ECOLOGICAL CONSEQUENCES OF THE TROPICAL ANT MOSAIC

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The Old World tropical forests carry a mosaic of dominant ants (Leston, 1972). When the habitat is partially degraded, as by a tree crop under thinned forest, much of the original mosaic remains: the substitute canopy carries a simplified simulacrum of the forest fauna, the only segment depleted is that of the subcanopy. With further deforestation we approach either plantation conditions, with a restricted mosaic, or mixed crop farms with the intrusion of a savanna fauna and the absence of true dominants due to habitat impermanence (Leston, 1973a, b). Circumstantial evidence indicates that an analogous mosaic occurs in the New World.

After details of the mosaic itself this paper gives indications of the sunecological consequences of the mosaic.

1. THE MOSAIC COMPONENTS These are the colonies of a restricted numbers of species: in Ghana about 5 percent of the forest zone fauna of c. 400 species may be dominants. These have a potential for rapid population increase, the ability to spread by saltation, a catholicity in food, static nests and workers tolerant of a wide range of conditions. In Ghana the dominants are species of myrmicines in the genera *Atopogyne*, *Atopomyrmex*, *Crematogaster*, *Macromischoides* and *Pheidole*, formicines in *Acantholepis*, *Camponotus* and *Oecophylla* (Leston, 1970, 1972, 1973a, c; Majer, 1972; Room, 1971). Elsewhere *Iridomyrmex* and *Anoplolepis* also provide dominants (Greenslade, 1971; Way, 1953) but neither dorylines nor ponerines ever do. In the neotropics, *Azteca* and its allies are probably among the dominants (Leston, 1973a).

Dominants are mutually exclusive, the result of aggression, in its widest sense (Room, 1971); but a range of chemical and behavioural phenomena minimises warfare. Competition is greatest between conspecifics, least between members of different genera. Thus *Atopogyne clariventris* and *Macromischoides aculeatus*, true dominants, share a common foraging area through the latter becoming more nocturnal in the presence of the former (Aryeetey and Leston, 1974).

2. LIMITING FACTORS Minor ones include storms, destructive of nests of *Oecophylla* and *Macromischoides* (Leston, 1973d), and fungal epizootics, affecting all West African dominants. More important are the species' nest requirements: the ability of a tree to supply leaves suitable for struction or to support desired homopters (Stictococcidae for *Oecophylla*, Pseudococcidae for *Atopogyne* and *Crematogaster*, Coccidae for *Macromischoides*, etc.) Vegetation *in toto* is critical too: *Oecophylla* nest in insolated canopies, *Macromischoides* in dense shade.

The main factor is space. In 2.3ha of cocoa lacunae there were few species in the mosaic (Majer, 1972). In the simpler mosaic of Solomon Islands' coconut, it was concluded that interspecific competition for space was the element mediating distribution (Greenslade, 1971). In another case, chemically-achieved reduction in one dominant, *Pheidole megacephala*, enabled a second, *Oecophylla smaragdina*, to spread extensively (Leston, 1973a; Stapley, 1972). This case is remarkable in that the first nests in the ground, the second in the canopy: they compete for foraging room.

3. MOSAIC PATTERNS These were investigated by mistblowing pyrethrum (table 1). Each quadrat contains the insects from 8 cu. m sampling volume. The samples fell into three groups.

Group I (table 2) was from forest understorey and is characterised by a moderate number of ant species and low ant numbers: the dominants are all ombrophiles. The lacunae result from gaps in the vegetation: the C-storey is discontinuous. The overlap of dominants in, say, A7 and A10 (table 1) is not real: the species were stratified. Group III is the pattern in dense shade with lots of dead wood. This results in a pure stand of Crematogaster striatula to the virtual exclusion of all other ants and a high total ant population.

Group II is representative of the pattern in broken vegetation with much insolation. It is the pattern of crop canopies under scattered shade trees and of the forest canopy, of irregular height beneath emergents. The number of ant species is high, as is the number of individuals. Overlaps between Macromischoides species and Atopgyne clariventris are real insofar as they forage in a common area, but the nests of the latter are high above the sampling space.

It is easy to conclude that vegetation density controls the total ant population, but a property of the ant species also seems involved and is suggested by the 'striatula bush' pattern.

4. ANT NUMBERS The 24 sq. m samples (table 2) had from 230 to over 10000 ants each: the same method gave 18800 Oecophylla longinoda in cocoa under scattered shade at Enchi. Relatively pure cultures have, in the main, higher populations than mixed ones, despite the wide no-man's-lands between colonies of the same species (Leston, 1971). Ants are by far the most abundant of free-living tropical insects and it is this which makes them of paramount ecological importance.

5. THE MOSAIC AND FAUNAL COMPOSITION The distribution of many homopters reflects the distribution of their mutualistic ant associates but is seldom specific (Strickland, 1951; Way, 1963): the dominant ants all practice mutualism. In other taxa many pests of tropical tree crops are negatively associated with some dominants (Leston, 1973a; Way, 1954). Room (1971, 1972) surveyed the dominants on loranths growing upon cocoa. Each was the centre of a positive and negative association of non-dominant ants, Homoptera and lepidopterous or coleopterous borers.

It is suggested that the insect orders can be placed in a dominant ant impact hierarchy. In addition to the evidence of the previous paragraph ant mimicry provides data. Mimicry of a dominant, it is postulated, reduces predation by a non-mimicked domenant, and is associated with mechanisms (behavioural, pigmentary or chemical) permitting coexistance in the model's foraging area. The early instars of many tropical Mantodea, Ensifera, especially a vast range of larval and adult Heteroptera, are ant mimics: unless ant impact was considerable such an evolutionary trend would be pointless. Further evidence comes from anti-ant defence devices: the repugnatorial secretions of many Coccinellidae and Chrysomelidae are so interpreted.

The hierarchy (table 3) does not necessarily cover all families or genera within an order; whilst Oecophylla preys upon many caterpillars others are protected. In Coleoptera the diversity of the order guarantees a range from obligate ant associates, e.g., Clavigeridae, through the innumerable ant mimics in, e.g., Carabidae, to the apparently unaffected Cicindelidae. Room (1972) shows that the distribution of Diptera is not associated with ant patterns: insects which flit in their daily activity are largely ant-neutral, including adult Parasitica. Endophytic and endoparasitic forms are unaffected whilst the maggot is usually distasteful to ants.

Hence a wide range of insects is positively or negatively associated with one or more dominant ant, which affect not only the species composition but also a species' abundance. In areas of faunal imbalance, as Hawaii or Melanesia, an introduced ant may become a dominant, with a profound impact upon the indigenous fauna. As some insects are vectors of plant diseases it follows that the incidence of sick or healthy plants is also influenced by the ant mosaic, e.g., the distribution of swollen-shoot in cocoa and forest trees in West Africa. Vegetational quality is also affected through the impact of dominant ants upon insects involved in plant dispersal and, less strongly, in pollination. The angiosperm revolution, the radiation of pollinators and the radiation of ants were contemporaneous (Leston, 1973a). This is best demonstrated by the great number of tropical plants with extra-floral nectaries: these evolved so as to space out strategically a limited number of vegetation protecting, but not species' specific, ants over the host plant.

6. CONCLUSION Every insect in the tropical forest zone has evolved within a field of dominant ants. Change in the mosaic inevitably leads to change in the composition, qualitative and quantitive, of the total insect fauna of the area and through this, affects floral composition too.

Table 1. Dominant ants in 1 sq. m quadrat subdivisions of 12 sampling sheets 3 x 8 m, the ants obtained by pyrethrum knockdown between 2 to 10 m above the ground. A, Atopogyne clariventris; B, Atopogyne buchneri; C, Crematogaster kneri; D, Macromischoides aculeatus; I, Macromischoides inermis; M, Macromischoides africanus; O, Oecophylla longinoda; P, Pheidole sp; S. Crematogaster prox. striatula; St, Crematogaster striatula. Sampling sites: A, Atewa Range Forest Reserve; B, secondary forest at Bunso; C, cocoa farm at Adeiso; K, secondary growth at Kade.

A1	P	P	P/M	M	M	–	–	P	B1	M	A	A	A	A	A	A	A
	P	P	P	–	–	–	P/I	P		M/A	M/A	M/A	A	A	A	A	A
	P	P	P	C	P	P	P/C	P/I		M/A	M/A	M/A	A	A	A	A	A
A4	P	–	–	–	M	–	–	C	B4	I	I	I	I	I	I	I	I
	–	C	C	C/M	M	–	C	M		I	I	I	I	I	I	I	I
	P	P	P	–	–	–	–	M		I	I	I	I	I	I	I	I
A7	S/M	S/M	S/M	S/M	M	–	–	–	B7	M	M/A	M	M	M/B	B	B	B
	S/M	S/M	M	M	M	–	M	M		M	M	M/B	M/B	M/B	B	B	B
	S/M	S/M	M	M	M	M	M	M		M	M/B	B	B	B	B	B	B
A10	–	P/S	P	P/S	S	S	S	S	C1	A	D	St	St	St	St	St	St
	P	P	P	P/S	S	S	P	–		A	D	D	St	St	St	St	St
	–	P	P	P	P/S	S	S	P		–	D	O	O	St	St	St	St
A13	–	–	M/C	M	M/C	M	M	–	K1	St	St	St	St	St	St	St	St
	–	–	–	C	M	–	C	C		St	St	St	St	St	St	St	St
	–	C	–	C	–	C	C	C		St	St	St	St	St	St	St	St
K7	S	–	S	S	S	S	S	S	K4	St	St	St	St	St	St	St	St
	S	S	–	S	S	S	S	S		St	St	St	St	St	St	St	St
	S	S	S	S	S	S	S	S		St	St	St	St	St	St	St	St

Table 2. Characteristics of some ant mosaic patterns in 24 sq. m samples.

Group	Sample	Totals ant spp	Totals ants	Spp/quadrat mean	Spp/quadrat mode	Dominants
1	A1	15	359	2.1	1	4
Primary	A4	19	371	2.9	2	3
forest	A7	16	492	3.2	4	2
C-storey	A10	22	305	3.5	3	2
	A13	18	232	2.2	2	2
....	K7	15	378	2.5	2	1
2	B1	30	3589	12.4	13	2
Secondary	B4	26	6561	9.1	9	1
forest or	B7	35	7094	7.8	5	3
ococa farm	C1	26	3663	8.2	9	4
3	K1	2	>10000	1.0	1	1
'striatula'	K4	2	>10000	1.0	1	1
bush						

Table 3. **Suggested hierarchy of the impact of ants upon some terrestrial insect groups.**

Homoptera Sternorrhyncha	very strong interactions
Other ants	very strong interactions
Heteroptera	strong interactions
Isoptera	strong interactions
Homoptera Auchenorrhyncha	moderate interactions
Orthoptera Ensifera	moderate interactions
Mantodea	moderate interactions
Blattodea	weak interactions
Lepidoptera	very variable: strong to weak
Coleoptera	very variable: strong to weak
Neuroptera	very variable: strong to weak
Dermaptera	neutral
Diptera	neutral
Hymenoptera Parasitica	no interactions.

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