Ecography 36: 1051–1057, 2013
doi: 10.1111/j.1600-0587.2012.00192.x

Subject Editor: Nathan J. Sanders. Accepted 17 December 2012

Ant mosaics occur in SE Asian oil palm plantation but not rain forest and are influenced by the presence of nest-sites and non-native species

Tom M. Fayle, Edgar C. Turner and William A. Foster

T. M. Fayle, Faculty of Science, Univ. of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic, and Forest Ecology and Conservation Group, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire, SL5 7PY, UK. – E. C. Turner (ect23@cam.ac.uk) and W. A. Foster, Insect Ecology Group, Univ. Museum of Zoology Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.

Interaction networks within biotic communities can be dramatically altered by anthropogenic habitat modification. Ants, an important ecological group, often interact competitively to form mosaic-like patterns in disturbed plantation habitats, in which dominant species form mutually exclusive territories. However, the existence of these ant mosaics in pristine forests is contentious. Here we assess the relative strengths of ant competitive interactions in oil palm plantation and primary rain forest in Sabah, Malaysia, using null models of species co-occurrence. We use two metrics: the C-score, which measures mean degree of overall co-occurrence, and a novel metric, the C_{var}-score, which measures the variance in degree of co-occurrence. We also investigate the role of nest sites by collecting ants from canopy and leaf litter microhabitats, and from epiphytic ferns, an important nest site for canopy ants. Furthermore, we assess whether non-native species, which were widespread in oil palm plantation (61 occurrences vs five in rain forest) are important in driving the formation of ant mosaics. We found no evidence for ant mosaics in any primary forest microhabitat. In oil palm plantation, segregation between species was pronounced in epiphytes, weak in the rest of the canopy and absent in leaf litter communities. Intriguingly, exclusion of non-native ant species from analyses increased the degree of negative species co-occurrence in all three microhabitats, with species segregation in the oil palm canopy becoming statistically significant. Our results suggest that invasion of plantation habitats by non-native species does not drive increased species segregation in ant communities. Rather, high degrees of species segregation might relate to changes in the importance of canopy nest sites, with colonies competing more strongly for these in plantations. In primary forests, weaker nest-site limitation and the highly complex, more vertically stratified, non-uniform canopy could lead to random co-occurrence between ant species at the scales studied here.

When natural habitats are exploited by humans, biotic communities are altered. Not only are there losses of species and changes in species composition, but the manner in which species interact can also shift (Morris 2010). While the former is well documented in a range of systems, data on the latter are relatively scarce (Floren et al. 2001, Tylianakis et al. 2007). Non-native species can also have profound impacts on species interaction networks (Vander-Zanden et al. 1999, Sanders et al. 2003), and this effect is often more pronounced in disturbed habitats (O'Dowd et al. 2003). Changes in the structure of these networks are expected to have contingent effects on ecosystem functioning (Fukami and Morin 2003).

Ants are an important ecological group in both degraded and natural habitats, interacting with many other taxa and mediating a range of ecosystem processes (Lach et al. 2010). Interaction networks within this group in forest canopies are often interpreted in the context of ant mosaics, where dominant species form territories from which they exclude each other (Leston 1973). Particular dominant species are associated with specific communities of ants ('subordinates') and other arthropods, potentially altering the functioning of ecosystems (Dejean et al. 1997). The existence of these mosaics is well-documented in simple, plantation habitats, but their presence in natural forest is more contentious (Floren and Linsenmair 2000, Blüthgen and Stork 2007, Davidson et al. 2007). Comparing the strength of mosaic patterns across habitats therefore represents a useful way of studying the impacts of anthropogenic habitat change on species interactions. Furthermore, plantations are often invaded by non-native species, which are sometimes behaviourally dominant (Pfeiffer et al. 2008, Dejean et al. 2010), and would therefore be expected to alter the structure of the mosaic. Either non-native species could decrease the overall abundance of negative species interactions, 'disassembling' the community (Sanders et al. 2003), or they might increase the abundance of these interactions, through competing strongly with native species

(Dejean et al. 2010). Since the existence of ant mosaics depends on interspecific competition, we would expect these patterns to be strongest at the resource for which there is most competition. For canopy ants, nest sites are thought to be an important limiting factor in both plantations (Philpott and Foster 2005) and in pristine habitats (Powell et al. 2011). Furthermore, only a small subset of species are expected to defend territories, while a larger proportion of species are likely to defend nest sites (Savolainen and Vepsäläinen 1988). Interaction networks in ground-dwelling ant communities are not usually interpreted in terms of ant mosaics; at small scales these species are often found to be distributed at random (Gotelli and Ellison 2002, Sanders et al. 2007b), although this has not been tested in plantations. We would therefore expect mosaic patterns to be most apparent in canopy nest sites, less apparent in the rest of the canopy and non-existent on the ground.

Here we use null models of species co-occurrence to test these hypotheses in primary rain forest and oil palm plantation in SE Asia. Oil palm plantation has expanded rapidly in the region, causing dramatic reductions in species richness and changes in species composition for a wide range of taxa (Fitzherbert et al. 2008, Turner et al. 2008, Foster et al. 2011). Ant mosaics are already known to exist in oil palm canopies in this area (Pfeiffer et al. 2008). In both forest and plantation, epiphytic bird's nest ferns (*Asplenium* spp.) are important nest sites for a range of arthropods (Fayle et al. 2009, Turner and Foster 2009) including canopy ants (Fayle et al. 2010, 2012, Fig. 1). Specifically, we test the hypothesis that there is a hierarchy in the strength of mosaic patterns across microhabitats: epiphytic ferns > canopy > ground leaf-litter, and that non-native species drive this pattern to some degree. We also assess the relative strengths of the mosaic pattern in forest and plantation.

Methods

Field sites

Sampling was conducted during May and June 2002 in oil palm *Elaeis guineensis* plantation (Sebrang Estate, 118°35′E, 5°02′N, altitude 150 m) and primary lowland dipterocarp rain forest (Danum Valley Conservation Area, 117°49′E, 5°01′N, altitude 170 m) in Sabah, Malaysia. Plantations were 14–18 yr old at the time of sampling. In each habitat 20 sites were chosen, each of which was centred on a tree supporting a bird's nest fern (*Asplenium* spp.). Distances between sites ranged from 0.1 to 4.2 km in oil palm plantation and from 0.1 to 3.2 km in rain forest. Further site details are presented elsewhere (Turner and Foster 2009, Fayle et al. 2010).

Sampling methods

Litter-dwelling ants were sampled by collecting four 1 m^2 samples of leaf litter on bearings of 0°, 90°, 180° and 360° from directly beneath the focal tree. These litter samples were then left in Winkler extractors for three days. Fern-dwelling ants were sampled in a similar manner, with ferns (one per focal tree) being collected into plastic bags, and finely chopped before extraction following Fayle et al. (2010). Canopy ants were sampled using ground-based insecticide fogging with pybuthrin 33BB non-persistent insecticide (Swingfog SN 50-10PE fogging machine). Four 1 m^2 trays were placed beneath the focal tree in the same locations as the litter samples to collect falling insects. Fogging was conducted after litter sampling and fern removal, to avoid any impacts of fogging on ants from these two microhabitats. This protocol is

Figure 1. Bird's nest ferns in (A) oil palm plantation and (B) primary lowland dipterocarp rain forest.

designed to sample ant communities at comparable, small spatial scales in the different microhabitats (sampling units being either a single fern, 1 m^2 of leaf litter, or 1 m^2 of canopy), and at the larger scales at which ant mosaics are usually studied (sampling units being whole trees, each of which was assessed using 4×1 m^2). Ants were identified to genus (Bolton 1994, Hashimoto 2007), split to morphospecies and where possible assigned species names. Species were assigned as native/non-native following previous studies (Pfeiffer et al. 2008, Fayle et al. 2010).

Statistical analyses

As a minimum requirement for inferring the presence of an ant mosaic, species need to occur non-randomly with respect to each other. Specifically it is expected that dominant species will co-occur less often than would be expected at random. If particular subordinates co-occur only with particular dominant species, then this will act to create larger sets of mutually non-co-occurring species (Fig. 2). To test this hypothesis we used null models of species co-occurrence. Since sample sizes precluded the use of pairwise assessments of co-occurrence between species (Supplementary material Appendix 1), we quantified co-occurrence across entire data matrices. Following previous studies testing for the existence of ant mosaics (Pfeiffer et al. 2008, Dejean et al. 2010), we used the C-score as our metric of community-wide species co-occurrence. The C-score counts the number of pairs of species and pairs of sites where each species occurs only once and the two species occur at different sites (Stone and Roberts 1990). The higher the C-score, therefore, the greater the numbers of non-overlapping species distributions. Randomisation of the original matrix is then used to create the distribution of C-scores expected under the null hypothesis that species co-occur at random, from which the probability of obtaining the observed C-score, or one more extreme, is obtained. Standardised effect sizes (SES; Sanders et al. 2003) are calculated as follows: $SES = (C_{observed} - C_{null})/\sigma_{null}$. Where $C_{observed}$ is the observed C-score, C_{null} is the mean C-score of the randomised null matrices, and σ_{null} the standard deviation of the C-scores of the randomised null matrices. Thus, a positive SES value indicates segregation between species, and a negative value, aggregation. The expected signal of an ant mosaic is a large proportion of negative pairwise interactions (P_{neg}), unless the number of dominants is very small, and the proportion of subordinates is very high, and even in this case P_{neg} is never less than 0.5 (Fig. 2). We therefore used one-tailed tests ($\alpha = 0.05$), since we were specifically looking for segregation between species. Tests were conducted using the oecosimu function in the R package vegan (Oksanen et al. 2008) with constant row and column sums, the sequential swap randomisation algorithm (see studies by Gotelli (2000)), and a burn in of 30 000 swaps. We used a further 30 000 swaps to generate null distributions, as smaller numbers of swaps can lead to high type 1 error rates (Fayle and Manica 2010).

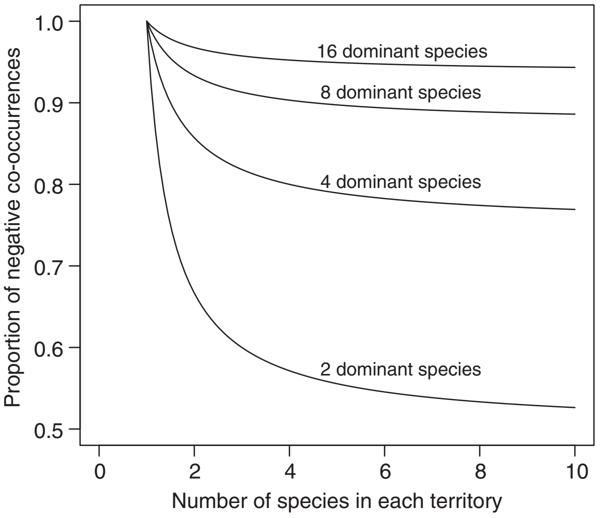

Figure 2. Expected proportion of pairwise negative co-occurrences between species in an ant mosaic in communities with different numbers of dominant and subordinate species. Consider an ant mosaic in which two or more dominant species hold mutually exclusive territories, in each of which occur subordinates peculiar to that dominant species. For simplicity, assume that the number of ant species (including the dominant) in any one territory is S, and this is constant between territories occupied by different dominants. There are therefore $S - 1$ subordinate species and one dominant species in each territory. If D is the number of different dominant species, then $D \times S$ is the total number of species in the whole community. Consequently the total number of pairwise interactions between species will be $DS(DS - 1)/2$. The number of positive interactions within a territory will be $S(S - 1)/2$, and therefore the total number of positive interactions in the community will be $DS(S - 1)/2$. The proportion of positive interactions is therefore $(DS(S - 1)/2)/(DS(DS - 1)/2)$ and so the proportion of negative interactions is simply calculated as $P_{neg} = 1 - (DS(S - 1)/2)/(DS(DS - 1)/2)$, simplified as $P_{neg} = 1 - (S - 1)/(DS - 1)$. P_{neg} is minimised when S tends towards infinity and $D = 2$ (the minimum number of dominant species required for the community to be considered a mosaic). P_{neg} can be written as $1 - 1/(D - (1/S)) + 1/(DS - 1)$, (from the simplified version of P_{neg}, above, separating out the two parts of the numerator of the fraction) which tends towards 0.5 only where $D = 2$ and S tends towards infinity. Therefore, given the assumptions above, there will always be more negative interactions between species than positive ones in an ant mosaic. Note that this analysis assumes that the territory of each dominant species is sampled only once. If multiple samples are taken from each territory type, then the predominance of negative interactions will become even more extreme (analyses not presented).

One criticism of metrics that sum co-occurrences across all species has been that they fail to detect non-random community structure where positive and negative interactions are present at similar frequencies (Blüthgen and Stork 2007). This is because metric values for datasets with many positively and negatively interacting species are similar to those where all species interact at random. Furthermore, when there are few dominants, and large numbers of subordinates, the ratio of negative to positive interactions is expected to tend towards 1:1 (Fig. 2). Here we implement a novel metric that allows the detection of such instances, without the need to explicitly conduct multiple pairwise comparisons. For all analyses for which the C-score did not differ significantly from that expected at random, we conducted a second analysis. We counted the numbers of chequerboard units for all pairs of species in the dataset, but instead of taking the mean of this value per species pair (the C-score), we calculated the variance in frequency of chequerboard units between species pairs (Supplementary material Appendix 2). We call this metric the C_{var}-score. We then compared the observed C_{var}-score to the distribution of this metric obtained from the randomised matrices generated above to calculate p-values. We were therefore able to assess whether there was a simultaneous increase in both positive and negative interactions. Note that tests were one tailed i.e. we only looked for instances in which the variance of pairwise chequerboard frequency was larger than would be expected if species co-occurred at random. We did not analyse matrices for which a significantly high C-score had been detected, since higher mean values of the metric are likely to lead to a higher variance, even in the absence of balancing positive and negative interactions.

Analyses of the C-score and C_{var}-score were conducted at two spatial scales for litter and canopy ant communities. For each dataset at the 1 m^2 scale, four data matrices were generated, one each from bearings of 0°, 90°, 180° and 360°. Each data matrix was randomised separately and the resulting observed and simulated metrics were summed across the four matrices. p-values were then calculated by comparing the distribution of the summed randomised null metrics with the observed metric summed across the four data matrices. This was done so that analyses were conducted at comparable scales across all microhabitats. We also conducted analyses at the scale of individual trees (whole tree scale) following previous studies (Pfeiffer et al. 2008), by combining the four data matrices from each tree before analysis.

To assess the role of non-native species in structuring oil palm communities, we reran these analyses with all non-native species excluded from the datasets, following the method of Pfeiffer et al. (2008). If non-native species compete strongly with all other ant species, then removing these species, and therefore their interactions, from the dataset, should result in a decreased degree of species segregation i.e. a lower C-score. Note that this approach is valid for detecting only direct interactions between ant species; indirect interactions will not be detected. Very few non-native species were found in rain forest (five occurrences across 200 samples from the three microhabitats, with 1 m^2 samples separate, compared with 61 occurrences in oil palm plantation), and so these data were not reanalysed. In order to ensure that species removal does not increase the probability of detecting species segregation per se we repeated the analyses described above, but instead of removing non-native species, we removed the same number of randomly selected species.

Results

Ant species in all three primary forest microhabitats co-occurred at random to one-another at the 1 m^2 scale (Fig. 3A–C, Table 1), with the observed C-scores being very close to the mean values expected under the null hypothesis. However, this was not the case in oil palm plantation, where there was evidence for species segregation in ant communities from bird's nest ferns and a non-significant trend for segregation in communities in the rest of the canopy

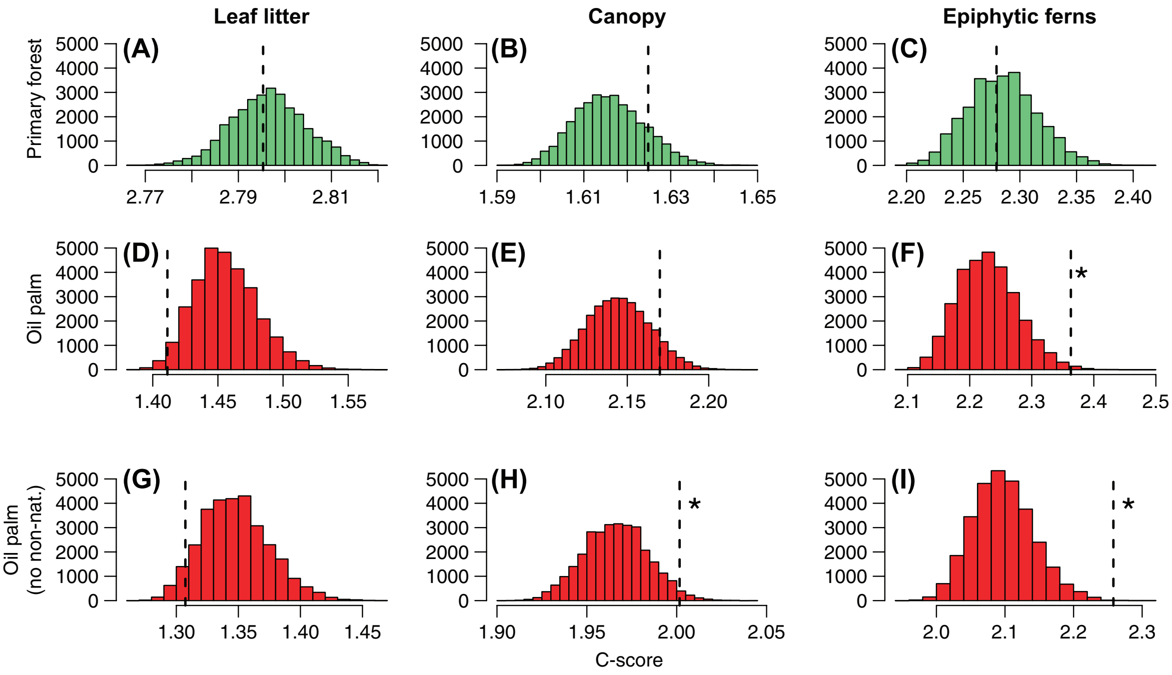

Figure 3. (A–I) The observed C-scores (broken lines) and the distributions of C-scores expected using null models in which there are no interactions between ant species for the 1 m^2 scale (histograms). A high C-score indicates that there is a high degree of segregation between species i.e. if the broken line is to the right of the histogram then there are fewer co-occurrences between species in that community than would be expected by chance. Histograms in green (A–C) show null distributions from primary forest microhabitats and those in red (D–I) oil palm microhabitats. Plots (G–I) show distributions for oil palm microhabitats with non-native ant species removed. Asterisks denote tests for which there was a significant degree of species segregation. See Table 1 for statistics.

Table 1. Observed C-scores and C_{var}-scores, mean metric values under null models, standardised effect sizes (SES) and related (one-tailed) p-values for ant communities from the three microhabitats in oil palm plantation and primary forest. Large C-score SES values indicate a greater degree of species segregation than would be expected at random. Large C_{var}-score SES values indicate greater degrees of both species segregation and aggregation. For leaf litter and canopy communities, analyses were conducted at two spatial scales: 1 m^2 and 'whole tree'. See Fig. 1 for graphical representations of full null distributions in comparison with observed metric values for C-score analyses at the 1 m^2 scale. p-values < 0.05 are given in bold. *Denotes oil palm communities with non-native species removed from the dataset.

		C-score				C_{var}-score			
Habitat	Microhabitat	Obs.	Mean null	SES	p	Obs.	Mean null	SES	p
1 m^2 scale:									
Rain forest	Epiphytic ferns	2.28	2.28	−0.18	0.573	0.05	0.05	−0.24	0.606
Oil palm	Epiphytic ferns	2.36	2.23	2.77	**0.006**	NA	NA	NA	NA
Oil palm*	Epiphytic ferns	2.26	2.10	3.59	**0.001**	NA	NA	NA	NA
Rain forest	Leaf litter	2.80	2.80	−0.14	0.560	0.65	0.66	−0.35	0.625
Rain forest	Canopy	1.62	1.62	1.10	0.147	0.18	0.16	1.30	*0.099*
Oil palm	Leaf litter	1.41	1.46	−1.85	0.983	0.13	0.17	−1.67	0.967
Oil palm	Canopy	2.17	2.14	1.30	0.107	0.10	0.10	0.29	0.381
Oil palm*	Leaf litter	1.31	1.35	−1.49	0.947	0.14	0.17	−1.11	0.882
Oil palm*	Canopy	2.00	1.97	1.98	**0.026**	NA	NA	NA	NA
Whole tree scale:									
Rain forest	Leaf litter	4.51	4.53	−0.98	0.834	2.07	2.43	−0.92	0.822
Rain forest	Canopy	2.60	2.61	−0.64	0.730	0.46	0.49	−0.78	0.784
Oil palm	Leaf litter	2.36	2.41	−1.42	0.932	0.28	0.34	−1.46	0.926
Oil palm	Canopy	3.04	2.99	1.41	*0.090*	0.24	0.23	0.43	0.328
Oil palm*	Leaf litter	2.04	2.09	−1.57	0.945	0.22	0.28	−1.61	0.958
Oil palm*	Canopy	2.61	2.54	2.32	**0.012**	NA	NA	NA	NA

(Fig. 3E, F, Table 1). Leaf-litter dwelling ant communities from oil palm plantations were randomly assembled (Fig. 3D, Table 1). We found no evidence for simultaneous increases in both positive and negative interactions (C_{var}-score) for any of the communities for which the above test was non-significant (Table 1). However, there was a non-significant trend for a higher C_{var}-score than would be expected at random in the canopy of rain forest (Table 1). Co-occurrence patterns at the whole tree scale for canopy and litter ants from the two habitats mirrored those observed at the 1 m^2 scale, with only a non-significant trend for species segregation being found in the oil palm canopy (Table 1).

We found seven non-native species in oil palm plantations: *Tetramorium simillimum*, *Tetramorium bicarinatum*, *Dolichoderus thoracicus*, *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Monomorium floricola* and *Cardiocondyla wroughtonii*. Across the 20 oil palm sites, non-native species were present in 10 sites in leaf litter, 11 sites in the canopy, and eight sites in epiphytic ferns. When these species were excluded and interactions between the remaining species analysed separately, this increased the degree of negative co-occurrence between species in leaf-litter, canopy and fern communities (Fig. 3G–I), as demonstrated by the larger SES values in all three microhabitats (Table 1). This effect was sufficiently pronounced such that oil palm canopy ant communities, which were initially not significantly segregated, became so after removal of non-natives from the dataset (Fig. 3E, H). This indicates that these non-native ant species are not the main drivers of the patterns of species segregation that we found. This was the case at both 1m^2 and whole tree scales (Table 1). Neither the leaf-litter nor the canopy oil palm ant communities showed evidence of simultaneous increases in positive and negative interactions (C_{var}-score) following removal of non-native species (Table 1). We found the method of species removal did not, of itself, increase species segregation. When species were selected for removal at random, the strength of segregation always decreased, as would be expected with reduced sample size and therefore reduced statistical power (Supplementary material Appendix 3). Results relating to differences in ant species richness and composition across habitats and microhabitats are presented elsewhere (Fayle et al. 2010).

Discussion

By using the same sampling methods in both forest and plantation we were able to compare directly the degree to which patterns of species segregation differed between these two habitats. Perhaps surprisingly, given the controversy over the existence of ant mosaics in undisturbed forest (Blüthgen and Stork 2007, Davidson et al. 2007), we have not been able to find any other study taking this approach in comparisons with oil palm plantation, or any other agricultural habitat. We found that none of the communities from primary forest showed any evidence of deterministic structuring (although see the non-significant trend for the C_{var}-score in primary canopy). This result echoes that found in comparisons of ant communities in pristine and disturbed rain forest (Floren et al. 2001), where disturbance increases the degree of species segregation. However, note that not all ant communities in disturbed forest are deterministically structured (Ribas and Schoereder 2002). It has previously been suggested that such results from pristine forests might relate to low statistical power or to positive and negative interactions cancelling out (Blüthgen and Stork 2007). However, this is unlikely to be the case in our study, since our dataset was large enough to clearly show the existence of ant mosaics in oil palm plantation, and there was no evidence for high variance in pairwise chequerboard count (C_{var}-score) in any microhabitat. Indeed, there were fewer species in plantation microhabitats than in those from rain forest and the same number of samples (Fayle et al. 2010), so any confounding effect of statistical power would be expected to give rise to the opposite pattern to that observed. One striking difference between the two habitats, and a potential factor explaining these patterns, is the structure of the canopy. In rain forest there are many more tree species (one species in oil palm vs 587 species in rain forest across 8 ha; Foster et al. 2011), and a single square metre of canopy could potentially consist of multiple species of trees across different canopy layers (even though the higher canopy layers may not have been completely sampled using our ground-based method). This might be expected to result in a more deterministic structuring in forest, since environmental filtering has a potentially greater role (Ellwood et al. 2009). However, the increased vertical heterogeneity could also potentially allow ant species to co-exist that would otherwise compete strongly. Alternatively, the high level of connectivity in the rain forest canopy might make it difficult to maintain a coherent territory, in contrast to the more simple structure of the plantation canopy. Indirect evidence for this postulation is the fact that the strength of segregation was, to some degree, scale dependent in plantations: a larger effect size was recorded at the whole-tree scale than at the 1 m^2 scale (controlling for differences in statistical power). A single canopy presumably makes for a more easily defendable territory than a 1 m^2 patch, which is well connected to other areas. There may even be differences in the way that ant communities are structured at different heights, something that it is not possible to detect using methods that combine communities from the upper and lower canopy. Recent work has found that ant communities at lower levels are structured randomly, while those from the very top of the canopy are more deterministic (Ribeiro et al. in press). A potential explanation for this is the high levels of insolation received by the upper canopy, which make it a similar environment to that found in plantations. Therefore our results do not necessarily rule out the possibility that competitive segregation exists in primary forests; rather they show that the mosaic pattern is much more pronounced in plantations. Our new metric, the C_{var}-score, may be useful for investigating such systems with more extensive datasets. Another promising option for detecting any weaker mosaic pattern in primary forests is to conduct sampling using continuous transects or plots, in which overlaps between territories can be explicitly identified (Davidson et al. 2007, Klimeš et al. 2012).

Our results also hint that competition for nest sites could be a driver of these mosaic patterns. To date it has been assumed that the major factor structuring ant mosaics is competition between dominant species for honeydew and extra-floral nectar (Blüthgen et al. 2003, Davidson et al. 2003, Blüthgen and Stork 2007). We found that in plantations deterministic, segregatory, community structuring was strong in an important canopy nest site (epiphytic ferns), weaker in the rest of the canopy and non-existent in ground-dwelling leaf litter communities. In hot, dry plantation canopies bird's nest ferns provide a cool, damp microclimate (Turner and Foster 2006), making them a valuable resource, and hence foci of competition. Nest sites could be less important in primary forests, since there are abundant accumulations of leaf litter elsewhere (Snaddon et al. 2012). If nest sites really are more limiting in plantations, then we would expect the more dominant species that monopolise honeydew resources (Blüthgen and Stork 2007) to take over these valuable resources. This is exactly what we observe: the most common species in primary forest ferns is *Diacamma* RF36 (8/20 ferns), a generalist predator and scavenger, while the most common species in plantation ferns are from two myrmicine genera, both of which are known to tend honeydew secreting homopterans or extrafloral nectaries (*Plagiolepis* Y1 (Eichhorn et al. 2011) and *Monomorium* J (Cuautle et al. 2005), both 6/20 ferns). An interesting exception to this has been found for some emergent trees in rain forest in Sarawak, in which the sole dominant ant species inhabits the rhizomes of *Leucanopteris* and *Platycerium* ferns and reduces the diversity of other canopy ants (Tanaka et al. 2012). However, although this shows that nest sites can sometimes influence ant interaction networks in primary forest canopies, this community could not strictly be called a mosaic, since there is only one dominant species.

Re-analysis of the data with non-native species excluded resulted in an increase in the strength of deterministic community structuring, with oil palm canopy-dwelling communities becoming significantly segregated (Table 1). The direct interactions mediated by non-native species therefore have the net impact of reducing the overall degree of segregation in arboreal plantation communities. Such a pattern might result from differential impacts of non-native species on residents (Sanders et al. 2003, Pfeiffer et al. 2008). For example, if a non-native species competed strongly with one native dominant species, but interacted at random with other native dominants (with which the native dominant competed; Sanders et al. 2007a), then this would effectively 'disassemble' the community, leading to a weaker overall degree of segregation. What is clear is that the effects of non-native species on species interaction networks are more subtle than them merely taking the place of native dominants, or competing strongly with all native species.

Our study demonstrates that high degrees of species segregation, congruent with the existence of ant mosaics, are present in oil palm plantation, and are absent, or at least much weaker, in primary rain forest. We also show that non-native species may act to disassemble ant communities in oil palm plantations, reducing the degree of species segregation, and that competition for nest sites potentially drives the assembly of these ant mosaics. Quantifying the impacts of habitat change on community interactions is central to our understanding of the long-term consequences of forest loss on biodiversity and for maintaining ecosystem function within plantations. This paper takes a step towards understanding the effect of habitat change on interaction networks, rather than assessing changes in species composition alone.

Acknowledgements – We are grateful to the EPU Malaysia, Yayasan Sabah, Danum Valley Management Committee and the Royal Society South East Asia Rainforest Research Programme for assistance with working in Malaysia and to Nico Blüthgen, Petr Klimeš, Kalsum Mohd Yusah, Jonathan Majer, and Nate Sanders for comments on the manuscript. We would also like to thank Chey Vun Khen and Arthur Y. C. Chung for acting as local collaborators during the data collecting phase of this work. Financial support was provided by the Natural Environment Research

Council, Yayasan Sime Darby and by the project 'Biodiversity of Forest Ecosystems' CZ.1.07/2.3.00/20.0064 co-financed by the European Social Fund and the state budget of the Czech Republic. TMF and ECT contributed equally to this work.

References

Blüthgen, N. and Stork, N. E. 2007. Ant mosaics in a tropical rainforest in Australia and elsewhere: a critical review. – Austral Ecol. 32: 93–104.

Blüthgen, N. et al. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. – Oecologia 137: 426–435.

Bolton, B. 1994. Identification guide to the ant genera of the world. – Harvard Univ. Press.

Cuautle, M. et al. 2005. Effects of ant behaviour and presence of extrafloral nectaries on seed dispersal of the Neotropical myrmecochore *Turnera ulmifolia* L. (Turneraceae). – Biol. J. Linn. Soc. 86: 67–77.

Davidson, D. W. et al. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. – Science 300: 969–972.

Davidson, D. W. et al. 2007. The tropical ant mosaic in a primary Bornean rain forest. – Biotropica 39: 468–475.

Dejean, A. et al. 1997. Ant mosaic in oil palm plantations of the southwest province of Cameroon: impact on leaf miner beetle (Coleoptera: Chrysomelidae). – J. Econ. Entomol. 90: 1092–1096.

Dejean, A. et al. 2010. Spatial distribution of dominant arboreal ants in a Malagasy coastal rainforest: gaps and presence of an invasive species. – PLoS One 5: e9319.

Eichhorn, M. P. et al. 2011. Attraction of ants by an invasive *Acacia*. – Insect Conserv. Divers. 4: 235–238.

Ellwood, M. D. F. et al. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. – Ecol. Lett. 12: 277–284.

Fayle, T. M. and Manica, A. 2010. Reducing over-reporting of deterministic co-occurrence patterns in biotic communities. – Ecol. Model. 221: 2237–2242.

Fayle, T. M. et al. 2009. The effect of rain forest canopy architecture on the distribution of epiphytic ferns (*Asplenium* spp.) in Sabah, Malaysia. – Biotropica 41: 676–681.

Fayle, T. M. et al. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. – Basic Appl. Ecol. 11: 337–345.

Fayle, T. M. et al. 2012. Public goods, public services, and by-product mutualism in an ant–fern symbiosis. – Oikos 121: 1279–1286.

Fitzherbert, E. B. et al. 2008. How will oil palm expansion affect biodiversity? – Trends Ecol. Evol. 23: 538–545.

Floren, A. and Linsenmair, E. 2000. Do ant mosaics exist in pristine lowland rain forests? – Oecologia 123: 129–137.

Floren, A. et al. 2001. Anthropogenic disturbance changes the structure of arboreal tropical ant communities. – Ecography 24: 547–554.

Foster, W. A. et al. 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of south east Asia. – Phil. Trans. R. Soc. B 366: 3277–3291.

Fukami, T. and Morin, P. J. 2003. Productivity–biodiversity relationships depend on the history of community assembly. – Nature 424: 423–426.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. – Ecology 81: 2606–2621.

Gotelli, N. J. and Ellison, A. M. 2002. Assembly rules for New England ant assemblages. – Oikos 99: 591–599.

Supplementary material (Appendix ECOG-00192 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.

Hashimoto, Y. 2007. Identification guide to ant genera of Borneo. – <http://homepage.mac.com/aenictus/AntsofBorneo.htm>.

Klimeš, P. et al. 2012. Why are there more arboreal ant species in primary than secondary tropical forests? – J. Anim. Ecol. 81: 1103–1112.

Lach, L. et al. 2010. Ant ecology. – Oxford Univ. Press.

Leston, D. 1973. The ant mosaic – tropical tree crops and the limiting of pests and diseases. – Trop. Pest Manage. 19: 311–341.

Morris, R. J. 2010. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. – Phil. Trans. R. Soc. B 365: 3709–3718.

O'Dowd, D. J. et al. 2003. Invasional meltdown on an oceanic island. – Ecol. Lett. 6: 812–817.

Oksanen, J. et al. 2008. vegan: community ecology package. – R package ver. 1.15-1, <http://cran.r-project.org/, http://vegan.r-forge.r-project.org/>.

Pfeiffer, M. et al. 2008. Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. – Ecography 31: 21–32.

Philpott, S. M. and Foster, P. F. 2005. Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. – Ecol. Appl. 15: 1478–1485.

Powell, S. et al. 2011. Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. – J. Anim. Ecol. 80: 352–360.

Ribas, C. R. and Schoereder, J. H. 2002. Are all ant mosaics caused by competition? – Oecologia 131: 606–611.

Ribeiro, S. P. et al. in press. Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy. – Myrmecol. News.

Sanders, N. J. et al. 2003. Community disassembly by an invasive species. – Proc. Natl Acad. Sci. USA 100: 2474–2477.

Sanders, N. J. et al. 2007a. An ant mosaic revisited: dominant ant species disassemble arboreal ant communities but co-occur randomly. – Biotropica 39: 422–427.

Sanders, N. J. et al. 2007b. Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. – J. Biogeogr. 34: 1632–1641.

Savolainen, R. and Vepsäläinen, K. 1988. A competition heirarchy among boreal ants: impact on resource partitioning and community structure. – Oikos 51: 135–155.

Snaddon, J. L. et al. 2012. Biodiversity hanging by a thread: the importance of fungal-litter trapping systems in tropical rainforests. – Biol. Lett. 8: 397–400.

Stone, L. and Roberts, A. 1990. The checkerboard score and species distributions. – Oecologia 85: 74–79.

Tanaka, H. et al. 2012. Effects of a fern-dwelling ant species *Crematogaster difformis*, on the ant assemblages of emergent trees in a Bornean rainforest. – Ann. Entomol. Soc. Am. 105: 592–598.

Turner, E. C. and Foster, W. A. 2006. Assessing the influence of bird's nest ferns (*Asplenium* spp.) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. – Selbyana 27: 195–200.

Turner, E. C. and Foster, W. A. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. – J. Trop. Ecol. 25: 23–30.

Turner, E. C. et al. 2008. Oil palm research in context: identifying the need for biodiversity assessment. – PLoS One 3: e1572.

Tylianakis, J. M. et al. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. – Nature 445: 202–205.

Vander-Zanden, M. J. et al. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. – Nature 401: 464–467.