

Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter

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Abstract

Oil palm cultivation is expanding rapidly into many of the world's most biodiverse tropical regions. One of the most functionally important and ecologically dominant animal groups in these environments is the ants. Here, we quantify the overall impacts of clear-felling lowland dipterocarp rainforest and conversion into oil palm plantation on ant diversity. At study sites in Sabah, Malaysia we collected ants from three microhabitats: 1 – the canopy, 2 – bird's nest ferns (*Asplenium nidus* complex, a common epiphyte in forest and oil palm), and 3 – leaf litter. We also measured temperature, humidity and light at collection sites to assess their impacts on ant community composition. Total ant species richness decreased from 309 to 110 (–64%) between forest and oil palm plantation. However, this impact was not the same across all microhabitats, with bird's nest ferns maintaining almost the same number of ant species in oil palm compared to forest (forest-oil palm, ferns: 36–35 (3% loss), canopy: 120–58 (52% loss), leaf litter: 216–56 (74% loss)). Relative abundance distributions remained the same for fern-dwelling ants, but became less even for oil palm ants in both the canopy and the leaf litter. These differences may be due in part to the ability of bird's nest ferns to provide a stable microclimate in hot, dry plantations. We also found that non-native ant species were more abundant in oil palm than in forest, and few forest ant species survived in plantations in any of the microhabitats. Only 59 of the 309 forest species persisted in oil palm plantations, corresponding to an 81% loss of forest species resulting from habitat conversion. Although oil palm supports many more ant species than has been previously reported, converting forest into plantation still leads to a dramatic reduction in species richness. The maintenance of forested areas is therefore vital for the conservation of ant biodiversity.

Zusammenfassung

Der Anbau von Ölpalmen expandiert in beschleunigtem Maße in viele tropische Regionen der Welt, die besonders hohe Biodiversitäten besitzen. Eine Tiergruppe, die in diesen Umwelten funktionell besonders wichtig und ökologisch dominant ist, sind die Ameisen. An dieser Stelle quantifizieren wir den gesamten Einfluss auf die Diversität der Ameisen, den der Kahlschlag von dipterokarpen Tieflandregenwäldern und die anschließende Verwandlung in Ölpalmenplantagen hat. Auf Untersuchungsflächen

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in Sabah, Malaysia, sammelten wir in drei Mikrohabitaten die Ameisen: (1) im Kronendach, (2) in Nestfarnen (*Asplenium nidus*-Komplex, einem verbreiteten Epiphyten im Wald und auf Ölpalmen) und (3) in der Streu. Wir maßen außerdem die Temperatur, die Luftfeuchte und das Licht an den Sammelorten, um den Einfluss auf die Zusammensetzung der Ameisengesellschaften zu bewerten. Die Gesamtartenzahl der Ameisen verringerte sich von 309 auf 110 (–64 %) vom Wald zur Ölpalmenplantation. Dieser Einfluss war jedoch nicht in allen Mikrohabitaten der gleiche, da in Nestfarnen fast die gleiche Anzahl von Ameisenarten in Ölpalmen wie im Wald erhalten blieben (Wald-Ölpalmen, Farnen: 36–35 (3% Verlust), Kronendach: 120–58 (52% Verlust), Laubstreu: 216–56 (74% Verlust)). Die Verteilungen der relativen Abundanzen blieben für farnbewohnenden Ameisen bestehen, waren jedoch in Ölpalmen sowohl im Kronendach als auch in der Laubstreu weniger gleichverteilt. Diese Unterschiede können zum Teil darauf zurückgeführt werden, dass die Nestfarnen in den heißen und staubigen Plantagen ein relativ stabiles Mikroklima zur Verfügung stellen können. Wir fanden außerdem heraus, dass nicht-einheimische Ameisenarten in den Ölpalmen häufiger als im Wald waren und dass nur wenige Waldameisenarten in sämtlichen Mikrohabitaten überlebten. Nur 59 der 309 Waldarten blieben in den Ölpalmenplantagen bestehen, so dass ein Verlust von 81% durch die Habitatumwandlung entstand. Auch wenn Ölpalmen sehr viel mehr Arten zulassen, als bisher berichtet wurde, führt die Umwandlung der Wälder in Plantagen immer noch zu dramatischen Verlusten im Artenreichtum. Der Erhalt bewaldeter Gebiete ist daher lebenswichtig für den Erhalt der Ameisenbiodiversität.

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Introduction

The extraction of resources and the continuing expansion of agriculture is an ongoing cause of many species extinctions (Tilman et al. 2001). Oil palm (*Elaeis guineensis* Jacq.) gives high vegetable oil yields relatively cheaply (Carter, Finley, Fry, Jackson, & Willis 2007; Corley 2009) and consequently is one of the most widespread and rapidly expanding crops. Since the majority of terrestrial biodiversity is supported in the tropical environments in which oil palm grows best (Fitzherbert et al. 2008; Turner, Snaddon, Fayle, & Foster 2008) and much oil palm expansion is into forested areas (Koh & Wilcove 2008), this trend is a major cause for concern.

While the overall impacts of converting forest into oil palm plantation on biodiversity are negative (Fitzherbert et al. 2008), relatively little research on this subject has been carried out (Turner et al. 2008), and some groups have similar, or even higher species richness in plantations (Chang, Hii, Buttner, & Mansoor 1997; Liow, Sodhi, & Elmqvist 2001). Consequently, it is vital that these impacts are properly documented for all ecologically important taxa, in particular those that carry out ecosystem services (e.g. Koh 2008a).

One of the most ecologically dominant groups of animals in tropical environments is the ants (Hölldobler & Wilson 1990). They comprise a large proportion of animal biomass and perform important ecosystem functions such as predation, soil turnover, nutrient cycling and seed dispersal (Alonso & Agosti 2000; Fayle et al. 2010). Ants also form mutualistic relationships with a diverse range of other animals (e.g. Dill et al. 2002) and plants (e.g. Edwards et al. 2010). To date, three studies have directly compared forest ant communities with those in oil palm plantations, using the same sampling techniques in both habitats (Brühl & Eltz 2010; Room 1975; Taylor 1977). These all documented reductions in species richness in plantations compared to forest. However, all three used methods that sample a single microhabitat (tuna baiting

and hand collecting; hand collecting; visual identification) and this is reflected in the low species richness of the forest sites in these three studies (26, 50 and 24, respectively). Two other collections have been made of ants from oil palm plantations, both of which found low ant species richness, although neither included ants from forested areas (Dejean, Djieto-Lordon, & Durand 1997; Pfeiffer, Tuck, & Lay 2008). Consequently, the impacts of conversion of forest to oil palm plantation on whole ant communities are not clear.

Most studies on the biodiversity impacts of habitat conversion do not distinguish between effects on animal communities in different parts of a habitat, such as those inhabiting the canopy, epiphytes and the leaf litter layer, referred to here as microhabitats. Such heterogeneity is important for smaller animals, which may be found exclusively in a particular microhabitat. This has been shown in oil palm plantations, where the impact of forest conversion on abundance of arthropod orders differs between microhabitats (Turner & Foster 2009), and for butterflies and birds, where habitat complexity explains some of the variation in species composition (Koh 2008b).

Although rarely sampled in studies of the impacts of habitat conversion, epiphytes are a microhabitat that can be of particular importance for ants, which often use them as a nesting substrate (Ellwood & Foster 2004; Ellwood, Jones, & Foster 2002; Stuntz, Linder, Linsenmair, Simon, & Zotz 2003). One of the most abundant of these in SE Asian forests and plantations is the bird's nest fern (*Asplenium nidus* complex), a litter basket epiphyte (forest: up to 180/ha; plantation: up to 112/ha; Fayle, Chung, Dumbrell, Eggleton, & Foster 2009; Turner & Foster 2009). The accumulations of aerial leaf litter in these plants provide a buffered microclimate away from the hot dry conditions prevalent in oil palm plantations (Turner & Foster 2006), and consequently are an ideal habitat for many groups of litter-dependent arthropods (Turner & Foster 2009).

Here we quantify how conversion of primary forest into oil palm plantation impacts on the composition of ant communities across three microhabitats (ground leaf litter, bird's nest ferns and canopy) by surveying existing areas of these two land-use types. Loss of forest ant species was predicted to occur in all three microhabitats, with communities in bird's nest ferns being least affected, due to their ability to buffer microclimate.

Materials and methods

Study site

We made collections of ants from primary forest (Danum Valley Conservation Area, 43,800 ha, 117°49'E, 5°01'N, altitude 170 m) and 14- to 18-year-old oil palm plantation (Sebrang Estate, 2576 ha, 118°35'E, 5°02'N, altitude 150 m) in Sabah, Malaysia between 10 May and 18 June 2002. This plantation is set within a continuous matrix of other plantations, within which some small fragments of secondary forest remain. This landscape is typical of highly intensive oil palm plantation in Sabah. Twenty transects were used in each habitat, with distances between transects ranging from 0.1 to 3.2 km in forest and 0.1 to 4.2 km in oil palm plantation. For further study site and sampling design details see Turner and Foster (2009).

Collection methods

In each habitat, collections were made at twenty sites centred on bird's nest ferns. Litter-dwelling ants were sampled on days without rain between 0900 and 1200 by collecting four 1 m² areas of leaf litter at bearings of 0°, 90°, 180° and 270° from the fern-bearing tree. Litter samples in forest sites were taken 1 m away from the tree, while those in oil palm plantation were taken 3 m away in order to avoid the area immediately around the tree that is sprayed with herbicides (Borneo Samudera, oil palm plantation manager, pers. comm.). These litter samples were then placed in Winkler extractors for 3 days (Krell et al. 2005), after which material was hand-sorted to collect any remaining ants.

We sampled ants inhabiting bird's nest ferns by collecting entire ferns ranging from 1 to 6 m in height above ground level (oil palm mean: 1.8 m, forest mean: 2.5 m) of the same range of diameters in the two habitats (0–50 cm frond tip to tip diameter: 6, 50–100 cm: 8, >100 cm: 6). We accessed ferns using ladders or single rope techniques and removed them by hand into plastic bags on the same day as the litter sampling was carried out. Litter contained within the bowl of the fern was removed and the fern core was dissected. Both the core fragments and litter were then processed in the same way as for ground litter (see above).

Canopy ants were fogged after litter and fern samples had been collected, using a Swingfog SN 50-10PE fogging

machine with pybuthrin 33BB non-persistent insecticide. At each sampling site four 1 m² fogging trays, with attached collecting pots containing 70% alcohol, were suspended 1 m above ground level at the same locations as the litter samples. Fogging was carried out for 1.5 min and the trays were left for 1 h after fogging had finished. There was adequate cover of fog up to approximately 15 m in the canopy, consequently sampling the entire oil palm plantation, but not the high canopy of forest.

Environmental variables

At each site, point readings of temperature and humidity were taken using a Vaisala HM 34 humidity and temperature meter, and of light levels using an Iso-tech ILM350 light meter in order to quantify the effects of microclimate on ant communities.

Ant identification

Worker ants were identified to genus using published keys (Bolton 1994) and then sorted to morphospecies (Oliver & Beattie 1996). Where possible, morphospecies were assigned species names using collections at the University Museum of Zoology, Cambridge, the antbase online image database (Pfeiffer 2009) and a number of genus-level taxonomic reviews (24% of the species collected, Appendix A: Table 1). For brevity, both species and morphospecies are hereafter referred to as species. We assessed the impact of habitat conversion on the proportion of non-native species (non-native being defined following Pfeiffer et al. 2008).

Statistical analysis

Generalised Linear Models (GLMs) were used to assess the effects of habitat conversion on ant abundance and species density (species per sample) across different microhabitats. Ant abundance and species density were analysed using GLMs with log-links and quasipoisson error distributions, with habitat as an explanatory factor and fern dry weight as a covariable for analyses within this microhabitat. Plots of residuals were inspected to ensure that variance was similar across different factor levels. Generation of species accumulation curves and analytical calculation of 95% confidence intervals were carried out in EstimateS v7.52 (Colwell 2009). Species occurrences were used as these are more likely to reflect the density of ant colonies than abundances. Kolmogorov–Smirnov tests were used to assess differences in relative abundance distributions of ant communities (as assessed by species occurrence) in forest and oil palm plantation across the different microhabitats (Sokal & Rohlf 1995, p. 435).

We used ordinations to assess the impacts of habitat conversion and subsequent changes in microclimate on ant community composition. Since species turnover was high,

Table 1. Numbers of species, numbers of species lost and gained, and levels of species similarity between the microhabitats in forest and oil palm.

Subhabitat	Forest sites	Oil palm sites	Total species	Species lost	Species gained	Species overlap	S_{class}	S_{inc}
Canopy	120	58	161	103	41	17	0.191	0.301
Fern	36	35	69	34	33	2	0.056	0.070
Litter	216	56	243	187	27	29	0.213	0.555
Total	309	110	360	250	51	59	0.282	0.689

Similarity indices used are S_{class} (Sørensen's classic similarity index) and \hat{S}_{inc} (Chao's incidence-based measure with a correction for unseen shared species).

Canonical Correspondence Analysis (CCA) was employed for this purpose (Leps & Smilauer 2003). Analyses were run first using the whole dataset, and then subsequently using only data from individual microhabitats to assess differing impacts of environmental variables in different parts of the environment. In order to assess turnover between communities while taking into account incompleteness of sampling, we calculated a modified version of Sørensen's similarity index in addition to the original Sørensen's index. This index corrects for bias in estimated community similarity caused by under-sampling by counting the number of shared singletons and doubletons in much the same way as classic species richness estimators do for single assemblages (Chao, Chazdon, Colwell, & Chen 2005). We used Generalised Linear Mixed Models with logit links and binomial error distributions fit with the Laplace approximation (which gives approximate P -values) to compare the proportion of occurrences of native and non-native ants in forest and oil palm plantation. The proportion of sites occupied by a species (out of a maximum of 20) was modelled as a function of the habitat and whether species was native or not (fixed effects). Species was included as a random factor in all models. For these models we looked for a significant interaction between the main effects of habitat type and classification as native/non-native species.

Results

We collected 16,085 worker ants from 309 species in forest, decreasing to 6081 ants from 110 species in oil palm plantation (Appendix A: Table 1). Ant abundance was lower in oil palm plantation than in forest for litter-dwelling ants (GLM: $t=3.63$, $df=38$, $P<0.001$, Fig. 1A), while the abundance of ants in the canopy remained the same (GLM: $t=-1.08$, $df=38$, $P=0.286$; Fig. 1A). Ferns collected from forest supported higher abundances of ants, as did larger ferns (GLM: forest/oil palm, $t=3.79$, $df=37$, $P<0.001$; fern dry weight, $t=3.28$, $df=37$, $P=0.001$; Fig. 1A). Ant species density (number of species per sample) was lower in oil palm plantation in both the leaf-litter and the canopy, but not in ferns (GLMs: litter, $t=9.64$, $df=38$, $P<0.001$; canopy, $t=3.94$, $df=38$, $P<0.001$; ferns, $t=0.67$, $df=37$, $P=0.506$; Fig. 1B), although larger ferns did support more ant species (GLM: $t=2.23$, $df=37$, $P=0.032$). Species accumulation curves show the ant communities in

the canopy and leaf litter to be more species-rich in forest than in oil palm plantation, while those in ferns are of similar species richness (Fig. 2). Between forest and oil palm plantation, total species richness decreased from 120 ± 14.4 (95% C.I.) to 58 ± 9.6 for canopy ants and from 216 ± 15.6 to 56 ± 9.7 for litter ants, while species richness of fern-dwelling ants remained the same (36 ± 7.1 and 35 ± 7.1 , respectively, Table 1). Levels of turnover were high for all microhabitats, although these decreased in the canopy and the litter once unsampled species had been taken into account (Table 1).

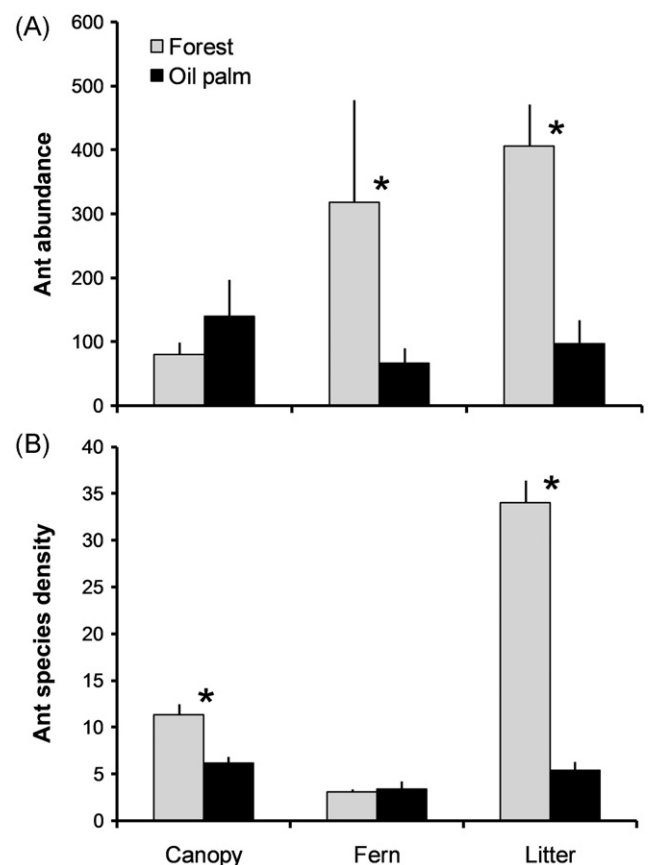


Fig. 1. Impacts of conversion of primary forest to oil palm plantation on (A) ant abundance and (B) ant species density. Canopy and litter values are totals from four 1 m² areas, while fern values are totals for single ferns. Means plus standard errors are plotted for each of the three microhabitats. Asterisks denote microhabitats for which significant differences were found between forest and oil palm habitats.

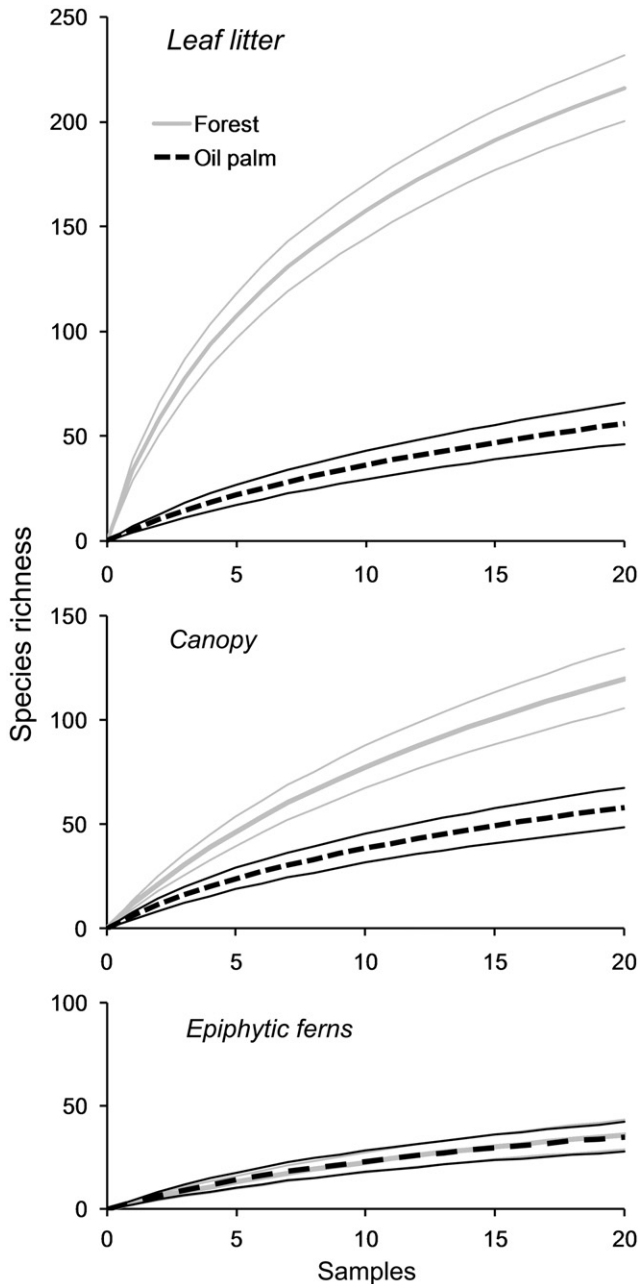


Fig. 2. Species accumulation curves for the habitats and microhabitats over 20 sampling points. Thicker lines denote mean species richness. Thinner lines denote 95% confidence intervals.

Relative abundance distributions differed between forest and oil palm plantation for canopy and litter-dwelling ants (K–S tests: canopy, $D=0.2731$, $P<0.01$; leaf litter, $D=0.3853$, $P<0.001$; Fig. 3B, C) but not for fern-dwelling ants (K–S test: $D=0.0591$, $P>0.05$; Fig. 3A). For both litter-dwelling and canopy-dwelling ants this difference was related to an increase in the abundance of the most numerous species in oil palm plantation compared to forest.

Both habitat (forest/oil palm plantation) and microhabitat (fern/canopy/litter) had significant effects on species compo-

Table 2. F -ratios and P -values for CCAs carried out on ant communities in forest and oil palm.

Explanatory variable	F -ratio	P -value
<i>All microhabitats</i>		
Oil palm	2.76	0.001
Litter	2.74	0.001
Fern	1.70	0.001
Temperature	1.22	0.016
Humidity	1.17	0.279
Light	1.15	0.131
<i>Separate microhabitats</i>		
Litter only (temperature)	1.26	0.012
Canopy only (temperature)	1.15	0.073
Ferns only (temperature)	0.87	0.658

Variables were tested sequentially using Monte Carlo permutation tests and then added into the model if the resulting P -value was less than 0.05. The number of permutations used for each test was 999. Note that the final category for each factor is not added, as the variance related to this has already been taken into account by the penultimate category for the factor. $N=180$ for all microhabitats. For separate microhabitats $N=40$ for leaf litter and canopy, and $N=35$ for ferns. P -values of less than 0.05 are in bold type. For separate microhabitats, habitat was included as a factor in all models and only the statistics for temperature are given, since no other environmental variables were significantly associated with ant community composition for any microhabitat.

sition of ant communities in the CCA (Table 2). Of the three continuous environmental variables measured, only temperature had a significant effect on overall species composition once differences between habitats and microhabitats had been taken into account (Table 2). For the microhabitats analysed separately, with the inclusion of habitat as a factor in all models, temperature had a significant effect on species composition of litter-dwelling ants, a marginally non-significant effect on canopy ants, and no effect on fern-dwelling ants (Table 2). Neither of the other environmental variables had an effect on species composition within any of the microhabitats.

Levels of species occurrence (the total number of samples that each species occurs in) of native and non-native species differed between oil palm plantation and forest (Fig. 4, Appendix A: Table 1) in the canopy (Generalised Linear Mixed Model: Habitat \times Species origin, $Z=-3.226$, $n=322$, $P=0.001$) and litter (GLMM: Habitat \times Species origin, $Z=3.706$, $n=486$, $P<0.001$) but not in ferns (GLMM: Habitat \times Species origin, $Z=-0.0104$, $n=138$, $P=0.992$). In both these cases non-native species occurred relatively more often in oil palm plantations, and less often in forest.

Discussion

The estimated levels of species losses sustained upon conversion of forest into oil palm plantation are very high, with 81% (250/309) of the ant species present in primary forest being absent in plantations. Our collections of ants are the first made from multiple microhabitats in oil palm plantation.

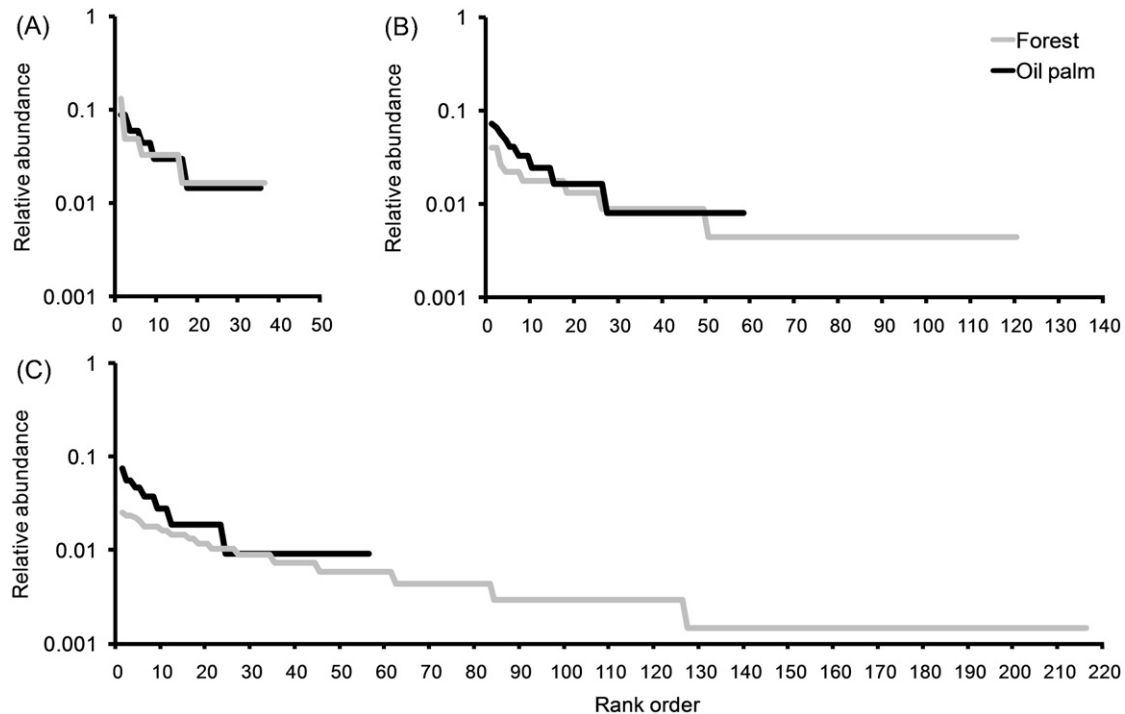


Fig. 3. Relative abundance distributions of ant species in forest and oil palm plantation for the three microhabitats: (A) Bird's nest ferns, (B) Canopy, (C) Leaf litter.

Consequently, we found a much higher species richness of ants in plantations (110 species) than previous studies (Brühl and Eltz 2009, 23 species; Dejean et al. 1997, six species; Pfeiffer et al. 2008, 39 and 36 species in different areas; Room 1975, 29 species; Taylor 1977, 20 species). However, the three studies that compared numbers of species in plantations to numbers in forest also found dramatic species losses upon habitat conversion (Fig. 5, Appendix A: Table 2).

We found that the impact of conversion to oil palm plantation was greatest for canopy and litter ants: the species density decreased and the relative abundance distributions also became less even. Impacts on the litter-dwelling ant communities may be due to both increase in disturbance and decrease in litter complexity in plantations. The impact on canopy-dwelling ants may also be due to simplification of the canopy structure in plantations. Finally, the microclimate in oil palm plantations tends to be hotter and drier than that in forest areas (Turner & Foster 2006; Appendix A: Table 3, this study), making them a more stressful environment for ants, leading to changes in community structure.

However, for fern-dwelling ants, species density and the shapes of relative abundance distributions did not differ between forest and oil palm. Relative abundance distributions with a larger proportion of the most dominant species are expected in disturbed habitats (Hill & Hamer 1998), and this was true for litter and canopy ants, but not for fern-dwelling ants. The apparent resilience of the fern-dwelling ant community structure (although not composition) to habitat change is probably due to the ferns' ability to buffer microclimate, since temperature affected the ant communities in the canopy and leaf litter, but not in the ferns (Table 2). This is plausible as temperature is known to be a major determinant of ant community composition in many ecosystems (e.g. Kaspari, Ward, & Yuan 2004). Bird's nest ferns are also one of the few plant species to be found in both forest and oil palm plantation, and may provide a similar nesting substrate for ant colonies, and consequently give rise to communities with similar structures, although with differing compositions.

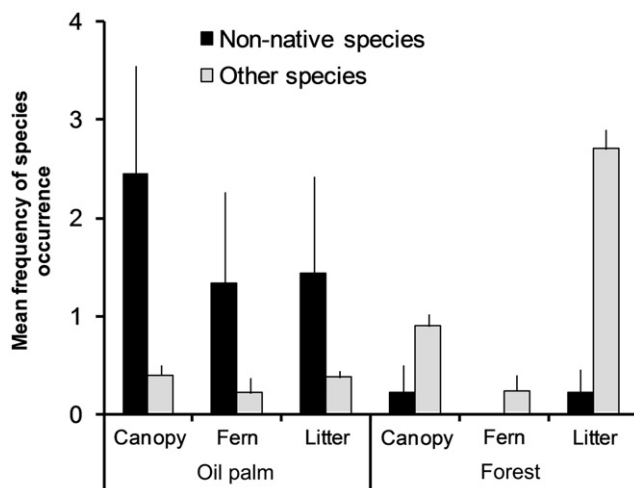


Fig. 4. The mean number of samples (out of a maximum of 20) containing non-native ants and all other species in the three microhabitats in oil palm plantation and forest. Number of non-native species=9, number of other species=351.

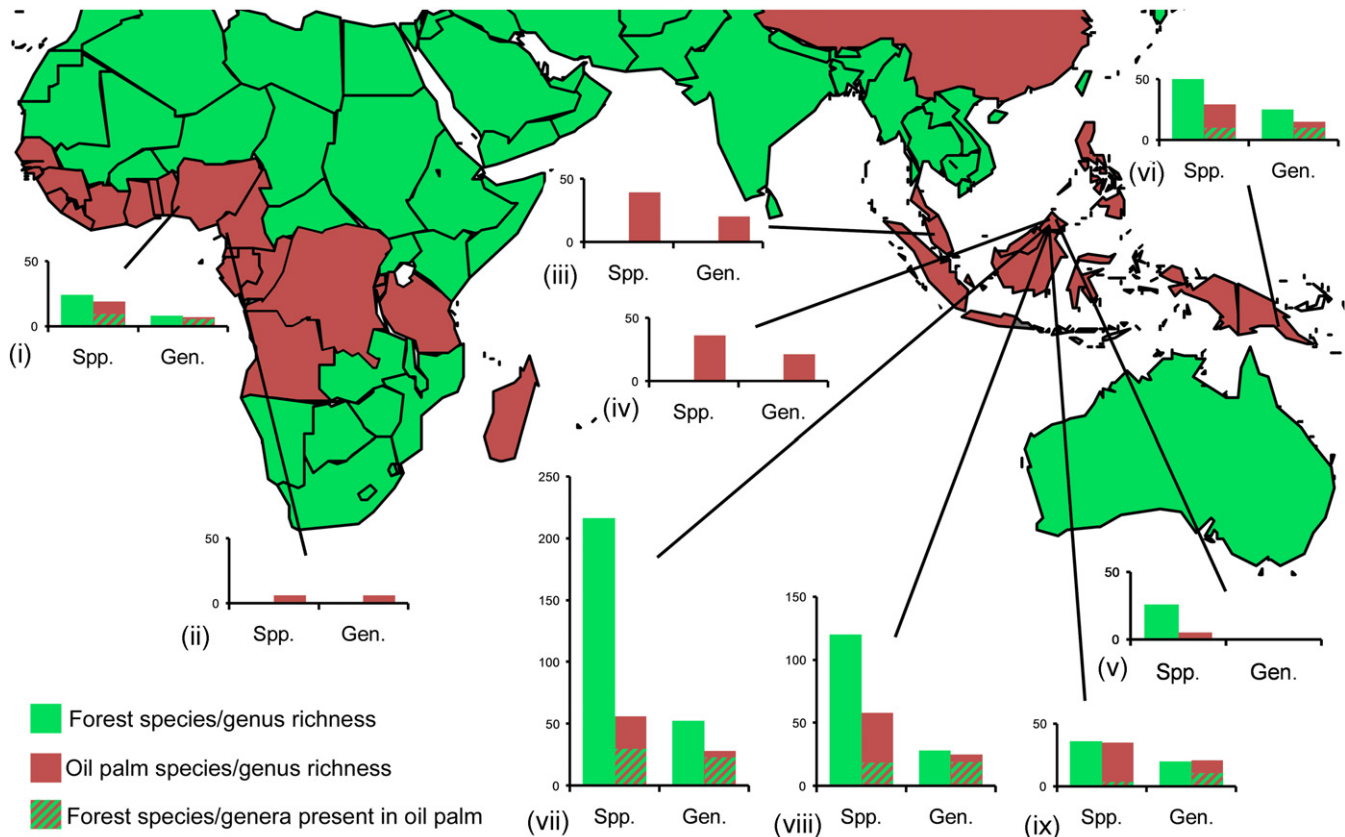


Fig. 5. Summary of the known impacts of conversion of forest to oil palm plantation on ant biodiversity. Countries in dark grey (red, online) are those in which oil palm is cultivated (from Koh & Wilcove 2008). Light grey bars (green bars, online) denote the numbers of species and genera of ants in forested areas and dark grey (red, online) bars the corresponding numbers for oil palm plantations. Hatched light and dark (green and red, online) blocks indicate forest species and genera that were found in plantations for each study from which data are available. All publications in which ants have been sampled to date in oil palm plantations are represented here, along with numbers for forested areas where surveys with the same methodology have been carried out as part of the same study. (i) Nigeria, visual identification *in situ* (Taylor 1977); (ii) Cameroon, inspection of cut fronds (Dejean et al. 1997); (iii) Peninsular Malaysia, inspection of cut fronds (Pfeiffer et al. 2008); (iv) Sabah, Malaysia, inspection of cut fronds (Pfeiffer et al. 2008); (v) Sabah, Malaysia, tuna baiting and hand collecting (Brühl & Eltz 2009), oil palm species richness rarefied; (vi) Papua New Guinea, hand collecting within 1 m² quadrats (Room 1975); (vii) Sabah, Malaysia, leaf litter sampling within 1 m² quadrats, Winkler extractors (this study); (viii) Sabah, Malaysia, canopy fogging (this study); (ix) Sabah, Malaysia, extracted from bird's nest ferns (*Asplenium nidus* complex) (this study). For species and genus numbers see Appendix A: Table 2.

The difference between the impacts of forest conversion on different microhabitats suggests that ant species richness in oil palm plantations could be increased by 15% if bird's nest ferns were left to grow (which is not always done (Piggott 1996)), since there were 96 species present in the canopy and litter combined with an additional 14 species present in the ferns. This is likely to be a conservative estimate of the potential impacts of this management strategy, since many other epiphyte species are common in plantations (Nadarajah & Nawawi 1993), and plantations have higher densities of bird's nest ferns than forests (oil palm, 112/ha; forest, 80/ha; Turner & Foster 2009). However, the increase in the number of forest ant species is negligible if ferns are left to grow, since the ferns are dominated by non-forest species (Table 1, Appendix A: Fig. 1). Consequently, this strategy would only be useful if these extra species were found to perform ecosystem ser-

vices, and is not recommended as a tactic for conserving ant biodiversity.

Only a small proportion of forest ant species were present in oil palm plantation, and non-native species were much more widespread (Fig. 4), occurring in all three microhabitats (Appendix A: Table 1). The reduction in ant species richness may therefore be due not only to physical differences in habitat structure, but to competitive interactions with non-native ants. For example, one of the non-native species found in this study, *Tetramorium bicarinatum* (Nylander), is known to be highly aggressive towards other ants (Astruc, Malosse, & Errard 2001). Other tramp species, such as *Cardiocondyla wroughtonii* (Forel), which do not show behavioural dominance, may nonetheless displace the less dominant of the native ant species (Heinze, Cremer, Eckl, & Schrempf 2006). The oil palm ant fauna is a combination of

forest species native to the area, and non-native species, some of which may have extensive geographical ranges. Some of the species that we found on oil palm in Sabah, are also found on oil palm in Papua New Guinea (*Tetramorium simillimum* (Smith), *Cardiocondyla wroughtonii* (Forel) and *Anoplolepis gracilipes* (Smith); Room 1975). However, there was no overlap between the SE Asian oil palm species and those found in Nigeria by Taylor (1977).

We have found that although oil palm plantations support a more diverse ant fauna than was previously thought, the impacts of converting rainforest into plantation are severe. While increasing habitat heterogeneity by encouraging the growth of epiphytes may lead to oil palm plantations supporting a greater number of ant species, most of these are not species that are found in primary forest. Consequently, the maintenance of forested areas is the only way of conserving a full complement of ant species.

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Appendix A. Supplementary material

The online version of this article contains additional supplementary data. Please visit 10.1016/j.baae.2009.12.009.

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