



Tropical forest fragments contribute to species richness in adjacent oil palm plantations



Jennifer M. Lucey^{a,*}, Noel Tawatao^{a,c}, Michael J.M. Senior^a, Chey Vun Khen^b, Suzan Benedick^c, Keith C. Hamer^d, Paul Woodcock^{d,f}, Robert J. Newton^e, Simon H. Bottrell^e, Jane K. Hill^a

^a Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK

^b Forest Research Centre, Sabah Forestry Department, PO Box 1407, 90715 Sandakan, Sabah, Malaysia

^c School of Sustainable Agriculture, Universiti Malaysia Sabah, Batu 10, Jalan Sg. Batang, 90000 Sandakan, Sabah, Malaysia

^d Institute of Integrative and Comparative Biology, University of Leeds, LS2 9JT, UK

^e School of Earth and Environment, University of Leeds, LS2 9JT, UK

^f School of Environment, Natural Resources and Geography, Bangor University, Bangor, Gwynedd LL57 2UW, UK

ARTICLE INFO

Article history:

Received 13 September 2013

Received in revised form 8 November 2013

Accepted 12 November 2013

Keywords:

Agricultural matrix

Ants

Borneo

Fragmentation

Spillover

Trophic level

ABSTRACT

In Southeast Asia, large-scale conversion of rainforest to oil palm plantations is one of the major causes of biodiversity declines. Recommendations for reducing species losses and increasing the sustainability of palm oil production advocate the retention of natural forest patches within plantations, but there is little evidence for the effectiveness of this strategy. Here, we examine to what extent rainforest remnants with different characteristics contribute to biodiversity within surrounding plantations. We sampled ground-dwelling ants in Sabah (Malaysian Borneo) using unbaited pit-fall traps along 1 km transects spanning forest-plantation ecotones of 10 forest fragments (area 5 ha–500 ha) and two continuous forest sites which bordered plantations. Ant species richness in plantations varied according to richness in adjacent forest fragments, which increased with fragment size. A trend of declining species richness in plantations with distance from the forest ecotone was consistent with spillover of forest species into plantations adjacent to forest remnants. Ant assemblages in plantations also contained more carnivorous species adjacent to large forest fragments, suggesting large fragments may have benefits for pest control in plantations, as well as benefits for local biodiversity. Our results indicate that large forest fragments support distinctive ant assemblages and increase diversity within the planted area, but small fragments (<~200 ha) contribute little to plantation diversity. Thus retaining large fragments of forest may help mitigate the loss of species within oil palm plantations.

Crown Copyright © 2013 Published by Elsevier Ltd. All rights reserved.

1. Introduction

Globally, the loss of natural habitats due to the continuing expansion of agriculture is a major threat to biodiversity (Millennium Ecosystem Assessment, 2005). In most regions, the relatively small area of land that is protected is not sufficient to prevent biodiversity losses (Franklin and Lindenmayer, 2009; Perfecto and Vandermeer, 2010) and research has shifted to investigating the potential for agricultural landscapes to help support diversity (Dauber et al., 2003; Tscharntke et al., 2005; Vandermeer and Perfecto, 2007). In Southeast Asia, forest clearance to make way for oil palm (*Elaeis guineensis* Jacq.) plantations is a major driver of biodiversity losses (Corley, 2009; Sodhi et al., 2010; Wilcove and Koh, 2010; Wilcove et al., 2013). Retaining natural habitat fragments within agricultural landscapes could improve species richness, as

well as provide source populations of beneficial species (e.g. for pest control) and other ecosystem services for agriculture (e.g. Duelli and Obrist, 2003; Ricketts, 2004; Ricketts et al., 2004). Accordingly, this method has been proposed as a way of improving the sustainable production of palm oil (RSPO, 2013). However, there is little information on the efficacy of forest fragments for maintaining or improving species richness within plantations (Edwards et al., 2010; Koh, 2008; Mayfield, 2005). It is important to identify the properties of forest patches necessary to support species richness within plantations, because retaining forest fragments that are too small, too isolated or with poor quality habitat may result in substantial economic losses from unplanted land in return for negligible conservation benefits.

Species richness in agricultural areas has been shown to increase with proximity to natural habitats (e.g. Dolia et al., 2008; Livingston et al., 2013; Perfecto and Vandermeer, 2002) due to “spillover” of individuals from source to sink habitats (Lucey and Hill, 2012), as well as the presence of edge species (De Vries

* Corresponding author. Tel.: +44 (0)1904 328645.

E-mail address: jennifer.lucey@york.ac.uk (J.M. Lucey).

et al., 1997). **Species-area relationships (SARs)** in which species richness increases with habitat patch size (MacArthur and Wilson, 1967) are well documented in tropical forest fragments (e.g. Benedick et al., 2006; Bruhl et al., 2003; Hill et al., 2011), and the habitat quality of forest fragments is also likely to influence their species richness (Thomas et al., 2001). Intuitively, higher species richness in larger, higher quality forest fragments might be expected to generate greater spillover effects of forest species into surrounding agricultural habitat. Forest fragments may also vary in their faunal composition, with potential consequences for spillover if species with particular ecological traits are more or less likely to cross ecotones. Previous studies have considered spillover of insects from single fragments (Dolia et al., 2008; Perfecto and Vandermeer, 2002; Ricketts et al., 2001), and how the quality of the agricultural matrix affects spillover (Perfecto and Vandermeer, 2002), but the effect of the characteristics of the forest fragment itself on the species richness in the surrounding matrix, has not been considered.

Ants were chosen as our study taxon because of their diverse functional roles and their potential benefits as predators of agricultural pests (Holldobler and Wilson, 1990; Philpott et al., 2008). Ants are sensitive to land-use changes (Woodcock et al., 2011), and their species richness is reduced in oil palm plantations compared with forest (Bruhl and Eltz, 2010; Faile et al., 2010; Lucey and Hill, 2012). They also occupy diverse trophic positions (Bluthgen et al., 2003) which may be an important determinant of extinction vulnerability in disturbed habitats (Bascompte and Sole, 1998).

The main objective of the study was to examine species richness and faunal composition of ants in forest sites and adjacent oil palm plantations. First, we examined factors affecting ant species richness within forest fragments in relation to forest fragment area, isolation, and habitat quality. We then examined relationships between species richness in fragments and adjacent plantations. In order to test whether these relationships could be due to spillover of forest ant species into adjacent oil palm, we tested whether species richness patterns in plantations varied in relation to distance from forest edges. Finally, we investigated changes in the faunal composition of ants between forest fragments and adjacent plantation sites, and used stable nitrogen isotope analysis to assess the trophic organisation of ant assemblages in each habitat.

2. Methods

2.1. Study sites

We sampled ground-dwelling ants along 1-km transects at 12 sites in Sabah, Malaysian Borneo (5°N, 117°5'E); 10 forest fragment sites and adjacent oil palm plantations, and two sites where plantations bordered continuous forest (Fig. 1). The study region experiences climate typical of the moist aseasonal tropics, with an average annual temperature of 27 °C and average annual rainfall of 2849 mm per year (Walsh et al., 2011).

The 10 forest fragment sites were located in, or adjacent to, five estate plantations belonging to three companies, one of which is a member of the Roundtable for Sustainable Palm Oil (RSPO, 2013, Fig. 1 and Table A1). Forest fragments ranged from 5 ha to 500 ha in size (Table A1). The two largest fragments (250 ha, 500 ha) were 'Virgin Jungle Reserves' (VJRs) and managed and protected by the Sabah Forestry Department. The eight smaller fragments (5–120 ha) were classified as 'High Conservation Value' (HCV) forest (www.hcvnetwork.org) and under the management of the plantation. The two sites where plantations bordered continuous forest were both in the Ulu Segama forest reserve within the Yayasan Sabah forestry concession (~1 million hectares of production forest, Reynolds et al., 2011, Fig. 1). This continuous forest had been

selectively logged in 1993 (~15 years before the study) when timber trees ≥ 0.6 m DBH were removed (Reynolds et al., 2011). There are no oil palm plantations bordering primary forest in the region.

All oil palm plantations that were sampled comprised mature fruiting palms between 10 and 19 years old, and palm trees were of similar height (10–15 m) and spread (~10 m diameter of palm tree crown from frond tip to frond tip), creating an even, closed canopy. Management practices were similar across plantations, with palms planted 10 m apart and vegetation kept clear around the palm bases. Ground cover was dominated by ferns and grasses, and herbicides were used to keep palm bases clear. Insecticide use is rare and was not applied at study sites during the study period.

2.2. Ant sampling and identification

We used unbaited pitfall traps to sample ants along transects. The traps consisted of 45 ml clear plastic tubes containing 15 ml of water with a small amount of detergent to reduce surface tension. The rims were lined with Fluon to prevent escape (Carney et al., 2003). Sampling took place in the drier season (March–September) between July 2008 and September 2010, when the sampling methods were not compromised by heavy rainfall. At each site, a 1-km transect was set-up perpendicular to the forest-plantation boundary, to sample 500 m into each habitat either side of the ecotone. The ecotones between forest and oil palm plantations at the sampling sites were sharp transition zones of ~1–3 m width, containing grasses and pioneer species. Stations were established at 100 m intervals along each transect (i.e. $N = 11$ stations per transect, five stations in forest, five in oil palm and one at the ecotone), except at the smallest remnant (Site 12, 5 ha), where stations were placed 50 m apart to avoid proximity to other edges of the fragment. Transects ran in straight lines except within forest in some small fragments, when the transect detoured, but minimum distances as previously described were always maintained between stations. At each station, five pitfall traps were placed in a square formation with the central traps placed directly on the transect and four other traps placed 10 m N, S, E and W of the central trap. Traps were buried flush with the ground, and sheltered beneath a suspended plastic cup to prevent rainfall displacing captured individuals. Traps were left in place for three days then collected and replaced with five new traps which were placed 5 m away from the original traps in the direction away from the ecotone in order to obtain greater spatial coverage, and left for a further three days. This sampling design resulted in a total sampling effort of 3960 trap-days (12 sites \times 11 stations \times 10 traps \times 3 days).

Ants were preserved in 95% alcohol and identified to genus following Hashimoto (2003). Some ants could be identified to species using reference collections at the Natural History Museum (London), and on-line resources (www.antweb.org; www.antbase.net). Reproductive individuals were excluded from identification and subsequent analyses because they do not necessarily indicate the presence of an established colony. Unnamed species that occur in www.antweb.org were given the same number as the on-line collection, and morphospecies not featured were subsequently submitted to the collection. Voucher specimens are deposited at the Forest Research Centre, Sandakan, Sabah.

2.3. Estimating ant species richness

We present analyses using raw species richness, but we also ran analyses with seven commonly-used species richness estimators in order to avoid biases associated with using any one estimator ('Estimate S' software, Colwell, 2006; Species Richness and Diversity v.2, Henderson and Seaby, 1998, see Table A2 for results). Ants live colonially in nests so individuals cannot be considered independent sampling units and abundance of individuals can be

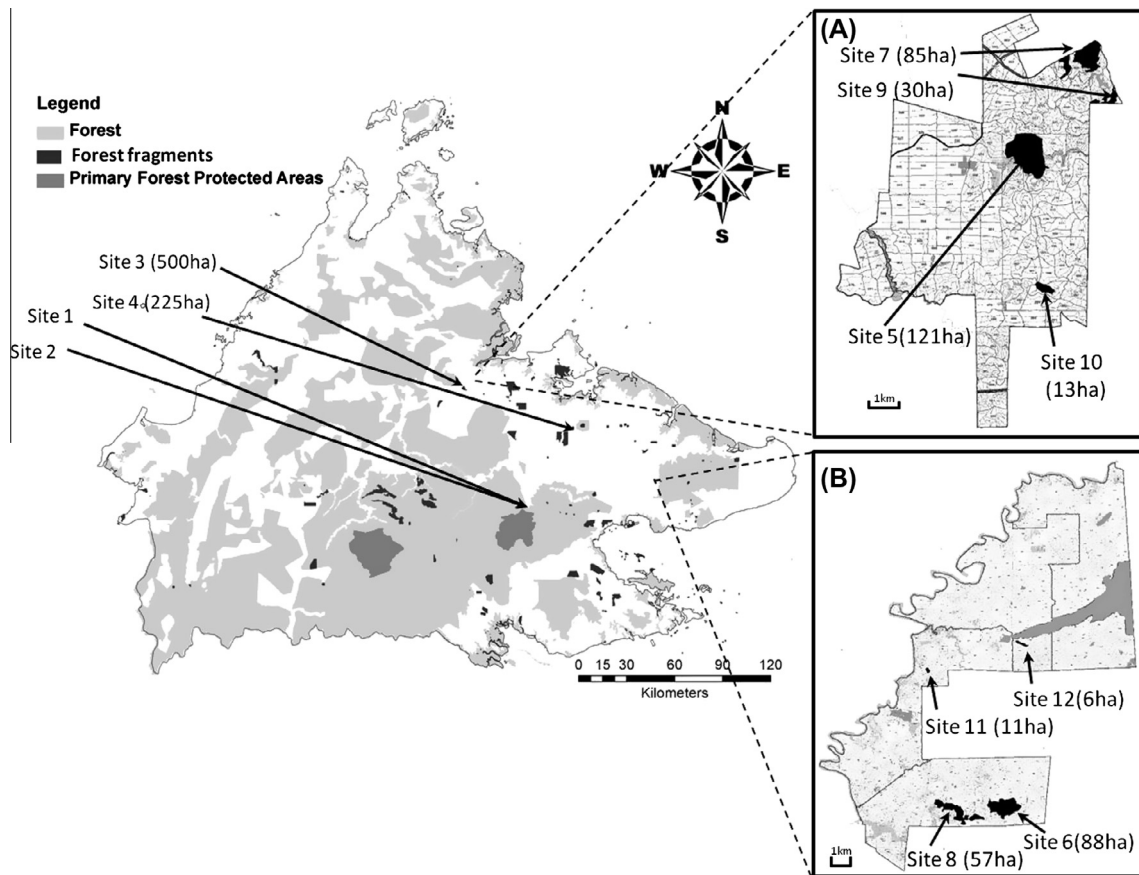


Fig. 1. Map of Sabah, indicating location and size of sampling sites. Insets show Rekahalus (inset A) and Sabahmas (inset B) oil palm plantations with sampling sites, which were compared in analysis of species richness with geographical location.

biased by proximity to large nests. We therefore used a measure of occurrence, based on presence/absence of species in each trap at a station (i.e. a species can have a maximum of 10 occurrences per station) for richness estimators which require an abundance value. A paired *t*-test was used to examine differences in species richness between forest and oil palm ($N = 12$ sites, in SPSS v.18, SPSS Inc., 2009).

2.4. Factors affecting species richness in forest fragments

We examined species richness of ants in forest fragments in relation to fragment area, forest quality, isolation of fragments from continuous forest. We also included distance from coast (as a proxy for time since isolation, Benedick et al., 2007). Continuous forest study sites were excluded from these analyses ($N = 10$ fragment sites). To assess forest quality the following measurements were recorded in the proximity of transects by JML (sites 1–4) and MJMS (sites 5–12; following Hamer et al., 2003): the distance and girth at breast height (GBH) of the two nearest large trees (>0.6 m GBH) in each of four quadrants within a 30 m radius of the centre of the station; the distance and GBH of the two nearest saplings (0.1–0.6 m) in each of the four quadrants; the percentage vegetation cover at canopy and ground levels estimated by eye by two independent observers within the 30 m radius, and shade cover measured using a densiometer (Lemmon, 1956). The number of locations where vegetation was measured differed depending on the size of the forest fragment (from 3 locations in site 12 to 15 locations in site 4). A measure of forest quality at each site was extracted from a Principal Components Analysis of vegetation structure (PCA, conducted in SPSS, Pearman, 2002; Hamer et al., 2003)

which included seven variables; mean tree GBH (cm), mean sapling GBH (cm), tree density (trees/ha = $10,000 \times \text{area, m}^2$, of four quadrants based on distance of furthest tree in each quadrant/No. trees), sapling density (saplings/ha), vegetation cover (%) at canopy and ground levels, and shade cover (%). Vegetation variables were transformed prior to analysis to normalise the data, and a mean PC1 value was computed for each site. Forest fragment areas (ha) were obtained from the Sabah Forestry Department and plantation owners' maps, and isolation was measured as the distance (km) from the edge of the fragment to the nearest continuous forest edge, from a regional map of Sabah.

We used generalised linear models (GLMs, in R; R Development Core Team, 2008) with a quasi-poisson error distribution to identify relationships of fragment species richness with forest quality, fragment area (ln transformed), fragment isolation (distance from continuous forest) and distance from coast. The initial model contained all predictor variables, and variables were removed from the model in order of least significance. Interaction terms were also included in initial models, and removed if found to be non-significant. There was an outlier associated with the isolation variable (Site 4) and so this data point was removed from the models which included this variable ($N = 9$ sites analysed), however the complete data set was used in subsequent models which did not include isolation ($N = 10$ sites). *F*-tests were used to test for significant differences in the goodness of fit between the best nested models, and if no significant difference was detected between two models, the simplest model was selected. Other richness estimators were analysed using using general linear models (LMs in R, see Table A2) but they did not qualitatively affect our conclusions and so we do not report them here.

2.5. Relationships between ant species richness in fragments and adjacent plantations

We used a GLM with quasi-poisson error distribution to test the hypothesis that species richness in oil palm was related to that of adjacent forest. Other richness estimators were tested (continuous indices were analysed LMs, see Table A2). In order to examine the effect of potential variation in habitat within plantations, mean percentage groundcover in plantations (estimated within a 30 m radius at each station) was also included in the model. We included the continuous forest sites in the analysis, but also re-ran the model to check whether the relationship held when only the fragment sites were included.

2.6. Spillover effects

We examined whether or not any observed relationships were due to a spillover of forest species from fragments into oil palm by using ANCOVA (in SPSS, $N = 12$ sites) to test for declines in species richness on oil palm transects with distance from the forest edge. Species richness at station was ln-transformed to account for exponential declines in richness which would be expected if spillover was due to dispersal effects (Hanski, 1999; Lucey and Hill, 2012). We also examined alternatives to spillover and looked for evidence that species richness patterns could be affected by the level of groundcover in plantations (see Supplementary information a4), or by pre-clearance geographic variation in forest biodiversity, using t -tests and by inspection of non-metric multi-dimensional scaling (NMDS) output plots (see below) for evidence of clustering of species assemblages in relation to proximity of study sites.

2.7. Faunal composition and trophic organisation of ant assemblages

To investigate similarity in species composition between sampling stations in forest fragments and adjacent oil palm, we used non-metric multi-dimensional scaling (NMDS using SPSS) and tested for significant differences among sites and habitat types using ANOSIM in R. We then investigated how the trophic organisation of ant communities in forest and oil palm was affected by forest fragment characteristics. Trophic positions of ant species collected from the forest floor in primary forest within Danum Valley Conservation Area were obtained from Woodcock et al. (2012), based on nitrogen isotope ratios ($\delta^{15}\text{N}$) converted to measures of trophic position following Post (2002). A trophic position of 2 indicates an obligate herbivore and a trophic position of 3 indicates a species that (on average) feeds one trophic level above obligate herbivores, with higher trophic positions indicating more carnivorous diets. A single trophic position value was assigned per species, and where there was no trophic level information for a species, a value at the genus level was allocated based on a mean of the known trophic positions of species within the same genus (Gibb and Cunningham, 2011). Using LMs (in R), weighted by sample size (number of species sampled per site), we first examined whether the average trophic position of ant species in forest fragment sites was related to forest area, vegetation quality or species richness in forest, or any combination of variables. We then examined factors affecting the average trophic position of ants in oil palm in relation to: average trophic position in adjacent forest, species richness in oil palm, species richness in forest, fragment area, quality of adjacent forest, and combinations of these variables. As previously, F -tests were used to test for significant differences in the goodness of fit between the best nested models, and if no significant difference was detected between two models, the simplest model was selected.

3. Results

3.1. Species richness

We sampled 36,657 ants, comprising 20,893 from forest, 11,484 from oil palm and 4280 from stations at the ecotone. This resulted in 1692 trap occurrences (i.e. presence of species in a pit-fall trap) in forest and 1316 trap occurrences in oil palm. Paired t -tests showed that occurrences were consistently lower in oil palm than in adjacent forest ($t_{11} = 2.66$, $p = 0.02$). We identified 237 species and morpho-species (together hereafter termed 'species'), comprising 167 species in forest and 130 species in oil palm. Species richness was 15% lower on average in oil palm sites than in adjacent forest sites (paired t -test, $t_{11} = 2.34$, $p = 0.04$, Table A1), and there was an overall decrease of ant species richness of 22% in oil palm compared to forest.

3.2. Determinants of species richness in forest fragments

In forest (including continuous forest), Principal Component Analysis of vegetation structure extracted three principal components, the first of which (PC1) accounted for 38% of variation in the data (for PCA results see Table A3). A high PC1 score represented forest with a high density of large trees and high canopy cover. Thus we conclude that PC1 describes relatively undisturbed high-quality forest. PC1 was highest at the continuous forest sites, but was not correlated with fragment area (GLM, $p = 0.2$) indicating that forest quality was not necessarily dependent on the size of fragments. Examination of GLMs found that fragment area alone was the best predictor of species richness in fragments (GLM, species richness by $\ln(\text{area})$; deviance explained = 0.52, $F_{1,8} = 8.93$, $p = 0.02$, Fig. 2). Isolation was not a significant predictor of species richness ($p = 0.6$) and so was removed from the model first. An F -test confirmed that neither area with vegetation quality ($p = 0.2$) nor area with distance from coast ($p = 0.5$) were significantly better at explaining variation in species richness than area alone (see Table 1). There were no significant interactions between covariates ($p > 0.05$).

3.3. Relationships between richness in fragments and adjacent plantations

The smallest forest fragment (Site 12) was an outlier with unusually high richness in the adjacent plantation (Fig. 3), possibly due to its close proximity to a large 122,500 ha forest reserve (Fig. 1). When this site was excluded there was a significant positive relationship between species richness in forest and adjacent oil palm (GLM, deviance explained = 0.6, $F_{1,9} = 13.84$, $p = 0.005$, Fig. 3; see Table A2 for results using other species richness estimators). This relationship was maintained when the two sites with continuous forest were also excluded from the analysis (GLM, deviance explained = 0.58, $F_{1,7} = 9.66$, $p = 0.02$). Percentage groundcover in plantations was not important for explaining ant species richness ($p = 0.6$ for $N = 9$ sites) and so was removed from the model (see Appendix A4). Thus ant species richness was higher in plantations adjacent to forest sites with high richness.

3.4. Spillover effects

The number of species sampled at each station (ln transformed) in plantations decreased significantly with increasing distance from the ecotone (ANCOVA combining data from 12 study sites, adjusted $R^2 = 0.28$, slope = -0.006 , distance effect, $F_{1,59} = 6.89$, $p = 0.01$; Fig. 4). There was no interaction between site and distance from the ecotone (ANCOVA, transect * distance,

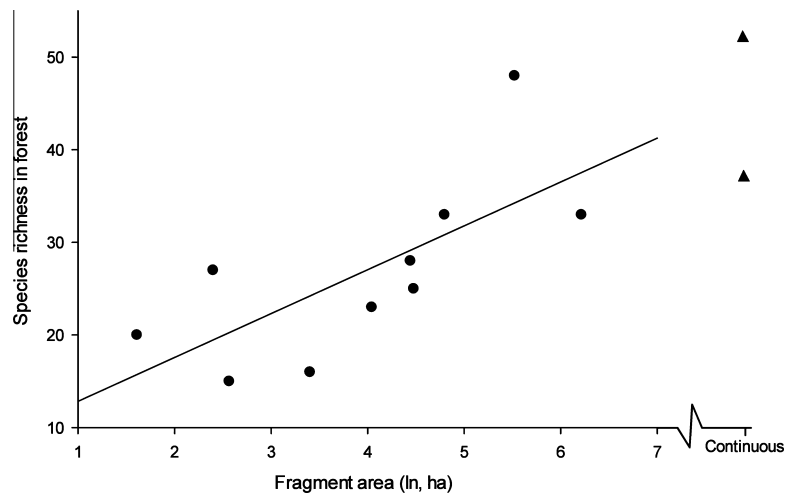


Fig. 2. Species-area relationship in forest fragments. Triangles show continuous forest sites, which were not included in the analysis but plotted for visual comparison with data from forest fragments.

Table 1
Results of generalised linear models which test for the best combination of variables for predicting ant species richness in forest fragments. Area of forest fragment is measured in ha, and PC1 is the first principal component of forest vegetation structure. PC1 measures forest quality (see main text for details).

	<i>n</i> ^a	Deviance explained	Degrees of freedom	<i>F</i> value	<i>P</i> value
ln(area) + PC1 + isolation	9	0.73	3,5	4.62	0.1
ln(area) + distance from coast	10	0.57	2,7	4.63	0.05
ln(area) + PC1	10	0.65	2,7	6.11	0.03
ln(area)	10	0.53	1,8	8.93	0.02

^a An outlier site in the isolation variable was removed in model 1, but included in subsequent models which did not include the isolation variable.

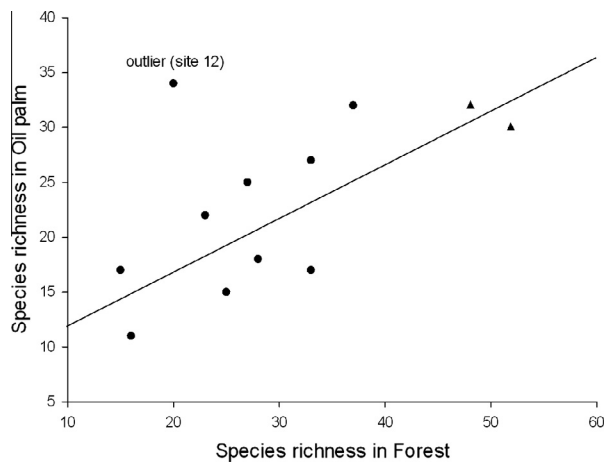


Fig. 3. The relationship between ant species richness in forest sites and adjacent oil palm plantations. Triangles show continuous forest sites. Line of best fit indicates relationship when outlying site was excluded from the analysis.

$F_{11,48} = 1.42$, $p = 0.2$), indicating that the slope of the relationship was similar across sites. There was no evidence of any effect of pre-clearance patterns on forest diversity because proximity of sites did not affect richness patterns (t -test comparing richness of sites in central northeast (Fig. 1 inset A) and eastern (Fig. 1 inset B) Sabah; $t_6 = 1.6$, $p = 0.8$), nor was there any evidence that the amount of groundcover in plantations was important for species richness at the local level (see Appendix A4). Thus we conclude that species richness of ants in plantations was affected by spillover from adjacent forest.

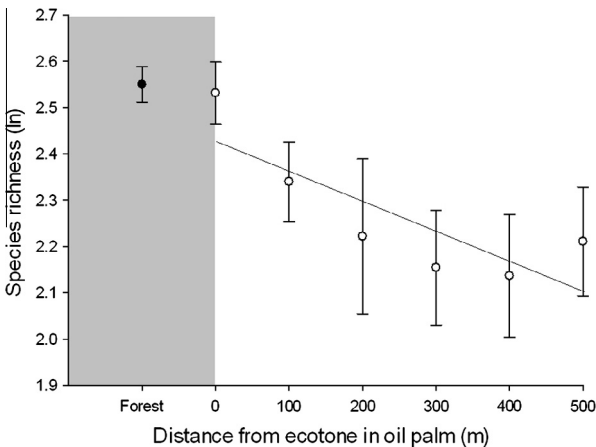


Fig. 4. Spillover of species into oil palm plantations. Decline in species richness along oil palm transects with distance from the forest edge. Grey shading and solid symbols represent forest sampling stations, white shading and hollow symbols represent oil palm sampling stations. Error bars are standard error of the mean number of species sampled at stations.

3.5. Faunal composition and trophic organisation

Non-metric multidimensional scaling showed that faunal composition was significantly different between large (>200 ha and continuous forest) and small (<200 ha) forest sites, and this separation by size was evident in both forest and oil palm assemblages (ANOSIM $R = 0.82$, $p < 0.001$, Fig. 5). There was also a significant difference in species composition between large forest fragments and adjacent oil palm (ANOSIM $R = 0.63$, $p = 0.03$, Fig. 5) but not

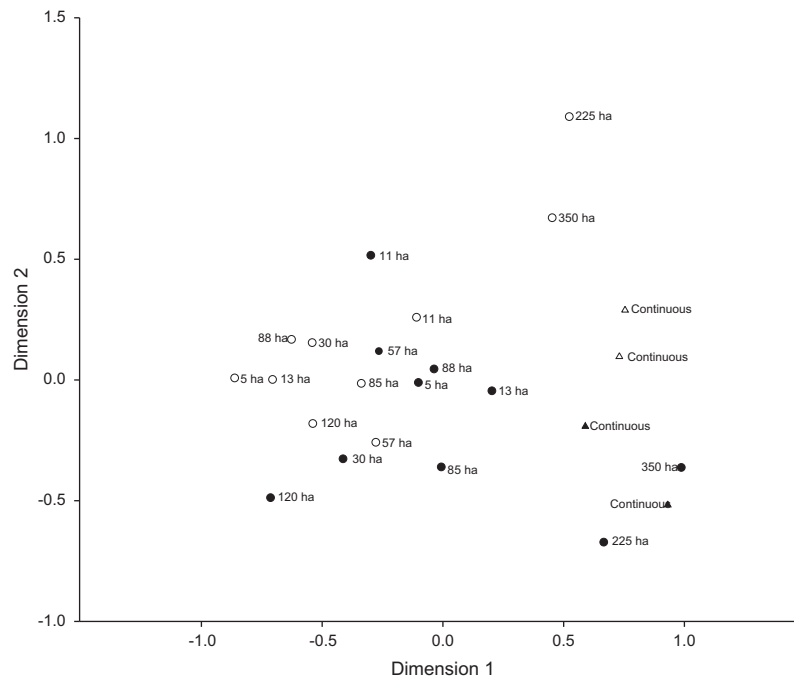


Fig. 5. Non-metric multidimensional scaling plot of species community similarity among forest (solid symbols) and oil palm (hollow symbols) sites. Triangles are sites in/adjacent to continuous forest. The area of the forest (or adjacent forest for oil palm sites) is annotated next to the data point.

between small fragments and adjacent oil palm ($R = 0.11$, $p = 0.1$, Fig. 5), indicating that small fragments contributed few additional species to the biodiversity of oil palm landscapes.

Data on trophic positions were available for 263 study species. The mean trophic position of species in forest was not predicted by fragment area (ln-transformed), isolation, species richness, or vegetation structure (PC1) (linear models of all combinations of predictor variables; all $p > 0.05$). However, the mean trophic position of species in oil palm was predicted by a combination of forest species richness and mean trophic position of species in adjacent forest (LM, *adjusted* $R^2 = 0.70$, $F_{2,7} = 11.35$, $p = 0.006$). This model was a significantly better fit than forest richness only (F -test, $F_{1,6} = 8.51$, $p = 0.02$). The mean trophic position of species in oil palm was also significantly related to the area (ln transformed) of adjacent forest (LM, *adjusted* $R^2 = 0.51$, $F_{1,8} = 10.44$, $p = 0.01$) but this variable did not significantly improve the model fit (LM, *adjusted* $R^2 = 0.65$, $F_{3,6} = 6.52$, $p = 0.03$; F test, $p = 0.9$). Thus trophic organisation of ant assemblages in oil palm was related to characteristics of adjacent forest sites, providing further support for spillover effects. Species with a trophic position > 3.5 (largely carnivorous, 20 species in oil palm, 71 species in total) comprised 10–25% of occurrences in oil palm adjacent to large and continuous forest but comprised between 0% and 0.09% of occurrences in oil palm adjacent to small forest fragments (Table A1), indicating that decreases in average trophic position were explained partly by the absence of carnivorous ants from plantations next to small forest fragments.

4. Discussion

4.1. Species richness in forest and adjacent plantations

Our study revealed an overall decline in species richness of 22% in oil palm compared to forest, thus confirming other studies showing that conversion of forest to oil palm plantations results in a reduction in species richness (Fitzherbert et al., 2008). We sampled only ground-level ants from a single microhabitat and so any beta diversity resulting from other aspects of habitat

complexity, such as canopy structure, was not included in our study. Including other aspects of habitat may increase the observed difference in diversity between forest and plantation sites (Faile et al., 2010).

Ant species richness within oil palm plantations could be predicted by the species richness in adjacent forest fragments, and fragment size was shown to be an important predictor of species richness within fragments, as expected from principles of island biogeography (MacArthur and Wilson, 1967). Studies of crops such as watermelon (Kremen et al., 2004) and coffee (Ricketts et al., 2004) showed that natural habitat within the agricultural landscape improved species richness and ecosystem services (e.g. pollination and pest control). Importantly, our results demonstrate a link between species richness within forest and species richness in nearby plantations, and identify that the size of the forest fragment is an important consideration for boosting species richness in the oil palm landscape, but that forest quality and isolation of forest fragments are less important. Habitat quality can vary within oil palm plantations (Luskin and Potts, 2011) and this might impact on species richness (Koh, 2008; Nájera and Simonetti, 2010). In our study, the vegetation structure of plantations was very homogeneous: palm trees at all sites were mature and fruiting, with a closed canopy several metres above ground level. The proportion of groundcover was the main source of variation within plantations, but there was no evidence that this affected ant species richness in plantations, and so we are confident that patterns of species richness were unlikely to be a consequence of variation in habitat quality in plantations.

4.2. Spillover effects

Our study also showed that species richness declined along oil palm transects with increasing distance from the forest edge, supporting the notion that fragments of natural forest contribute to boosting diversity within plantations via spillover effects. Richness declined with distance from forest edge when combining data from all sites, and a trend of decline was evident at the majority of sites

(8 out of 12) when data were analysed separately by site. This contrasts with our previous study reporting little evidence of spillover by ants when just two sites were examined (Lucey and Hill, 2012). Unfortunately there was not sufficient statistical power in our data in this study to examine whether the slope or intercept of the richness decline was affected by forest site properties, but evidence that ant diversity in oil palm was related to adjacent forest sites (Fig. 3) suggests that spillover patterns may be affected by properties of the adjacent forest habitat. Proximity to forest might also affect environmental conditions in the plantation making it more suitable for ants, but evidence from this study and other studies (Livingston et al., 2013; Lucey and Hill, 2012; Luskin and Potts, 2011) suggests that microclimate and vegetation structure do not vary within plantations over the distances covered by our study, therefore local environmental conditions are unlikely to be responsible for the patterns in ant species richness we report. In support of our conclusions about spillover affecting richness patterns, we found no evidence that our findings were an artefact of pre-conversion landscape-level variation in ant species richness, because sites that were closer to each other did not share more similar species richness. The number of species in habitat fragments may take time to decline to a new equilibrium post-isolation (Tilman et al., 2001) and so species richness could have been higher at sites further from the coast, assuming that forest clearance began in coastal areas and progressed inland (Benedick et al., 2007), but we found no evidence of this. The strength of relationships between species richness in forest and forest fragment size suggests that it is properties of the forest which are important for maintaining local diversity, and this has a knock-on effect on species richness within plantations. Taken together, our findings indicate that spillover effects, with forest species colonising adjacent plantations, are the most likely explanation for the observed relationships.

Our study indicates that while some ant species persist successfully in plantations, increased plantation diversity near the ecotone may result from source-sink dynamics (Pulliam, 1988), with sink populations in plantations supported by source populations within adjacent forest. We included only flightless workers in our study, which indicate the presence of established colonies at sample sites (Longino et al., 2002), and we excluded potentially transient reproductive individuals. Therefore, our results contrast with other studies, such as those of butterflies and birds, where spillover effects may also include dispersal of non-breeding individuals (Dolia et al., 2008; Koh, 2008; Lucey and Hill, 2012). Our studies of ants and butterflies suggest that there are differences in the strength of spillover between taxa, and that spillover effects may be stronger in vagrant non-breeders than in residents (Lucey and Hill, 2012). This implies that fragments may not only boost local diversity but also aid movement of forest-dependent species through the agricultural matrix.

4.3. Faunal composition and predatory species

We showed that large (>200 ha fragments and continuous sites) forest areas contained species assemblages which were distinct from those in oil palm, but that assemblages in small fragments (<200 ha) were less distinguishable from adjacent oil palm assemblages. This indicates that small (<200 ha) fragments provide few additional ant species which do not already persist in the planted area, hence lower species richness in oil palm plantations which are adjacent to small fragments may be caused by a lack of spillover of additional species from these fragments.

Theory suggests that species at the highest trophic levels are most vulnerable to extinction from habitat disturbance (Bascompte and Sole, 1998; Hill et al., 2011). We found that the average trophic position of species in forest was not related to any of the forest properties we measured, but that the average

trophic position of species within oil palm could be predicted from the richness and average trophic position of species in the adjacent forest. Because species richness in forest was strongly associated with forest area, we conclude that the size of forest fragments affects the proportion of predatory ants within plantations, even though trophic organisation did not appear to alter within the forest fragments themselves. This is an important consideration from an agricultural perspective, because predators can play an important role in pest management (Way and Khoo, 1992). Other studies have shown that proximity to forest can boost ecosystem functions such as pollination and predation by parasitoids (Klein et al., 2006; Ricketts, 2004), and our results suggest that forest fragment size could affect ecosystem functioning within oil palm plantations. The fact that the trophic organisation of ant assemblages varied within plantations with respect to features of the adjacent forest, but did not vary within forest fragments might suggest that composition of ant assemblages in plantations adjacent to large fragments are not only affected by spillover of forest predatory species from large fragments, but that conditions in the plantation near to large fragments are more favourable for predators. For example, there may be more spillover of prey species from adjacent forest, which enables more predatory species to persist in plantations closer to large areas of forest. More research is needed to examine whether the increase in predatory species could benefit pest control in plantations, or whether this benefit is negated by the presence of more prey.

Trophic positions of ant species were obtained from specimens collected in primary forest, and could differ between habitats as a result of changes in diet or, for predators, in the trophic positions of prey (Edwards et al., 2013; Woodcock et al., 2013). This will be an important issue for future research. However, our results are robust in showing that the presence of large areas of natural forest impacts on the trophic composition of ant species within plantations.

4.4. Conservation implications

There has been much debate in recent years as to whether a land-sharing or a land-sparing conservation approach is more appropriate in tropical agricultural landscapes (Green et al., 2005). Some studies suggest that biodiversity conservation should focus on making agricultural areas “wildlife-friendly” (e.g. Koh et al., 2009; Perfecto and Vandermeer, 2010) whilst others argue that agriculture should be intensified so that greater areas of continuous natural habitat can be protected (e.g. Edwards et al., 2010; Ghazoul et al., 2010). In this study, we showed that species richness in plantations can be improved by the presence of large patches of forest. If there are pest control benefits or other ecosystem services provided by the forest to the plantation, this might reduce the necessity for intensive plantation management thereby **further improving the plantation matrix for biodiversity** (Hole et al., 2005; Koh, 2008; Maas et al., 2013; Ricketts, 2004). However, very small fragments provided negligible species diversity benefits, even when the contribution of species within the fragments themselves was considered. Although these small forest fragments might be better given over to agriculture, such small fragments may persist if, for example, they are too steep or have poor soil and so remain unplanted (RSPO, 2013). These small fragments might benefit from forest restoration to enhance their habitat quality (Edwards et al., 2009, 2012), and could also act as “stepping stone” habitats for some vagile species to move across the landscape (Proctor et al., 2011; Uezu et al., 2008), although our results indicated that habitat quality was not important for maintaining ant species richness once fragment area had been accounted for. Therefore, we conclude that conservation efforts and sustainable plantation design should focus primarily on protecting larger forest

patches. Our study of ten fragments in Sabah indicates that for ants this area should be at least 200 ha, but more research is required to establish whether this would be a suitable recommendation for other taxa and other regions. The challenge is to determine the optimum size and placement of fragments within agricultural landscapes that balance economic yields and landscape biodiversity.

Acknowledgements

We thank the Economic Planning Units of the Prime Minister's Department, Yayasan Sabah, Danum Valley Management Committee, A. Wong, Mr. Chin, C. Beamish and Wilmar International Ltd. for permission to work at sites, G. Reynolds, the Royal Society SE Asia Rainforest Research Programme, M. Tarman, R. Lim, U. Jami and staff at Danum Valley Field Centre for logistical support, Yen Yee Loh, C. Beamish and Wilmar international Ltd for providing the maps in Fig. 1 and two anonymous reviewers for comments which greatly improved the manuscript. The project was funded by the UK Natural Environment Research Council and the UK Government Darwin Initiative (Defra). This paper constitutes Publication no. 614 of the Royal Society SEARRP.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.11.014>.

References

- Ant Base. <www.antbase.net>. (accessed 10.9.2013).
- AntWeb. <www.antweb.org>. (accessed 10.9.2013).
- Bascompte, J., Sole, R.V., 1998. Effects of habitat destruction in a prey-predator metapopulation model. *J. Theor. Biol.* 195, 383–393.
- Benedick, S., Hill, J.K., Mustaffa, N., Chey, V.K., Maryati, M., Searle, J.B., Schilthuisen, M., Hamer, K.C., 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *J. Appl. Ecol.* 43, 967–977.
- Benedick, S., White, T.A., Searle, J.B., Hamer, K.C., Mustaffa, N., Vun Khen, C., Mohamed, M., Schilthuisen, M., Hill, J.K., 2007. Impacts of habitat fragmentation on genetic diversity in a tropical forest butterfly on Borneo. *J. Trop. Ecol.* 23, 623–634.
- Bluthgen, N., Gebauer, G., Fiedler, K., 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. *Oecologia* 137, 426–435.
- Bruhl, C., Eltz, T., 2010. Fueling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodivers. Conserv.* 19, 519–529.
- Bruhl, C.A., Eltz, T., Linsenmair, K.E., 2003. Size does matter - effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. *Biodivers. Conserv.* 12, 1371–1389.
- Carney, S., Byerley, M.B., Holway, D., 2003. Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia* 135, 576–582.
- Colwell, R.K., 2006. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8. Persistent URL <purl.oclc.org/estimates>.
- Corley, R.H.V., 2009. How much palm oil do we need? *Environ. Sci. Policy* 12, 134–139.
- Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agric. Ecosyst. Environ.* 98, 321–329.
- De Vries, P.J., Murray, D., Lande, R., 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* 62, 343–364.
- Dolia, J., Devy, M.S., Aravind, N.A., Kumar, A., 2008. Adult butterfly communities in coffee plantations around a protected area in the Western Ghats, India. *Anim. Conserv.* 11, 26–34.
- Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic Appl. Ecol.* 4, 129–138.
- Edwards, D.P., Ansell, F.A., Ahmad, A.H., Nilus, R., Hamer, K.C., 2009. The value of rehabilitating logged rainforest for birds. *Conserv. Biol.* 23, 1628–1633.
- 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.
- Edwards, D., Backhouse, A., Wheeler, C., Khen, C., Hamer, K., 2012. Impacts of logging and rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *J. Insect Conserv.* 16, 591–599.
- Edwards, D.P., Woodcock, P., Newton, R.J., Edwards, F.A., Andrews, D.J.R., Docherty, T.D.S., Mitchell, S.L., Ota, T., Benedick, S., Bottrell, S.H., Hamer, K.C., 2013. Trophic flexibility and the persistence of understory birds in intensively logged rainforest. *Conserv. Biol.*, n/a–n/a.
- Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y.C., Eggleton, P., Foster, W.A., 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic Appl. Ecol.* 11, 337–345.
- Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brulh, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* 23, 538–545.
- Franklin, J.F., Lindenmayer, D.B., 2009. Importance of matrix habitats in maintaining biological diversity. *Proc. Nat. Acad. Sci.* 106, 349–350.
- Ghazoul, J., Koh, L.P., Butler, R.A., 2010. A REDD light for wildlife-friendly farming. *Conserv. Biol.* 24, 644–645.
- Gibb, H., Cunningham, S.A., 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. *J. Anim. Ecol.* 80, 119–127.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M., Chey, V.K., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *J. Appl. Ecol.* 40, 150–162.
- Hanski, I., 1999. Metapopulation Ecology. Oxford University Press.
- Hashimoto, Y., 2003. Identification Guide to ant Genera of Borneo. HCV resource network. URL: <www.hcvnetwork.org>. (accessed 10.9.13).
- Henderson, P.A., Seaby, R.M.H., 1998. Species Richness and Diversity v. 2, PICSES Conservation Ltd., Oxford.
- Hill, J.K., Gray, M.A., Khen, C.V., Benedick, S., Tawatao, N., Hamer, K.C., 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? *Philos. Trans. Royal Soc. B: Biol. Sci.* 366, 3265–3276.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? *Biol. Conserv.* 122, 113–130.
- Holldobler, B., Wilson, E.O., 1990. The Ants. Harvard University Press, Cambridge, Mass. (USA).
- Klein, A.M., Steffan-Dewenter, I., Tscharnkte, T., 2006. Rain forest promotes trophic interactions and diversity of trap-nesting hymenoptera in adjacent agroforestry. *J. Anim. Ecol.* 75, 315–323.
- Koh, L.P., 2008. Birds defend oil palms from herbivorous insects. *Ecol. Appl.* 18, 821–825.
- Koh, L.P., Levang, P., Ghazoul, J., 2009. Designer landscapes for sustainable biofuels. *Trends Ecol. Evol.* 24, 431–438.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* 7, 1109–1119.
- Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstory density. *Forest Sci.* 2, 314–320.
- 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.
- Longino, J.T., Coddington, J., Colwell, R.K., 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology* 83, 689–702.
- Lucey, J.M., Hill, J.K., 2012. Spillover of insects from rain forest into adjacent oil palm plantations. *Biotropica* 44, 368–377.
- Luskin, M.S., Potts, M.D., 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic Appl. Ecol.* 12, 540–551.
- Maas, B., Clough, Y., Tscharnkte, T., 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecol. Lett.* 16, 1480–1487.
- MacArthur, R.H., Wilson, E.O., 1967. Theory of Island Biogeography. Princeton University press, New Jersey.
- Mayfield, M., 2005. The importance of nearby forest to known and potential pollinators of oil palm (*Elaeis guineensis* Jacq.; Areaceae) in southern Costa Rica. *Econ. Bot.* 59, 190–196.
- Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. <www.maweb.org>. (accessed 10.9.13).
- Nájera, A., Simonetti, J., 2010. Can oil palm plantations become bird friendly? *Agrofor. Syst.* 80, 203–209.
- Pearman, P.B., 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understory. *Ecol. Monogr.* 72, 19–39.
- Perfecto, I., Vandermeer, J., 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv. Biol.* 16, 174–182.
- Perfecto, I., Vandermeer, J., 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *PNAS USA* 107, 5786–5791.
- Philpott, S.M., Perfecto, I., Vandermeer, J., 2008. Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. *J. Anim. Ecol.* 77, 505–511.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumption. *Ecology* 83, 703–718.
- Proctor, S., McClean, C., Hill, J., 2011. Protected areas of Borneo fail to protect forest landscapes with high habitat connectivity. *Biodivers. Conserv.* 20, 2693–2704.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *Am. Nat.* 132, 652–661.
- R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <<http://www.R-project.org>>.

- Reynolds, G., Payne, J., Sinun, W., Mosigil, G., Walsh, R.P.D., 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philos. Trans. Royal Soc. B: Biol. Sci.* 366, 3168–3176.
- 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.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. *Proc. Nat. Acad. Sci. USA* 101, 12579–12582.
- RSPO. 2013. Roundtable on Sustainable Oil Palm (RSPO): Principles and Criteria for the Production of Sustainable Palm Oil 2013. <<http://www.rspo.org/file/revisedPandC2013.pdf>>. (accessed 10.10.13).
- Sodhi, N., Posa, M., Lee, T., Bickford, D., Koh, L., Brook, B., 2010. The state and conservation of Southeast Asian biodiversity. *Biodivers. Conserv.* 19, 317–328.
- SPSS Inc., 2009. PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc.
- Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., Goodger, B., 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc.: Biol. Sci.* 268, 1791–1796.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8, 857–874.
- Uezu, A., Beyer, D., Metzger, J., 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? *Biodivers. Conserv.* 17, 1907–1922.
- Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation. *Conserv. Biol.* 21, 274–277.
- Walsh, R.P.D., Bidin, K., Blake, W.H., Chappell, N.A., Clarke, M.A., Douglas, I., Ghazali, R., Sayer, A.M., Suhaimi, J., Tych, W., Annammala, K.V., 2011. Long-term responses of rainforest erosional systems at different spatial scales to selective logging and climatic change. *Philos. Trans. Royal Soc. B: Biol. Sci.* 366, 3340–3353.
- Way, M.J., Khoo, K.C., 1992. Role of ants in pest-management. *Annu. Rev. Entomol.* 37, 479–503.
- Wilcove, D., Koh, L., 2010. Addressing the threats to biodiversity from oil-palm agriculture. *Biodivers. Conserv.* 19, 999–1007.
- Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.*
- Woodcock, P., Edwards, D.P., Fayle, T.M., Newton, R.J., Khen, C.V., Bottrell, S.H., Hamer, K.C., 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. *Philos. Trans. Royal Soc. B: Biol. Sci.* 366, 3256–3264.
- Woodcock, P., Edwards, D., Newton, R., Edwards, F., Khen, C., Bottrell, S., Hamer, K., 2012. Assessing trophic position from nitrogen isotope ratios: effective calibration against spatially varying baselines. *Naturwissenschaften* 99, 275–283.
- Woodcock, P., Edwards, D.P., Newton, R.J., Vun Khen, C., Bottrell, S.H., Hamer, K.C., 2013. Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. *PLoS ONE* 8, e60756.