

Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics

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A functional group model of ant community composition has been widely used in Australia to analyse biogeographical patterns of ant community structure and the responses of ant communities to disturbance. The model has provided valuable support to the widespread use of ant communities as bioindicators of ecological change. However, the model was developed from studies of arid-zone faunas, and its applicability to the World Heritage rainforests of Queensland's humid tropics has not yet been validated. Here we test predictions based on the functional group model for ant communities in Queensland's humid rainforests, by documenting ant community composition and its responses to disturbance on the Atherton Tablelands. Five sites were studied, comprising two relatively undisturbed reference sites representing contrasting rainforest types, and three previously cleared sites, two of which were undergoing revegetation. A variety of sampling techniques were employed, including pitfall trapping, litter extractions, baiting, and general searching. A total of 50 ant species from 29 genera were collected. Site species richness was highest at the reference sites, and lowest at the unvegetated disturbed site, and overall was negatively related to mean ground temperature. As predicted by the functional group model, behaviorally dominant dolichoderines were uncommon or absent at the reference sites, and the most common ants were Generalized myrmicines and Opportunists. Also as predicted, habitat disturbance favored Opportunists, and, as the disturbance involved canopy clearance, this led to colonization by *Iridomyrmex* and other Dominant dolichoderines. Opportunists represented about 40% of total ants in traps at the reference sites, compared with 80–95% at the disturbed sites. Except one species, Tropical Climate Specialists and Specialist Predators were absent from disturbed sites.

In conclusion, patterns of ant composition in relation to disturbance on the Atherton Tablelands conform to the functional group model that has been widely applied to ant faunas elsewhere in Australia. The model may therefore play an important role in the use of ants as bioindicators of ecological change in the World Heritage rainforests of this region.

Keywords: Ant communities; bioindicators; disturbance; functional groups; tropical rainforest.

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Introduction

There is considerable interest in the identification of robust bioindicators for use in land monitoring and assessment programmes (Noss, 1990; Spellerberg, 1993; McKenzie *et al.*, 1995), and attention has recently focused on terrestrial invertebrates in this role (Disney, 1986; Rosenberg *et al.*, 1986; Kremen, 1992; Williams, 1993). In a recent analysis of various insect groups as potential bioindicators, ants scored highest (Brown, 1997). In Australia, ants have been used extensively as bioindicators (Majer, 1983; Greenslade and Greenslade, 1984; Andersen, 1990, 1997a), particularly in relation to minesite restoration (Majer *et al.*, 1984; Majer, 1985; Andersen, 1997b), but also to other disturbances such as fire, grazing and logging (Neumann, 1992; York, 1994; Vanderwoude *et al.*, 1997a). Changes in ant community structure following disturbance have been found to reflect changes in many other invertebrate groups (Majer, 1983; Andersen, 1997b).

The use of invertebrate bioindicators is most effective when supported by a predictive understanding of community composition in relation to environmental stress and disturbance. The use of ants as bioindicators is supported by a macro scale functional group scheme (Table 1; Andersen, 1997a), which has been used extensively to analyse biogeographic patterns of community composition (Greenslade and Thompson, 1981; Greenslade, 1985; Andersen, 1993a; Andersen and Clay, 1996; Reichel and Andersen, 1996) and the responses of ant communities to disturbance (Anderson, 1990, 1991a, 1993b; Burbidge *et al.*, 1992; Vanderwoude *et al.*, 1997a). Ant richness and biomass are

Table 1. Summary of functional groups of Australian ants (giving characteristics and major taxa), based on their relationships to environmental stress and disturbance (see text)

Dominant Dolichoderinae:	Abundant, highly active and aggressive species, exerting a strong competitive influence on other ants. These favour hot and open habitats. <i>Iridomyrmex</i> , <i>Anonychomyrma</i> .
Subordinate Camponotini:	Co-occurring with, and behaviourally submissive to Dominant dolichoderines. With large body size and, often, nocturnal foragers. <i>Camponotus</i> , <i>Polyrhachis</i> , <i>Opisthopsis</i> .
Hot Climate Specialists:	Taxa adapted to arid environments with morphological, physiological or behavioural specializations which reduce their interaction with Dominant dolichoderines. <i>Melophorus</i> , <i>Meranoplus</i> , <i>Monomorium</i> (part).
Cold Climate Specialists:	Distribution centred on the cool-temperate zone. Occur in habitats where Dominant dolichoderines are generally not abundant. <i>Prolasius</i> , <i>Notoncus</i> , <i>Monomorium</i> (part).
Tropical Climate Specialists:	Distribution centred on the humid tropics. Occur in habitats where Dominant dolichoderines are generally not abundant. <i>Oecophylla</i> , <i>Tetraponera</i> , many other tropical taxa.
Cryptic Species:	Forage predominantly within soil and litter, having relatively little interaction with epigeaic ants. <i>Solenopsis</i> , <i>Hypoponera</i> , many other small myrmecines and ponerines.
Opportunists:	Unspecialized, ruderal species characteristic of disturbed sites, or other habitats supporting low ant diversity. <i>Rhytidoponera</i> , <i>Paratrechina</i> , <i>Aphaenogaster</i> , <i>Tetramorium</i> .
Generalized Myrmicinae:	Cosmopolitan, sub-dominant ants occurring in most habitats, with an ability to find and defend, rapidly, clumped food resources. <i>Crematogaster</i> , <i>Pheidole</i> , <i>Monomorium</i> (part).
Specialist Predators:	Little interaction with other ants due to specialist diet, large body size, and small size. <i>Myrmecia</i> , <i>Cerapachys</i> , <i>Bothroponera</i> , <i>Leptogenys</i> .

typically greatest in warm, open habitats, and in Australia these communities are usually dominated both numerically and functionally by dolichoderines, primarily species of *Iridomyrmex* (Greenslade, 1976; Andersen, 1992; Andersen and Patel, 1994). Generalized myrmicines (species of *Crematogaster*, *Monomorium* and *Pheidole*) are sub-dominant ants in these communities (Andersen, 1995), but often assume behavioural dominance in warm, shady habitats. Behavioural dominance is generally low in highly stressed (low temperature) or disturbed communities, where Opportunists such as species of *Rhytidoponera* or *Paratrechina* often predominate (Andersen, 1990, 1995).

Although the ant functional group model was developed, primarily, from studies of arid-zone faunas (Greenslade, 1978), it has successfully been applied to almost all major Australian biomes (Andersen, 1995), including monsoonal rainforests of the seasonal tropics of northwestern Australia (Andersen and Burbidge, 1991; Andersen and Majer, 1991; Andersen and Reichel, 1994; Reichel and Andersen, 1996). However, the applicability of the model to rainforests of the humid tropics of northern Queensland remains to be validated. These rainforests cover extensive areas and represent a variety of structural types (Webb and Tracey, 1981), and have recently been afforded World Heritage status due to their ecological, biogeographic and taxonomic interest and aesthetic appeal. Despite the taxonomy and biogeography of the ant fauna being known reasonably well by Australian standards (Taylor, 1972), we are unaware of any published accounts providing quantitative data on community composition at individual sites, although the abundances of selected species have been examined in relation to habitat fragmentation (Hill, 1995).

The functional group model makes the following predictions in relation to patterns of ant composition in humid rainforests of northern Queensland. First, behaviourally dominant dolichoderines, and especially species of *Iridomyrmex*, are likely to be uncommon or absent in undisturbed habitats, due to heavy shading. As a result, the most common ants are likely to be Generalized myrmicines and Opportunists (Andersen, 1995). Habitat disturbance is likely to favour Opportunists, as it does throughout much of the rest of Australia (Andersen, 1990, 1995). Where habitat disturbance involves canopy clearance (i.e. removal of shade), colonization by species of *Iridomyrmex* is also likely.

This paper aims to: (1) provide for the first time quantitative descriptions of ant community composition in humid tropical rainforest of northern Queensland; (2) describe the effects of disturbance on ant community composition; and (3) test the extent to which these patterns of composition conform to predictions arising from the functional group model.

Methods

Study sites

The study was conducted at five sites (Table 2) on the Atherton Tablelands in north-eastern Queensland, representing two relatively undisturbed reference sites, and three disturbed sites. The two reference sites were chosen to represent the range of rainforest types occurring in the area. The first was located at Gadgarra State Forest (GSF), in the Toohey's Creek region. GSF is a mature stand of rainforest that was selectively logged approximately 40 years ago. Our study site was approximately 100 m inside the south-western edge of the forest where it was bordered by a cattle paddock. The dominant canopy trees were *Elaeocarpus angustifolius* Blume (Elaeocarpaceae), *Flindersia* spp. [Rutaceae (segregated, occasionally, as Flindersiaceae)], *Euodia xanthoxyloides* F. Muell. (Rutaceae), and *Castanospermum australe* A. Cunn and C. Fraser ex Hook. (Legumi-

Table 2. Summary microclimate variables at each site. Data are means, with standard deviations in parentheses. Measurements of air and ground temperature were taken at each site using a temperature probe, at the same time litter samples were collected. Percentage canopy cover was determined using a spherical densiometer, and percentage and type of ground cover was estimated visually

Site	Air temp. (°C)	Ground temp. (°C)	Litter depth (cm)	Canopy cover (%)
GSF	24.8 (0.0)	19.6 (0.0)	2.4 (0.5)	95.6 (1.5)
TS	27.3 (0.7)	22.8 (0.7)	2.9 (1.2)	89.6 (2.6)
R95	23.6 (2.2)	22.2 (0.8)	0.8 (0.7)	78.9 (5.9)
R96	26.5 (0.7)	22.9 (0.6)	1.5 (0.5)	0.0 (0.0)
P	30.3 (0.8)	28.6 (2.4)	0.8 (0.6)	0.0 (0.0)

nosae). *Cryptocarya* spp. including *C. corrugata* C.T. White and Francis (Lauraceae), *Neolitsea dealbata* (R.Br.) Merr. (Lauraceae), *Acronychia acidula* F. Muell. (Rutaceae), *Blechnum cartilagineum* Sw. (Blechnaceae), *Cryptocarya triplinervis* R.Br. (Lauraceae), and *Calamus australis* Mart. (Palmae) were common in the sub-canopy or understorey.

The second reference site was located at the Tolga Scrub (TS) forest fragment (26 ha), located 15 km from GSF. TS is an isolated complex notophyll rainforest fragment that was selectively logged 80–100 years ago. The dominant canopy trees of our study site were *Ficus superba* Miq. (Moraceae), *F. obliqua* F. Forst. (Moraceae), *F. hispida* L.f. (Moraceae), *Toona ciliata* (F.Muell.) Harms (Meliaceae), *Argyrodendron peralata* (F.M. Bailey) Edlin ex J. Boas (Sterculiaceae), and *C. australe*. *Calamus caryotoides* A. Cunn. Ex Mart. (Palmae), *Dendrocnide moroides* (Wedd.) Chew (Urticaceae), *N. dealbata*, and *Gardenia* spp. (Rubiaceae) were common in the sub-canopy or understorey. The study site was bordered on two sides by roads that ran through the northern end of the fragment, and surrounded by agricultural fields and urban development.

The three disturbed sites were three completely cleared paddocks used for cattle production. One (R95) had been revegetated for 1 year, another (R96) had been revegetated for 2 months, and the other (P) had not been revegetated at all. R95 was located on the eastern bank of Toohey's Creek approximately 1 km upstream from GSF. Many species of tree were planted in January 1995 to restore the riparian zone of the paddock to rainforest. A total of 42 rainforest species were planted, mostly *Omalanthus novo-guineensis* (Warb.) K. Schum. (Euphorbiaceae), *E. angustifolius*, *Melicopeelleryana* (F. Muell.) T.G. Hartley (Rutaceae), and *Alphitonia whitei* Braid (Rhamnaceae). All of the trees at this site were approximately 1–2 m in height (estimated visually), closely planted, and provided some ground shade. R96 was located on the eastern bank of Toohey's creek approximately 2 km upstream from GSF. Here, planting was in February 1996, and was similar to that in R95, with the exception that 49 species were planted. All of the trees at this site were approximately 40–50 cm tall (estimated visually), evenly spaced, and provided little or no shading. P was located on the eastern bank of Toohey's Creek approximately 20 m from R96, and its vegetation consisted of pasture grasses.

Sampling

Our aim was to obtain comparative data on species richness and composition at each site, rather than to compile comprehensive species lists. We used a variety of techniques in order to sample a range of ant guilds (Olson, 1991; Andersen and Reichel, 1994). First, a

5 × 4 grid of pitfall traps, with 10 m spacing, was established at each site. Traps were 34 mm diameter test tubes, partly filled with ethanol as a preservative and operated for 48 h. Second, ants were extracted from five litter samples (72 h extraction time) at each site using Winkler sacs (Olson, 1991). The samples included the top 3–5 cm of soil as well as surface litter, and were collected at 8 m intervals along a transect adjacent to the trapping grid. Finally, ants were collected at ten combined sardine, tuna and honey baits located for 24 h at each site. Baits were located on tree trunks and logs (where available), as well as on the ground. All sampling was conducted during April (end of wet season) 1996. Previous studies of Queensland ant faunas indicate that functional group composition of ants shows little seasonality (Andersen, 1993a; Vanderwoude *et al.*, 1997b).

Analysis

Specimens collected from all samples were combined to produce species lists for each site, and pitfall catches were used as quantitative data on species relative abundances. Species abundances in individual traps were transformed to a five point scale (1 = 1 ant, 2 = 2–5 ants, 3 = 6–20 ants, 4 = 21–50 ants, 5 = <50 ants) to avoid misleadingly high abundances due to sampling near foraging paths or nest entrances (Andersen, 1991b). These individual abundance scores were tallied to provide estimates of site relative abundances. Ant species were assigned to functional groups following Andersen (1995), and to a biogeographical category [Torresian (tropical) Bassian (cool-temperate), Eyrean (arid), Widespread] according to the distribution of the species-groups to which they belong.

Results

We collected a total of 50 ant species from 29 genera (Table 3), with the richest genera being *Polyrhachis* (seven species), *Pheidole* (six), *Hypoponera* (four), *Rhytidoponera* (four) and *Paratrechina* (three). The most abundant species was *Rhytidoponera victoriae*, followed by *Aphaenogaster pythia*, *Paratrechina* sp. A and *Solenopsis* sp. A. The list includes two introduced species, *Tetramorium bicarinatum* and *Pheidole megacephala*.

Species richness ranged from seven at P to 21 at GSF, with TS having the highest number of genera (14) (Table 3). Species richness at R95 (19) was higher than at R96 (12), which was higher than at P (7). Overall, species richness was negatively related to mean ground temperature (Fig. 1). In contrast to total species richness, ant abundance in traps was lower at GSF and TS than at the disturbed sites. These abundance patterns may be partly explained by decreased ant 'trappability' with increasing vegetative cover. However, they also reflect site differences in ant species composition, with the distributions of the most common species listed above all heavily centered on the disturbed sites.

Analyses of species turnover across sites are constrained by sampling intensity, but turnover appeared high, with 35 (69%) of the 50 species recorded from a single site, and only two species (*Paratrechina* sp. A and *Rhytidoponera victoriae*) recorded at all five sites (Table 3). In terms of shared species, highest site similarities (about 25% shared species) were between P and the two revegetated sites (Table 4). GSF tended to have the lowest similarities with other sites (mean of 10.5%), including a very low similarity (7%) with TS.

Thirty (60%) of the species belong to Torresian, six (12%) to Bassian, and the remainder (28%) to widespread species-groups (Table 3). No Eyrean taxa were recorded. Biogeographical profiles varied markedly across sites; for example, the proportion of widespread species ranged from 24% at GSF to 57% at P. Four out of the six Bassian

Table 3. Distribution of ants across study sites (GSF = Gadgarra rainforest; TS = Tolga Scrub rainforest fragment; R95 = 1995 revegetation planting at Toohey's Creek; R96 = 1995 revegetation planting at Toohey's Creek; P = cattle paddock at Toohey's Creek). Data are numbers of ants recorded in pitfall traps, with records in litter samples (L) and hand collections at baits (H) also indicated

	Biog. ^a	FG ^b	Site records					Total in traps
			GSF	TS	R95	R96	P	
Myrmeciinae								
<i>Myrmecia rowlandi</i>	B	SP	H	-	-	-	-	-
Aenictinae								
<i>Aenictus</i> sp.nr. <i>ceylonicus</i>	T	C	-	-	-	2	-	2
Ponerinae								
<i>Amblyopone australis</i>	W	C	-	H	-	-	-	-
<i>Anochetus ?graefferi</i>	T	SP	-	H	-	-	-	-
<i>Cryptopone rotundiceps</i>	T	TCS	H	-	-	-	-	-
<i>Heteroponera relictata</i>	B	CCS	L	-	-	-	-	-
<i>Heteroponera ?imbellis</i>	B	CCS	-	L	-	-	-	-
<i>Hypoponera</i> sp. A	W	C	L	-	-	-	-	-
<i>Hypoponera</i> sp. B	W	C	L	L	H	-	-	-
<i>Hypoponera</i> sp. C	W	C	-	L	L	-	-	-
<i>Hypoponera</i> sp. D	W	C	-	L,H	-	-	-	-
<i>Mesoponera australis</i>	T	SP	-	L,H	-	-	-	-
<i>Myopias</i> sp. A	T	SP	-	-	-	1	-	1
<i>Onychomyrmex hedleyi</i>	T	SP	H	-	-	-	-	-
<i>Rhytidoponera impressa</i>	T	OP	-	-	H	-	-	-
<i>Rhytidoponera purpurea</i>	T	OP	2,H	-	3,H	-	-	5
<i>Rhytidoponera scaberrima</i>	T	OP	2	-	-	-	-	2
<i>Rhytidoponera victoriae</i>	B	OP	13,L	10,L	3,L	46,L	22,H	94
Myrmicinae								
<i>Aphaenogaster pythia</i>	W	OP	-	-	26,L	11,L	32,L	69
<i>Cardiocondyla ?nuda</i>	T	OP	-	-	-	-	L	-
<i>Crematogaster</i> sp.A (<i>laeviceps</i> gp.)	W	GM	-	H	H	-	-	-
<i>Meranoplus</i> sp. A	T	HCS	-	H	-	-	-	-
<i>Myrmecina rugosa</i>	T	TCS	-	L	-	-	-	-
<i>Oligomyrmex</i> sp. A	T	C	L	-	-	-	-	-
<i>Pheidole megacephala</i>	T	GM	-	-	L	-	-	-
<i>Pheidole</i> sp. A	T	GM	14,L,H	-	H	-	-	14
<i>Pheidole</i> sp. B	T	GM	L	-	H	-	-	-
<i>Pheidole</i> sp. E	W	GM	L	-	-	-	-	-
<i>Pheidole</i> sp. F	T	GM	L	-	H	-	-	-
<i>Pheidole</i> sp. G	T	GM	5,H	-	H	-	-	5
<i>Pristomyrmex thoracicus</i>	T	TCS	-	L	-	-	-	-
<i>Solenopsis</i> sp. A	W	C	-	16,L	11,L	-	3,L	30
<i>Strumigenys philiporum</i>	T	C	H	-	-	-	-	-
<i>Strumigenys friedae</i>	T	C	-	-	-	1	-	1
<i>Tetramorium bicarinatum</i>	T	OP	L	-	-	-	-	-

Table 3. (Continued)

	Biog. ^a	FG ^b	Site records					Total in traps
			GSF	TS	R95	R96	P	
Dolichoderinae								
<i>Anonychomyrma</i> sp. A (<i>nitidiceps</i> gp.)	B	D	-	-	H	-	-	-
<i>Iridomyrmex</i> sp. A (<i>anceps</i> gp.)	W	D	-	1	1,H	10,L,H	L	12
<i>Leptomyrmex ruficeps</i>	T	TCS	-	3	-	-	-	3
<i>Ochetellus</i> sp. A (<i>glaber</i> gp.)	W	OP	-	-	H	9,L,H	2	11
<i>Technomyrmex</i> sp. A	T	OP	L	-	-	-	-	-
Formicinae								
<i>Paratrechina</i> sp. A (<i>vaga</i> gp.)	T	OP	2,L	L,H	13,L	10	20,L	45
<i>Paratrechina</i> sp. B (<i>minutula</i> gp.)	W	OP	L	-	H	-	-	-
<i>Paratrechina</i> sp. C	W	OP	-	L,H	-	-	-	-
<i>Polyrhachis clio</i>	T	S	-	H	-	-	-	-
<i>Polyrhachis rufifemur</i>	T	S	-	-	-	L	-	-
<i>Polyrhachis senilis</i>	T	S	-	-	-	H	-	-
<i>Polyrhachis</i> sp. B (<i>appendiculata</i> gp.)	T	S	-	-	L	-	-	-
<i>Polyrhachis flavibasis</i>	B	S	L	-	-	-	-	-
<i>Polyrhachis</i> sp. nr. <i>rastellata</i>	T	S	-	H	-	H	-	-
<i>Polyrhachis urania</i>	T	S	-	-	-	H	-	-
Total no. ants			47	30	57	90	79	294
Total no. species			21	18	19	12	7	(50)
Total no. genera			13	14	11	9	7	(29)
No. 'exclusive' species			12	11	4	6	1	

^a Biogeographic affinities as follows: B = Bassian; T = Torresian; W = widespread.

^b Functional groups, as follows: D = Dominant Dolichoderinae; S = Subordinate Camponotini; HCS = Hot Climate Specialist; TCS = Tropical Climate Specialist; CCS = Cold Climate Specialist; C = Cryptic Species; OP = Opportunist; GM = Generalized Myrmicinae; SP = Specialist Predator.

species were recorded at GSF, compared with only two at the three disturbed sites combined.

In terms of numbers of species, the most important functional groups were Opportunists (12 species), and Generalized Myrmicinae and Subordinate Camponotini (seven each; Table 3). Only two Dominant dolichoderines and one Hot Climate specialist were recorded. Opportunists were particularly prominent at P, comprising five (71%) of the seven species. Considering the nine Tropical Climate Specialists and Specialist Predators collectively, eight were recorded at one or the other of the reference sites, but at none of the disturbed sites. Functional group abundance varied even more markedly across sites (Fig. 2). In particular, Dominant dolichoderines were abundant at disturbed sites, but

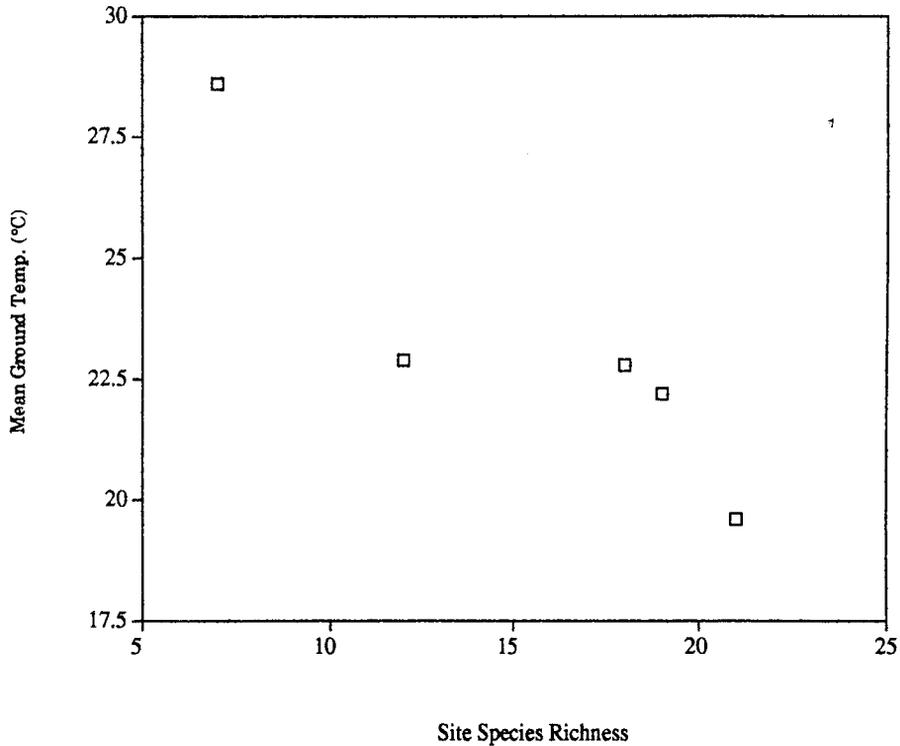


Figure 1. Relationship between site species richness and mean ground temperature.

absent from GSF, and Opportunists represented about 40% of total ants in traps at both GSF and TS, compared with about 80% at R95 and R96, and 95% at P.

Discussion

The fauna

As predicted for Queensland's tropical rainforests by the functional group model, behaviourally Dominant dolichoderines were uncommon or absent in our undisturbed habitats (GSF and TS), and the most common ants were Generalized myrmicines and Opportunists. On the basis of biogeographical patterns of ant distribution elsewhere in

Table 4. Percentage of shared species [(no. of shared spp./total no. of spp.) × 100] for each pair of sites

Site	GSF	TS	R95	R96	P	Mean
GSF	100	7.5	22.5	6.1	7.1	
TS		100	18.4	12.9	15.4	
R95			100	16.1	23.1	
R96				100	26.3	
P					100	
Mean						15.5

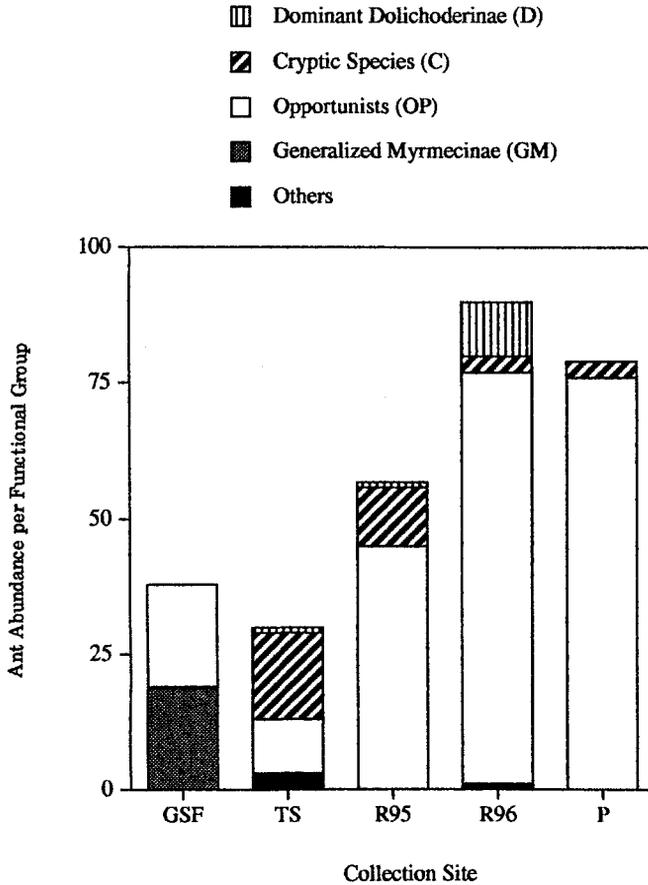


Figure 2. Functional group composition at each study site. Data are abundances in pitfall traps.

Australia, Andersen (1995) predicted that Queensland’s tropical rainforests would support structurally similar ant communities to those known to occur in monsoonal rainforests of northwestern Australia, but with a greater representation of Tropical Climate Specialists. Using the key to structural types of ant communities in Andersen (1995), GSF and TS support DD0GM (Dominant Dolichoderinae and Generalized Myrmecinae representing <10% and >30% respectively of the total of ants in traps) and DD0OPP (Dominant Dolichoderinae and Generalized Myrmecinae representing <10% and <30% respectively) communities, the predominant occurrence in monsoonal rainforests (Andersen, 1995).

Considering GSF and TS together, 11% of recorded species are Tropical Climate Specialists, which is only slightly higher than in monsoon rainforests of the Northern Territory (8%) and Kimberley (5%; Reichel and Andersen, 1996). Again considering GSF and TS together, 56% of recorded species have Torresian affinities, compared with 59% and 48% in monsoon rainforests in the Northern Territory and Kimberley respectively (Reichel and Andersen, 1996). The proportion of tropical species recorded at GSF and TS is therefore not substantially different from that in monsoonal rainforests. However, given the relatively high elevation and cool climate of the Atherton Tablelands, the proportion of tropical species is likely to be higher elsewhere in northern Queensland. Moreover, such

comparisons are likely to be influenced by the higher sampling intensity in the Northern Territory and Kimberley studies. Two Cold Climate Specialists were recorded in the present study, whereas this group is not present in monsoonal rainforests of northwestern Australia (Reichel and Andersen, 1996).

Similarity in species composition was very low between GSF and TS. In particular, five species of *Pheidole* (Generalized Myrmicinae) were recorded at GSF, where they contributed 60% of total pitfall catches, whereas *Pheidole* was not recorded at all at TS. It is not possible to judge the extent to which these differences have been influenced by fragmentation at TS, or simply reflect different faunas associated with different rainforest types.

Response to disturbance

As predicted by the functional group model, habitat disturbance favoured Opportunists, and, as the disturbance involved canopy clearance, this led to colonization by *Iridomyrmex* and other Dominant dolichoderines. Opportunists represented about 40% of total ants in traps at both GSF and TS, compared with 80–95% at the disturbed sites. Except for one species, Tropical Climate Specialists and Specialist Predators were absent from disturbed sites. Disturbance therefore had a marked and predictable effect on functional group composition.

Disturbance is also indicated by the presence of the tropical tramp species *Pheidole megacephala* at R95. This ant has had a devastating impact on native ants and other invertebrates where it has been introduced on Pacific islands (Lieberberg *et al.*, 1975; Gillespie and Reimer, 1993), and has a major impact on native ants at disturbed sites elsewhere in Queensland (Majer, 1985; Heterick, 1997). It has decimated the native ant fauna of a rainforest patch near Darwin in Australia's Northern Territory (Hoffmann, 1966) and, undoubtedly, has the capacity to do likewise in Queensland rainforests, particularly if its invasion is facilitated by habitat disturbance.

In conclusion, patterns of ant composition in relation to disturbance on the Atherton Tablelands conform to the functional group model that has been widely applied to ant faunas elsewhere in Australia. The model may therefore play an important role in the use of ants as bioindicators of ecological change in the World Heritage rainforests of this region.

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