

Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal

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Abstract

The ant fauna of 12 sand-mined plots representing a range of rehabilitation ages and three undisturbed vegetation controls was surveyed during 1982. Physical and botanical parameters were also measured in each plot.

Sixty-four ant species were collected from the 15 study plots, of which 44 had colonized one or more of the mined plots. Ant recolonization proceeded rapidly in plots up to 6 years old and may have been influenced by the passage of time, plant cover, density and diversity variables, the amount of litter and by the paucity of logs. In terms of ant species composition, the mined plots were most different from the undisturbed areas. The older plots exhibited a lower ant species richness and this is believed to have resulted from interspecific competition with the tramp ant, *Pheidole megacephala*. Ant succession proceeded in a slower fashion in the plots dominated by *P. megacephala*.

The influence of ants on seeds applied during broadcast seeding of rehabilitated areas was also investigated. Seed removal by ants was greatest for the arillate seeds of *Acacia concurrens* but moderate quantities of *Allocasuarina* spp., *Eucalyptus* spp. *Xanthorrhoea* sp. and *Banksia* spp. were taken also.

Seed removal by ants was low in the areas which had recently had topsoil applied except where ants foraged from adjacent rehabilitation areas; here they exerted their influence up to 50 m across the fresh topsoil. Seed removal rates in topsoil adjacent to forest were low. Removal rates in a revegetated area 2.5 years old approached those in forest. This indicates that the previous ant-seed relationship had been partially restored by this time, although the relative contribution of seed harvesters and elaiosome collectors still needs to be assessed.

Introduction

North Stradbroke Island is a large sandmass, about 40 km east of Brisbane in south-east Queensland. It is bounded by latitudes 27° 20'–27° 45' S and longitudes 153° 20'–153° 33' E and measures approximately 32 km in the north-south direction and up to 11 km in the east-west direction (Fig. 1).

One company which is mining for mineral sand in the north of the Island is Associated Minerals Consolidated Ltd (AMCL). Mining, now under the jurisdiction of AMCL, first started in 1950 and in 1956 dredging of the frontal dunes commenced. Broadly speaking, three of the Island's dune systems have been affected by this company's mining operations; the frontal dunes along almost the entire eastern side of the Island, the exposed high dunes immediately behind the frontal dunes of the northern half of the Island and the high dunes situated near

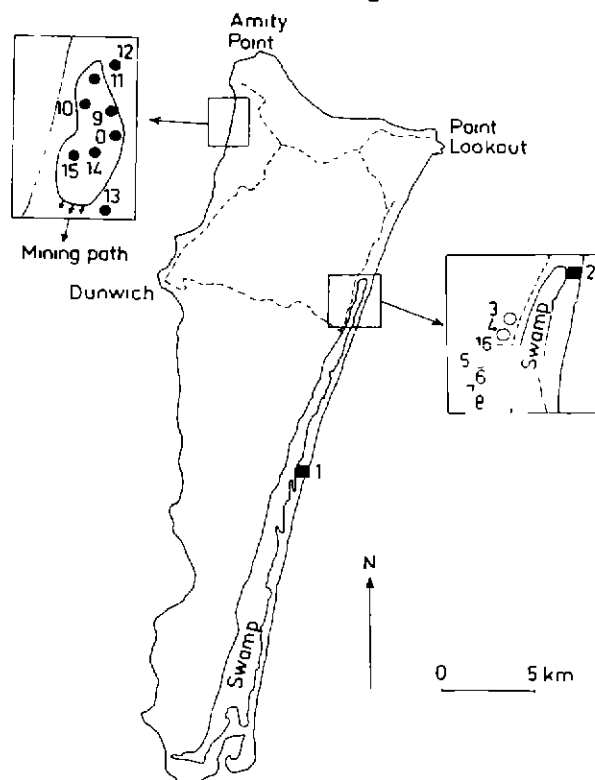


FIG. 1. Position of mined and control plots where ant surveys were performed and also the plots in which seed removal was assessed. Plot numbers are explained in the text; ■ frontal dune plots, ○ exposed high dune plots and ● high dune plots

Amity Point on the northern tip of the Island. Each dune system has its own characteristic vegetation association. Although a number of plant communities occur within each dune system, the principal ones affected by AMCL mining operations are the open-herbland (or coastal dune grassland) on the frontal dunes, the closed-scrub (or coastal dune scrub) on the exposed high dunes and the open forest on the high dunes (Clifford & Specht 1979).

In each case the areas are rehabilitated by recontouring the dunes using silica tailings, spreading topsoil (except frontal dunes), stabilizing the surface using stubblemulch (frontal dunes only), covering the area with brush matting, Terolas (a bitumenous substance) and/or cover crops and then applying a seed mixture of exotic and native plants. Planting of additional species is often carried out at a later date (Brooks 1976, 1980).

Majer (1981) and Majer *et al.* (1982, 1984) outlined the importance of recolonization of invertebrates for the successful rehabilitation of reclaimed areas. Briefly this results from their involvement in soil aeration, soil drainage, litter decomposition, nutrient cycling, pollination, plant predation, vertebrate food webs, seed distribution and survival. Ants are particularly important in the latter two processes as they may either harvest the seed and consume the contents (harvesters) or gather and disperse the seed in response to ant-attracting structures on the diaspore (collectors). Recently it has been suggested that in view of their frequent ecological dominance, elevated position in the food chain and their tendency to occupy specialized niches (Greenslade 1979), ants may act as good bioindicators of the abundance, species richness and species composition of other invertebrate taxa and also of the nature of the flora (Majer 1983). An investigation of ant recolonization in mined areas may therefore reveal much about the restoration of the biota in general. Such studies have already been performed in mineral sand-mined areas at Myall Lakes, NSW by Fox and Fox (1982) and at Eneabba, WA, by Majer *et al.* (1982).

Attention recently has been focused on ants of North Stradbroke Island by Drake (1981) who investigated ant-seed interactions in open forests of the Island. She concluded that diaspore removal by ants was extremely rapid and that the readily available seed supply for germination was significantly depleted.

Greenslade and Thompson (1981) studied the relationships between ant distribution, vegetation and soil in the Cooloola-Noosa River area of

Queensland, 130 km north of North Stradbroke Island. In the present study the exposed high dunes correspond to landscape units 1C and 1D and the Amity Point high dunes to landscape unit 5 of Greenslade and Thompson. The present study used a similar nomenclature of ant taxonomy to that for Cooloola so the results are comparable.

The aim of the present study was threefold:

- (1) to assess the recolonization by ants of mined areas and compare this with baseline data in undisturbed vegetation;
- (2) to investigate the factors contributing to the return of the ant fauna;
- (3) to assess the degree of seed removal by ants in mined areas.

Methods

Description of experimental plots

Ant recolonization was assessed in 12 mined and three unmined areas (Table 1, Fig. 1). Mined areas were selected to represent the three dune systems and also a range of times since rehabilitation (0 to 15 years). Vegetation and general invertebrate composition of plots 1 and 2 were assessed recently by Chandler (1982) and soil, litter and vegetation composition were measured in plots 5 and 6 by Cartwright (1982).

All mined plots were rehabilitated by seeding with a mixture of plant species and the approximate species composition of the blends is shown in Table 1. Enrichment planting was also carried out in some of the plots.

Control plots 12 and 13 were situated at either end of the Amity Point high dune mining path while plot 8 was near the southern end of the exposed high dune mining operations (Fig. 1). No control plots were established on the frontal dunes since all areas, except for a small blowout at Point Lookout, had been mined.

Plot 12 was in layered open forest of 20–25 m height. The upper canopy was dominated by *Eucalyptus signata* and *Eucalyptus pilularis* with *Eucalyptus intermedia*, *Allocasuarina torulosa* and *Allocasuarina littoralis* as subdominants. *Banksia aemula* formed a tall shrub layer while the medium shrub layer comprised *Monotoca elliptica*, *Leucopogon* sp., *Dodonea triquetra* and *Ricinocarpus pinifolius*. The grassy ground cover was dominated by *Eriachne* spp. and *Themeda australis*. The area had not been burnt recently.

TABLE 1. Age of rehabilitation and composition of seed blends applied to the 12 mined plots. Species which were planted or introduced with the brush matting are also shown.

Dune system	Frontal dunes		Exposed high dunes				High dunes					
	1	2	4	16	3	5	6	7	11	10	9	0
Plot number	9.0 5.0		15.0 10.0		8.0 6.0		2.0 0.5		2.5 1.7 1.1 0.1			
Time since rehabilitation (yrs)												
Species												
+ <i>Acacia concurrens</i>	P		S	S	S	S		S				S
° <i>A. cyanophylla</i>				S	S	S		S				S
+ <i>A. sophorae</i>	S											
+ <i>A. suaveolens</i>			S	S	S	S						
+ <i>Banksia aemula</i>				B/P	B/P	B/P/S		B/P				P
+ <i>B. integrifolia</i>	P											
+ <i>B. serrata</i>			B	B/P	B/P	B/P/S		B/P				P
+ <i>Callitris columellaris</i>												P/S
+ <i>Canavalia maritima</i>	S											
+ <i>Carpobrotus glaucescens</i>	S		P									
+ <i>Allocasuarina equisetifolia</i>	P		P									
+ <i>A. littoralis</i>			B		B/P	B/P/S		B/P/S				P/S
+ <i>A. torulosa</i>												P/S
+ <i>Ipomoea pes-caprae</i>	S											
+ <i>Eucalyptus intermedia</i>			B	B/P	B/P	B/P/S		B/P/S				P/S
+ <i>E. pilularis</i>												P/S
+ <i>E. signata</i>					B/P	B/P/S		B/P/S				P/S
+ <i>Hibbertia scandens</i>			P									
° <i>Leptospermum laevigatum</i>	P											
+ <i>Spintex hirsutus</i>	S											
+ <i>Tristania conferta</i>			B	B/P	B/P	B/P/S		B/P/S				
+ <i>Xanthorrhoea johnsonii</i>								S				
° Cover crop-Sudax (Sorghum Cross)				S	S	S		S				S
° Other cover crop grasses			S/P	S	S	S						

P planted; S direct seeded; B seed provided from brush matting; + native to area; ° non native species.

Plot 13 was in open forest (20–25 m height) which had been burnt 1 year previously. The upper canopy was dominated by *E. pilularis* and *E. intermedia* and also some *Callitris columellaris*. The tall shrub layer consisted of *B. aemula*, *A. torulosa* and *A. littoralis* while the medium shrub layer was absent due to the effects of fire. A well developed ground cover was dominated by *Imperata cylindrica*, *Eriachne* spp. and *Pteridium esculentum*.

Control plot 8 was in a 6–8 m high closed scrub with upper canopy consisting of *Acacia concurrens*, *Banksia integrifolia*, *Banksia serrata* and *Tristania conferta*. The shrub layer was dominated by *M. elliptica* and *A. littoralis* and the ground layer by *P. esculentum*, *Lomandra longifolia* and various grasses.

Measurement of physical and vegetation variables

The mean mid-day soil temperatures (at 2.5 cm depth) and rainfalls for the Amity Point high dune and 'Plant 01' exposed high dune (close to plot 7,

Fig. 1) areas were obtained from company records for the pitfall trap and litter sampling periods and for each month of 1982 (Table 2).

A 100 m transect was marked out in the centre of each mined plot and in the three control plots. The penetrability of the soil to a depth of 2 cm was assessed using a hand-held Soiltest densiometer at 10 m intervals along each transect. One square metre quadrats were then established at 10 m intervals along each transect. Within each quadrat the percentage bare ground, the depth and percentage of ground covered by litter, and the percentage plant cover were recorded. A litter volume index [(depth × percentage cover)/100] was calculated. The numbers of individual plants of each species occurring within the quadrats were also recorded. Projected foliage cover was assessed by scoring the presence or absence of vegetation covering a wire cross mounted in a vertical sighting tube which was placed at 50 equidistant points along each transect.

The vegetation structure and density was further investigated using a 2 m rod (adapted from Levy &

TABLE 2. Monthly rainfall totals and mean soil temperatures (2.5 cm depth) measured on the Amity high dunes and the exposed frontal dunes (mine plant 01) during 1982

Time interval	Total rainfall (mm)		Mean soil temperature (°C)	
	Amity	Plant 01	Amity	Plant 01
January	351.0	347.5	*	*
February	145.5	128.0	37.2	37.3
March	326.0	235.0	36.6	36.6
April	136.0	159.5	32.8	32.9
May	63.0	66.0	28.8	29.1
June	62.0	54.5	27.1	27.0
July	40.0	44.0	22.0	21.9
August	90.0	62.0	24.1	24.1
September	109.0	89.5	27.6	27.6
October	98.5	126.0	29.4	29.4
November	12.0	14.0	39.9	39.4
December	141.0	163.0	37.9	38.3
28 September–3 October 1982 (pitfall trap & first litter fauna samples)	0.0	0.0	29.5	29.5
9–13 December 1982 (second litter fauna samples)	19.0	58.0	39.6	37.8
12 December 1982 (seed Expt. 1)	0.0	0.0	39.0	39.5
6–7 October 1982 (seed Expt. 2)	0.0	0.0	29.0	29.5
14–15 December 1982 (seed Expt. 3)	0.0	0.0	41.0	42.0

* No data available.

Madden 1933), which was divided into 25 cm intervals. Fifty equidistant rod placings were made along each transect. The numbers of contacts of vegetation touching the rod at each 25 cm interval were counted, and records were made of incidence of tree canopy situated vertically above the rod. From these data, percentage area cover of vegetation (trees and understorey) was obtained by calculating the percentage of the 50 recordings which touched any plant. Plant cover density was obtained by dividing the total number of plant contacts by the number of rod placings which resulted in any vegetation contact; this calculation was performed for the total length of the rod in order to obtain an overall measurement of cover density and also for each 25 cm interval in order to construct a vertical profile of cover density.

The number of pieces of dead wood within a 2 m wide strip adjacent to each transect was recorded. Wood was divided into three categories: 1–9.9 cm, 10–29.9 cm and > 30 cm diameter. The items in each category were also summed to give a measure of total dead wood.

Plant species richness in each plot was investigated by further searching the plot for a 30 min period to record all species present.

The plot means or computations for all physical and vegetation recordings were calculated. Com-

position of vegetation was further examined by summing the plant species lists collected in the 10 quadrats from each plot. Thus plant species richness was expressed in three ways: mean plant species per quadrat, total plant species in 10 quadrats and total plant species collected from a plot in 30 min. The diversity of plants was expressed by the Shannon and Weaver (1949) H' index:

$$H' \text{ (decits)} = (n \log n - \sum_i n_i \log n_i) / N$$

where n = total number of individuals and n_i = the importance value of the i th species. The bulked 10 quadrat data were used for this calculation. The plant diversity index also was used to calculate the plant evenness index. This was the equitability of the apportionment values among species in each plot and was obtained by the following formula:

$$J' = H' \text{ (decits)} / \log S$$

where S = total number of species in the population.

Ant recolonization census

Four complimentary ant sampling techniques were used.

(1) Ten pitfall traps, consisting of 43 mm internal diameter plastic bottles containing 30 ml of alcohol/

glycerol (70/30 v/v) were installed at 10 m intervals along the transect. Traps were operated for 6 days from 28 September 1982.

(2) Hand collections were performed in the vicinity of each transect for 2 person-hours during the daytime and 1 person-hour at night. The daytime collections were always made during the relatively cool periods of 0800–1100 h or 1500–1800 h.

(3) Tall vegetation was struck with a stout baton in order to dislodge ants onto a plastic sheet beneath. Beating was performed for about 30 min during the daytime and the resulting collections were amalgamated with those from (2).

(4) A 4 l container of leaf litter was collected from sites scattered along each transect and ants were extracted by heat and light over a 24 h period in a Berlese-Tullgren funnel with 150 W bulb (Southwood 1966). All samples were taken between 26 September and 8 October 1982 and repeated 9–13 December 1982.

The ants were sorted to species level and, where possible, named. In most cases this was not possible so specimens were allocated code numbers which corresponded to those used in the Cooloola study (Greenslade & Thompson 1981). Species labelled 'new' had not yet been found at Cooloola so their original North Stradbroke code number is given. The full collection of voucher specimens, labelled 'North Stradbroke Island Collection' is housed at the School of Biology, Western Australian Institute of Technology.

A checklist of ants for each transect was obtained by combining the collection data from the four sampling methods. The total species obtained for each transect was referred to as ant species richness.

Pitfall trap catches are not a faithful representation of species abundance since they are influenced by the relative activity of species, ant behaviour and the amount and type of litter (Southwood 1966). However, they were considered to provide an approximate representation of ant community composition, and accordingly the mean number of individuals per plot and also the Shannon-Weaver diversity and evenness indices for the pitfall trap samples were calculated.

Analysis of ant recolonization data

Principal components analysis (PCA) was first employed to compare the ant species composition of the various plots. By using species presence/absence per plot as the data base, the PCA technique first

compared the species content of the plots using Orloci's (1966) weighted similarity coefficient:

$$\text{WSC} = \frac{n}{\sum_{i=1}^n} (x_{ij} - \bar{x}_i) (x_{ih} - \bar{x}_i)$$

where x_{ij} , x_{ih} were the species scores for plots j and h , \bar{x}_i was the species score for the average plot and n was the number of plots. Then the plots were arranged along axes, termed components, so that the plots with the least similar species content occurred farthest apart. The first component represented the combination of variables with maximum variance, subsequent components represented ones with lessening variance. The components were then identified with environmental factors since it was these which contributed to the variation in species composition. This was done by visually inspecting the plot groupings on the diagram, by inspecting the trends in certain plot parameters along axes or, finally, by correlating plot environmental variables with the plot's principal component score.

An understanding of the relative abundance of species in plots is an important aspect of community analysis. However, the ordinations were performed using species presence/absence data in order to minimize the influence of extremely abundant species. Plot 0 was excluded from this analysis as it contained no ants. The ordination was first performed on all plots except plot 0 and secondly, in view of the markedly different ant community composition of the frontal dunes and the remaining dune systems, on all plots except 0, 1 and 2.

In order to provide further information on the relationship between ant recolonization and plot variables a correlation analysis was performed on the matrix of vegetation, physical, and ant community parameters. Two groups of plots were excluded from this analysis: the unmined control plots (in view of the large discontinuity between many mined and unmined plot parameter values) and frontal dune plots 1 and 2. The latter two plots were excluded because other aspects of the data analysis indicated that the ant community of this dune system was of lower richness and subject to different constraints when compared with other dune types. The analysis was therefore performed on all exposed high dune and high dune mined plots ($n = 10$). It was also repeated on all exposed high dune and high dune mined plots where *P. megacephala* had not yet dominated the ant community ($n = 7$; i.e. all plots \leq

6 years old). All variables which were significantly correlated ($P < 0.05$) with the variables of interest, namely ant species richness, diversity and evenness and also time since rehabilitation, were noted.

Seed removal by ants

Removal of seed by ants was assessed in a number of different situations, namely (1) unmined forest, (2) fresh topsoil adjacent to unmined forest, (3) fresh topsoil adjacent to recent rehabilitation and (4) an area which had been rehabilitated 2.5 years previously. Five areas (Fig. 1) were selected to represent these situations:

Plot 14 — unvegetated topsoil adjacent to forested high dune;

Plot 15 — unvegetated topsoil adjacent to 1.1-year-old high dune rehabilitation;

Plot 11 — 2.5-year-old high dune rehabilitation;

Plot 12 — unmined forested high dune and

Plot 13 — unmined forested high dune.

The seed depot technique of Majer (1980, 1984) was used to assess seed removal. Here 12×12 or 12×24 cm Masonite boards were set in the ground with their rough side uppermost. Batches of 20 seeds were then placed on the boards during early morning and the numbers removed were assessed at 2 h intervals. Ants which were observed taking seeds were collected and the pattern of seed disturbance on boards checked to ensure that no other agents had taken seeds. Boards were set up at 10 m intervals as follows:

Plot 14 — eight small boards established at right angles to forest edge, with two in the forest and six in the fresh topsoil (Fig. 1).

Plot 15 — eight small boards established at right angles to the topsoil interface with the previous rehabilitation, with two in the revegetation and six in the fresh topsoil (Fig. 1).

Plots 11, 12 and 13 — 10 large boards established at 10 m intervals along the previously marked ant-sampling transect.

Experiment 1. The aim of this experiment was to assess the rate of seed removal in native vegetation (plot 13), in fresh topsoil (plots 14 and 15) and in the 2.5-year-old rehabilitation area (plot 11). The fresh topsoil experiment was also designed to assess the edge-effects from forest and adjacent rehabilitation area since ants are known to forage into new topsoil from such areas and remove seed (Majer 1980, 1983). The older rehabilitation area was included to assess the likely fate of seed shed by plants growing in the mined sites. Twenty *A. concurrens* seeds were

placed on each board at 0800 h on 12 December 1982 in order to compare seed removal between sites.

Experiment 2. This experiment was designed to assess which seeds used in the company's rehabilitation programme (Tables 1 and 3) were vulnerable to being taken by ants. Twenty seeds each of *A. concurrens*, *B. aemula*, *B. serrata*, *E. pilularis*, *A. torulosa*, *T. conferta* and *Xanthorrhoea johnsonii* were placed on each of the boards from forest plot 12 at 0800 h on 6 October 1982.

Experiment 3. This was a repeat of experiment 2 and was performed during a warmer period in forest plot 13 where the major seed-collecting ants described by Drake (1981) were found to be more abundant. Twenty seeds each of *A. concurrens*, *B. aemula*, *B. serrata*, *A. littoralis*, *A. torulosa*, *E. intermedia*, *E. pilularis*, *E. signata*, *T. conferta* and *X. johnsonii* were placed on boards at 0800 h on 14 December 1982.

Seed removal counts were made over an 8 h period in experiment 1 and over a 30 h period in experiments 2 and 3. The mean weights and linear dimensions of the seeds used are given in Table 3. Data on rainfall and soil temperature for the duration of the three experiments were obtained from company records (Table 2).

TABLE 3. Size of seeds used in ant seed removal experiments ($n = 20$).

Species	Length (mm)	Width (mm)	Mass (mg)
<i>Acacia concurrens</i>	4.9 (3.5*)	1.8	9.2
<i>Banksia aemula</i>	12.1	10.5	101.1
<i>B. serrata</i>	14.3	8.2	53.5
<i>Allocasuarina littoralis</i>	6.0	2.9	1.9
<i>A. torulosa</i>	7.7	4.0	4.9
<i>Eucalyptus intermedia</i>	7.5	3.0	4.7
<i>E. pilularis</i>	2.2	1.9	2.8
<i>E. signata</i>	1.7	1.1	0.9
<i>Tristania conferta</i>	2.7	0.6	0.3
<i>Xanthorrhoea johnsonii</i>	8.4	4.1	11.8

* Length without elaiosome.

Results

Physical and vegetation measurements

Data on physical and vegetation factors (Table 4) were arranged to illustrate trends with time since rehabilitation and also to enable ready comparison to be made between mined and control plots.

TABLE 4 Mean or total measurements of soil penetrability, litter variables, ground cover variables and vegetation composition in the 12 mined and three control study plots

Plot number	0	7	9	10	6	11	2	5	3	1	16	4	12	13	8
Time since rehabilitation (y)	0.1	0.5	1.1	1.7	2.0	2.5	5.0	6.0	8.0	9.0	10.0	15.0	— controls —		
Soil penetrability (hg cm ⁻²)	4.8	5.4	5.3	6.6	5.8	6.4	3.2	7.4	7.1	2.6	6.4	9.2	5.8	6.3	4.8
Bare ground (%)	99.9	81.0	76.5	74.5	60.0	53.0	58.1	32.5	0.5	28.4	36.5	2.3	2.2	15.4	2.7
Litter cover (%)	0.0	14.7	21.5	9.2	23.5	25.7	26.8	65.0	99.5	64.8	63.5	92.5	90.5	76.1	97.3
Litter depth (mm)	0.0	3.3	3.7	3.3	4.0	2.8	6.1	18.6	10.5	8.0	14.3	17.6	18.9	8.0	25.0
Litter index (depth × % - 100)	0.0	0.5	0.8	0.3	0.9	0.7	1.6	12.1	10.5	5.2	9.1	16.3	17.1	6.1	24.3
Total logs (1-9.9 cm)	0	84	74	21	84	17	20	59	24	4	30	21	52	38	34
(10-29.9 cm)	0	0	4	0	0	0	0	0	0	0	0	0	3	3	0
(> 30 cm)	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0
(all sizes)	0	84	78	21	84	17	20	59	24	4	30	23	72	45	35
Ground cover (% by quadrats)	0.1	9.7	12.0	28.1	30.5	38.5	30.0	27.9	2.7	58.0	37.0	13.2	39.1	18.1	17.3
Ground cover (% by Levy rod)	6	40	22	42	48	50	52	48	16	64	80	38	70	52	42
Projected foliage cover (%)	0	0	0	1	2	1	2	14	92	12	18	58	46	60	60
Plant cover density															
(0-24.9 cm)	1.0	1.5	2.6	2.9	3.3	5.4	1.7	3.5	1.5	1.6	2.4	1.7	3.1	1.8	2.3
(25-45.9 cm)	0.0	1.3	2.0	2.0	2.2	4.3	2.4	3.0	4.0	1.3	1.9	1.0	2.4	2.1	3.6
(50-74.9 cm)	0.0	0.0	1.3	2.1	1.0	1.8	1.9	1.3	2.5	1.6	2.9	0.0	3.8	2.0	1.3
(75-99.9 cm)	0.0	0.0	1.0	1.4	1.0	2.0	1.5	2.0	3.5	2.6	2.6	0.0	7.1	5.5	2.0
(100-124.9 cm)	0.0	0.0	1.0	1.0	1.0	3.0	1.5	1.2	1.0	2.5	2.0	1.5	4.6	0.0	1.0
(125-149.9 cm)	0.0	0.0	0.0	0.0	3.3	1.0	0.0	1.7	1.0	2.6	2.7	2.0	6.0	0.0	2.0
(150-174.9 cm)	0.0	0.0	0.0	1.0	0.0	2.0	1.5	2.5	1.8	3.5	3.7	1.6	1.4	0.0	1.6
(175-200 cm)	0.0	0.0	0.0	0.0	2.0	0.0	3.0	1.5	1.3	3.5	3.0	6.0	2.0	0.0	1.3
(all strata)	1.0	1.7	2.8	3.7	4.0	8.6	3.0	3.4	4.8	5.8	5.8	3.2	6.5	3.2	3.9
Mean plant species per quadrat	1.0	3.2	3.3	5.9	6.7	6.1	2.1	3.5	2.1	1.8	2.3	1.8	4.7	5.2	4.0
Total plant species in 10 quadrats	1	9	15	23	22	20	7	16	7	5	9	9	18	23	15
Total plant species in plot	1	34	35	33	41	36	24	35	18	24	13	29	39	36	30
Plant species diversity (H')	—	0.38	0.95	1.09	1.21	1.15	0.58	1.07	0.58	0.41	0.71	0.61	1.10	0.82	0.91
Plant species evenness (J')	—	0.41	0.81	0.80	0.91	0.88	0.68	0.89	0.70	0.59	0.91	0.64	0.87	0.63	0.78

The correlation analysis of the all-mined plot ($n = 10$) indicated that the amount of bare ground significantly decreased with time since rehabilitation while litter cover, depth and litter index values, projected foliage cover and plant cover density (150-174.9 cm and 175-200 cm), mean ants per pitfall trap and total *P. megacephala* in traps all increased with time (Table 5). The numbers of logs of the upper two size classes were less abundant or absent in the mined plots when compared with the control ones. Smaller logs (1-9.9 cm diameter) were often as abundant in the mined plots as in the controls due to dead wood being introduced with the brush matting (Table 4).

The percentage ground cover obtained by both quadrat and Levy rod methods showed no linear time-trends or marked differences between control and mined plots. Plant cover densities of the lower layers showed time-trends in that they peaked at certain rehabilitation ages and then generally declined (0-24.9 cm and 25-49.9 cm layers peaked at 2.5 years, the 75-99.9 cm layer peaked at 8 years and the 100-124.9 cm layer peaked at 9 years, Table

4). The three plant species richness parameters and the plant species diversity index also increased in the early stages of rehabilitation but all showed some degree of decline in plots older than 2.5 years. The relationship between plant species evenness and time was also non-linear although there was an increase in species evenness in plots up to 2 years old.

Description of ant data

The checklist of ants, obtained by all four methods, contains 64 species from the 15 study plots; of these, 44 had colonized at least one of the mined plots, 20 were confined to the control plots and 18 were confined to the mined plots (Table 6).

Before considering the recolonization data further the affinities of the ant fauna of the three dune systems should be considered. In the high dune and exposed high dune plots ant species richness increased rapidly in a linear or curvilinear fashion from 0 to 6 years and the data for the two high dune systems fell on the same line; that of frontal dune

Time since rehab. (y)	0.1	0.5	1.1	1.7	2.0	2.5	5.0	6.0	8.0	9.0	10.0	15.0	— controls —		
Plot Number	0	7	9	10	6	11	2	5	3	1	16	4	12	13	8
Dune system*	ED	ED	HD	HD	ED	HD	FD	ED	ED	FD	ED	ED	HD	HD	ED
<i>Meranoplus</i> sp. 1								+							
<i>Monomorium</i> sp. 5					+	+	+	+		+		+	+	+	+
<i>Monomorium</i> sp. 4								+							
<i>Monomorium</i> sp. 8									+						+
<i>Pheidole megacephala</i>					+			+	+	+	+	+			+
<i>Pheidole</i> sp. 1			+					+					+	+	+
<i>Pheidole</i> sp. 4															+
<i>Pheidole</i> sp. 5								+							
<i>Pheidole</i> sp. 10														+	
<i>Pheidole</i> sp. new (72)								+							
<i>Solenopsis</i> sp. 1			+	+		+	+	+	+	+	+	+	+	+	+
<i>Tetramorium</i> sp. 2								+	+	+					
Dolichoderinae															
<i>Bothriomyrmex</i> sp. 1					+									+	+
<i>Iridomyrmex</i> (A) sp. 2								+		+	+	+			
<i>Iridomyrmex</i> (A) sp. 3						+		+							
<i>Iridomyrmex</i> (B) sp. 6				+									+		+
<i>Iridomyrmex</i> (C) sp. 1												+		+	
<i>Iridomyrmex</i> (D) sp. 2				+	+			+							+
<i>Iridomyrmex</i> (E) sp. 2		+		+	+	+	+	+		+					
<i>Iridomyrmex</i> (F) sp. 1		+	+		+	+	+	+					+		+
<i>Iridomyrmex</i> (F) sp. 2			+	+	+	+	+	+							
<i>Iridomyrmex</i> (F) sp. 3			+	+	+	+	+	+							
<i>Iridomyrmex</i> (G) sp. 3		+	+	+	+	+	+	+							
<i>Iridomyrmex</i> (J) sp. 1													+	+	+
<i>Leptomyrmex</i> sp. 4															
<i>Tapinoma</i> sp. 1						+	+	+		+					+
<i>Tapinoma</i> sp. 2											+			+	+
<i>Technomyrmex</i> sp. 2								+				+		+	
Formicinae															
<i>Camponotus (consobrinus</i> gp.) sp.4)			+	+		+							+	+	+
<i>Camponotus (variegatus</i> gp.) sp. 3)								+		+			+	+	+
<i>Camponotus (innexus</i> gp.) sp. 1)													+	+	
<i>Melophorus</i> sp. 1															+
<i>Melophorus</i> sp. 3													+	+	+
<i>Notoncus</i> sp. 2												+	+		+
<i>Paratrechina</i> sp. 2										+				+	
<i>Paratrechina</i> sp. 3													+	+	+
<i>Paratrechina</i> sp. 6		+	+	+	+	+	+	+		+				+	+
<i>Paratrechina</i> sp. new (41)					+					+				+	+
<i>Polyrhachis ammon</i>							+	+					+	+	+
<i>Polyrhachis hookeri</i>															+
<i>Polyrhachis (Campomyrma)</i> sp. new (56)							+	+							
<i>Polyrhachis (Cyrtomyrma)</i> sp. new (52)												+		+	+
<i>Stigmacros</i> sp. 7												+	+	+	+
<i>Stigmacros</i> sp. new (47)								+		+					
<i>Stigmacros</i> sp. new (62)															+

* FD frontal dune, ED exposed high dune, HD high dune

plot 2 fell beneath the fitted curve (Fig. 2). There was a decline in ant species richness in older high dune plots although the decrease in frontal dune plot 1 was not as great. The non-concordance of the frontal dune plot values with those of the two high

dune systems indicates that its ant fauna is of different composition.

The results of the principal components analysis also enable comparisons to be made between dune systems. The 14 plot ordination separated the control

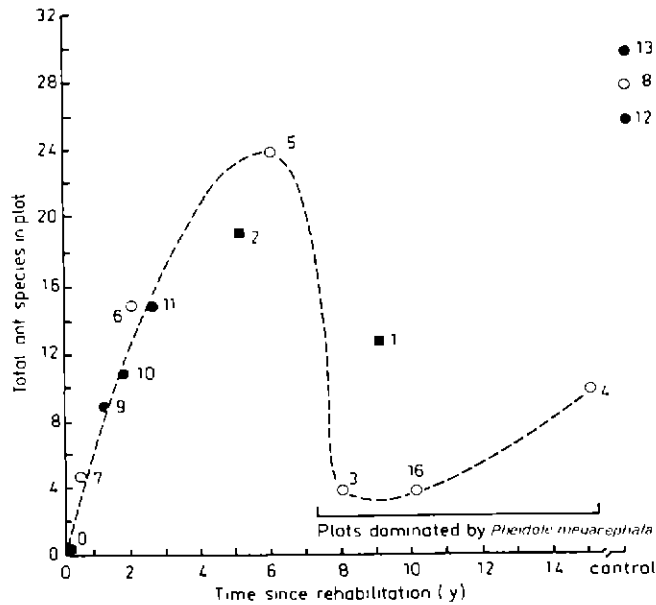


FIG. 2 Relationship between return of ant species per mined plot and incidence of the introduced ant, *Pheidole megacephala*, in sand-mined areas of North Stradbroke Island, Queensland. Key to dune type symbols given Fig. 1

and mined plots along axis 1. The inclusion of frontal dune plots which, by comparison with plots from the other two dune systems had an ant fauna of relatively low species richness and dissimilar species composition, made axis 2 difficult to interpret. The first two axes of the ordination which excluded these two plots is therefore shown in Fig. 3. Most factors were investigated for fit on the first, second or third axes of the ordination but axis 3 was not identified. Axis 1 once again separated the control plots from the mined plots and, since high dune plots 12 and 13 were grouped with exposed high dune plot 8, these two dune systems were indicated as having relatively similar ant faunas (Fig. 3). Axis 2 represented a component of the ant fauna which may be found in plots ranging from 0.5 to 6 years old. The age values of these plots were positively correlated with their corresponding second axis principal component values ($r = 0.94$, $P < 0.001$). Three of the older plots, where *P. megacephala* was dominant, were grouped separately on the negative part of axis 2 and this appeared to be associated with the extremely low species richness and dissimilar species composition of these plots. The ordination therefore indicated that a history of mining, time since rehabilitation and presence of *P. megacephala* all had an influence on the composition of the ant fauna. The concordance of the younger, high dune and exposed high dune plots along axis 2 indicated that time had a greater influence on the developing ant fauna than did type of high dune system.

In view of the similar trends in the ant fauna in the two high dune systems these two dune types are

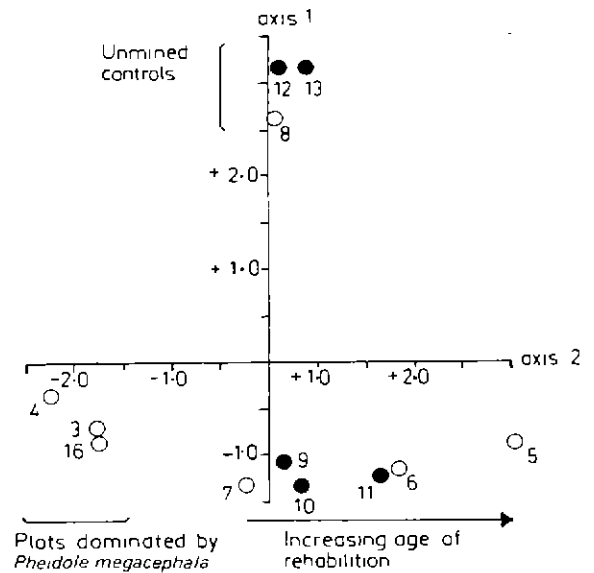


FIG. 3 First and second axes of mined high dune and control plot ordination derived using ant species presence/absence data. Axes 1 and 2 represent 32% and 18% of variance respectively. Code numbers of plots are explained in Table 1 and key to dune type symbols is given Fig. 1. Plots are grouped in terms of age and presence of the dominant ant, *Pheidole megacephala*

treated as a single entity; the frontal dune plots are treated separately.

The most obvious feature of ant recolonization was the presence of large densities of *P. megacephala* in the older mined plots of the exposed high dunes (Table 6 and 7). Although found in some plots which were < 6 years old (plots 5 and 6), this ant only attained large densities in the older plots; it was present in all rehabilitated plots > 6 years old (Table 6). Ant species richness increased rapidly in a linear or curvilinear fashion from 0 to 6 years but declined in the older plots which were dominated by *P. megacephala*. The older plots exhibited species richness more characteristic of plots < 2 years old (Table 7, Fig. 2). A similar pattern was observed for ant species diversity (Table 7). Ant species richness, but not diversity, exhibited a positive trend in the 8–15 year old plots although values never reached those in younger plots which lacked *P. megacephala* (Table 7, Fig. 2).

Particular species of ants colonized and dominated plots of different ages (Tables 6 and 7). There was a steady accession of additional species up to 6 years with only two new species (*Monomorium* sp. 8 and *Paratrechina* sp. 3) colonizing mines between 6 and 10 years. Thereafter, six additional species, unrecorded from the younger plots where *P. megacephala* was not dominant, colonized mined areas. These were *Iridomyrmex* (C) sp. 1; *Tapinoma* sp. 2; *Paratrechina* sp. 2; *Polyrhachis* (*Cyrtomyrma*) sp. new (52); *Stigmacros* sp. 7 and an unidentified ponerine.

TABLE 7. Mined and control plots arranged by dune system and rehabilitation age to show the ants which are most numerous in each plot and also the ant summary measures of mean number of ants per pitfall trap, ant species richness, evenness and diversity

Plot no. Rehab age (y) Mean no. ants per trap* >15	Amity high dune			Exposed high dune			Frontal dune					
	9 1.1	11 2.5	12 Control	0 0.1	7 0.5	6 2.0	5 6.0	3 8.0	4 15.0	8 Control	2 5.0	1 9.0
5-15	<i>Iridomyrmex</i> (F) sp. 3	<i>Iridomyrmex</i> (F) sp. 3	<i>A. longiceps</i> <i>Notoncus</i> sp. 2	<i>Iridomyrmex</i> (F) sp. 3 <i>Iridomyrmex</i> (F) sp. 1 <i>Iridomyrmex</i> (E) sp. 2	<i>Cardiocondyla</i> sp. 1	<i>Iridomyrmex</i> (F) sp. 3 <i>Iridomyrmex</i> (E) sp. 2	<i>Iridomyrmex</i> (E) sp. 3 <i>Iridomyrmex</i> (E) sp. 2	<i>Iridomyrmex</i> (E) sp. 3 <i>Paratrechina</i> sp. 6	<i>P. megacephala</i> <i>P. megacephala</i>	<i>Iridomyrmex</i> (F) sp. 3	<i>Iridomyrmex</i> (E) sp. 2 <i>Paratrechina</i> sp. 6 <i>Cardiocondyla</i> sp. 1 <i>Monomorium</i> sp. 5 <i>Pheidole</i> sp. 1 <i>Iridomyrmex</i> (A) sp. 2	<i>P. megacephala</i>
1-5	<i>Iridomyrmex</i> (E) sp. 2 <i>Paratrechina</i> sp. 6	<i>Paratrechina</i> sp. 6	<i>Crematogaster</i> sp. 3 <i>Pheidole</i> sp. 1 <i>Iridomyrmex</i> (J) sp. 1	<i>Cardiocondyla</i> sp. 1 <i>Paratrechina</i> sp. 6	<i>Iridomyrmex</i> (F) sp. 1 <i>Paratrechina</i> sp. 6	<i>Paratrechina</i> sp. 6	<i>Iridomyrmex</i> (E) sp. 3 <i>Iridomyrmex</i> (E) sp. 2	<i>Pheidole</i> sp. 1 <i>Notoncus</i> sp. 2	<i>Pheidole</i> sp. 1 <i>Notoncus</i> sp. 2	<i>Iridomyrmex</i> (E) sp. 3 <i>Paratrechina</i> sp. 6 <i>Cardiocondyla</i> sp. 1 <i>Monomorium</i> sp. 5 <i>Pheidole</i> sp. 1 <i>Iridomyrmex</i> (A) sp. 2	<i>Paratrechina</i> sp. 6 <i>Cardiocondyla</i> sp. 1 <i>Monomorium</i> sp. 5 <i>Pheidole</i> sp. 1 <i>Iridomyrmex</i> (A) sp. 2	<i>P. megacephala</i>
0.5-1	<i>Cardiocondyla</i> sp. 1 <i>Paratrechina</i> sp. 6	<i>Iridomyrmex</i> (G) sp. 3 <i>Paratrechina</i> sp. 6	<i>R. (metallica)</i> sp. 6 <i>Crematogaster</i> sp. 1	<i>Iridomyrmex</i> (B) sp. 6 <i>R. (metallica)</i> sp. 6 <i>Crematogaster</i> sp. 1	<i>Iridomyrmex</i> (B) sp. 6 <i>R. (metallica)</i> sp. 6 <i>Crematogaster</i> sp. 1	<i>Iridomyrmex</i> (B) sp. 6 <i>R. (metallica)</i> sp. 6 <i>Crematogaster</i> sp. 1	<i>Iridomyrmex</i> (E) sp. 2 <i>Paratrechina</i> sp. 6	<i>Iridomyrmex</i> (E) sp. 2 <i>Paratrechina</i> sp. 6 <i>Solenopsis</i> sp. 1 <i>Tetramorium</i> sp. 2 <i>Iridomyrmex</i> (F) sp. 1	<i>Monomorium</i> sp. 5 <i>R. (metallica)</i> sp. 5 <i>Monomorium</i> sp. 5 <i>Pheidole</i> sp. 5 <i>Solenopsis</i> sp. 1 <i>Iridomyrmex</i> (F) sp. 2 <i>Paratrechina</i> sp. (new) 41	<i>Monomorium</i> sp. 5 <i>R. (metallica)</i> sp. 5 <i>Monomorium</i> sp. 5 <i>Pheidole</i> sp. 5 <i>Solenopsis</i> sp. 1 <i>Iridomyrmex</i> (F) sp. 2 <i>Paratrechina</i> sp. (new) 41	<i>Solenopsis</i> sp. 1 <i>Solenopsis</i> sp. 1 <i>Iridomyrmex</i> (F) sp. 2 <i>Paratrechina</i> sp. (new) 41	<i>Solenopsis</i> sp. 1 <i>Solenopsis</i> sp. 1 <i>Iridomyrmex</i> (F) sp. 2 <i>Paratrechina</i> sp. (new) 41

* (community structure)

The quantity of ants in pitfall traps also indicated a change in the species dominating plots through time (Table 7). *Cardiocondyla* sp. 1 and *Iridomyrmex* (F) sp. 3 dominated the 0.5-year-old plot, and these were succeeded by other *Iridomyrmex* spp., *R. (metallica)* gp., *Pheidole* spp., *Crematogaster* sp. 1, other myrmicines and *Paratrechina* sp. 6 at various times during the 1.1 to 6 year time span. All of these species were less abundant or absent in the plots dominated by *P. megacephala*.

The separation of mined and control plots along axis 1 of the ordination diagram (Fig. 3) and a comparison of the ant species lists in these plots (Table 6) indicated that the ant fauna of the mined plots was most unlike that of the controls both at 6 years, and after 15 years when *P. megacephala* was dominating the fauna. Twenty ant species from 17 genera [*Hypoponera* (1 sp.), *Mesoponera* (1 sp.), *Platythyrea* (1 sp.), *Prionopelta* (1 sp.), *Rhytidoponera* (2 spp.), *Aphaenogaster* (1 sp.), *Chelaner* (1 sp.), *Crematogaster* (1 sp.), *Dacryon* (1 sp.), *Pheidole* (2 spp.), *Iridomyrmex* (1 sp.), *Leptomymex* (1 sp.), *Camponotus* (1 sp.), *Melophorus* (2 spp.), *Notoncus* (1 sp.), *Polyrhachis* (1 sp.), and *Stigmacros* (1 sp.)] were present in the control plots but absent from any rehabilitated areas. Many of these were cryptic litter dwelling species, dead wood nesters or ants which had a strong arboreal foraging or nesting habit (e.g. *Crematogaster*, *Leptomymex*, *Camponotus* and *Polyrhachis*).

Ant correlation analyses

The plot variables, which were significantly correlated ($P < 0.05$ level) with either ant species richness, diversity or evenness are given for two data sets: (1) all high dune mined plots where *P. megacephala* was rare ($n = 7$) and (2) all high dune mined plots ($n = 10$).

Ant species diversity and evenness were positively inter-correlated in both data sets (Table 5). This was to some extent expected since ant diversity contains an evenness component. This section therefore will concentrate on the richness and evenness measures and only refer to the diversity index where supplementary information was added.

Ant species richness was correlated with several plot parameters in the mined plots in which *P. megacephala* was rare. Those which were positively associated with ant species richness were time since rehabilitation, the three litter variables, both percentage ground cover measures, projected foliage cover, plant cover density (3 strata), plant species

diversity and plant species evenness. Percentage bare ground was negatively correlated with ant species richness. Ant species evenness was not correlated with any of the site variables (Table 5).

Since some of the parameters which were correlated with ant species richness were also associated with time since rehabilitation (Table 5), their contribution to ant species recolonization cannot be confidently implicated on the basis of these simple correlation coefficients alone.

When the mined plots dominated by *P. megacephala* were also included in the analysis, all but two of the previously noted correlations (plant species diversity and evenness) were no longer significant. This was related to the non-linearity of the dependent variable as a function of time and suggested that the influence of these variables was over-ridden by some additional factor. Two features of the larger data set are of interest. First was the positive correlation between ant species richness and plot plant species richness, diversity and evenness. This resulted from both ant richness and these plant parameters tending to peak at around 2.5 to 6 years (Table 4, Fig. 2). The other interesting correlations were the negative ones between the number of *P. megacephala* trapped and ant species richness (-0.33) and evenness (-0.55). Although these correlations are not significant, they suggest that the reduced ant richness, and evenness values in the older plots may have been caused by the presence of *P. megacephala*. This is discussed later.

Assessment of the simple correlation coefficients has provided a guide to, but not conclusive evidence of, the factors contributing to ant return. The potentially interesting variables were therefore screened for inclusion in a stepwise multiple regression analysis using the larger data set and with ant species richness as the dependent variable. The independent variables were litter depth, percentage ground cover (by quadrat method), plant cover density (75–99.9 cm), and the total plant species in plot. To allow for the dominance of plots by *P. megacephala*, a dummy variable was included (0 = absent or only present in traces, 1 = dominant in plot). The analysis was run for every possible combination of variables, using two, three, four or five variables, in order to find the number and sequence of variables which accounted for the greatest variation in ant species richness. The adjustment for dominance by *P. megacephala* accounted for 0.13 of the total variance in ant species richness.

The contribution of variables which accounted for the greatest amount of variance in ant species rich-

ness, after adjustment for *P. megacephala*, was litter depth (R square change = 0.57) and total plant species in plot (R square change = 0.15). Inclusion of additional variables in the regression equation accounted for very little extra variance in the dependent variable. Thus, apart from *P. megacephala*, increasing litter depth and plot plant species richness make an important contribution to increasing ant species richness in rehabilitated areas.

Assessment of seed removal

Experiment 1. Application of one-way analysis of variance followed by use of the Sheffé test (Nie *et al.* 1975) indicated there was no significant difference in amount of *A. concurrens* seed taken in native vegetation, the 2.5-year-old rehabilitation region and unvegetated topsoil adjacent to the 1.1-year-old rehabilitation zone (Table 8). No seed was taken from the fresh topsoil adjacent to forest.

Figure 4 shows the number of seeds removed from depots situated at various distances from forest/topsoil and rehabilitation/topsoil interfaces. The results suggest that although no seed-taking ants foraged from the forest into the topsoil, they exerted their influence in topsoil up to 50 m from the rehabilitated area. The lack of seed removed from the

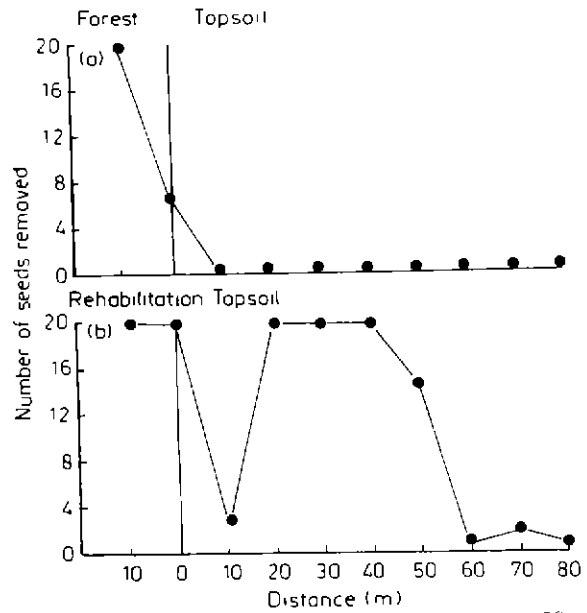


FIG 4. Total *Acacia concurrens* seeds removed (max = 20) after each 8 h from depots situated along (a) a forest/fresh topsoiled area interface and (b) a 11-year-old rehabilitated area/topsoiled area interface. Observations performed 12 December 1982

depot immediately adjacent to the rehabilitation probably reflected the patchy distribution of ant territories (Fig. 4).

The ants observed taking seed were *Rhytidoponera (metallica)* gp., *Iridomyrmex* (B) sp. 6, *Pheidole* sp. 1, *Monomorium* sp. 5 and *Paratrechina* sp. 6 in the forest plots, *R. (metallica)* gp. and *Iridomyrmex* (F) sp. 3 in the 2.5-year-old mined area and *Iridomyrmex* (F) sp. 3 and *Monomorium* sp. 5 in the topsoil adjacent to the rehabilitation area.

Experiments 2 and 3. Considerably more seed was taken during December than in October (Table 9). The results for *E. signata* and *T. conferta* are not shown as the small seeds of these species were scattered by wind. Observations suggest that they were not taken in large quantities by ants.

TABLE 8. Mean number of *Acacia concurrens* seeds removed (max = 20) after 8 h from depots situated in open forest (plot 13), 2.5-year-old rehabilitation (plot 11), unvegetated topsoil adjacent to 11-year-old rehabilitation (plot 15) and unvegetated topsoil adjacent to forest (plot 14). Italics implies plots do not exhibit statistically different seed removal levels.

Survey date	Plot number							
	13		11		15		14	
	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.
12 December 1982	17.70	5.74	12.50	7.72	12.20	9.14	0.00	0.00

TABLE 9. Mean number of seeds removed (max. = 20) after 30 h from depots situated in open forest during the two periods 6-7 October 1982 and 14-15 December 1982. The horizontal bars connect seed species which do not exhibit statistically different removal levels

Survey date	<i>Acacia concurrens</i>		<i>Allocasuarina torulosa</i>		<i>Allocasuarina littoralis</i>		<i>Eucalyptus pilularis</i>		<i>Eucalyptus intermedia</i>		<i>Xanthorrhoea johnsonii</i>		<i>Banksia serrata</i>		<i>Banksia aemula</i>	
	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.	\bar{x}	s.d.
6-7 Oct. 1982	5.40	8.19	2.20	6.27	n.s.		4.30	8.03	n.s.		0.00	0.00	0.00	0.00	0.00	0.00
14-15 Dec 1982	19.70	0.95	16.50	7.47	13.40	6.77	11.40	8.66	7.70	7.02	5.20	3.88	1.90	1.37	0.20	0.42

n.s. not studied.

Moderate quantities of *A. concurrens*, *A. torulosa* and *E. pilularis* were taken during October but *X. johnsonii* and *Banksia* spp. seeds were not removed. Numbers removed of the first three species did not statistically differ from each other. *R. (metallica)* gp. was observed removing seed of all three species. In addition, *Iridomyrmex* (B) sp. 6, *Pheidole* sp. 1, *Monomorium* sp. 5 and *Paratrechina* sp. 6 were observed taking *A. concurrens* seeds.

Seed of all species studied were taken by ants during December (Table 9). A number of significant differences exist. The elaiosome-possessing *A. concurrens* were the most frequently removed seeds and the *Banksia* spp. were seldom taken. Most seeds were removed by *R. (metallica)* gp. although *Aphaenogaster longiceps* removed *A. concurrens* seed and *Monomorium* sp. 5 were observed chewing *A. concurrens* elaiosomes *in situ*. *Polyrhachis ammon* was observed removing one *E. pilularis* seed and an unidentified grasshopper (Acrididae) ate at least one *A. littoralis* seed at the depot.

There was no direct relationship between quantity, and size, of seeds removed (Table 3) although large size was no doubt one reason why few of the massive *Banksia* spp. seeds were taken. The *Banksia* spp. and *X. johnsonii* seeds were removed from depots after the apparently more attractive seeds had been taken.

Discussion

Ant recolonization of rehabilitated areas

The non-conformity of temporal trends in species richness of the frontal dunes with those in the other two dune systems (Fig. 2) suggested that the ant fauna of the former was subject to different constraints. Collections of ants from unmined frontal dunes on nearby Moreton Island (Majer unpublished data) suggested that the fauna of this dune system was of lower species richness than in the high and exposed high dune systems. This was probably associated with the lower plant species richness in this primary colonizing zone (Clifford & Specht 1979) and also with the instability of the substrate (Thompson & Ward 1975).

The proximity of the high and exposed high dune control plots on the ant species ordination (Fig. 3), and the concordance of their ant colonization patterns in rehabilitated areas (Fig. 2), indicated that their ant fauna was of relatively similar species composition and subject to similar constraints.

Greenslade and Thompson (1981) also noted that these two dune systems shared a moderate proportion of ant species and, in terms of ant community organization, were closely related. In view of the relatively large differences in ant fauna between the frontal dunes and the high or exposed high dunes, the following discussion concentrates on the latter two dune systems.

It was difficult to assess the contribution of site factors to the recolonization of ant fauna over the first 6 years since ant species richness and diversity and most of the associated site factors were correlated with time (Table 5). Correlated factors which could have contributed to ant recolonization in younger plots were time since rehabilitation, percentage ground cover, projected foliage cover, plant cover density in certain strata, plant species richness, diversity and evenness, the amount of litter and the disappearance of bare ground. Litter cover, bare ground and time since rehabilitation were most highly correlated with ant species richness (Table 5) and it was probable that at least one of these inter-correlated variables played an important part in encouraging ant recolonization.

Dominance by *P. megacephala* undoubtedly played a major role in influencing the composition of the ant fauna of older plots; correlation analysis (Table 5) indicated that its presence outweighed the influence of the above-mentioned factors. However, when allowance was made for dominance by *P. megacephala*, the stepwise multiple regression analysis indicated that litter depth and plot plant species richness make a particularly important contribution to increasing ant species richness in the mined areas.

Additional evidence for assessing site factor contribution to ant recolonization may be derived from similar studies performed elsewhere in which the use of greater numbers of plots enabled more detailed statistical analyses to be performed. Majer *et al.* (1984) assessed the contribution of site factors to ant recolonization in south-west Australian bauxite mines, also by stepwise-multiple-regression analysis, and found that ant recolonization was positively influenced by plant species richness and diversity, time since rehabilitation, percentage plant cover and percentage litter cover. The presence of large logs was also found to be an important factor. Fox and Fox (1982) performed a similar study in coastal sand mines in central New South Wales. Of the site factors investigated, they found that a floristic component (the absence of a group of plant species found in mature heath), foliage height diversity, vegetation

density in two mid-strata and soil penetrability were all associated with ant recolonization. Comparison of the factors derived from these studies with the candidate list from the present one suggested that time, percentage plant cover, plant cover density, plant species richness, diversity and evenness and the amount of litter may have contributed to recolonization by ants. The absence, or paucity, of most of the ponerines associated with dead-wood and one log-nesting *Camponotus* sp. in the rehabilitated areas (Table 6) may indicate that the absence of logs in mined areas is restricting colonization by certain species.

Recolonization by ant species occurred rapidly in plots up to 6 years old and more slowly in the older plots where *P. megacephala* dominated the ant fauna (Fig. 2). This raised the question of whether the older plots always had a low ant species richness or had experienced a sudden decline when they exceeded 6 years of regrowth. A number of hypotheses may be advanced to explain this apparent dichotomy in ant species richness. These are either based on the influence of fertilizers, of plant species richness or the presence of *P. megacephala*, and the stepwise-multiple-regression analysis certainly suggests a joint influence of the last two factors.

The fertilizer hypothesis suggests that the initial rapid build-up of ants may be related to high primary productivity associated with the applied fertilizers. Fertilizer availability may be exhausted after some time, admittedly well before 6 years (D. R. Brooks, pers. comm.), causing a decline in productivity and a change-over to a slower succession mediated by more natural ecological constraints (C. H. Thompson, pers. comm.). There is evidence for this hypothesis derived from soil endomycorrhizal studies (Jehne & Thompson 1981; C. H. Thompson, pers. comm.) and the pattern of ant species richness over time may reflect this phenomenon.

The second hypothesis is based upon the known positive correlation between plant and ant species richness in rehabilitated mines (Majer *et al.* 1982, 1984). Accordingly, the low plant species richness in the older plots (Table 4), which partly resulted from the less varied seed blends and plantings in older plots (Table 1), may have prevented ant richness building up in these areas. Alternatively, small-scale plant species richness (at the metre quadrat level) may have declined in the older plots due to interspecific competition between plants (Clark 1975) and the decline of pioneer species and thus caused a reduction in plant species richness. Such trends in plant species richness have already been alluded to

on the frontal dunes (Chandler 1982) and on the exposed high dunes (Cartwright 1982) although data provided by Brooks (1976) suggest that species richness at the broader level may not decline. The relative influence of plant species richness promoted during initial rehabilitation and the later-stage decline in plant species richness clearly should be investigated since it may tell us whether plant species richness, and therefore possibly ant species richness, was never high in the older plots or whether plant richness, and possibly that of ants, is destined to decline in all plots after 6 years.

The influence of *P. megacephala* is certainly a major cause of the discrepancy in ant species richness in the younger and older plots. Evidence for this hypothesis may be derived from a number of sources. First, Fox and Fox (1982) noted a similar abrupt replacement of ant species in NSW at approximately 9 years after rehabilitation. This was related to the replacement of the dominant ant species by new dominants (native dolichoderines) which, as a result of interspecific competition, caused changes in the structure and function of the ant community. The low numbers of other ant species, and resulting low evenness values (Table 7), in plots where *P. megacephala* was present, indicated strongly that this ant was having a major competitive effect on the remaining ant community. The ability of this species to outcompete, and replace, other ant species is well known in various parts of the world (Haskins & Haskins 1965; Lieberburg *et al.* 1975) and in Queensland (R. W. Taylor, pers. comm.). A further indication that interspecific competition was the reason for low ant species richness was that six new species colonized the mines dominated by *P. megacephala* (Table 6). Possibly these are species which may co-exist with *P. megacephala* but not with ants dominating the younger plots.

There are two reasons why *P. megacephala* may be present in the older frontal dune and exposed high dune plots. Since these plots are all on the eastern side of the island (Fig. 1), their position may correspond to an outbreak area of *P. megacephala* which possibly resulted from the long history of mining and mine-road building in this area. The second possibility is that *P. megacephala* may colonize all plots older than 6 years.

Although possible, the first suggestion does not seem likely since plots 2, 5, 6, 7 and 8 were also in this region (Fig. 1) and were not dominated by this ant (Fig. 1, Table 7). Small colonies were found in exposed high dune plot 8 (on a track) and also mine

plots 5 (6 years old) and 6 (2 years old) but these bore no resemblance to the extensive outbreaks in plots 1, 3, 4 and 16 (Table 7).

The attainment of dominance by *P. megacephala* in the older plots is consistent with observations made by Greenslade (1972) on the ecology of this species. Firstly, it prefers areas of relatively high humidity, being unable to withstand desiccation and also preferring relatively low temperatures. The species may be unable to proliferate in mined plots until the vegetation has built up to a certain density and a dense litter layer has formed. Inspection of litter index, foliage cover and plant density values in certain strata (Table 4) is consistent with this suggestion. Presumably the ant was unable to spread widely in undisturbed areas, such as the major part of control plot 8, due to competitive exclusion by the relatively rich native ant fauna of the ground layer (Greenslade 1972).

If the first of these explanations regarding *P. megacephala* is correct, the maturing plots of the Amity Point high dunes will probably not be invaded by *P. megacephala*. If the second is correct, as appears most likely, ant richness in all plots will ultimately decline as *P. megacephala* invades and dominates the fauna. The answer to this question may only confidently be found by resurveying the younger plots when they are over 6 years old.

Majer (1983) showed that the abundance and species composition of ants can provide a useful bioindicator of the abundance and type of invertebrate fauna present. Although the current study confined itself to the ant fauna, I postulate that the general findings on ant recolonization rates, species composition and community organization may also apply to the invertebrate fauna in general, at least in the absence of *P. megacephala*. Some of the conclusions of this study may therefore be used to describe other aspects of faunal recovery following rehabilitation.

The sand-mined areas are on dune systems of low nutrient status (Thompson & Ward 1975) so the re-establishment of efficient nutrient cycling agents in the rehabilitated areas is essential. Soil and litter invertebrates play an important regulatory role in nutrient cycling (Kitchell *et al.* 1979) so it is important that satisfactory soil and litter invertebrate communities are re-established. The trends in ant recolonization, and casual inspection of the Berlese-Tullgren funnel samples, indicate that substantial soil and litter invertebrate recolonization has taken place. The situation following colonization by the

generalist *P. megacephala*, which must have a substantial prey requirement (Greenslade 1972), is unclear and merits urgent investigation.

Pheidole megacephala may have two other influences which are undesirable. Firstly, by out-competing the native ant fauna, it is providing a conservation threat to native ants. To date, this species seems to be largely confined to the mined areas although its possible spread into undisturbed areas should be monitored. Secondly, it was found to remove *A. concurrens* seed when they were placed out on depots within their territory (Majer, unpublished data). The relationship between elaiosome-bearing seeds, such as *Acacia* spp., and ants is reputed to be of benefit to the seed (Berg 1975) and this relationship is particularly well developed in Australia. The response of *P. megacephala* to seeds of plants with which it has not co-evolved may not be beneficial. This aspect of the study was not pursued although in South Africa Bond and Slingsby (1984) found that the normally beneficial proteaceous plant-ant mutualism collapsed following invasion by the non-native Argentine ant (*Iridomyrmex humilis*). Since *P. megacephala* is a voracious seed harvester the same problem may exist here.

Finally, the question of whether this study has indicated how long it will take for the mined areas to resemble the original biota should be investigated. The ordination diagram indicates that, in terms of their ant fauna, the mined plots are still most unlike the undisturbed areas (Fig. 3). Although mined plot ant species richness and diversity approached that in the control plots after 6 years, relatively few of the species were shared. The presence of *P. megacephala* has hindered the recovery. Fox and Fox (1982) applied regression lines to their NSW sand mine ant data and predicted that total ant faunal recovery might take 17 years. In view of the presence of *P. megacephala* in many of the plots used in this study it is not possible to put a realistic time scale on ecosystem recovery, but it is certainly longer than 17 years.

Seed removal by ants

Seed-taking by ants, as suggested by *A. concurrens* removal rates, took place at high levels within undisturbed vegetation (Table 8). Removal rate was affected by season (Table 9), and presumably temperature, and this was also noted on North Strad-

broke Island by Drake (1981). The *Acacia* removal rates were similar to those observed in south-west Australian and northern Australian forests (Majer 1980, 1984).

The attainment of forest seed removal rates in the 2.5-year-old revegetation (Table 8) is encouraging since it suggests that the original broad ant-seed relationship may have been restored partially. To support this statement it is necessary to investigate the balance between seed harvesters, which actually destroy the seed, as *R. metallica* often does, and elaiosome collectors, such as *A. longiceps*, which probably benefit the seed in some way. Although seed was taken in approximately equal proportions by seed eaters and elaiosome collectors in the forest, only elaiosome collectors were involved in the mine. The relative contributions of seed harvesters and elaiosome collectors in rehabilitated and control areas needs further investigation before restoration of the ant-seed relationship can be confidently claimed.

Restoration of the ant-seed relationship is particularly important since these areas are vulnerable to accidentally and naturally-lit fires. The burying of seed by elaiosome collecting ants in mined areas should ensure that seeds survive and germinate following such fires (Shea *et al.* 1979).

The seed-taking experiments in fresh topsoil indicated that seed removal by ants was likely to be of little significance adjacent to native vegetation although it was considerable where the topsoil was next to rehabilitation areas. Seed removal was 100% up to 40 m into the topsoiled area (Fig. 4), and this was associated with the rapid build-up of seed-taking ants in recently restored areas.

The seed-choice experiments indicated those species most susceptible to removal by ants (Table 9). Generally speaking, the relative removal rates of these species concurred with those noted by Drake (1981) although her data indicated that *E. signata* seed was removed rapidly. The hitherto unreported removal of *Banksia* spp. and *X. johnsonii* seed on the island may have resulted from ants being attracted to depots by seed of more desirable plant species. No other taxa were suspected of removing seed during these observations. *A. concurrens* was the most frequently removed species and the only one possessing an elaiosome. Although this species was taken by both the generalist *R. (metallica)* gp. and the elaiosome collecting *A. longiceps*, most other plant species were removed by the former species. This concurs with predictions based on their lacking an elaiosome.

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