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Biodiversity of leaf-litter ants in fragmented tropical rainforests of Borneo: the value of publically and privately managed forest fragments

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Abstract

In view of the rapid rate of expansion of agriculture in tropical regions, attention has focused on the potential for privately-managed rainforest patches within agricultural land to contribute to biodiversity conservation. However, these sites generally differ in their history of forest disturbance and management compared with other forest fragments, and more information is required on the biodiversity value of these privately-managed sites, particularly in oil-palm dominated landscapes of SE Asia. Here we address this issue, using tropical leaf-litter ants in rainforest fragments surrounded by mature oil palm plantations in Sabah, Borneo as a model system. We compare the species richness and composition of ant assemblages in privately-managed forest fragments (‘high conservation value’ fragments; HCVs) with those in publically-managed fragments of forest (virgin jungle reserves; VJRs) and control sites in extensive tracts of primary forest. In this way, we test the hypothesis that privately-managed and publically-managed forest fragments differ in their species richness and composition as a result of differences in history and management and hence in habitat quality. In support of this hypothesis, we found that HCVs had much poorer habitat quality than VJRs, including lower sizes and densities of trees, less canopy cover, fewer dipterocarp trees and shallower leaf litter. Consequently, HCVs supported only half the species richness of ants in VJRs, which in turn supported 70 % of the species richness of control sites, with vegetation structure and composition explaining 77 % of the variation among forest fragments in ant species richness. HCVs were also much smaller than VJRs but there was only a weak relationship between fragment size and habitat quality, and species richness was not related to fragment size. VJRs supported 78 % of the 156 species found in extensive tracts of forest whereas HCVs supported only 22 %, which was only slightly higher than the proportion previously recorded in oil palm (19 %). These data support previous findings that publically-managed VJR fragments can make an important contribution to biodiversity conservation within agricultural landscapes. However, we suggest that for these HCVs to be effective as reservoirs of biodiversity, management is required to restore vegetation structure and habitat quality, for instance through enrichment planting with native tree species.

Keywords

Biodiversity crisis
Extinction

Habitat loss
Oil palm
Species–area relationship
Sustainable agriculture

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Electronic supplementary material

The online version of this article (doi:10.1007/s10531-014-0768-5) contains supplementary material, which is available to authorized users.

Introduction

Throughout the world, previously extensive tracts of natural habitat now exist as fragments scattered across predominantly agricultural landscapes. In tropical regions, the conversion of forests to agricultural crops, often grown in monoculture, is a major threat to biodiversity, and reducing biodiversity losses in landscapes dominated by agriculture is a critical conservation concern (Tilman et al. 2001; Sodhi et al. 2010; Laurance and Edwards 2011). In view of the rapid rates of expansion of farmland and agroforestry in tropical regions and the small proportion of formally protected natural and semi-natural forest, attention has recently focused on the potential for privately owned or managed remnants of forest within agricultural crops to contribute to biodiversity conservation (Scherr and McNeely 2008; Koh et al. 2009; Lucey et al. 2014). However, whilst the value of such an approach has been evaluated for a range of agricultural systems in the neotropics (Tarabelli et al. 2005; Chan and Daily 2008; Muñoz et al. 2013), there are few such data for other tropical regions.

One of the most rapidly expanding crops in the tropics is oil palm *Elaeis guineensis* (Foster et al. 2011). Most palm oil (80 % of the global total) is produced in Malaysia and Indonesia (Fitzherbert et al. 2008), where over half of the expansion of oil palm between 1990 and 2005 occurred at the expense of forest (Koh and Wilcove 2008). About half the original cover of lowland rainforest in Southeast Asia has been lost (Sodhi et al. 2010), resulting in the sharpest declines in biodiversity of any biogeographical region (Myers et al. 2000; Butchart et al. 2004). Many of the largest palm oil producers have expressed a desire to implement environmentally-friendly management, resulting in the Roundtable on Sustainable Palm Oil (RSPO) certification program, which promotes the protection of natural forest remnants within oil palm plantations as a means of mitigating losses of biodiversity (Bhagwat and Willis 2008). However, the effectiveness of such fragments for conserving forest species has seldom been evaluated (Edwards et al. 2010).

The persistence of species within forest fragments may be influenced by vegetation structure in addition to fragment area, but the interactions between these factors and their impacts within different landscapes and species assemblages are poorly understood (Laurance and Cochrane 2001; Prugh et al. 2008), especially within complex systems such as tropical forests (Carvalho and Vasconcelos 1999; Hill et al. 2011; Uezu and Metzger 2011). For instance, many studies have examined biodiversity in fragments of near-primary rainforest (Kattan et al. 1994; Benedick et al. 2006; Muñoz et al. 2013), yet agricultural crops usually replace forest that has already been highly degraded by activities such as timber extraction (McMorrow and Talip 2001; Edwards et al. 2011). Hence the biodiversity of forest fragments remaining within agricultural landscapes may have been reduced prior to fragmentation. In addition, fragments may experience further disturbance post-fragmentation, for example, as a consequence of natural disturbance from edge effects (Laurance 1991, 2000) and from further human disturbance related to the management and protection of fragments. However, the ability of degraded forest fragments to support biodiversity is not clear, and the relative importance of fragment size and habitat quality remains obscure (Fischer and Lindenmayer 2002; Lozano-Zambrano et al. 2009; Magrach et al. 2012).

Within the State of Sabah in northern Borneo, there are long-established remnants of primary or near-primary rain forest (‘virgin jungle reserves’, VJRs), typically surrounded by oil palm plantations but managed and protected by the Sabah Forestry Department (Marsh and Greer 1992). These VJRs were first established between 1930 and 1957, and re-gazetted in 1984 for research and conservation of plant genetic resources. They support high-quality forest, although some lowintensity selective logging possibly including some illegal logging has occurred at a few sites (Sabah Forestry Department 2005). These VJR fragments contrast with patches of forest retained within oil palm plantations in keeping with RSPO principles and guidelines for increasing sustainability. RSPO-certified plantations are required to protect ‘high conservation value’ forest (HCVs) within their concessions. HCVs are defined as habitats of critical biodiversity or social value, although identification of HCV areas is more stringent for newer plantations established after 2005, and plantations that were established before 2005 also retain HCV forest in marginally plantable areas such as steep slopes. Thus, pre-2005 HCVs may not specifically have been retained to protect biodiversity, but could nonetheless provide the only semblance of remaining natural habitat within plantations. These different types of fragments provide an opportunity to examine the retention of biodiversity within a landscape of intensive agriculture. Previous studies of invertebrates in Sabah indicated that even relatively small VJRs supported populations of forest-dependent species that would not otherwise be able to persist in the agricultural landscape (Benedick et al. 2006; Hill et al. 2011). This contrasts with data indicating that HCVs supported few species of forest birds or ants (Edwards et al. 2010; Lucey et al. 2014). These studies suggest a qualitative difference in the conservation value of these different types of forest fragment, but direct comparisons have previously been lacking.

Here, we focus on ground-dwelling ants, which attain high densities and species richness in tropical forests and play important functional roles in seed dispersal, nutrient cycling and improving soil structure, and as both predators and prey (Wilson and Holldobler 2005; Milton and Kaspari 2007; Philpott et al. 2008; Woodcock et al. 2013). We compare privately-managed HCVs and publically-managed VJRs with ‘control’ sites in extensive tracts of forest, and we examine the relative importance of habitat quality and size of fragments for ant species richness and composition. In this way, we test the hypothesis that privately-managed and publically-managed forest fragments differ in their species richness and composition as a result of differences in history and management and hence in habitat quality.

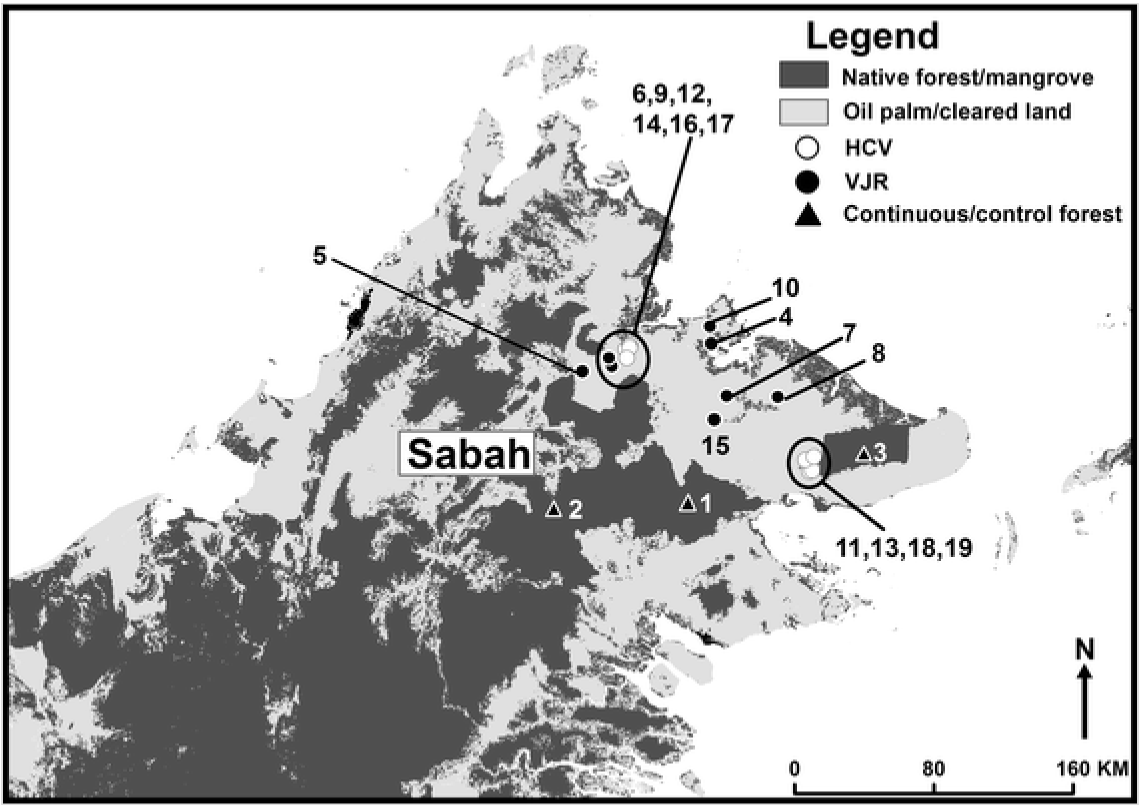
Methods

Study sites

Ground-dwelling ants were sampled at 19 forest sites in Sabah (Fig. 1), comprising three control sites in extensive tracts of protected forest, eight VJRs and eight HCVs (sizes of VJRs and HCV study sites we examined spanned the range of sizes present within the landscape). Two of the control sites (Danum Valley and Maliau Basin Conservation Areas) were within a single large area (*c.* 1 million ha) of continuous forest, with the third (Tabin Wildlife Reserve) comprising >120,000 ha of protected forest (Fig. 1; Table S1). All VJRs and HCV fragments were surrounded by oil palm plantations comprising mature fruiting trees (>7 years old) that were 10–15 m high and planted about 10 m apart. Data on fragment areas were obtained from plantation owners and the Sabah Forestry Department. Climate at study sites is typical of the moist aseasonal tropics, with an average annual temperature of 27.2 °C and average annual rainfall of 3,049 mm per year (Walsh et al. 2011).

Fig. 1

Sampling sites in Sabah, Malaysian Borneo. *Dark grey* shading shows forest cover and *light grey* shaded areas are non-forest areas, which are generally oil palm plantations. Land cover classifications are based on Miettinen et al. (2011). Locations of control sites (*triangles*), VJRs (*solid circles*) and HCVs (*hollow circles*) are shown. *Numbers* refer to site locations listed in Table S1



Sampling of ants

Ground-dwelling ants were sampled between July 2006 and September 2010 at stations 500 m apart along transects at each of 19 study sites (1 transect per site; 73 stations in total; most sites had five stations but small fragments (<90 ha) could support only 1–3 stations). All sampling years were similar in terms of environmental conditions (no mast-fruiting, droughts or floods at study sites). Leaf litter and loose topsoil were collected from five 1 m^2 quadrats positioned 10 m apart (forming a cross shape) at each station (365 quadrats in total). Quadrats were placed at least 10 m apart to ensure that sampled individuals were likely to have come from different nests (Kaspari 1993; Bruhl et al. 2003). Soil and leaf litter was sieved (mesh = 1 cm^2) to remove debris and samples were then emptied into mesh bags and hung inside modified Winkler bags in the shade for three days to extract ants (Bestelmeyer 2000), which were stored in 95 % alcohol. To ensure efficient sampling of ants, samples were taken only after three or more days without heavy rain (Woodcock et al. 2011).

Worker ants were identified (by N.T.) first to genus following existing keys (Bolton 1994; Hashimoto 2003) then to species using reference collections at the Natural History Museum (London), the California Academy of Sciences and Borneensis Collection (Universiti Malaysia Sabah), and on-line resources (http://www.antweb.org; http://www.antbase.net). Undescribed species that occur in www.antweb.org were given the same number as the on-line collection, and morphospecies not featured were given new reference numbers (http://www.antweb.org/borneo.jsp) and submitted to the collection. Voucher specimens have been deposited at the Forest Research Centre, Sandakan, Sabah.

Assessment of habitat quality

To characterize the structure and composition of the vegetation in forest fragments, the following data were recorded at stations in 15 of the 16 fragments where ants were sampled (all except Sepilok; VJR site 4 in Fig. 1): circumference at breast height, identity (Family Dipterocarpaceae or other) and height to the point of inversion (site of first major branch, recorded as upper or lower half of the trunk; Torquebiau 1986) of the two nearest large trees (circumference > 0.6 m) in each of four quadrants (i.e. four non-overlapping circular arcs, each of 90°) centred at the station (eight trees per station in total); number of large trees in each quadrant with 30 m of each station; circumference at breast height and number of saplings (circumference 0.1–0.6 m) within 10 m of each station; estimated vegetation cover (%) at ground level, canopy level and combined vegetation cover (%) above head height (i.e. canopy closure; Jennings et al. 1999) within 30 m of each station. Tree circumferences were measured to the nearest 1 cm with a tape-measure. Trees were identified with the assistance of staff from Danum Valley Field Centre ~~Centre~~, Sabah, using diagnostic features in Meijer and Wood (1964) and Newman et al. (1996, 1998). Ground cover and canopy cover, to the nearest 5 %, were recorded as the means of at least two independent visual estimates; these varied among recorders by no more than 10 %. Canopy closure was the mean of four estimates in each cardinal direction, measured with a spherical densiometer (Jennings et al. 1999). In addition, we measured leaf litter depth in five 1 m^2 quadrats per station (the same as those used to sample ants), to the nearest 1 cm with a ruler prior to sampling of ants.

Data were used to calculate the density of trees and saplings at each station. They were then normalized where necessary (see Table 1 for transformations of each variable) and analyzed by a principal components analysis (PCA; Picozzi et al. 1992; Hamer et al. 1997). This allowed ordination of differences among stations in vegetation structure, by generating a number of independent factors comprising sums of weighted variables, with each variable standardized (i.e. mean across all stations = 0, SD = 1).

Table 1

Contributions of different variables to two principal components of variation in vegetation structure

	PC1	**PC2**
Canopy closure (%, logit)[a]	0.0794	**−0.5984**
Canopy cover (%, asin)[a]	**0.3898**	−0.1107
Ground cover (%, ln)	−0.0107	**0.4626**
Tree cbh[b] (cm, lnln)	**0.4128**	0.2572
Point of inversion (ln)	**0.4658**	0.0753
Tree density (ha^{-1}, sqrt)	**0.3423**	0.0155
Prop dipterocarps (asin)	**0.3572**	−0.2097
Sapling cbh (cm, ln)[a]	0.0546	**0.5241**
Sapling density (ha^{-1}, sqrt)	0.2282	−0.1413
Leaf litter depth (cm, sqrt)	**0.3929**	0.0703

Variables making main contributions to each principal component (factor loading ≥ 0.3) are in bold. Terms in brackets indicate units, followed by transformations made to normalize each variable prior to analysis

[a] See "Results" section, "Assessment of habitat quality" section for differences between canopy closure and cover

[b] Circumference at breast height

Ant species richness

Species richness is highly sensitive to sample size and so the numbers of species recorded at sites could have reflected the numbers of individuals sampled rather than the numbers of species inhabiting different forest patches. Hence we used a jack-knifed estimate to assess the likely species pool (S_{max}) at each station from the number of species observed (S_{obs}), using the formula $S_{max} = S_{obs} + a(n - 1/n)$ where *n* is the number of samples (i.e. 5 quadrats per station) and *a* is the number of species in only one sample (Heltshe and Forrester 1983; Smith and Van Belle 1984).

To account for the lower number of sampling stations in small fragments, our response variable for analysis of species richness was the mean of S_{max} values for stations in each fragment. We used general linear modelling (GLM) to relate species richness in forest fragments to $\log_{10}$ fragment area, vegetation structure (principal component scores) and type of fragment (VJR or HCV). Fragment areas and principal component scores were included in the model as covariates and type of fragment as a fixed effect. To find the best-fitting model and check the robustness of our results, non-significant terms ($P \geq 0.05$) were serially deleted to ensure that this did not qualitatively affect the significance of the remaining terms, producing a minimum adequate model (MAM; Crawley 2007). In addition, as a further check of robustness, we repeated the analysis including only $\log_{10}$ fragment area and fragment type, and then including only $\log_{10}$ fragment area, to check that our results were not confounded by any covariance among fragment type, area and habitat quality.

Species composition

Ants live colonially in nests and so conspecific individuals sampled in the same quadrat cannot be considered independent sampling units. We therefore used a measure of occurrence, based on presence/absence of species in quadrat samples, to compare ant communities between different types of forest (HCVs, VJRs and control sites). We first converted the occurrence data for each species into a proportion of the total number of occurrences per site, in order to account for differences among sites in the total number of ant occurrences. Ordination of sites according to species similarity (Bray-Curtis index; Magurran 2004) was then achieved using non-metric multi-dimensional scaling (NMDS; Clarke and Warwick 2001). We also used analysis of similarity

(ANOSIM, using the Vegan package in R; Oksanen et al. 2013) to examine differences between forest types in patterns of species occurrence.

Results

Fragment sizes and habitat quality

VJRs were much larger on average than HCVs (back-transformed mean of $\log_{10}$ area = 264.0 ha, *n* = 8, SD ± 5.0 and 31.7 ha, *n* = 8, SD ± 3.2, respectively; *t* test using equal variance estimate; $t_{14} = 3.01$, $P < 0.01$). PCA extracted two components of variation in vegetation structure (PRIN1 and PRIN2) which accounted for 33 and 17 % of the variability in the vegetation data, respectively. The first factor increased with increasing size and density of trees, proportion of dipterocarps and height to point of inversion, and with increasing canopy cover and leaf litter depth (Table 1). A high PRIN1 score thus represented dense forest with deep leaf litter and large, closely-spaced trees comprising mainly dipterocarps branching in the upper half of the trunk. The PRIN2 score increased with decreasing canopy closure and increasing ground cover and sizes of saplings, indicating a relatively open canopy and understory, with vigorous growth of the lower strata of the vegetation (Table 1).

There was a weak but significant positive correlation between $\log_{10}$ fragment area and PRIN1 score (Pearson correlation; $r = 0.53$, $n = 15$, $P < 0.05$) and no correlation with PRIN2 score ($r = -0.24$, $n = 15$, $P < 0.4$). Both PRIN1 scores and PRIN2 scores varied significantly between the two types of forest fragment ($F_{2,13} = 4.2$, $P < 0.05$ and $F_{2,13} = 5.8$, $P < 0.05$, respectively), with PRIN1 scores being higher in VJRs, whereas PRIN2 scores were higher in HCVs (Table 2).

Table 2

Vegetation characteristics and PCA factor scores (mean ± SE) in Virgin Jungle Reserves (VJRs) and High Conservation Value (HCV) plantation forest fragments ($n_{\text{stations}} = 35$ in VJRs, 18 in HCVs)

Variables	VJRs	HCVs
Canopy closure (%)	93.2 ± 0.6	88.7 ± 1.6

Variables	VJRs	HCVs
Canopy cover (%)	48.7 ± 5.7	23.0 ± 7.7
Ground cover (%)	33.2 ± 3.5	41.8 ± 2.8
Tree cbh (cm)	96.7 ± 7.1	86.7 ± 5.2
Point of inversion	10.0 ± 0.8	6.5 ± 0.8
Tree density (ha^{-1})	78.2 ± 9.1	79.5 ± 21.7
Prop. dipterocarps	0.31 ± 0.04	0.04 ± 0.02
Sapling cbh (cm)	16.0 ± 0.7	18.5 ± 0.9
Sapling density (ha^{-1})	1071 ± 139	1040 ± 126
Leaf litter depth (cm)	1.7 ± 0.2	1.2 ± 0.2
PRIN1	0.55 ± 0.44	−1.14 ± 0.56
PRIN2	−0.47 ± 0.20	0.31 ± 0.19

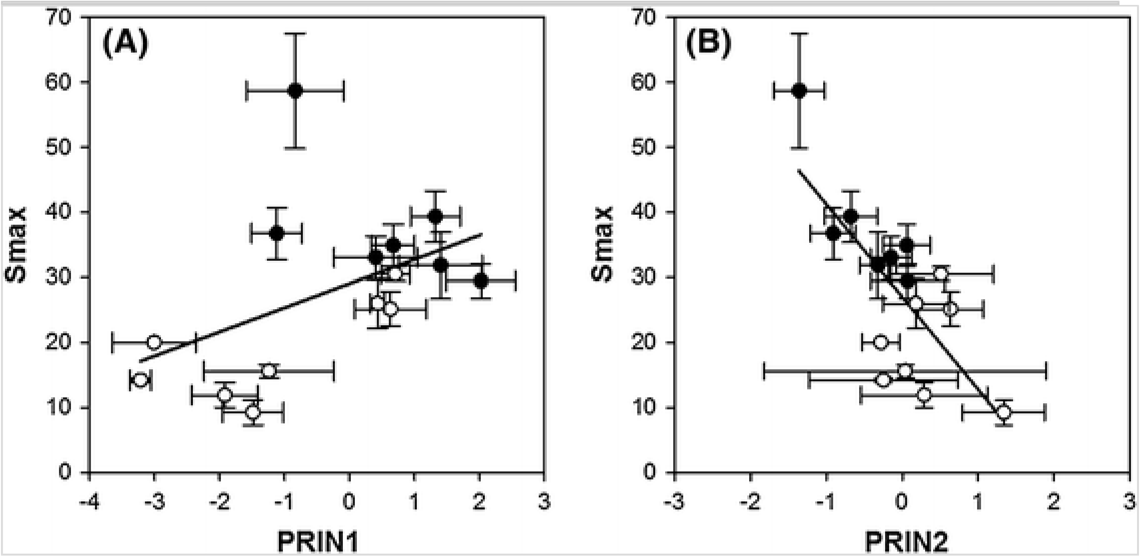
Species richness in forest fragments

We sampled 25,528 individuals of 230 species of ant at 19 sites (Table S2). Mean S_{max} differed significantly among the three types of forest (ANOVA; $F_{2,16} = 13.6$, $P < 0.001$) and was highest in continuous forest (mean = 55.1, $n = 3$, SE ± 12.3), intermediate in VJRs (mean = 37.9, $n = 8$, SE ± 3.2) and lowest in HCVs (mean = 19.1, $n = 8$, SE ± 2.7). Comparing S_{max} with S_{obs} indicated that we sampled ~64 % of species at each station, with a negligible difference in this respect between continuous forest (63.5 %), VJRs (63.6 %) and HCVs (64.0 %). Across all 15 forest fragments where vegetation structure was assessed, there was a significant positive relationship between S_{max} and PRIN1 score (GLM; $F_{1,12} = 13.0$, $P < 0.01$) and a significant negative relationship between S_{max} and PRIN2 score ($F_{1,12} = 29.3$, P < 0.001). PRIN1 and PRIN2 scores together explained 77 % of the variance in S_{max} among fragments (R^2 of minimum adequate model = 0.77; Fig. 2) but neither fragment type nor $\log_{10}$ fragment area were retained in the minimum adequate model ($P > 0.6$ in each case). In a separate GLM including only fragment type and $\log_{10}$ fragment area as predictor variables, S_{max} differed significantly between the two types of fragment ($F_{1,13} = 11.4$,

$P < 0.01$) but was not related to fragment area ($F_{1,13} = 0.09$, $P = 0.8$), whilst a model including only $\log_{10}$ area was not significant ($F_{1,14} = 4.3$, $P = 0.1$), thus confirming that species richness differed significantly between the different types of fragment as a result of differences in habitat quality and not fragment size.

Fig. 2

Estimated species richness (S_{max}) of leaf-litter ants in relation to vegetation structure **a** PRIN1 and **b** PRIN2 at rainforest sites in Sabah, Borneo (*solid circles* VJRs; *hollow circles* HCV fragments within oil palm plantations). Data show mean values ± SEs



Species composition

Of 230 species sampled, only 30 species (13.0 %) were recorded in all three habitats (control sites, VJRs and HCVs) and there was a significant difference among habitats in species composition (ANOSIM, $r = 0.74$, $P = 0.002$), with 92 species (40.0 %) unique to continuous forest and VJRs but only 5 species (2.2 %) unique to continuous forest and HCVs (Fig. 3). Further examination of species composition using non-metric multi-dimensional scaling showed that ant assemblages in continuous forest and VJRs clustered closely together whereas those within HCVs clustered separately (Fig. 4).

Fig. 3

Numbers of species unique to samples from VJRs, HCVs and continuous forest, together with numbers of species common to more than one type of forest. *Numbers in brackets* are percentages of the total number of species recorded across all sites

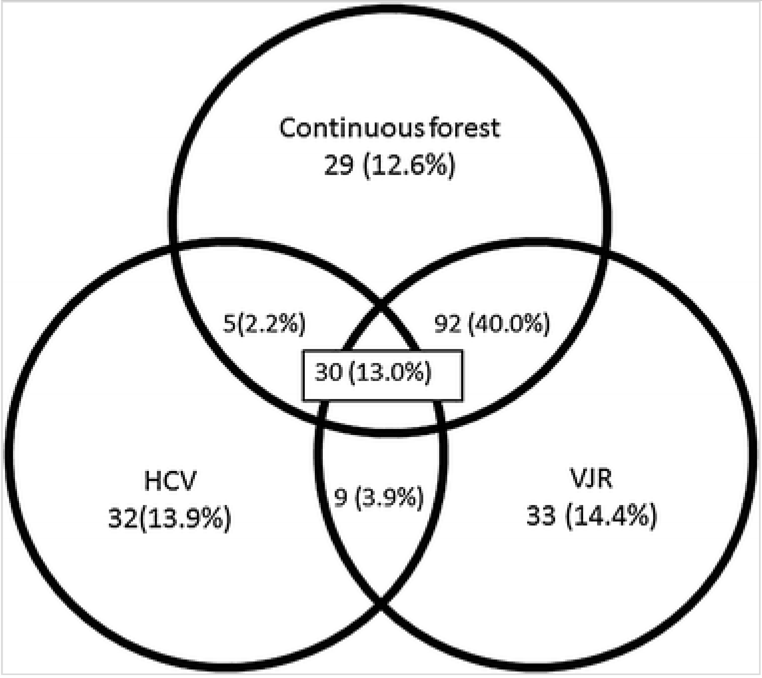
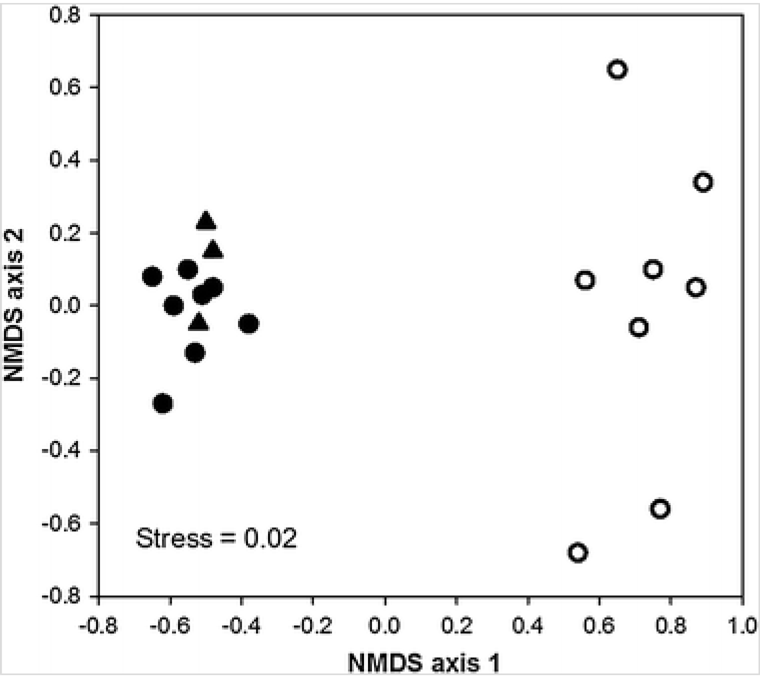


Fig. 4

Non-metric multi-dimensional scaling (NMDS) of species similarity (Bray-Curtis index) between control sites (*triangles*), VJRs (*solid circles*) and HCVs (*hollow circles*). The matrix has a stress value 0.02 indicating a large disparity in variance in the data between HCVs and the other sites



Discussion

Results of this study provide strong support for our hypothesis that privately-managed and publically-managed forest fragments differ in their species richness and composition as a result of differences in history and management and hence in habitat quality. We did not sample every HCV within our study area but an analysis of all HCVs within 23,000 ha of oil palm plantings in southern Sabah (Edwards et al. 2014) found a similar range of sizes to our study (mean area ± SE = 11.5 ± 4.2 ha, *n* = 307) supporting the notion that we sampled a representative range of HCVs in this study. HCVs had much poorer habitat quality than VJRs in terms of vegetation structure and composition, with a lower density and size of large trees, fewer dipterocarps, lower canopy cover, higher ground cover and shallower leaf litter, all of which are characteristic of highly disturbed forest (Hamer et al. 2003; Benedick et al. 2006). We conclude that this difference was largely associated with the history and management of each type of fragment; VJRs were established by the mid-1960s on land that had not previously been logged, and hence comprise mostly primary forest with only minimal disturbance, whereas HCVs were typically logged, and sometimes intensively so, prior to their isolation. HCVs were also smaller than VJRs and so may have experienced higher mortality of large trees and greater changes in vegetation structure compared with VJRs due to greater edge effects within small fragments (Laurance et al. 2000; Pardini et al. 2005), although there was only a weak relationship between fragment size and habitat quality.

We found that ant species richness in forest fragments was significantly affected by habitat quality but not by fragment size, highlighting the importance of separating the effects of habitat alteration per se from those of patch area (Marsden et al. 2001; Gomes et al. 2010). The effects of habitat quality probably occurred because tree density, canopy cover and leaf litter depth affect microclimatic conditions such as humidity and temperature at ground level, whilst leaf litter depth also affects the availability of nest-sites and food resources (Kaspari 1996; Campos et al. 2003). Extensive tracts of forest had significantly higher ant species richness than HCVs or VJRs, probably due to differences among sites in vegetation structure (Benedick et al. 2006), and possibly also due to differences in leaf litter composition and diversity (Silva et al. 2011) resulting from the fewer large dipterocarps in forest fragments.

Most animal taxa decline in species richness, abundance and functional diversity following conversion of forest to oil palm, with a severe loss of forest species and an increased abundance of non-native species (Edwards et al. 2010, 2013a, b; Fayle et al. 2010, 2013; Foster et al. 2011; Senior et al. 2012). In contrast to oil palm, we found that VJRs supported 78 % of the species sampled at control sites (calculated from data in Fig. 3), supporting previous evidence that such forest remnants make an important contribution to biodiversity within agricultural landscapes (Benedick et al. 2006; Lucey et al. 2014). However, HCVs supported only 22 % of the species recorded at control sites, which is only slightly higher than the proportion of forest species recorded within the oil palm itself (19 %; Fayle et al. 2010). Assessment of beta-diversity between habitats may be hampered by incomplete species inventories with a high proportion of unrecorded species (Pfeiffer and Mezger 2012) but in our study, a similar and reasonably high proportion of species (~64 %; see “Results” section) was sampled in each type of forest, confirming that HCVs support a depauperate assemblage of forest ant species.

In keeping with our findings, Edwards et al. (2010) found that HCVs had low biodiversity value for birds, whilst Edwards et al. (2014) found no relationship between oil palm yield and proximity to unplanted forest, suggesting that fragments provide no net benefit in terms of ecosystem services such as herbivore suppression. Lucey et al. (2014) found that fragments can contribute to plantation diversity through spillover effects but also concluded that small (<200 ha) fragments provided few biodiversity benefits. These data call into question the effectiveness of small poor-quality HCVs in enhancing biodiversity or providing ecosystem services within plantations. It is also not known whether HCVs with few mature dipterocarp trees are able to regenerate adequately and therefore improve in quality over time. RSPO principles and criteria for the sustainable production of palm oil include the retention of HCV forest fragments within oil palm plantations (Bhagwat and Willis 2008) but there are currently no clear guidelines relating to fragment characteristics or management to improve quality. Since 2005, assessment and identification of HCV areas for conserving biodiversity by RSPO-compliant plantations has been more stringent, and conservation of large tracts of forest is one of the six high conservation values to be identified prior to new plantings (www.hcvnetwork.org). Nonetheless, many small poor-quality fragments of HCV exist, and we suggest that rehabilitation to restore vegetation structure and improve habitat quality, for instance through enrichment planting with native tree species (Edwards et al. 2009; Ansell et al. 2011), is required for these HCVs to be effective as reservoirs of biodiversity.

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Electronic Supplementary Material

Below is the link to the electronic supplementary material.

Supplementary material 1 (DOCX 30 kb)

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