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# Microhabitat Requirements and Behaviors of Ant Functional Groups that Allow for their Co-existence: A Recommendation for Restoration Practices

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Microhabitat Requirements and Behaviors of Ant Functional Groups that Allow for their  
Co-existence: A Recommendation for Restoration Practices

by

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## ABSTRACT

Ants are commonly used as bioindicators for assessing restoration sites because of the speed and sensitivity at which they respond to environmental changes. I compared ant genera among restoration sites to determine the influence of microhabitat and behavior on ant structure. I collected ants and microhabitat features (percent canopy cover, vegetation density and dry leaf litter weight) in three differently aged restoration plots (1998, 2004, 2009) in Queensland, Australia. Twenty ant genera were collected and assigned to functional groups. I concentrated on four genera to study ant communities: *Iridomyrmex* (functional group = dominant dolichoderinae), *Pheidole* (generalized myrmicinae), *Paratrechina* (opportunist) and *Sphinctomyrmex* (cryptic species). Among the 20 ant genera, ant composition was most similar between age-plots 1998 and 2004, and most dissimilar to age-plot 2009. Percent canopy cover and leaf litter weight were negatively correlated with *Iridomyrmex* and *Paratrechina* frequency and may be responsible for low frequencies of *Iridomyrmex* and *Paratrechina* in age-plots 1998 and 2004. In contrast, the frequencies of *Pheidole* were high in age-plots 1998 and 2004; *Pheidole* may have usurped the dominant role, therefore keeping the frequencies of opportunists low. *Sphinctomyrmex* had high frequencies in age-plots 1998 and 2004 possibly because of its cryptic behaviors. Age-plot 2009 showed no significant difference between the four ant genera - niche separation and ant structure has not had time to establish in younger restoration sites. Microhabitat features and niche partitioning between ant functional groups are important for developing ant communities. Recommendations were made for improving restoration sites with respect to ants.

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## 1 INTRODUCTION

2 The destruction of rainforests is one of the greatest threats to biodiversity and the  
3 ecosystem services that regulate environmental processes (Gradwhol and Greenberg,  
4 1988, Chazdon 2008). Rainforests are quickly being degraded at an alarming rate as a  
5 result of agricultural practices, salinization, mining, invasive species and other human  
6 activities (Jansen 1997, Andersen 1990). Restoration efforts attempt to restore the  
7 biological diversity, structural complexity, and ecological synergy of heavily degraded  
8 ecosystems (Berger 1990).

9 The ecological consequences of most human land-use practices are not  
10 immediately known and can be difficult to measure (Andersen 1990). Indicator species  
11 have been used to assess ecosystem responses to environmental perturbation (Andersen  
12 1997). Invertebrates make particularly good indicators because of their sensitivity to  
13 microclimate differences, their significant role in nutrient cycling as decomposers, and in  
14 the trophic system as a food resource for predators that are important for a well  
15 functioning rainforest ecosystem (Jansen 1997).

16 Ants are widely used as indicators of recovery from environmental disturbances  
17 (Connell 1978, Piper *et al.* 2009). Ants have many advantages over other invertebrates  
18 because of their abundance, diversity and functional importance (Jansen 1997, Andersen  
19 1990). In cool, wet regions, more than 50 ant species have been found to occur in one  
20 hectare of land (Andersen 1990). Ants are ideal insects to measure ecosystem health and  
21 stress because of their involvement in a wide range of key ecological processes, and the  
22 speed and sensitivity at which they respond to environmental changes (Piper *et al.* 2009,  
23 Andersen 1990). The composition of ants can be correlated to forest health, vegetation

24 composition and microhabitat features (Jansen 1997, Andersen 1990). In order to  
25 effectively use ants as bio-indicators, complex ant communities were condensed into a  
26 small number of categories called functional groups. Designed by P.J.M. Greenslade in  
27 1978, functional grouping recognizes species by their ecological function and behavior  
28 rather than taxonomic affinity (Piper *et al.* 2009, Andersen 1990). Functional grouping  
29 operates on a generic level that allows patterns and meaningful comparisons to be made  
30 (Andersen 1995).

31 Australian ants make up 15% of the world's ant species (Shattuck 1999). They fill  
32 important niches, from seed distributors and scavengers in harsh environments such as  
33 the Australian outback, to nutrient cycling and soil aeration in Australian rainforests  
34 (Shattuck 1999). Ants have been used widely in Australia as bioindicators for restoration  
35 of mining sites, but the development and function of ant communities in rainforest  
36 restoration sites remain understudied (Andersen *et al.* 2003, Andersen *et al.* 2004, King *et*  
37 *al.* 2008).

38 In my study, I assessed ant composition in three differently aged year plots in a  
39 restoration corridor. I related the age of the restoration plot and the microhabitat features  
40 of each age-plot to the ecological functions and the behaviors of observed ant genera,  
41 collectively called functional groups. Specifically I looked at the frequency (presence or  
42 absence) and ecological functions of dominant and subordinate ant genera to explain their  
43 capacity to coexist. I tested two hypotheses: 1) Subordinate ant genera are expected to  
44 coexist with dominant ant genera because of different habitat requirements, and  
45 ecological behaviors and services; 2) Opportunist ants are expected to be absent in age-  
46 plots where dominant ant genera exist because of high competition by dominant ant

47 genera and lack of specialization by the opportunists. The study aimed to identify the  
48 diversity and fulfillment of ecological functions performed by specific functional groups  
49 of ants and to recommend ways to improve restoration sites with respect to ant genera  
50 composition.

51



## 52 **METHODS**

### 53 **Study Site**

54 The study site was located in Maroobi park (S 17° 26.919, E 145° 63.988), Atherton  
55 Tablelands, Northeast Queensland, Australia. Maroobi park is part of the lakes corridor  
56 that connects Lake Eacham to Lake Barrine. The sampling sites were composed of  
57 several reforested plots that were labeled with the year the trees were planted. Sampling  
58 was conducted 6-8 April and 12-16 April, 2010 during which the area experienced  
59 stochastic periods of rain.

60 Three distinct plots for each age category were sampled: restoration plantings from  
61 old growth (1998/1999), medium aged growth (2004), and new growth (2009) (Table 1  
62 and Plate 1 in Appendix B). (One 1999 plot was used in place of a 1998 simply because  
63 of site area limitations. Differences between 1998 and 1999 plots were assumed to be  
64 negligible for the purpose of our study, and will collectively be referred to as ‘1998 age-  
65 plot’). Data were collected to gather information about ant abundance, ant genera  
66 composition, and microhabitat features.

### 67 **Ant Collection**

68 A 40 m transect was established in the approximate center of each age-plot. Pitfall traps  
69 were constructed from PVC tubing that was 5 cm in diameter and 20 cm in length with a  
70 cap at one end. Traps were buried so that the opening of the tube was flush with the  
71 ground. We filled the traps with approximately 10 mL of detergent diluted with water and  
72 covered the traps with a plastic cover 3 to 4 cm above-ground to prevent rain and debris  
73 from entering the trap. Two traps were placed 4 m apart, equidistant from the transect, at  
74 increments of 0 m, 20 m and 40 m along the transect for a total of six pitfall traps or three

75 sampling repeats in each age-plot. Traps were set at 17:30 and contents were collected  
76 twice within 24 hours, at 5:30 and 17:30, to get a sample of nocturnal and diurnal ants,  
77 respectively. Traps were exposed for a total of 48 hours yielding four collections for each  
78 repeat. Upon collection, the contents of the pitfall traps were suctioned into labeled  
79 bottles using a pipette with 2 to 3cm cut off the tip to increase the diameter to ensure all  
80 the content was collected.

81 Samples were sorted from sediment and by-catch and kept in vials filled with  
82 70% ethanol. The ants were identified at 4x magnification using a T1A Prism Optical  
83 microscope to the genus level using an ant key from *Australia Ants and Their Biology*  
84 *and Identification* (Shattuck 1999). Identifying to the genus level in monitoring is  
85 taxonomically sufficient because genus-level analysis can show species-level patterns  
86 (Schnell et al. 2003, Andersen 1995).

### 87 **Microhabitat Features**

88 Microhabitat features measured included percent canopy cover, dry leaf litter weight, and  
89 horizontal vegetation density.

### 90 **Canopy Cover**

91 Percent canopy cover was measured at each repeat using a spherical densiometer (Model-  
92 A; Robert E. Lemmon). Four measurements in the cardinal directions were taken at each  
93 repeat of all transects. The 24 squares of the densiometer were individually and equally  
94 divided into 4 smaller squares. Canopy cover was recorded as 100%, 75%, 50%, 25% or  
95 0%. Measurements from each direction were averaged to calculate percent canopy cover  
96 for each repeat in all age-plots.

97

**98 Leaf Litter**

99 Leaf litter was collected within a 25 x 25 cm square along the 40 m transect at 10  
100 m and 30 m in all age-plots. The leaf litter was then left in a Berlese funnel for 15 hours  
101 under 60 W lights. An opaque jar was filled with approximately 50 mL of isopropyl  
102 alcohol and was placed under the funnels to collect organisms migrating away from the  
103 light and heat. The dry mass weight of the leaf litter was obtained by drying it at 60°C in  
104 a lab oven (Memmert, type BE 400) until constant mass was reached (3 to 4 days).

**105 Horizontal Vegetation Density**

106 Horizontal vegetation density was measured using a 500 x 200 cm, 10-square  
107 checkered cover-board held at three different heights: above the feet (0 to 20 cm), at knee  
108 level (40to 60 cm) and across the chest (110 to 130 cm). Readings were recorded in  
109 opposite directions at each repeat of all transects. An observer standing at a 6 m distance  
110 recorded the number of squares fully- and half-obscured by vegetation. Measurements  
111 from both directions were averaged to calculate percent vegetation for each level at every  
112 repeat in all age-plots.

**113 Abiotic Conditions**

114 Temperature and humidity were taken with a Kestrel 3000 Pocket Weather Meter  
115 (Kestrel Weather) at each age-plot at time of collection. This may be helpful in future  
116 studies at different times of the year to explain ant genera richness and complexity (Table  
117 2 in Appendix B).

**118 Statistical Analyses**

119 A cluster analysis based on Kulczynski's similarity index was done to show similarities  
120 in the composition of ant genera between the differently aged age-plots using the stats

121 program PAST (version 1.94b, Oyvind Hammer, 2009).

122         Frequency scores were used instead of abundance (number of specimens) to avoid  
123 a bias caused by traps being placed beside colony entrances or along foraging trails. This  
124 is often done with invertebrates because of their considerable population size (Andersen  
125 2003). The frequency of ants was tallied using a binary scale of present (1) or absent (0)  
126 for each collection at every repeat of each age-plot. Ant frequency scores for each repeat  
127 of every age-plot were calculated and assigned a score of 0 to 4, based on four total times  
128 we collected ants from the pitfall traps at each repeat.

129         Univariate statistics (ANOVA) using Microsoft Excel compared the frequency of  
130 ant genera that had a frequency score of at least 1 in each-plot year. A Tukey test using  
131 PAST compared the difference between the frequency scores of those ant genera between  
132 the age-plots. Based on the results, four most frequently occurring ant genera were  
133 chosen as focus ant genera. A second ANOVA for each age-plot was done to compare the  
134 frequency of the four ant genera. A Tukey test was done to identify which ant genera  
135 occurred significantly more or less frequently than other ant genera in each year.

136         Multiple regression analyses using PAST were performed separately on each of the  
137 four ant genera to see which microhabitat feature was most influential on the frequency  
138 of these genera. Single regression analyses were run between microhabitat features that  
139 influenced the frequency of a particular ant genus.

140

141 **RESULTS**

142 Among the three differently aged age-plots, we collected a total of 20 different ant  
 143 genera. Based on Kulczynski's similarity index, the cluster analysis showed similarities  
 144 in the composition of ant genera in age-plots 1998 and 2004 while 2009 has a different  
 145 composition of ant genera (Figure 1; Table 1 and 2 in Appendix A).

146 Seven ant genera were found *Pheidole*, *Iridomyrmex*, *Sphinctomyrmex*,  
 147 *Paratrechina*, *Solenopsis*, *Cryptopone* and *Lordomyrmex* in at least one repeat at every  
 148 age-plot. From these seven ant genera, *Pheidole*, *Iridomyrmex*, *Sphinctomyrmex* and  
 149 *Paratrechina* were chosen for increased focus because of their relative high frequency at  
 150 each age-plot (Table 3 in Appendix B). There was a significant difference between the  
 151 four select genera and the other three less frequent ant genera (1998: ANOVA  $F_{6,56}$   
 152  $=18.30$ ,  $p < 0.05$ ; 2004: ANOVA  $F_{6,56} = 29.78$ ,  $p < 0.05$ ; 2009: ANOVA  $F_{6,56} =$   
 153  $13.81$ ; Table 1 in Appendix C).

154 In age-plot 1998, there was a significant difference between the frequency of the  
 155 four chosen different ant genera (ANOVA  $F_{3,32} = 15.16$ ,  $p < 0.05$ ; Figure 2). *Pheidole*  
 156 occurs significantly more than *Iridomyrmex* (Tukey test,  $p = 0.00057$ ) and *Paratrechina*  
 157 (Tukey test,  $p = 0.00092$ ). *Iridomyrmex* occurs significantly less than *Sphinctomyrmex*  
 158 (Tukey test,  $p = 0.00022$ ). *Sphinctomyrmex* occurs significantly more than *Paratrechina*  
 159 (Tukey test,  $p = 0.00027$ ). In age-plot 2004, there was a significant difference between  
 160 the frequency of the four ant genera (ANOVA  $F_{3,32} = 37.33$ ,  $p < 0.05$ ). *Pheidole* occurs  
 161 significantly more than *Iridomyrmex* (Tukey test,  $p = 0.05313$ ) and *Sphinctomyrmex*  
 162 (Tukey test,  $p = 0.00017$ ). *Iridomyrmex* occurs significantly less than *Sphinctomyrmex*  
 163 (Tukey test,  $p = 0.00017$ ). *Sphinctomyrmex* occurs significantly more than *Paratrechina*

164 (Tukey test,  $p = 0.00017$ ; Figure 3). *Iridomyrmex* never occurs more than any other  
165 genus in 2009 or in 2004. There was no significant difference between the frequency of  
166 the four ant genera in age-plot 2009 (ANOVA  $F_{3,32} = 0.50$ ,  $p = 0.69$ ; Figure 4).  
167 Multiple regressions analyses were performed to test the significance of microhabitat  
168 features on the frequency scores of each of the four select ant genera to show that  
169 vegetation densities at different heights, canopy cover and leaf litter in combination were  
170 correlated with the frequency of some of the four selected genera. None of the  
171 microhabitat features had an impact on *Pheidole's* frequency score (R square = 0.2386;  $F$   
172 = 1.3164;  $p = 0.2952$ ) or the frequency score of *Sphinctomyrmex* (R square = 0.165;  $F$  =  
173 0.8315;  $p = 0.5418$ ). Canopy cover and leaf litter affected frequency scores of  
174 *Iridomyrmex* (R square = 0.8029;  $F = 17.11$ ;  $p = <0.05$ ) in combination with other  
175 microhabitat features (Figure 5). Multiple regression shows that *Paratrechina's*  
176 frequency scores are also mostly affected by canopy cover and leaf litter (R square =  
177 0.7532;  $F = 12.822$ ;  $p = <0.05$ ) in combination with the other measured microhabitat  
178 features (Figure 6).

179 Based on the results of the multiple regression analyses, single linear regressions  
180 were run between the frequency score of *Iridomyrmex* and canopy cover (R square =  
181 0.7657;  $F = 81.7071$ ;  $p = <0.05$ ; Figure 7) and dry leaf litter mass (R square = 0.5903;  $F$   
182 = 36.0259;  $p = <0.05$ ; Figure 8). Single linear regressions were also run between the  
183 frequency of *Paratrechina* and canopy cover (R square = 0.6543;  $F = 45.4150$ ;  $p = <0.05$ ;  
184 Figure 9) and dry leaf litter mass (R square = 0.6370;  $F = 42.1118$ ;  $p = <0.05$ ; Figure 10).

## 185 **DISCUSSION**

186 Analyzing ant composition and the response of functional groups to microhabitat features  
187 to evaluate how functional groups co-exist is a valuable approach for using ants as bio-  
188 indicators to assess the state of a restoration site and to suggest improvements. My  
189 findings support my two hypotheses: 1) Subordinate ant genera are expected to coexist  
190 with dominant ant genera because of different habitat requirements, and ecological  
191 behaviors and services; 2) Opportunist ants are expected to be absent in age-plots where  
192 dominant ant genera exist because of high competition by dominant ant genera and lack  
193 of specialization by the opportunists.

194       Of the three differently aged restoration plantings, age-plots 1998 and 2004 were  
195 most similar in ant genera composition, whereas age-plot 2009 was different from the  
196 other two years. Young sites are distinctly different in composition than more mature re-  
197 growth forests (Majer 1997). Distinctions between the soil compositions of differently  
198 aged plots can be associated with invertebrate presence. For example, cultivated soils that  
199 have compacted zones beneath the soil surface, and therefore relatively little invertebrate  
200 inhabitants, are prone to run-off. Over time, experiments on soil have shown substantial  
201 recovery toward virgin soil levels in association with recovery of soil invertebrate  
202 populations (Majer 1997). In Australia, studies have focused on the colonization of  
203 invertebrates and in particular ants to monitor biodiversity and success of mining site  
204 restoration (Andersen *et al.* 2003, Andersen *et al.* 2004, King *et al.* 2008).

205       In this study, 20 ant genera were collected in total, seven of which were present in  
206 all age-plots at least once. Of the seven genera found ubiquitously, I focused on four ant  
207 genera because their high relative frequency and affiliation to highly contrasting

208 functional groups that may assist in explaining mechanisms of coexistence in ant  
209 communities. *Iridomyrmex* (functional group = dominant dolichoderinae), *Pheidole*  
210 (generalized myrmicinae), *Paratrechina* (opportunist) and *Sphinctomyrmex* (cryptic  
211 species), as categorized by Andersen (1995), served as a case study to correlate the  
212 establishment of ant communities with ecological functions and behaviors of ants, as well  
213 as microhabitat features of restoration sites.

214 Age-plots 1998 and 2004 both have a significantly higher frequency of *Pheidole*  
215 and *Sphinctomyrmex* than *Iridomyrmex* and *Paratrechina*. Our results indicate that this  
216 ratio can be explained by the specific microhabitat requirements of the species. The low  
217 frequency of *Paratrechina* and *Iridomyrmex* can be explained by the negative  
218 relationships with canopy cover and leaf litter weight. Microhabitat features take priority  
219 in determining the distribution of *Iridomyrmex* whereas opportunists have a very broad  
220 habitat distribution (Andersen 1995).

### 221 **Functional Grouping**

222 Excluding species-specific microhabitat requirements, interspecific interactions  
223 between ant genera in different functional groups also contributed to the establishment of  
224 observed ant communities. The four genera being investigated in this paper, *Pheidole*,  
225 *Sphinctomyrmex*, *Iridomyrmex*, and *Paratrechina* belong to distinct functional groups  
226 that often have contrasting behaviors and preferences. (Andersen 1995).

### 227 **Generalized Myrmicinae - *Pheidole***

228 Generalized myrmicines (*Pheidole*) are characterized by having widespread  
229 nesting and foraging habits in warm, heavily shaded areas. Individual generalized  
230 myrmicinae are not highly active or aggressive and they depend on rapid recruitment and



231 mass mobilization for their success. Generalized myrmicines exemplify priority effects  
232 such that they become competitive and recruit rapidly to rich, clumped food resources  
233 (Andersen 1995, Hoffmann and Andersen 2003, Andersen 2008).

#### 234 **Cryptic Species - *Sphinctomyrmex***

235 Cryptic species (*Sphinctomyrmex*) are usually inconspicuous and nest and forage  
236 exclusively below the ground under heavy leaf litter where they may avoid interactions  
237 with other ants, or use the cover as a predation strategy. Cryptic species have highly  
238 specialized requirements and a restricted distribution that makes them sensitive to  
239 disturbances, especially when there is a change in leaf litter composition (Andersen 1995,  
240 Shattuck 1999, Hoffmann and Andersen 2003, Andersen 2008, Piper *et al.* 2009).

#### 241 **Dominant Dolichoderinae - *Iridomyrmex***

242 Dominant dolichoderines (*Iridomyrmex*) are dominant ants with high abundance  
243 and activity density. Ants under this functional group provide a fundamental framework  
244 for ant communities because of their pervasive authority and strong competition with  
245 other taxa (Andersen 1995). They demonstrate inter- and intra-specific combat, and they  
246 aggressively defend resources and territories (Blüthgen and Stork 2007). Dominant  
247 dolichoderines have extensive foraging ranges that often move into the canopy where  
248 they will have large aggressive colonies and absolute, mutually exclusive territories.  
249 (Hölldobler and Wilson 1990, Majer and Camer-Pesci 1991, Philpott *et al.* 2008).

250 Terrestrially, dominant dolichoderines are scavengers and prefer warm, open territories  
251 away from well-shaded areas (Andersen 1995, Hoffmann and Andersen 2003, Piper *et al.*  
252 2009). Despite having a wide foraging range, the distribution of dominant dolichoderines  
253 is usually patchy, they are only physically able to monopolize resources on a local level,

254 as seen in the canopy of isolated trees and on small islands (Hölldobler and Wilson 1990,  
255 Andersen 1995, Piper *et al.* 2009).

### 256 **Opportunist - *Paratrechina***

257       Opportunists (*Paratrechina*) are unspecialized and poor competitors who  
258 predominate only under conditions of stress or disturbance that puts other ants at a  
259 competitive disadvantage (Andersen 1995, Hoffmann and Andersen 2003). They are  
260 scavengers and predators that feed on items that are more scattered, less predictable and  
261 are replenished quickly after consumption (Blüthgen and Stork 2007). They are found  
262 mostly in ruderal habitats but can expand ecologically and take control of larger niches if  
263 conditions are favorable (Andersen 1995, Hölldobler and Wilson 1990).

264       Our results can be explained by linking relationships between ant functional  
265 groups to their ecological services and microhabitat requirements. *Iridomyrmex* occurs in  
266 low frequency in older age-plots because of its preference for life in the canopy over the  
267 shaded forest floor laden with heavy leaf litter that can induce stress by constraining rapid  
268 rates of activity (Andersen 1995, Hoffmann and Andersen 2003, Piper *et al.* 2009).  
269 Many studies have shown that a majority of trees, especially in tropical forests, are used  
270 by dominant ants for foraging and nesting, (Majer and Camer-Pesci 1991, Andersen  
271 1995) and supporting high levels of trophobioses with sap-sucking insects that produce  
272 honeydew as a byproduct (Fritz 1983, Gibb 2005). *Iridomyrmex* will migrate to the  
273 canopy of older regrowth areas where they can take advantage of their adaptations to  
274 exploit a seemingly unlimited supply of nutrient-rich honeydew. Aggressive behaviors  
275 and rapid recruitment allows them to readily dominate and control the abundant resources  
276 found in the canopy (Andersen 1995, Gibb 2005). The shift of *Iridomyrmex* to higher

277 forest strata is likely to provide a valuable service for old growth sites. Plant herbivory is  
278 reduced as the ants defend their food source by killing or knocking off any organisms that  
279 comes into proximity with honeydew producing insects such as homopterans. Plants rely  
280 on homoptera to attract ants, and by tolerating homoptera, plants can gain benefits that  
281 exceed the costs incurred because of the homoptera (Fritz 1983). It is much less costly for  
282 a plant to maintain a colony of homoptera or produce their own ant-specific extrafloral  
283 nectaries than to produce other defenses such as nitrogen-rich, cyanide-like secondary  
284 compounds to prevent herbivory (Forsyth and Miyata 1984, Majer 1997). Irrespective of  
285 the source of nutrients, ants will recruit nest mates to a tree, defend it, and return to it  
286 regularly to harvest the nutrients in the interest of themselves while maintaining a  
287 mutualistic symbiosis with plants and homoptera (Fritz 1983, Forsyth and Miyata 1984).  
288 Some ants, such as the *Pseudomyrmex* in the New World tropics, will trim vines and  
289 neighboring foliage within several yards of a tree to reduce competition while  
290 inadvertently reducing the risk of fire damage (Forsyth and Miyata 1984, Hölldobler and  
291 Wilson 1990). Our study did not collect arboreal ants, however the low frequency of  
292 *Iridomyrmex* in our pitfall traps, along with the dominant tendencies of this functional  
293 group, suggests this genus has colonized arboreally. The migration of *Iridomyrmex* into  
294 the canopy indicates important spatial niche partitioning and trophic variances throughout  
295 the forest strata.

296         Generalized myrmicines, such as Pheidole, will exhibit aggression even against  
297 dominant dolichoderines, but competitive influence is only expressed locally if dominant  
298 dolichoderines inhabit the same area; Generalized myrmicines will often take on a  
299 dominant role in their absence (Andersen 1995, Hoffmann and Andersen 2003, Piper *et*

300 *al.* 2009). On the forest ground of the older age-plots 1998 and 2004, where little sunlight  
301 penetrates through the canopy and leaf litter gathers, it is probable that *Pheidole* usurped  
302 the dominant role in light of the low abundance of *Iridomyrmex* (Piper *et al.* 2009). In  
303 the New World tropics *Pheidole* has been observed as an aggressive predator and  
304 scavenger - feeding primarily on dead arthropods and seeds (Wilson 2003).

305 High frequencies of *Pheidole* helps explain low frequencies of *Paratrechina* in  
306 the older age-plots 1998 and 2004. *Pheidole* and *Paratrechina* respond oppositely to  
307 disturbance and have different habitat preferences and competitive abilities (Hoffmann  
308 and Andersen 2003). Habitat type is most important for opportunists like *Paratrechina*  
309 (Gibb 2005). Initial recruitment into a site by *Paratrechina* is the key to their persistence  
310 in a site. It is likely that the colony size of *Paratrechina* was reduced, rather than being  
311 completely excluded, when the older age-plots were younger and still developing -  
312 microhabitat became unfavorable and competition was increasing. Opportunists distribute  
313 themselves complementary to superior competitors and will keep abundances low until  
314 conditions are favorable for them to expand (Andersen 2008). *Paratrechina* serve as an  
315 ecological 'backup' against environmental disturbances because of their modularity and  
316 sociality. They will assume the functions of other ants, although not as proficiently, until  
317 conditions stabilize and more suitable ant groups can reoccupy their niches (Hölldobler  
318 and Wilson 1990, Andersen 2008).

319 In contrast, the relative high frequencies of *Pheidole* and *Sphinctomyrmex* in the  
320 older age-plots provide more immediate benefits to the ecosystem. Both ant genera are  
321 important ground dwellers and predators that are able to coexist together, despite  
322 *Pheidole* taking on a dominant role. Many ant species are able to co-exist with dominant

323 ants by having different foraging times, habitat requirements and resource use, or by  
324 reducing colony size to minimize confrontation (Gibb 2005, Andersen 2008).  
325 *Sphinctomyrmex* exclusively nests deep in the soil and predares on other ants and termites  
326 such that they are important regulators of the invertebrate community. The elusive  
327 behavior of these ants may be a strategy for coexisting with *Pheidole* without being  
328 excluded (Hölldobler and Wilson 1990, Andersen 1995, Shattuck 1999). *Pheidole* and  
329 *Sphinctomyrmex* are important saprophytes that break down dead or residual organic  
330 plant matter that creates a considerable nutrient reservoir. Pedogenesis by ants improves  
331 soil structure and creates bio-pores within the soil that help conduct water movement and  
332 stimulate root growth (Hölldobler and Wilson 1990, Majer 1997). The nesting and  
333 foraging habits of *Sphinctomyrmex* and *Pheidole* are important in reducing organic matter  
334 into smaller particles for enhanced microbial attack and for microbial inoculation of the  
335 material that they process through their guts (Killham 1994). *Pheidole* and  
336 *Sphinctomyrmex* contribute to nutrient turnover and over all soil maintenance while they  
337 forage and create a medium for nesting (Majer 1997).

338 Myrmecochory, seed dispersal by ants, is another important ecological service  
339 provided by *Pheidole* and *Iridomyrmex*. Myrmecophytes, plants that have evolved to live  
340 in a mutualistic association with ants, produce propagules that are attractive to ants  
341 (Mathews and Kitching 1984). This is an effective way to spread seeds because ants are  
342 not interested in consuming the endosperm, rather their intentions are aimed at the oily  
343 nutrient laden elaiosome, thus allowing the seed to remain viable. The plant benefits  
344 from myrmecochory by avoiding interspecific competition, fire, and parental competition.  
345 The seeds are brought in the care of *Iridomyrmex* and *Pheidole* to an ant nest that has

346 nutrient-superior microsites that are isolated from predators (Hölldobler and Wilson  
347 1990, Majer 1997, Shattuck 1999). Restoration sites may benefit from myrmecochory by  
348 increasing the rate and success of seedling germination.

349 Age-Plots 1998 and 2004 have clearly distinguished ratios of the 4 major functional  
350 groups, while this is not the case in the younger 2009 age-plot. This one-year-old plot  
351 has no significant difference in the frequency of the 4 functional groups being analyzed.  
352 This can be explained by considering the 2009 age-plots as highly disturbed. Responses  
353 of species to disturbance are unlikely to be linear, meaning that abundance and diversity  
354 will often increase during the establishment phase and vary overtime; In our study, no  
355 one genus will be competitively superior during the early development of a site  
356 (Hoffmann and Andersen 2003). If the current frequency of ant genera persists for too  
357 long a period, the Gause-witt theory may take effect. In short, the Gause-witt theory  
358 states that if two species interfere with one another, one will always replace the other  
359 unless population densities of the two species become self-limiting in such a way that  
360 densities will stop increasing before either species becomes extinct (Hölldobler and  
361 Wilson 1990). The goal in creating a diverse, successful restoration site is establishing an  
362 equilibrium of different niches that are occupied in a way for ecological services to be  
363 performed at maximum efficiency while maintaining sufficient diversity. In tropical  
364 communities, past and present interspecific competition results in species occupying the  
365 habitat or resource on which it is the most effective predator. This can often take time or  
366 it may not happen at all (Connell 1978).

### 367 **Conclusion**

368 In conclusion, the ant composition found at the older age-plots is representative of a

369 balanced community at a functional level. It provides evidence emphasizing the role of  
370 dominant ants as a fundamental framework for ant communities and the mechanisms  
371 subordinate ant genera use to co-exist with dominant ant genera in relation to  
372 microhabitat requirements and behaviors (Andersen 1995). It emphasizes the important  
373 biological processes individual functional groups possess that contribute to create a  
374 healthy ecosystem. My findings support my two hypotheses that 1) Subordinate genera  
375 are expected to be able to coexist with dominant genera because of different habitat  
376 requirements, ecological behaviors and services and 2) Opportunists are expected to be  
377 absent in age-plots where dominant genera exist because of high competition by  
378 dominant genera and lack of specialization.

### 379 **The Future**

380         Several important implications emerge from this study as ways to better manage a  
381 young restoration site in a way that encourages and supports the development of  
382 ecologically valuable ant communities. The distribution of leaf litter in a newly planted  
383 restoration site will encourage *Iridomyrmex* to move into the canopy which will open up  
384 niches for other functional groups at an epigeic level. Heavier leaf litter will encourage  
385 *Pheidole* and *Sphinctomyrmex* to establish themselves in the area to promote soil nutrient  
386 turnover and aeration (Killham 1994, Shattuck 1999, Andersen 1995, Hölldobler and  
387 Wilson 1990). High frequencies of *Iridomyrmex* and *Pheidole* will provide better success  
388 rates for propagules (Shattuck 1999, Hölldobler and Wilson 1990). In addition, it may be  
389 important to select trees that are known to produce ant-specific sweet exudates or trees  
390 that are associated with aphid-ant interactions when planning a restoration site.  
391 Encouraging the movement of dominant *Iridomyrmex* into the tree canopy by adding leaf

392 litter may be especially important in the early stages of a restoration site because of the  
393 terminal consequences of herbivory on young trees whose leaves are few but crucial to  
394 their development (Forsyth and Miyata 1984, Floate and Whitham 1994, Gibb 2005).

395         Future studies may test the behaviors of each functional group to get an idea of  
396 the extent of ant ecological services. It may be interesting to survey arboreal ant  
397 communities at this site to assess the extent *Iridomyrmex* is using honeydew and plant  
398 exudates as a food source and at which tree species. It would be valuable to observe  
399 species-specific behaviors on the new age-plot and precisely define how well the ant  
400 species coexist and the duration in which there becomes a significant difference between  
401 ant compositions. Due to the arrangement of the study area, establishing a control site  
402 would be easy and an effective way of testing the suggestions.

403



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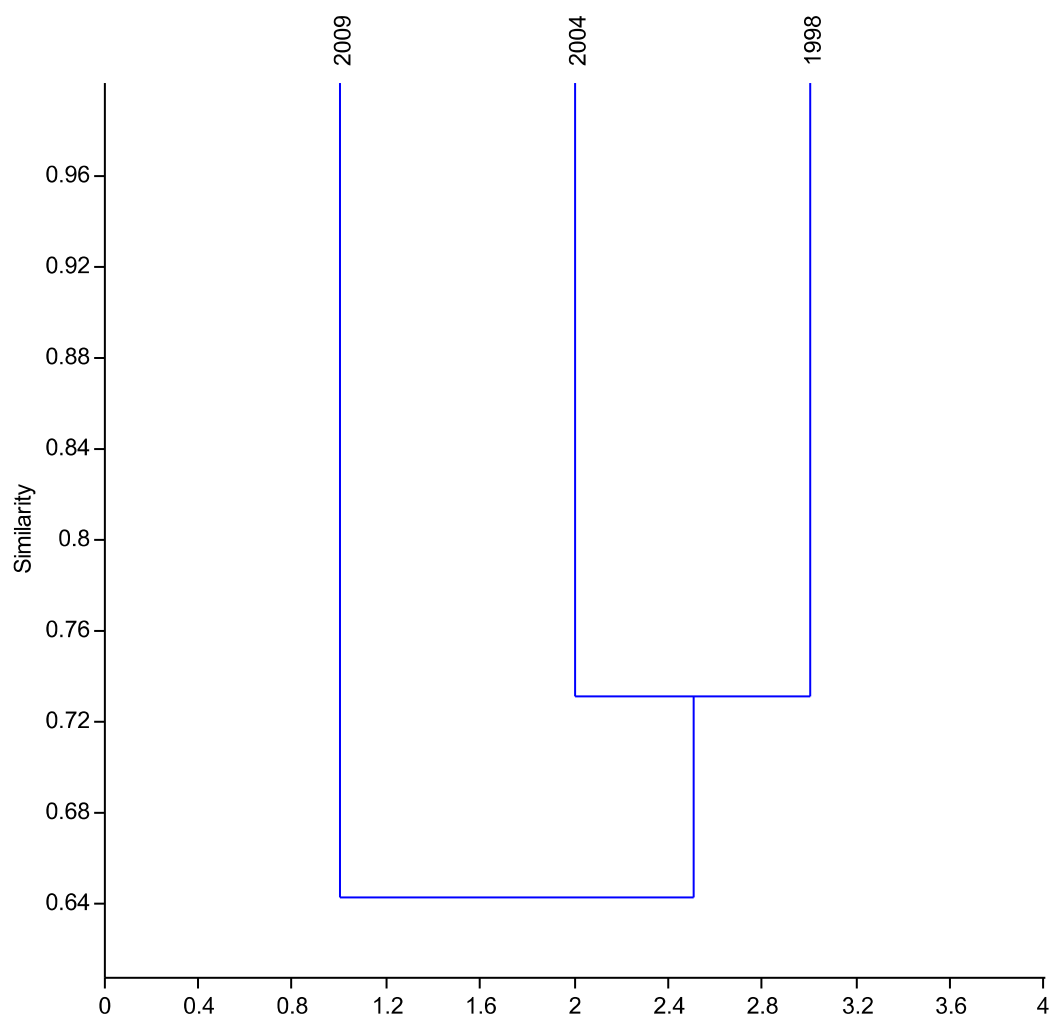
**FIGURES**

Figure 1. Kulczynski's similarity index. Cluster analysis shows similarities in total ant genera composition between age-plots 2004 and 1998.

Figure 2. In age-plot 1998, there was a significant difference between the frequency of the different ant genera *Pheidole*, *Iridomyrmex*, *Sphinctomyrmex* and *Paratrechina*, (ANOVA  $F_{3,32}=15.16$ ,  $p = <0.05$ ). *Pheidole* and *Sphinctomyrmex* occurred more frequently than *Iridomyrmex* and *Paratrechina*.

Figure 3. In age-plot 2004, there was a significant difference between the frequency of the different ant genera *Pheidole*, *Iridomyrmex*, *Sphinctomyrmex* and *Paratrechina*, (ANOVA  $F_{3,32}=37.33$ ,  $p = <0.05$ ). *Pheidole* and *Sphinctomyrmex* occurred more frequently than *Iridomyrmex* and *Paratrechina*.

Figure 4. In age-plot 2009, there was no significant difference between the frequency of the different ant genera *Pheidole*, *Iridomyrmex*, *Sphinctomyrmex* and *Paratrechina*, (ANOVA  $F_{3,32}=0.50$ ,  $p = 0.69$ ).

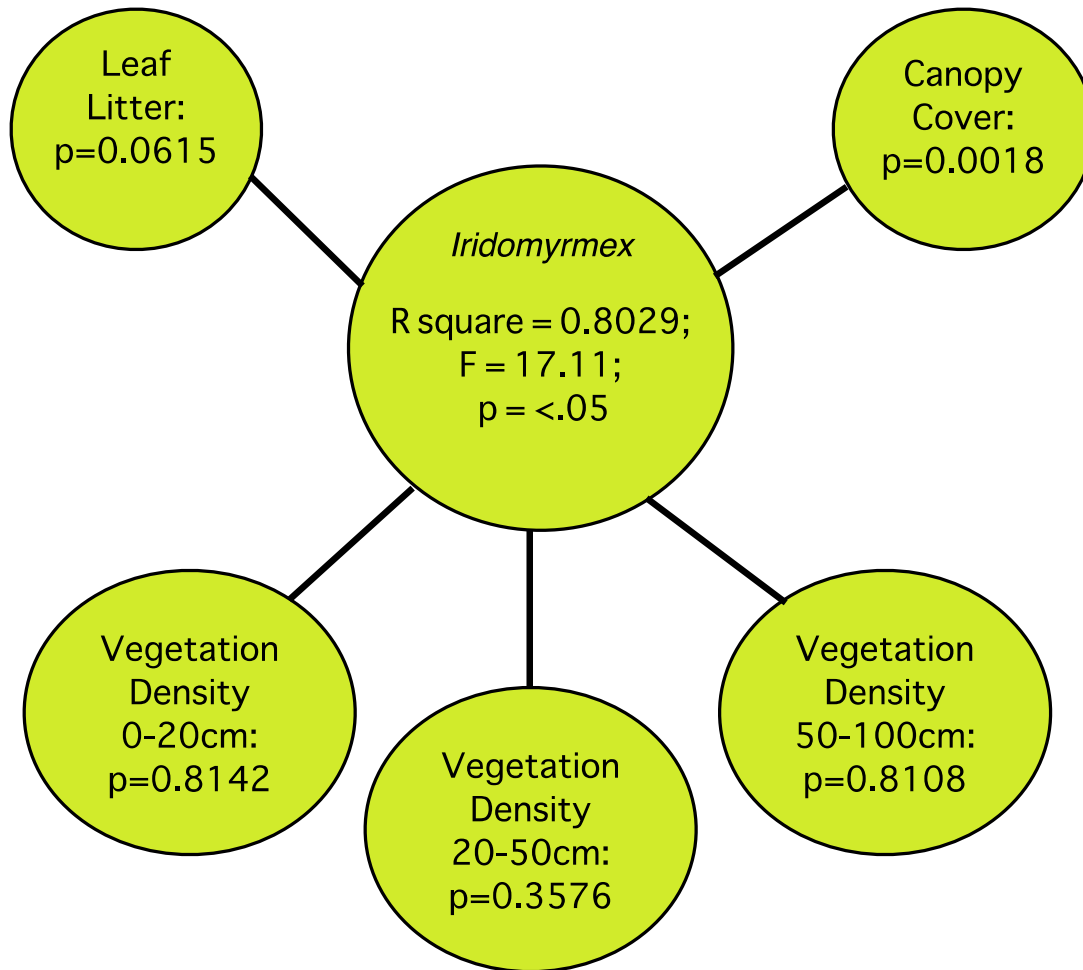


Figure 5. Multiple Regression of frequency scores of *Iridomyrmex* against microhabitat features.



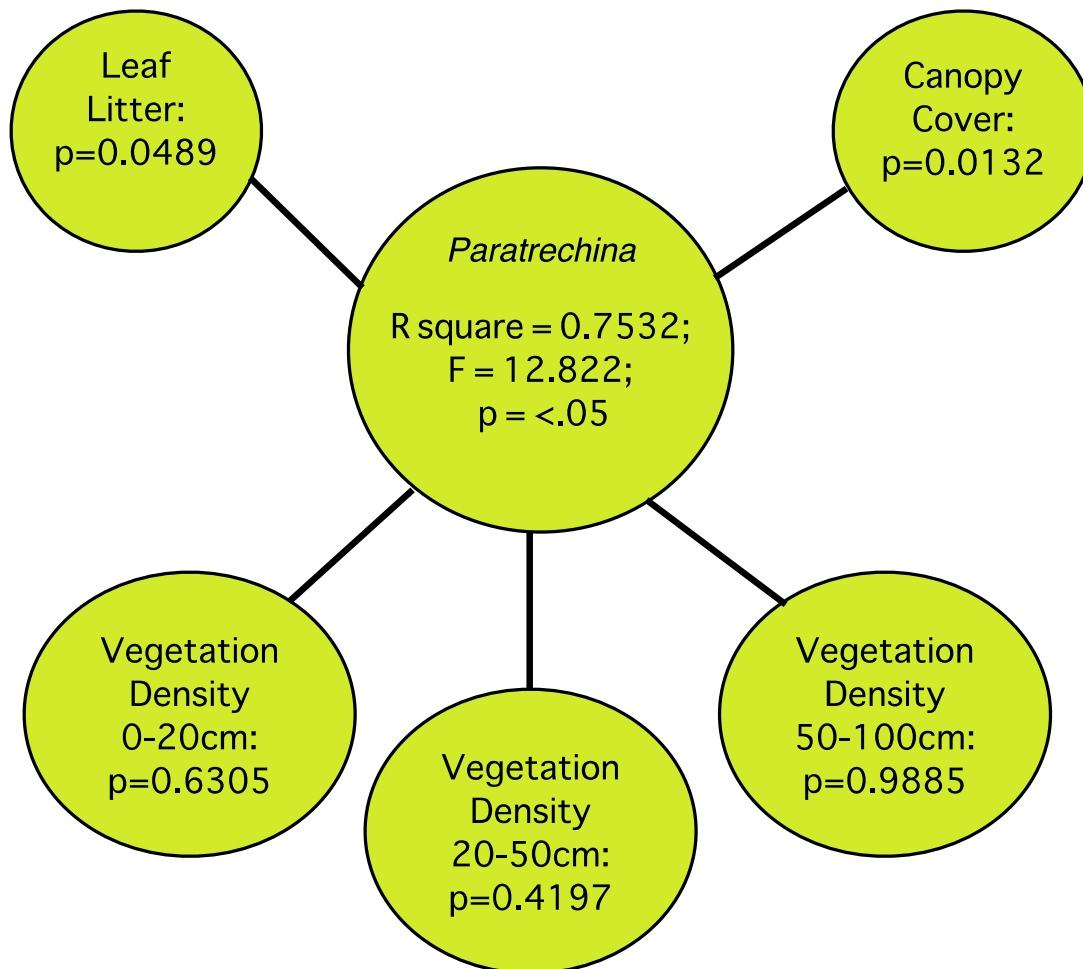


Figure 6. Multiple Regression of frequency scores of *Paratrechina* against microhabitat features.

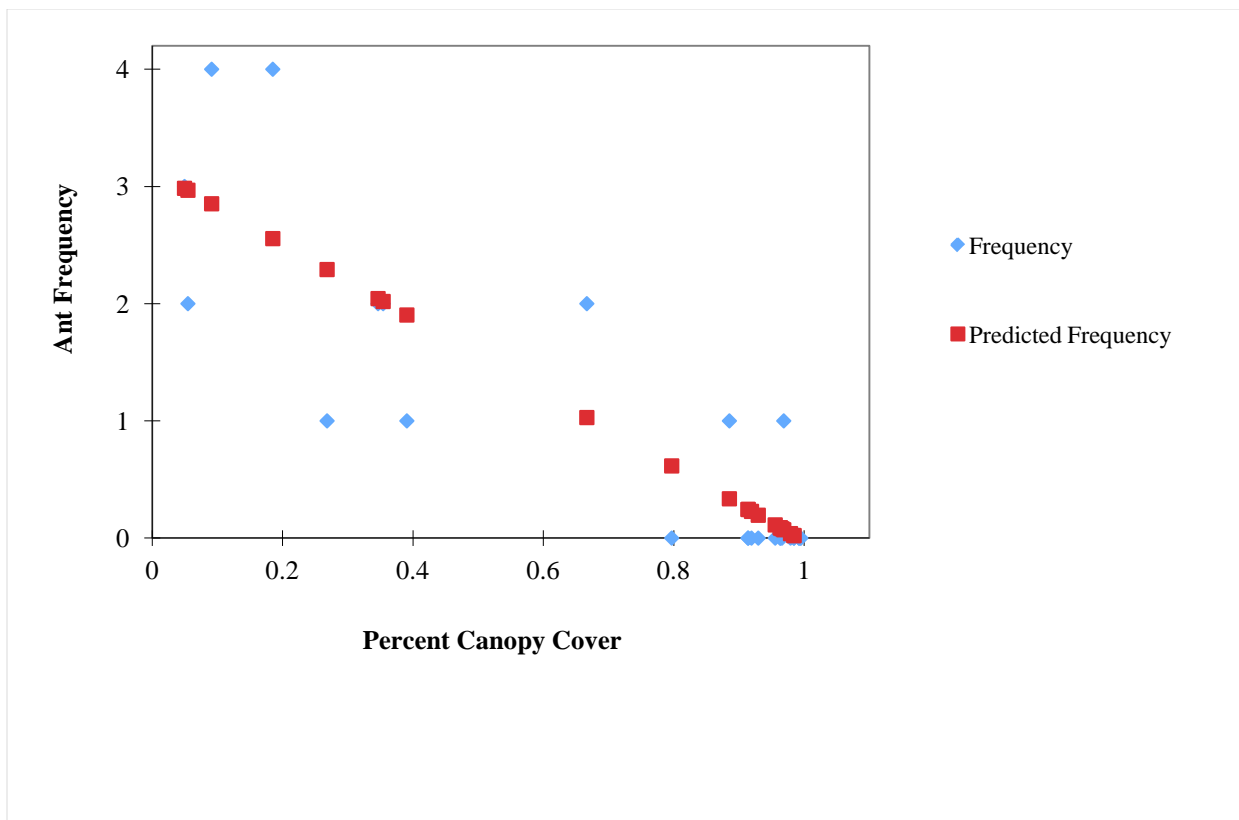


Figure 7. Single linear regression between the frequency scores of *Iridomyrmex* and canopy cover. 76.57% of the variability was explained by canopy cover (R square = 0.7657; F = 81.7071; p = <0.05).

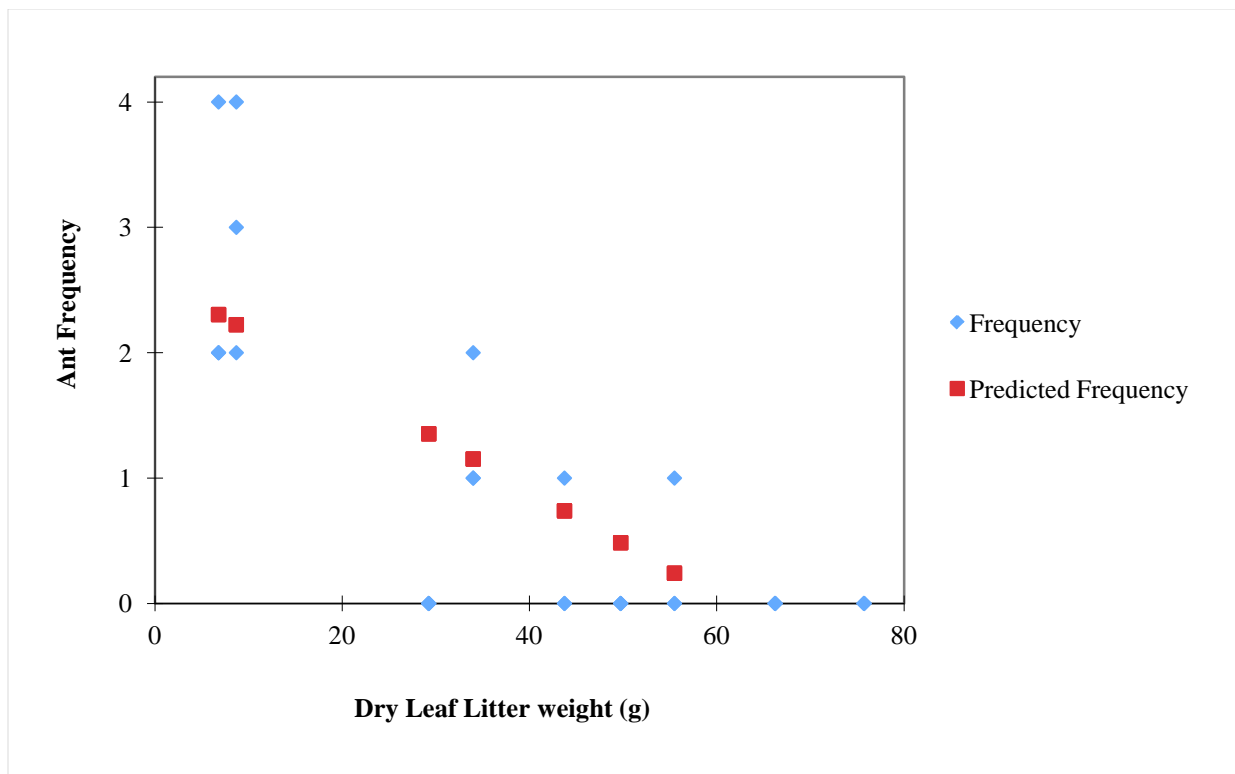


Figure 8. Single linear regression between the frequency scores of *Iridomyrmex* and dry leaf litter mass. 59.03% of the variability was explained by leaf litter weight (R square = 0.5903; F = 36.0259; p = <0.05).

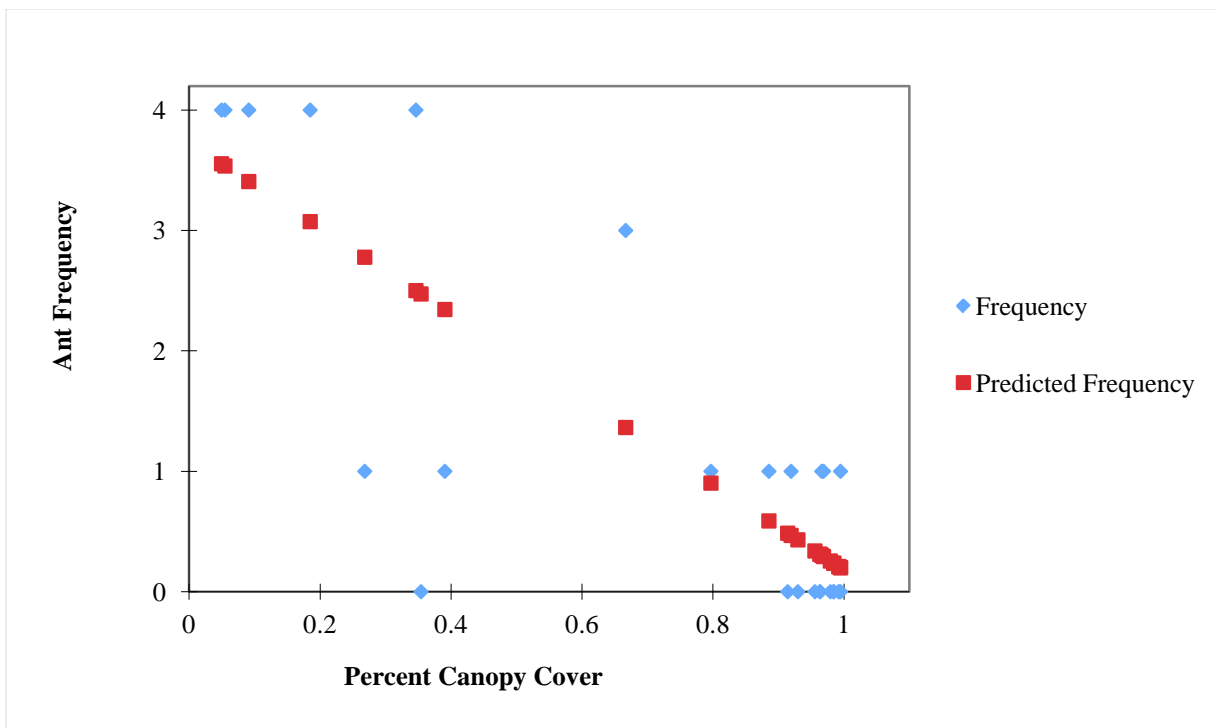


Figure 9. Single linear regression between the frequency scores of *Paratrechina* and canopy cover. 65.43% of the variability was explained by canopy cover (R square = 0.6543; F = 45.4150; p = <0.05).

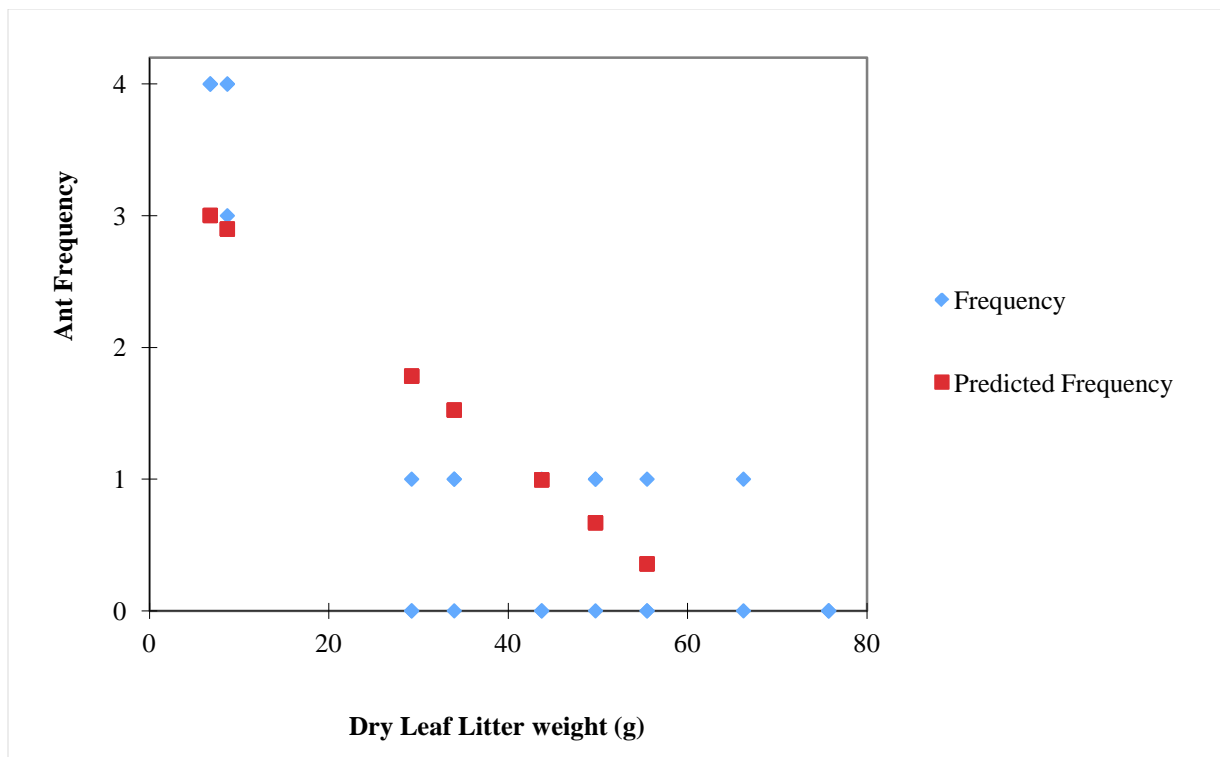


Figure 10. Single linear regression between the frequency scores of *Paratrechina* and dry leaf litter mass. 63.70% of the variability was explained by leaf litter weight (R square = 0.6370; F = 42.1118; p = <0.05).

**APPENDIX A**

Table 1. Kulczynski similarity index

Age-Plot	1999	2004	2009
1999	1	0.73052	0.64935
2004	0.73052	1	0.63636
2009	0.64935	0.63636	1

Table 2. Cluster analysis of total ant genera; 0 = absent, 1 = present

<b>Ant Genus</b>	<b>1998</b>	<b>2004</b>	<b>2009</b>
Pheidole	1	1	1
Iridomyrmex	1	1	1
Sphinctomyrmex	1	1	1
Paratrechina	1	1	1
Solenopsis	1	1	1
Notoncus	1	0	1
Rhytidoponera	1	1	0
Rhopalomastix	0	1	0
Cryptopone	1	1	1
Lordomyrmex	1	1	1
Tapinoma	0	0	1
Tetramorium	0	0	1
Anonychomyrma	1	0	0
Technomyrmex	1	1	0
Camponotus	1	0	0
Cerapachys	0	0	1
Strumigenys	1	0	0
Calyptomyrmex	1	0	0
Ochetellus	0	1	0

**APPENDIX B**

Table 1. GPS Coordinates of age-plots in Maroobi Park

Year Plot	Coordinate
1999A	S 17° 26.919
	E 145° 63.988
1998B	S 17°26.732
	E 145° 64.035
1998C	S 17°26.810
	E 145° 64.009
2004A	S 17° 26.716
	E 145° 64.183
2004B	S 17° 26.731
	E 145° 64.171
2004C	S 17° 27.033
	E 145° 64.174
2009A	S 17° 26.934
	E 145° 64.018
2009B	S 17°26.781
	E 145° 64.108
2009C	S 17°26.907
	E 145° 64.032



Table 2. Temperature (°F) and Humidity (%) taken at collection times at each transect

Table 2.1. 1998 age-plots

Plot	Date	Time	Temperature (°F)	Humidity (%)
1999A	7-Apr	6:55	67.3	100
1999A	7-Apr	17:51	70.4	100
1999A	8-Apr	6:20	66.9	96.3
1999A	8-Apr	17:12	70.7	91.5
1998B	13-Apr	6:17	59.3	93.9
1998B	13-Apr	17:45	73.9	87.7
1998B	14-Apr	7:00	69.5	93.6
1998B	14-Apr	17:14	68.9	96.3
1998C	15-Apr	6:32	64	100
1998C	15-Apr	17:47	69.8	93.9
1998C	16-Apr	6:28	64.5	97.2
1998C	16-Apr	17:51	67.1	98.5

Table 2.2. 2004 age-plots

Plot	Date	Time	Temperature ( °F)	Humidity (%)
2004A	7-Apr	7:14	69.1	100
2004A	7-Apr	18:10	69.6	100
2004A	8-Apr	6:55	67.4	98.6
2004A	8-Apr	17:46	68.9	99.2
2004B	13-Apr	6:42	58.7	94
2004B	13-Apr	18:05	73	91.3
2004B	14-Apr	7:15	71.1	96.9
2004B	14-Apr	17:38	68.3	100
2004C	15-Apr	6:44	64.5	100
2004C	15-Apr	18:16	69.7	93.5
2004C	16-Apr	6:42	64.8	98
2004C	16-Apr	18:07	66.2	100

Table 2.3 2009 age-plots

Plot	Date	Time	Temperature (°F)	Humidity (%)
2009A	7-Apr	6:30	67.3	98.7
2009A	7-Apr	17:40	71.3	100
2009A	8-Apr	6:00	66.8	94.7
2009A	8-Apr	17:29	70.2	95.6
2009B	13-Apr	6:50	58.8	96.5
2009B	13-Apr	18:08	73.3	91.7
2009B	14-Apr	7:30	67.8	100
2009B	14-Apr	17:48	67.9	98.4
2009C	15-Apr	6:20	63.7	100
2009C	15-Apr	18:02	69	93.9
2009C	16-Apr	6:12	64.7	96.4
2009C	16-Apr	17:57	66.5	98.1

Table 3. Frequency scores of the four focus ant genera in each repeat of every age-plot

Table 3.1 1998 age-plot

Plot	Repeat	Pheidole	Iridomyrmex	Sphinctomyrmex	Paratrechina
1998A	0m	3	0	0	0
1998A	20m	3	0	0	1
1998A	40m	2	0	3	0
1998B	0m	3	1	4	1
1998B	20m	2	0	3	0
1998B	40m	1	0	3	0
1998C	0m	0	0	4	0
1998C	20m	4	0	4	0
1998C	40m	4	0	4	0

Table 3.2 2004 age-plot

Plot	Repeat	Pheidole	Iridomyrmex	Sphinctomyrmex	Paratrechina
2004A	0m	1	0	4	0
2004A	20m	0	0	4	0
2004A	40m	0	0	3	1
2004B	0m	1	0	3	0
2004B	20m	2	0	4	1
2004B	40m	4	0	4	1
2004C	0m	0	0	4	0
2004C	20m	0	0	4	0
2004C	40m	2	1	3	1

Table 3.3 2009 age-plot

Plot	Repeat	Pheidole	Iridomyrmex	Sphinctomyrmex	Paratrechina
2009A	0m	2	4	2	4
2009A	20m	1	2	3	4
2009A	40m	3	2	3	4
2009B	0m	3	2	4	0
2009B	20m	3	1	2	1
2009B	40m	1	1	3	1
2009C	0m	4	2	4	3
2009C	20m	4	4	2	4
2009C	40m	2	3	4	4

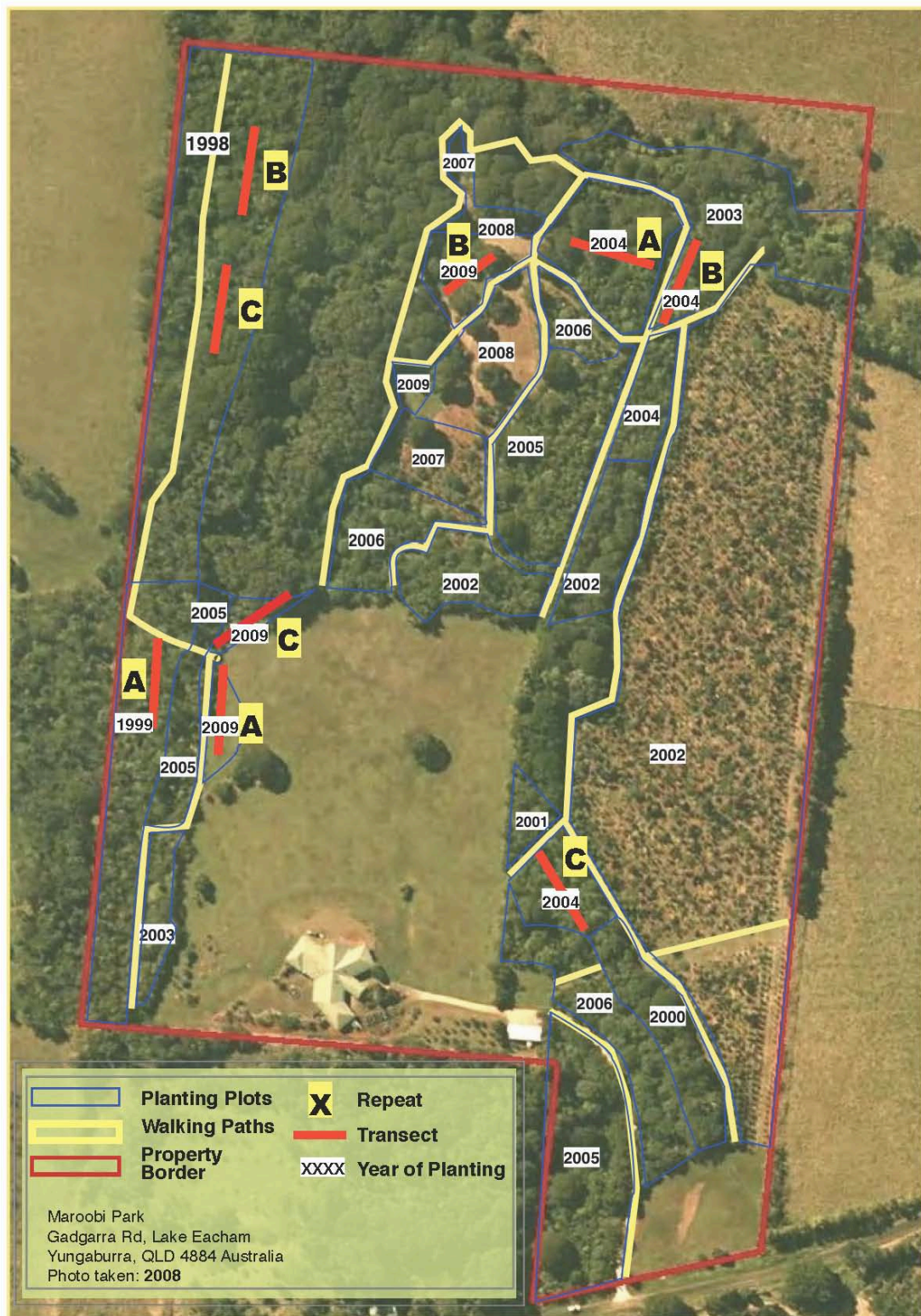


Plate 1: Map of Maroobi Park with age-plots and transects