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The effect of forest disturbance on the leaf litter ant fauna in Ghana

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In order to observe the effect of forest loss on the leaf litter ant fauna in Ghana, West Africa, samples were taken in primary forest, secondary forest and in cocoa plots. Ants were extracted from the leaf litter by sieving followed by suspension in Winkler bags. The species composition and species richness in the three different habitats were compared and no significant difference was found between them. It was concluded that most primary forest leaf litter ant species continue to survive in parts of the agricultural landscape which has largely replaced their original habitat.

Keywords: Formicidae; biodiversity; conservation; tropical forest; habitat disturbance

Introduction

Tropical forests have a particular importance in biological conservation for two reasons: they are home to a large proportion (probably at least half) of the world's species (Myers, 1986) and are currently being destroyed at an estimated rate of almost 1% per year (Whitmore and Sayer, 1992). The loss of global species richness likely to result from this destruction has been estimated by a number of authors (reviewed in Paoletti *et al.*, 1992; Jenkins, 1992). Their estimates vary but together they suggest that in a few more decades it may have been reduced by perhaps one-quarter. Such figures have been widely quoted in the conservation literature (e.g. Western, 1989; Osborn, 1991; McNeely, 1992).

Fundamental to most estimates for future extinctions are the relationships between species richness and habitat area, which are well documented for some groups of organisms (e.g. see Begon *et al.*, 1990). A common broad generalization is that a 90% reduction in the area of a habitat results in a 50% reduction in the number of species present (Reid and Miller, 1989). However, as Lugo (1988) points out (with some examples), such calculations do not take into account the ability of many species to survive in the disturbed or agricultural habitats which commonly remain following the loss of primary forest. We see a need for quantitative studies on selected taxa aimed specifically at this question. Previous studies on ants (Room, 1975a; Leston, 1979; Torres, 1984), although not primarily addressing this question, have shown that many primary forest ant species also occur in tree-crop plantations. In this paper we examine the leaf litter ant fauna of Ghana, West Africa, comparing species composition and

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species richness in primary forest with that in secondary forest and the main tree crop, cocoa. We aim to show the extent to which the primary forest fauna survives in the agricultural habitats that replace its original home.

Ants are important components of tropical forests. They comprise over one-third of the total insect biomass (and with termites approximately one-third of the total animal biomass) in a Brazilian forest (Fittkau and Klinge, 1973). They dominate the arthropod fauna numerically, both in the canopy (see Discussion) and on the ground; they comprised approximately one-half of all arthropods in the leaf litter in a Panamanian forest (Levings and Windsor, 1982). They are also commonly keystone species in tropical systems, e.g. via their predation of other invertebrates and their mutualisms with plants (reviewed in LaSalle and Gauld (1993)).

In West Africa ants are, for a tropical insect group, well studied taxonomically, largely as a result of research into cocoa pest control. Ghana has many areas of primary forest within its forest reserves, which together comprise approximately 20% of the forest zone in the country. Outside the reserves are many areas of abandoned or fallow agricultural land which has developed secondary forest of varying age, as well as an estimated 4–6 million acres of cocoa (Abbiw, 1990).

Materials and methods

Sampling

Between December 1991 and November 1992 we sampled the leaf litter ant fauna at 34 different sites scattered across the forest zone of Ghana. Almost all of these sites were in the Moist Semi-Deciduous forest type of Hall and Swaine (1976). The sites included 14 areas of primary forest, ten of secondary forest and ten cocoa plots (see Fig. 1).

It is very difficult to demonstrate that an area of forest is primary in the sense of never having been disturbed by man (i.e. is virgin forest). Therefore, we use the term primary forest to mean sites with a closed high canopy. Only two of these sites showed any signs of logging, which in these cases had been selective and had occurred at least 20 years ago. There is evidence that such low-intensity selective logging does not significantly affect the leaf litter ant fauna (Olson and Andriamiadana, in press). All primary forest sites were within forest reserves except for one in an arboretum and two in sacred groves, areas where for religious reasons the vegetation is undisturbed.

The secondary forest sites were areas regenerating following clearance for agriculture, except for two which were from marginal areas of forest reserves badly burnt in 1983. These clearances had only been partial because in Ghana some primary forest trees are left to provide shade for the crops. The sites varied widely in stage of regeneration (resulting not only from differences in age but also from differences in the history of previous land-use), but all had a broken, mostly low canopy and tangled undergrowth, i.e. impossible to walk through without a machete. The youngest site was 8 years old and the oldest approximately 40–50.

At each site we sampled the leaf litter ant fauna by placing ten 1 m^2 quadrats at random within an area of approximately 1000 m^2. All the leaf litter was collected from each quadrat and the ants extracted from it by sieving through a 1 cm mesh and leaving the residue in Winkler Bags for 3 days. The method is similar to extraction by Berlese funnel except that the material is suspended in a mesh bag and left to dry in air rather than exposed to a heat source. It is a more appropriate sampling method for leaf litter

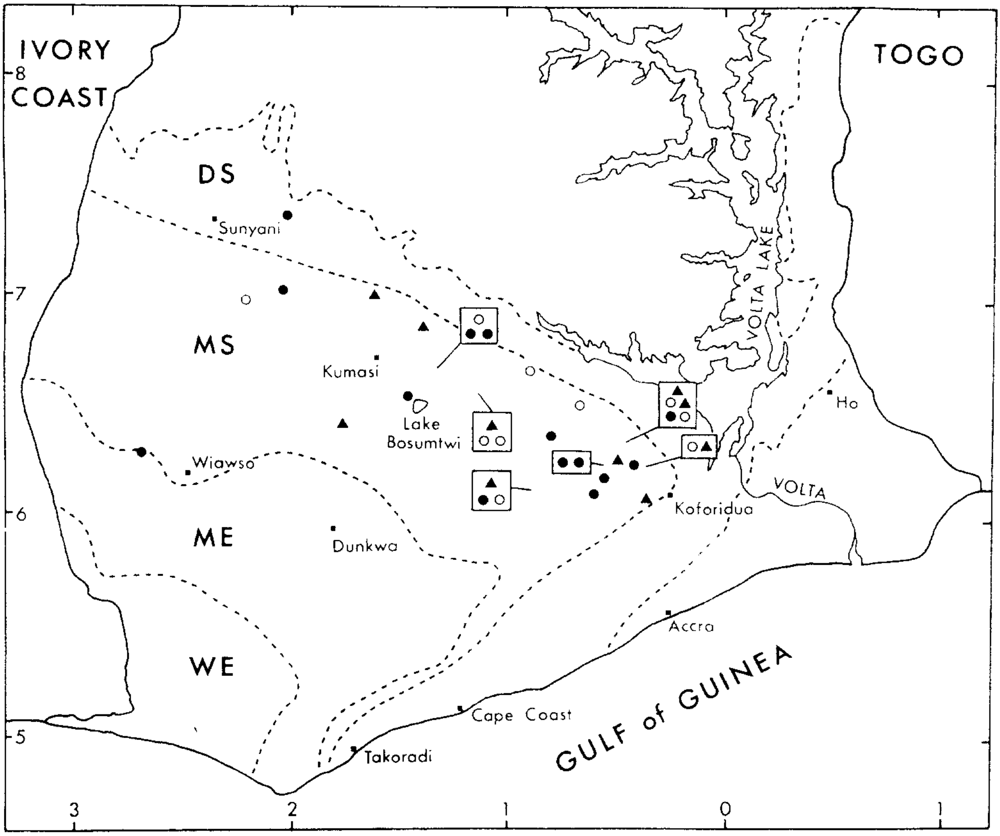

Figure 1. Locations of sites in Ghana, West Africa. Symbols: ● = primary forest; ○ = secondary forest; ▲ = cocoa. Forest and forest-type boundaries are shown by broken lines (– – –). Forest-type abbreviations: WE = Wet Evergreen; ME = Moist Evergreen; MS = Moist Semi-deciduous; DS = Dry Semi-deciduous. From Hall and Swaine (1981).

ants than pitfall trapping, which appears to underestimate the proportion of small species and specialized predators (Olson, 1991). At each site all the ants extracted from the ten quadrats were combined to form a single figure, which is used in the subsequent analyses. We excluded as tourists (1) species known not to forage in the leaf litter (mostly arboreal species), (2) winged reproductives and (3) isolated queens except for those species where the queens forage.

ANALYSES

Species composition

We compared the species composition of the sites in the three habitats in two ways.

(1) To see if the sites in one habitat tended to be more similar, in terms of their species composition, to those in other habitats, we first measured the similarity between all possible pairs of sites using the Morisita Index (see Wolda, 1981 for an assessment of this). We then used the CLUSTER option in the statistics package SYSTAT (Wilkinson, 1990) to link the sites into groups according to these similarity measures.

(2) It is possible that, even if there are not distinct groups, a gradient in species composition may be present in the data, possibly caused by the differing degrees of disturbance among the sites. Therefore we also used the ordination programme DECORANA (Malloch, 1988). This arranges the sites in a low dimensional space so that the more similar ones (according to their species composition) are placed closer together and the more dissimilar ones further apart (see Gauch, 1982).

Species richness

We compared the species richness of the habitats in two ways.

(1) We calculated the mean number of species found at sites in the three habitats. In addition we used a rarefaction programme derived from Hurlbert (1971) to estimate for each site how many species would be represented in a random sub-sample of n individuals, where n equals the smallest number of individuals found at a site. By using rarefaction we can compare the species richness of sites having allowed for variation caused merely by differences in the number of individuals collected. A limitation to this is the assumption in Hurlbert's equation that individuals are randomly dispersed; this probably does not hold for ants.

The statistical significance of differences between the habitats was tested using analysis of variance (ANOVA).

(2) Habitats may have similar mean species richness at sites but have different degrees of variation in species composition between component sites. This could lead to differences in the overall species richness of the habitats. We therefore plotted a species accumulation curve for each habitat. In each case we produced five randomly arranged sequences of sites and then found the mean number of species represented in site 1, site 1 + site 2, site 1 + site 2 + site 3, and so on.

Results

Our sampling at 34 sites produced a total of 39 809 ants in 176 species (excluding tourists). The average number of individuals found at a site was 1171 (minimum = 267, maximum = 2846). A full list of the species, along with more detailed descriptions of the sampling locations, is included in a separate publication (Belshaw and Bolton, 1993).

Species composition

The results of the CLUSTER analysis are presented in Fig. 2. It is clear that distinct groups are not present in the data. Not only are sites in the three habitats spread fairly evenly among the groups but the distances in terms of average similarity between the groups are very small.

The results of the DECORANA analysis are presented by plotting the first two axes against each other (Fig. 3). As with the result of the CLUSTER analysis, this shows the high degree of overlap in species composition between the habitats. The first axis does however produce what appears to be a small separation of the three habitats, with secondary forest appearing intermediate between primary forest and cocoa, but the difference is not statistically significant (one-way ANOVA with respect to habitat, $F = 2.17$, $p = 0.131$).

A possible factor causing the wide separation of cocoa sites on the second axis is age. The most distant outlier is the youngest (7 yr old) while the one on the X axis may be the oldest (perhaps over 50 y with regraftings). Unfortunately exact ages are not available for most plots.

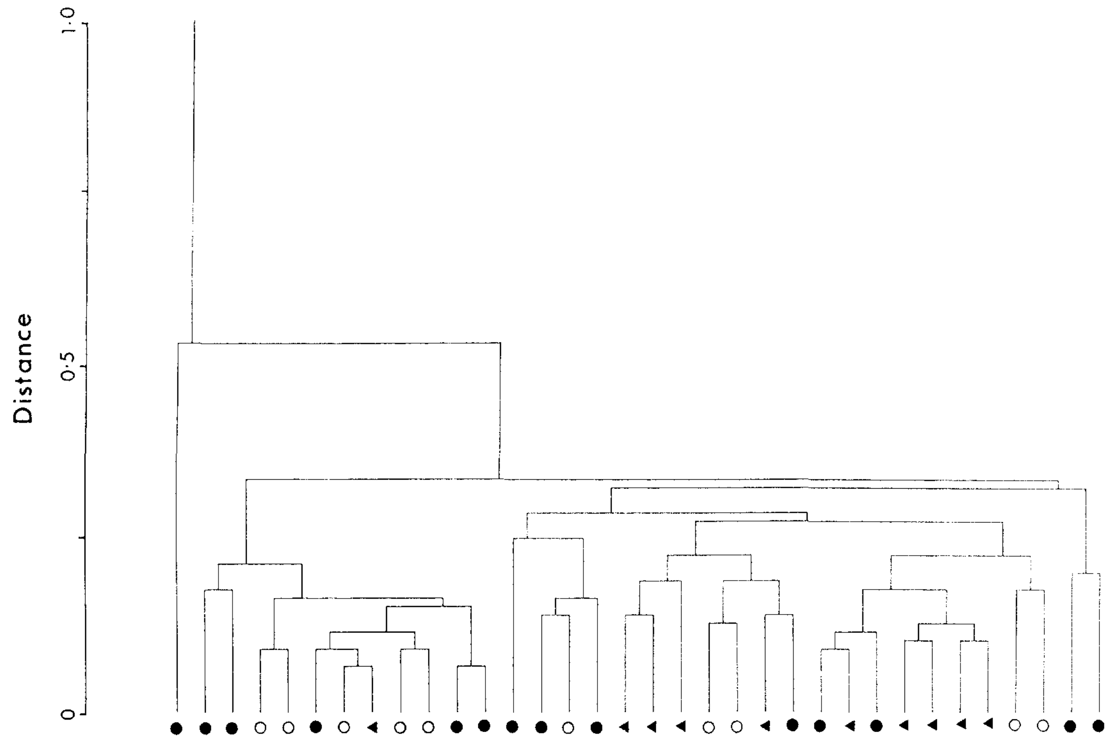

Figure 2. Sites grouped according to similarity of species composition (Morisita Index) by CLUSTER analysis in SYSTAT (distance is EUCLIDEAN, linkage is AVERAGE). Symbols: ● = primary forest; ○ = secondary forest; ◀ = cocoa.

We repeated the above analyses using logarithms of species abundances. Logarithmic transformation reduces the influence of abundant species, which are often generalists and hence may be less vulnerable to habitat disturbance. This procedure did not, however, produce more distinct groupings or gradients in the results.

Species richness

The mean number of species at each site in the three habitats is shown in Table 1. There is no significant difference between the means, with or without rarefaction.

Table 1. Mean species richness of sites in the three habitats (see text for explanation of rarefaction). One-way ANOVA with respect to habitat, $F = 0.307$ and 0.334, $p = 0.719$ and 0.738 (before and after rarefaction respectively)

Habitat	Number of sites	Mean number of species (SE)	Number of species after rarefaction
Primary forest	14	39.1 (3.1)	27.7
Secondary forest	10	35.5 (3.8)	26.2
Cocoa	10	36.6 (3.1)	26.2

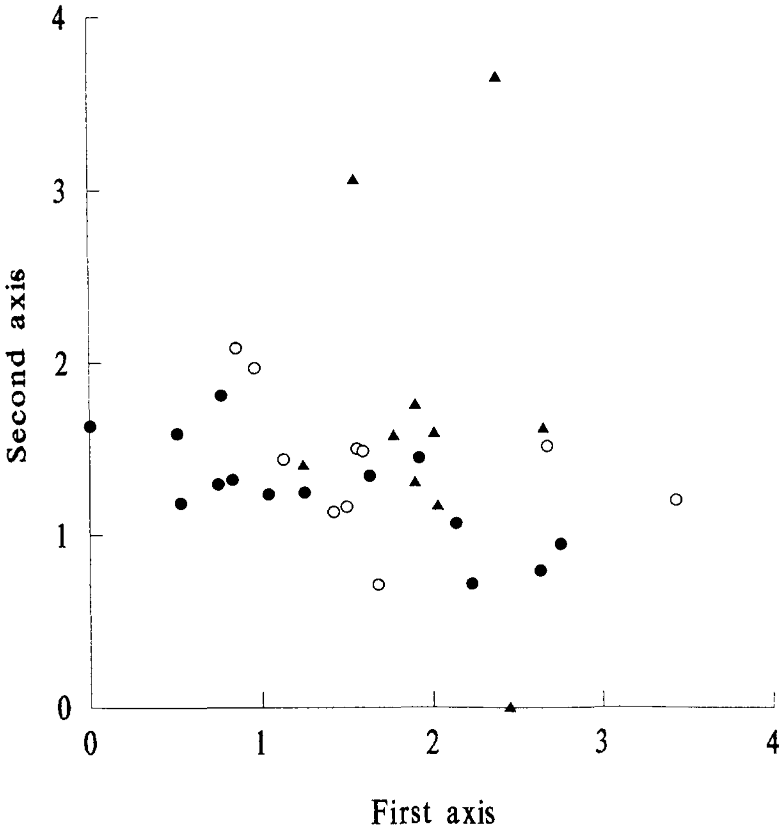

Figure 3. Species composition of sites compared using DECORANA. Symbols: ● = primary forest; ○ = secondary forest; ▲ = cocoa. (Eigenvalues of axes: first = 0.442, second = 0.372, third = 0.186, fourth = 0.133).

Figure 4 shows the species accumulation curve, averaged over five series, for the three habitats. After ten sites the cumulative numbers of species for primary forest and cocoa are identical; indeed, the curve is steeper for cocoa, suggesting that had more sites been sampled it may even have risen above the one for primary forest. The cumulative number of species after ten sites for secondary forest is only slightly smaller than for cocoa and primary forest (114 species compared to 126).

Discussion

We find in our data no evidence for a significant difference in species composition or species richness between primary forest and the agricultural habitats sampled. We conclude therefore that in Ghana disturbance of the original primary forest habitat (i.e. conversion to secondary forest or cocoa) has had little or no long-term effect on the species composition or the species richness of the leaf litter ant fauna.

The act of forest clearance drastically alters the habitat causing major changes in the ant fauna (MacKay *et al.*, 1991). Olson (1991) found evidence for a reduction in the

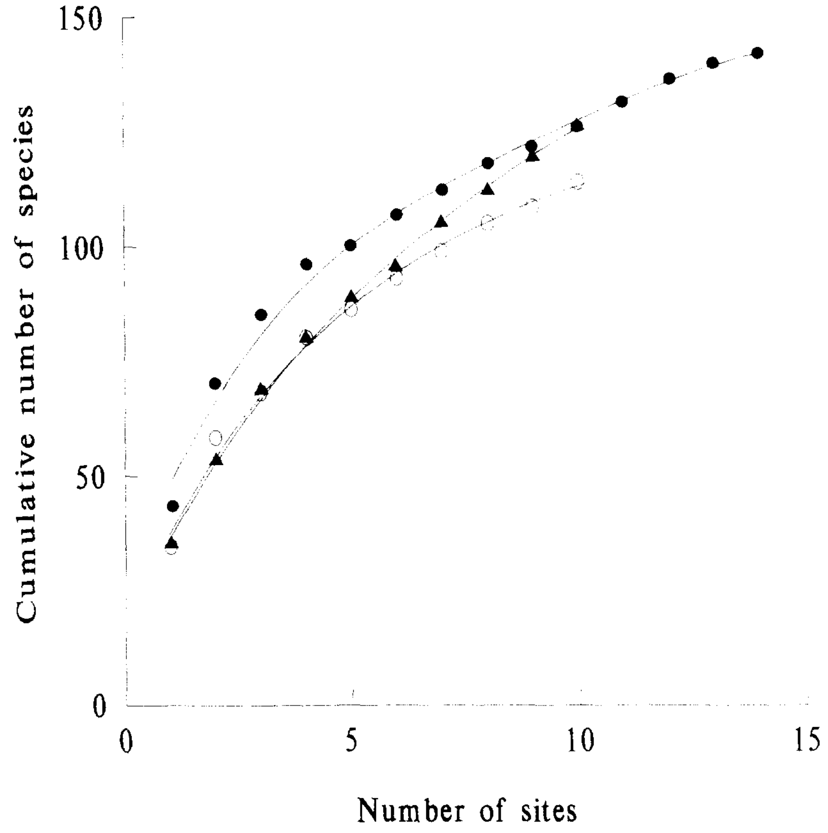

Figure 4. Species accumulation curves for the three habitats. Symbols: ● = primary forest; ○ = secondary forest; ▲ = cocoa.

species richness of the leaf litter fauna in young successional sites. However, it appears from our study that after ten or so years the primary forest species are again thriving in the leaf litter of these new habitats. It is likely therefore that these three different habitats – despite pronounced differences in plant species composition, architectural profile, degree of closure of the canopy etc. – offer a similar leaf litter microhabitat. Burghouts *et al.* (1992) found that the annual leaf fall, leaf litter mass, and rate of litter decomposition in primary and recently logged forests were indeed similar.

A few cautionary remarks are required here. Our sampling may not have been sufficiently intensive to detect a loss of rare species resulting from deforestation. Also, the remaining areas of primary forest may be necessary sources for recolonization of these continually recycling agricultural habitats. In which case, further deforestation in Ghana would have a significant effect on the leaf litter ant fauna. Two additional points need to be addressed.

(1) We have no data on the response to disturbance of the canopy ant fauna, which is taxonomically very different from that in the leaf litter. Erwin (1990), following recent advances in sampling techniques, has suggested that in tropical forests a greater

proportion of insect diversity is in the canopy as compared with the ground. Many studies have found ants to dominate numerically the arthropod fauna in the canopy, comprising 4% (Sulawesi, Stork and Brendell, 1990), 18% (Brunei, Stork, 1988), 43% (Seram Indonesia, Stork, 1988), 44% (Cameroon, Basset *et al.*, 1992), 51% (Brazil, Adis *et al.*, 1984) and 70% (Peru, Tobin, 1991) of individuals collected. As the canopy is greatly changed by disturbance, both in architecture and in plant species composition, there may be important changes in the total ant fauna which we have not observed.

In cocoa, ants are known to be relatively species-poor in the canopy (Room, 1971, 1975b), where a small number of aggressive species defend large territories forming a 3-dimensional mosaic. Territories are defended against conspecifics and a particular range of other species. Such associations between species-poor communities and the presence of territory-defending species appear to be common in ants (Hölldobler and Wilson, 1990). These so called *ant mosaics* are a common feature of tropical tree crops (see Majer, 1993).

The canopy fauna in non-agricultural habitats has been much less well studied. We assume that it is also dominated by ant mosaics, examples of which have been recorded in both secondary (Leston, 1978) and primary tropical forest (Hölldobler, 1983). Wilson (1987) discusses the ants – over 100 000 workers – extracted by insecticide fogging within a few square kilometres of a Peruvian forest. He found a maximum of 43 species from a single tree and an estimated 135 species in total. These figures suggest a species richness broadly comparable with our study. Olson and Ward (1993) found that the collection of arboreal species in an approximate 6 km^2 area of Madagascan forest added only 26 species to the 50 found from litter sifting and pitfall trapping. Allowing for this study being in a tropical dry forest, where the canopy may present a less favourable environment to ants, it gives further support for the species richness of canopy and ground ant faunas being generally similar.

Hammond (1992) has questioned Erwin's view that the canopy contains a high proportion of the total forest insect fauna. For example, after a comprehensive sampling programme in an area of Sulawesi (see Hammond, 1990) he concluded that probably less than 10% of the beetle species found were true canopy specialists.

(2) Ants may be less vulnerable to habitat disturbance, and hence unrepresentative, owing to their being social. Sociality is almost certainly the most important factor behind the ecological dominance which ants have achieved. Wilson (1990) discussed the ecological advantages conferred by sociality but found no evidence for a reduced vulnerability to habitat disturbance. Indeed, he saw the restrictions of colony establishment as factors permitting the persistence of non-social insects in the face of a general competitive superiority of social insects.

Clearly one cannot extrapolate from a single taxon in a single microhabitat to the entire global fauna. It remains to be shown if other taxa in the leaf litter resemble ants in their ability to survive the loss of primary tropical forest. It also remains to be shown what proportion of the global fauna this represents. Nevertheless, if many other forest insect groups are found to survive well in agricultural habitats, current predictions of the global species loss resulting from tropical deforestation will begin to look very exaggerated.

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