from rain forest into adjacent oil palm plantations. *Biotropica* 44, 368–377. <http://dx.doi.org/10.1111/j.1744-7429.2011.00824.x>.
- Lucey, J.M., Tawatao, N., Senior, M.J.M., Chey, V.K., Benedick, S., Hamer, K.C., Woodcock, P., Newton, R.J., Bottrell, S.H., Hill, J.K., 2014. Tropical forest fragments contribute to species richness in adjacent oil palm plantations. *Biol. Conserv.* 169, 268–276. <http://dx.doi.org/10.1016/j.biocon.2013.11.014>.
- Luskin, M.S., Potts, M.D., 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic Appl. Ecol.* 12, 540–551. <http://dx.doi.org/10.1016/j.baae.2011.06.004>.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2013. *Cluster: cluster analysis basics and extensions*. R Package Version 1.14.4.
- Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L., Richardson, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecol. Appl.* 20, 126–134.
- McDermott, C.L., Cashore, B., Kanowski, P. (Eds.), 2010. *Global Environmental Forest Policies: An International Comparison*. Earthscan, London.
- Nakashima, Y., Nakabayashi, M., Sukor, J.A., 2013. Space use, habitat selection, and daybeds of the common palm civet (*Paradoxurus hermaphroditus*) in human-modified habitats in Sabah, Borneo. *J. Mammal.* 94, 1169–1178. <http://dx.doi.org/10.1644/12-MAMM-A-140.1>.
- Newbold, T., Hudson, L.N., Phillips, H.R.P., Hill, S.L.L., Contu, S., Lysenko, I., Blandon, A., Butchart, S.H.M., Booth, H.L., Day, J., Palma, A.D., Harrison, M.L.K., Kirkpatrick, L., Pynegar, E., Robinson, A., Simpson, J., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2014. A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proc. R. Soc. B* 281, 20141371. <http://dx.doi.org/10.1098/rspb.2014.1371>.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcua, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141, 1461–1474.
- Ochi, T., Kon, M., Kikiuta, T., 1996. Studies on the family Scarabaeidae (Coleoptera) from Borneo. I. Identification key to subfamilies, tribes and genera. *G. Ital. Entomol.* 8, 37–54.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. *Vegan: community ecology package*. R Package Version 2.0-10.
- Procheş, Ş., Wilson, J.R.U., Veldtman, R., Kalwij, J.M., Richardson, D.M., Chown, S.L., 2005. Landscape corridors: possible dangers? *Science* 310, 779–783. <http://dx.doi.org/10.1126/science.310.5749.779>.
- Rand, T.A., Tylianakis, J.M., Tschamntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603–614. <http://dx.doi.org/10.1111/j.1461-0248.2006.00911.x>.
- Ricketts, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.* 18, 1262–1271.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Fay, J.P., 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv. Biol.* 15, 378–388. <http://dx.doi.org/10.1046/j.1523-1739.2001.015002378.x>.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. *Science* 294, 1920–1923. <http://dx.doi.org/10.1126/science.294.5548.1920>.
- Sabah water resources enactment, 1998. *LEX-FAOC033659*.
- Savilaakso, S., Garcia, C., Garcia-Ulloa, J., Ghazoul, J., Groom, M., Guariguata, M.R., Laumonier, Y., Nasi, R., Petrokofsky, G., Snaddon, J., Zrust, M., 2014. Systematic review of effects on biodiversity from oil palm production. *Environ. Evid.* 3, 4. <http://dx.doi.org/10.1186/2047-2382-3-4>.
- Sekercioglu, C.H., 2009. Tropical ecology: riparian corridors connect fragmented forest bird populations. *Curr. Biol.* 19, R210–R213. <http://dx.doi.org/10.1016/j.cub.2009.01.006>.
- Simberloff, D., Farr, J.A., Cox, J., Mehlman, D.W., 1992. Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* 6, 493–504.
- Slade, E.M., Burhanuddin, M.L., Caliman, J.P., Foster, W.A., Naim, M., Prawirosukarto, S., Snaddon, J.L., Turner, E.C., Mann, D.J., 2014. Can cattle grazing in mature oil palm increase biodiversity and ecosystem service provision? *Planter* 90, 655–665.
- Slade, E.M., Mann, D.J., Lewis, O.T., 2011. Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biol. Conserv.* 144, 166–174. <http://dx.doi.org/10.1016/j.biocon.2010.08.011>.
- Snaddon, J.L., Willis, K.J., Macdonald, D.W., 2013. Biodiversity: oil-palm replanting raises ecology issues. *Nature* 502, 170–171. <http://dx.doi.org/10.1038/502170d>.
- Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A., Rossiter, S.J., 2008. Conservation value of forest fragments to Palaeotropical bats. *Biol. Conserv.* 141, 2112–2126. <http://dx.doi.org/10.1016/j.biocon.2008.06.009>.
- Tschamntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes — a review. *J. Appl. Ecol.* 48, 619–629. <http://dx.doi.org/10.1111/j.1365-2664.2010.01939.x>.
- Walsh, R.P., Newbery, D.M., 1999. *The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact*. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 354, 1869–1883.
- Wich, S.A., Garcia-Ulloa, J., Kühl, H.S., Humle, T., Lee, J.S.H., Koh, L.P., 2014. Will oil palm's homecoming spell doom for Africa's great apes? *Curr. Biol.* 24, 1659–1663. <http://dx.doi.org/10.1016/j.cub.2014.05.077>.
- Willson, M.F., Morrison, J.L., Sieving, K.E., de Santo, T.L., Santisteban, L., Díaz, I., 2001. Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conserv. Biol.* 15, 447–456.
- Zurita, I., Gates, J.E., Castellanos, I., 2007. Artificial nest predation in hedgerows and scrub forest in a human-dominated landscape of central Mexico. *Acta Oecol.* 31, 158–167. <http://dx.doi.org/10.1016/j.actao.2006.07.005>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Springer New York, New York, NY.