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Ant dispersal and predation affects the availability of seeds for old-field recolonisation in Western Australia

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Abstract

Seed arrival onto abandoned farmlands (old-fields) in south-western Australia can be limited by their proximity to native remnant vegetation. As the major seed-harvesting guild, ants could affect seed availability on old-fields by either: (1) affecting the dispersal of elaiosome-bearing seeds from adjacent remnants; (2) thieving the elaiosome from seeds without affecting their dispersal onto old-fields; or (3) predating seeds, which reduces the availability of seeds for dispersal. The relative importance of these ant-seed interactions will depend on the rates of ant-mediated seed dispersal from the remnants onto the old-field, as well as the rates of seed predation across these habitats. We sampled the ant communities within two old-fields, within the adjacent eucalypt woodland remnants and at the boundaries of these two habitats, using pitfall traps to determine the relative proportions of seed dispersers, elaiosome thieves and seed harvesters within each zone–ants were assigned to these groups on the basis of our observations of ant-seed interactions. During these observations, we followed the fate of elaiosome-bearing *Acacia* seeds that were offered to ants within each zone, primarily to estimate rates of seed dispersal and elaiosome thieving. We also offered eucalypt seeds to ants in feeding stations to estimate seed predation within each zone. We found that the relative proportions of seed dispersers, elaiosome thieves and seed harvesters were similar across zones, despite differences in the species composition between sites and a reduction in species richness in the old-fields. None of the *Acacia* seeds that we offered were dispersed from either remnant into the adjacent old-field. The majority of dispersal events were less than 3.6 m from the seed source (61%; *n* = 74) and dispersal beyond 20 m was rare (4%; maximum 28.1 m). Rates of elaiosome thieving and seed predation were not elevated in the old-fields compared with their rates in the other zones. Overall, the data indicate that ant-mediated seed dispersal onto old-fields was rare and seed predation by ants was similar across habitats.

Keywords: elaiosome, myrmechory, *Acacia acuminata, Eucalyptus loxophleba* subsp. *loxophleba*, old-field succession

Introduction

Seed availability onto abandoned farmlands (old-fields) in south-western Australia is limited–soil seed storage is uncommon and seed dispersal onto old-fields is generally limited by the distance to the seed source (Standish *et al.* 2007). However, the latter observation has not been confirmed for species whose seeds are dispersed by ants. Ants could potentially affect the dispersal of legumes and other native plants with elaiosome-bearing seeds adapted for this purpose (Davidson & Morton 1984; Beattie 1985). Indeed, myrmechory is a common dispersal mode among the flora of south-western Australia (Berg 1975; Milewski & Bond, 1982). Conversely, ants could remove the elaiosome without dispersing the seed ('aril robbing'; Andersen & Morrison 1998). We term this 'elaiosome thieving' to be consistent with the well-established terminology used to describe floral larceny (Inouye 1980). Ants can also predate seeds, usually without affecting their dispersal (Parsons 1968; Bell *et al.* 1993; Yates *et al.* 1995 but see Retana *et al.* 2004); we term these species 'seed harvesters' after Briese & Macauley (1977). So, ant-seed interactions can have both positive and negative outcomes (Berg 1975; Beattie 1985; Andersen 1988) which have implications for the availability of seeds on old-fields. The net outcome will depend on the movement of seed-dispersing ants between the native woodlands and the adjacent old-field, as well as the rates of seed predation across these habitats.

For many invertebrate taxa, the boundaries between habitats are broad transition zones rather than sharply defined edges (Dangerfield *et al.* 2003). Therefore, the movement of ants across boundaries is likely, and will be determined by the foraging distances and the competitive interactions between the species present in each habitat (Haering & Fox 1987; Adler & Gordon 2003; Ness 2004). The species present in old-fields are likely to include those that can survive the disturbances induced by clearing and cultivation, and will probably include seed

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dispersers such as *Melophorus* and *Rhytidoponera* and seed harvesters, such as *Pheidole* and *Monomorium* (Majer *et al.* 1987; Lobry de Bruyn 1990 cited in Hobbs *et al.* 1993).

The aim of our study was to determine the effect of ants on the availability of seeds within two old-fields in south-western Australia. We sampled the ant communities within two old-fields, their adjacent remnants and across the boundaries of these habitats to determine the relative proportions of seed dispersers, elaiosome thieves and seed harvesters. We assigned ant species to these groups on the basis of our observations during studies of ant-seed interactions. In these studies, we estimated rates of ant-mediated seed dispersal, elaiosome thieving and seed predation using feeding stations placed within the same zones. We considered the implications of our data for the recolonisation of old-fields by native woodland species.

Methods

Study sites

The study sites were two old-fields and their adjacent eucalypt woodland remnants ~4 km apart in the central wheat and sheep farming region of Western Australia. The climate of the region is extra-dry Mediterranean (Beard 1990). Native plant recolonisation of both old-fields is limited; the dispersal of wind-dispersed species decreases with distance from the adjacent woodland remnants (Standish *et al.* 2007). The woodland remnants included species of *Acacia*, *Gastrolobium*, *Lepidosperma*, *Daviesia*, *Goodenia* and *Velleia* (Standish *et al*. 2007), all of which might possess myrmechorous seeds (Berg 1975).

The Letchford Road old-field (7.3 ha; 31°18'S, 117°43'E) is bordered by Letchford Road along one length, a road reserve along another side, and by woodland on the other two sides. It is dominated by vegetative cover of non-native annual grasses (*Avena* spp., *Pentaschistis airoides*) and native grasses (*Aristida holathera, Austrostipa eremophila*). The adjacent remnant is a York gum (*E. loxophleba*)–wandoo (*Eucalyptus capillosa*)–mallee (probably *E. subangusta*) woodland; it is ~100 ha in size. The old-field at Pullen Road (22.3 ha; 31°20'S, 117°44'E) is bordered by Pullen Road, woodland and, on opposite sides, two cultivated paddocks. It is dominated by vegetative cover of non-native annual grasses (*Avena* spp.) with scattered *Acacia acuminata*. The adjacent remnant is York gum–wandoo–salmon gum (*E. salmonophloia*) woodland; it is ~100 ha in size. Both remnants that we studied are unusually large and intact compared with other remnants in the region (Yates & Hobbs 1997). Further details of the land-use histories of these sites are provided in Standish *et al*. (2006).

Five transects were set out at each site, 65 to 80 m apart and perpendicular to the boundaries of the old-field and remnant. The boundaries were separated by a dirt track ~2 m wide that ran between the woodland remnant and old-field at each site. Four zones along each transect were used throughout this study: 50 m into the remnant (50R) and 50 m into the old-field (50OF) and at the boundaries of the two habitats (*i.e.* 0 m into each habitat; 0R and 0OF). A map of this layout is provided in Standish *et al*. (2007).

Ant assemblages

Pitfall traps were used to sample the surface-active ant community at each site; five replicate pitfall traps (*i.e.* one per transect) were placed at each of the four zones. Pitfall traps consisted of a 44 mm diameter (150 mL) specimen vial inserted into the ground after removing a plug of soil with a purpose-built auger. Traps were flush with the ground and two-thirds filled with a 70:30 95%-ethanol:glycol mix. Traps were collected after 7 days and the samples were stored in 70% ethanol. Ants were identified to morphospecies and, where possible, to species, using the reference collection of Western Australian ants held at Curtin University of Technology. Samples are housed at Curtin University of Technology.

Ant-mediated seed dispersal

The observational unit was a 6 x 6 grid of filter paper discs (50 mm diameter) spaced 2 m apart, similar to that of Andersen (1988a). At each site, two replicate grids were placed at each of the four zones; grids were placed at transects 1 and 5 so as to minimise repeated sampling of ants from the same nests. The grids at 0R and 0OF were approximately 3 m apart. One *Acacia acuminata* seed was placed on each disc. We chose *A. acuminata* (hereafter *Acacia*) because it is common at the study sites and its seeds are readily available. The seeds were collected by Greening Australia (Northam) prior to May 2004 and weighed ~16 mg each; they were not fresh but this did not seem to diminish their attractiveness to ants. We did not expect, nor observe, seed rain from the *Acacia* trees within the study area as this usually occurs soon after pod development and seed set in December (R J Standish, pers. obs.).

Sampling was conducted between 13 and 20 March 2005 and was stratified so that one replicate was conducted in the morning (started between 7.25 and 7.55 hrs) and one in the evening (started between 14.25 and 15.45 hrs). The maximum daily temperatures for this period recorded at the nearest (Kellerberrin) climate station ranged from 26.2–38.5 °C (Bureau of Meterology 2005). Initiation of the evening sample was deliberately delayed on the hottest days until ant foraging was observed. After three hours the fate of seeds was recorded as either: dispersed (seed not within 3 cm of the disc); elaiosome thieved (seed minus elaiosome within 3 cm of the disc); or unmoved (seed with elaiosome within 3 cm of the disc).

When an ant was seen collecting a seed during the observation period, the ant was followed until it reached its nest or abandoned the seed. If the ant took the seed into its nest, then dispersal was inferred; the dispersal distance was measured, and an ant was sampled for later identification. Also, ants seen feeding on the elaiosome but not dispersing the seed (*i.e.* eliasome thieves) were sampled for later identification. If a seed was removed but the ant not seen, that seed was recorded as dispersed and an additional seed added to the disc to allow further observations. We assumed these seeds were dispersed by ants rather than by other seed-dispersing fauna (*i.e.* birds or rodents) because these animals were relatively inactive during our observations.

Seed predation by ants

At each site, five replicate feeding stations (one per transect) were placed at each of the four zones. A feeding station consisted of a 5 cm plastic petri dish and lid glued to a 10 cm x 10 cm plywood board; there were three 5 mm entrances spaced equidistant around the perimeter of the dish (Yates *et al.* 1995). Each feeding station contained 10 *Eucalyptus loxophleba* subsp. *loxophleba* (York gum) seeds. The York gum seeds are small (*i.e.* < 1 mm in diameter) and have no elaiosome. Eucalypt seeds are generally eaten by ants (Yates *et al.* 1994a; Yates *et al.* 1995; Ruthrof *et al.* 2002). In addition, non-feeding stations were placed at each of the four zones on transects one and five to estimate the removal of seeds by the wind. The non-feeding stations had Tac-gel (Formula 3, Rentokil Initial Pty Ltd, NSW, Australia) applied to plywood board to prevent ants from entering the feeding station. Feeding and non-feeding stations were placed out on 12 March 2005 and left in place for 24 hrs when the seeds remaining were counted. Stations that had seeds missing upon collection were restocked and left in place for a further 24 to 48 hours, during which time they were frequently checked to establish if seeds were removed by ants, and to sample these ants for identification.

Statistical analysis

Detrended correspondence analysis (DCA; Hill & Gauch 1980) was used to explore differences in ant assemblages among zones. DCA arranges groups along ordination axes, based on the composition of taxa, and does not force association among groups. Relative to other ordination techniques, DCA has improved performance when data are heterogeneous (Hill & Gauch 1980). Abundance data was transformed to log (x + 1) before ordination, which reduced the impact of very abundant species on the result. The program PC-ORD (McCune & Mefford 1999) was used for these analyses.

We used a two-factor ANOVA to compare the abundance of seed dispersers, eliasosome thieves, and seed harvesters in the pitfall traps; and to compare the species richness of the ants sampled using pitfall traps. The factors were zone (fixed) and site (fixed). We used the same test to compare the numbers of *Acacia* seeds that were dispersed, had their elaiosomes thieved or were unmoved from the discs. Data were log transformed where necessary to meet the assumptions of ANOVA. Analyses were done using SPSS (SPSS Inc. 2002).

Results

Ant assemblages

Ant assemblages were separated primarily by site along axis 1 of the ordination (Fig. 1). Within each site, ant assemblages within the remnant (zones 50R and 0R) were distinct from those within the old-field (zones 50OF and 0OF) along axis 2, and these differences more distinct at Pullen (Fig. 1). However, these differences were primarily due to those ants not associated with seeds (Table 1). Of the 22 taxa associated with seeds in the studies of ant-seed interactions and sampled in at

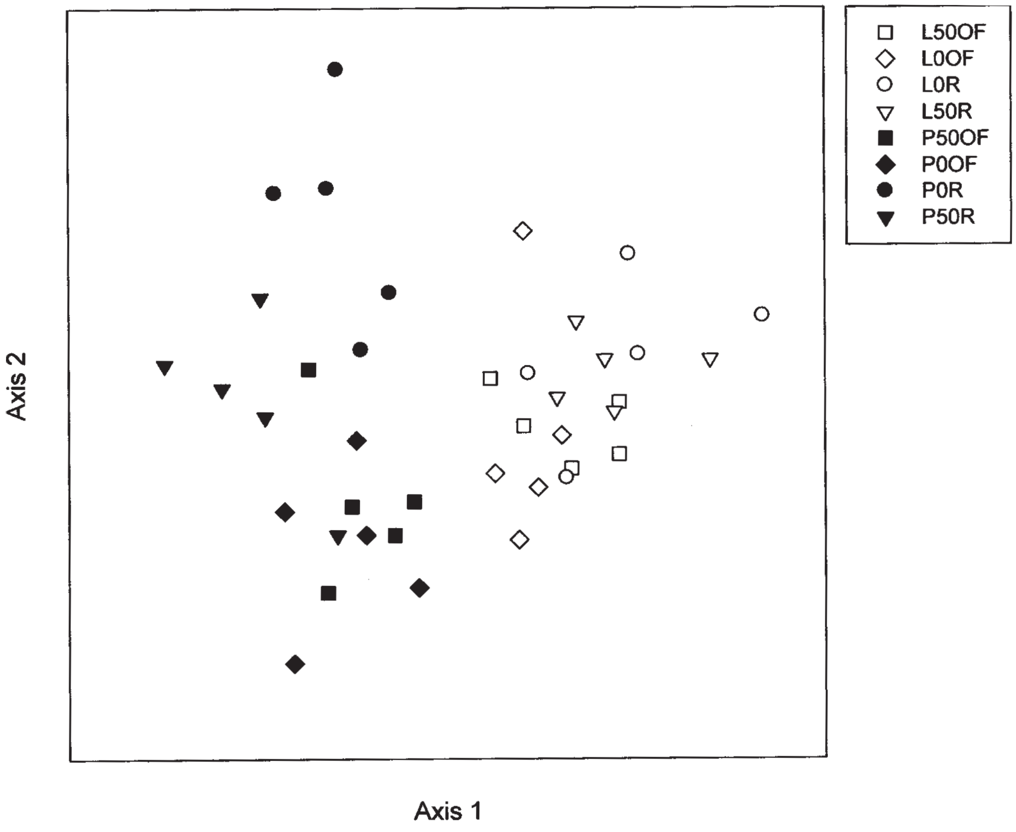


Figure 1. Ordination of ant assemblages at Letchford (open symbols) and Pullen (filled symbols) located within zones. Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field. R^2 axis-1 = 0.28; R^2 axis-2 = 0.13.

Table 1

Summary of ant assemblages sampled using pitfall traps at Letchford and Pullen. The ants associated with seed dispersal, elaiosome thieving and seed predation in the studies of ant-seed interactions are shaded grey and labelled 'Y' = commonly associated; '1' = observed on a single occasion. The other ants that were not observed interacting with seeds (*i.e.* not associated with seeds) are unshaded. Data are mean ± SE.

Taxon	Letchford 50OF	OOF	0R	50R	Pullen 50OF	0OF	0R	50R	Seed disperser	Elaiosome thief	Seed harvester
Dolichoderinae											
Iridomyrmex bicknelli	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Iridomyrmex chasei	103 ± 79	573 ± 211	656 ± 263	959 ± 266	0 ± 0	0 ± 0	0.4 ± 0.4	0 ± 0		Y	
Iridomyrmex chasei concolor	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3.6 ± 2.4	24.4 ± 9.1	59 ± 58	8.8 ± 7.5		Y	
Iridomyrmex dromus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.8 ± 1.8			
Iridomyrmex hartmeyeri gp. sp. JDM849	0 ± 0	0 ± 0	0.4 ± 0.4	0.4 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Iridomyrmex mattiroloi splendens	0 ± 0	1.6 ± 1.3	0 ± 0	0.2 ± 0.2	4.4 ± 4.1	0.2 ± 0.2	1 ± 1	4.8 ± 4.8			
Iridomyrmex rufoniger suchieri POP1	0.2 ± 0.2	0.6 ± 0.6	1 ± 0.6	1.2 ± 0.9	0.2 ± 0.2	4.4 ± 3.9	0 ± 0	9.6 ± 9.6			
Iridomyrmex viridiaeneus	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	1 ± 1	0.6 ± 0.4	2.4 ± 2.2	Y		
Irodomyrmex bicknelli brunneus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0.6 ± 0.4	0.2 ± 0.2			
Tapinoma sp.	2 ± 2	0.8 ± 0.8	0.6 ± 0.6	1.8 ± 1.2	0.2 ± 0.2	2.2 ± 0.8	0.4 ± 0.2	0.6 ± 0.6			
Formicinae											
Camponotus capito ebeninithorax	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0.2 ± 0.2			
Camponotus cinereus amperei	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Camponotus cowlei	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Camponotus nigriceps	0 ± 0	0 ± 0	0.2 ± 0.2	0.4 ± 0.4	0 ± 0	0 ± 0	0.4 ± 0.4	0.6 ± 0.2			
Camponotus claripies	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2			
Camponotus oetkeri	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Camponotus gibinotus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0			
Melophorus bruneus complex sp. JDM791	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0 ± 0	1 ± 1	0 ± 0	1.2 ± 0.4	Y		
Melophorus bruneus gp JDM 600	0 ± 0	0 ± 0	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1		
Melophorus insularus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.4			
Melophorus JDM176	0.8 ± 0.8	2.4 ± 2.4	2.8 ± 1.7	6 ± 3.8	0 ± 0	2.6 ± 1.2	0 ± 0	26.4 ± 13.5			
Melophorus JDM472	0.4 ± 0.4	3.4 ± 3.1	0.4 ± 0.4	0 ± 0	3 ± 3	1.6 ± 1.1	3.2 ± 3.2	4 ± 3.7			
Melophorus JDM787	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus ludius sulla	0 ± 0	1.8 ± 1.8	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	7.6 ± 4.3			
Melophorus mjobergi	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus potteri	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.4	0 ± 0	0.4 ± 0.2			
Melophorus sp. near *aeneovirens* (JDM545)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	2 ± 1			
Melophorus sp.	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus turneri	1.2 ± 0.8	0.2 ± 0.2	1.4 ± 1.1	1 ± 0.7	6.2 ± 5.9	0 ± 0	0 ± 0	7.8 ± 3	Y		
Melophorus turneri perthensis	0 ± 0	2.6 ± 2.6	0.8 ± 0.5	0.8 ± 0.8	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	Y		
Melophorus wheeleri	7 ± 2	6.4 ± 4.5	1 ± 1	5.6 ± 5.6	8.8 ± 5.3	7.2 ± 4.1	0 ± 0	0 ± 0	Y	1	

Stigmacros ?JDM1015	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Stigmacros JDM341	0 ± 0	0 ± 0	0.6 ± 0.4	0.4 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Ponerinae											
Anochetus armstrongi	0 ± 0	0.4 ± 0.4	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0			
Odontomachus ruficeps	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.6 ± 1.3			
Ectatomminae											
Rhytidoponera metallica	0.4 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.2	5.2 ± 1.4	0.8 ± 0.3	Y	1	
Rhytidoponera violacea	2.2 ± 0.5	4 ± 1.9	3.6 ± 1.6	0.8 ± 0.3	1.2 ± 0.8	0.8 ± 0.3	1.4 ± 0.6	4.8 ± 1.8	Y		
Myrmicinae											
Crematogaster frivola	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.8		1	
Crematogaster JDM428	0 ± 0	0 ± 0	0.4 ± 0.4	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1		
Epopostruma lattini	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Meranoplus diamidiatus	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Meranoplus diversus	0 ± 0	0.2 ± 0.2	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Meranoplus JDM423	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		1	
Monomorium aithoderum	3.2 ± 3.2	0 ± 0	0 ± 0	1.8 ± 1.1	0 ± 0	0 ± 0	0.8 ± 0.8	29 ± 24		Y	Y
Monomorium anthracinum	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium bicorne	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium centrale	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.4 ± 0.9	0 ± 0	0.2 ± 0.2	0 ± 0		1	
Monomorium fieldi	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		1	
Monomorium laeve	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.8 ± 0.8	0.2 ± 0.2	3.2 ± 2.7			
Monomorium rothsteini	20 ± 12	24 ± 11	3 ± 2.7	8.4 ± 6	119 ± 80	116 ± 39	1 ± 0.7	0 ± 0		Y	
Monomorium rufonigrum	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium silaceum	2.4 ± 1.6	1.2 ± 0.7	2.4 ± 1.1	0.4 ± 0.2	0 ± 0	1 ± 1	0 ± 0	0 ± 0			
Monomorium sordidum	2.6 ± 2.6	1.8 ± 1.8	2.2 ± 1.3	0.8 ± 0.8	21 ± 7	23 ± 10	48 ± 38	34 ± 10		Y	
Monomorium stictonotum	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium sydneyense	1 ± 1	0 ± 0	0.2 ± 0.2	4 ± 3.5	0 ± 0	0 ± 0	0 ± 0	2.2 ± 1.9			
Pheidole ampla	0.2 ± 0.2	0 ± 0	0 ± 0	0.4 ± 0.4	4 ± 3.5	0 ± 0	1 ± 1	0.2 ± 0.2			Y
Pheidole ampla perthensis	0.4 ± 0.4	1 ± 0.7	0.8 ± 0.5	0 ± 0	4.6 ± 4.6	0.6 ± 0.6	0 ± 0	2.4 ± 1.7	1		
Pheidole hartmeyeri	1.6 ± 1.3	0 ± 0	0.2 ± 0.2	0 ± 0	15 ± 14	15 ± 12	0.2 ± 0.2	0 ± 0	1		
Pheidole JDM164	0 ± 0	1.2 ± 1.2	1.8 ± 1.3	0.6 ± 0.4	0.8 ± 0.8	0 ± 0	0 ± 0	9.4 ± 7.1			
Pheidole JDM177	2 ± 2	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0.2 ± 0.2	2 ± 2	1		
Solenopsis clarki	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Tetramorium impressua	0.4 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1	1	Y
Tetramorium striolatum	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0 ± 0			
Tetramorium viehmeyeri	1.2 ± 1.2	1.4 ± 0.9	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.5	0 ± 0	0 ± 0			

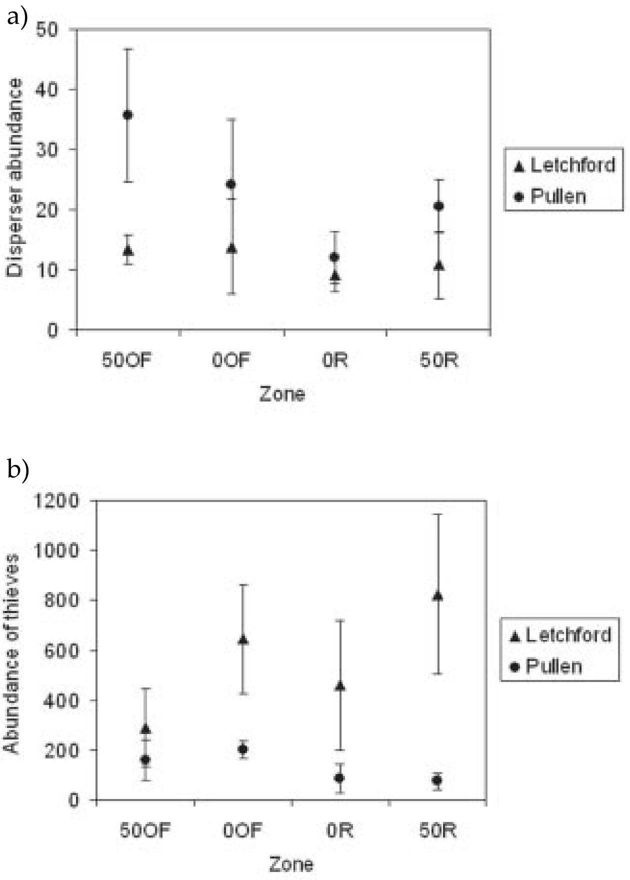


Figure 2. Mean abundance (± SE) of a) *Acacia*-seed dispersers and; b) elaiosome thieves sampled using pitfall traps (n = 5). Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field.

least two pitfall traps, 21 were sampled on both sides of the boundary and one, *Tetramorium impressua*, was only sampled in the Letchford old-field (Table 1). Also, this species was recorded dispersing an *Acacia* seed 93 cm within the Pullen old-field. Two taxa (*Meranoplus* JDM423 and *Crematogaster* JDM428) were recorded during the studies of ant-seed interactions and not sampled in the pitfall traps.

Acacia seed dispersers were more abundant at Pullen than at Letchford and tended to be more abundant in the old-field than in the woodland at Pullen (Fig. 2a; MS (site) = 0.88; d.f. = 1,32; P = 0.01; MS (zone) = 0.31; d.f. = 3,32; P = 0.08; MS (site x zone) = 0.12; d.f. = 3,32; P = 0.43). Thieves were more abundant at Letchford than at Pullen, and at Letchford the 50R zone had much higher abundance of thieves than the 50OF zone (Fig. 2b). This is principally due to the high abundance of *Iridomymex chasei* in the woodland compared to its abundance in the old-field at Letchford (Table 1). At Pullen, the abundance of thieves was similar across zones (Fig. 2b; MS (site) = 3.60; d.f. = 1,32; P < 0.001; MS (zone) = 0.47 ; d.f. = 3,32; P = 0.1; MS (site ′ zone) = 0.66; d.f. = 3,32; P = 0.04). The abundance of the three (confirmed) York gum seed harvesters was too low and variable to establish a pattern.

The species richness of ants was similar between sites and zones except for the 50R zone at Pullen, which had a much higher species richness (Fig. 3a; MS (site) = 30.63; d.f. = 1, 32; P = 0.03; MS (zone) = 36.83; d.f. = 3,32; P = 0.002; MS (site x zone) = 27.49; d.f. = 3,32; P = 0.009). The species richness of seed dispersers and seed harvesters was similar between sites and zones (data not shown). The species richness of thieves was higher at Pullen (Fig. 3b; MS (site) = 8.1; d.f. = 1, 32; P= 0.015) and the species richness of others (those not recorded on seeds) was highest in the 50R zone (Fig. 3c; MS (zone) = 0.378; d.f. = 3, 32; P < 0.001). The ant which was numerically dominant differed between the two sites; *I. chasei concolor* was abundant at Letchford and *I. chasei* was abundant at

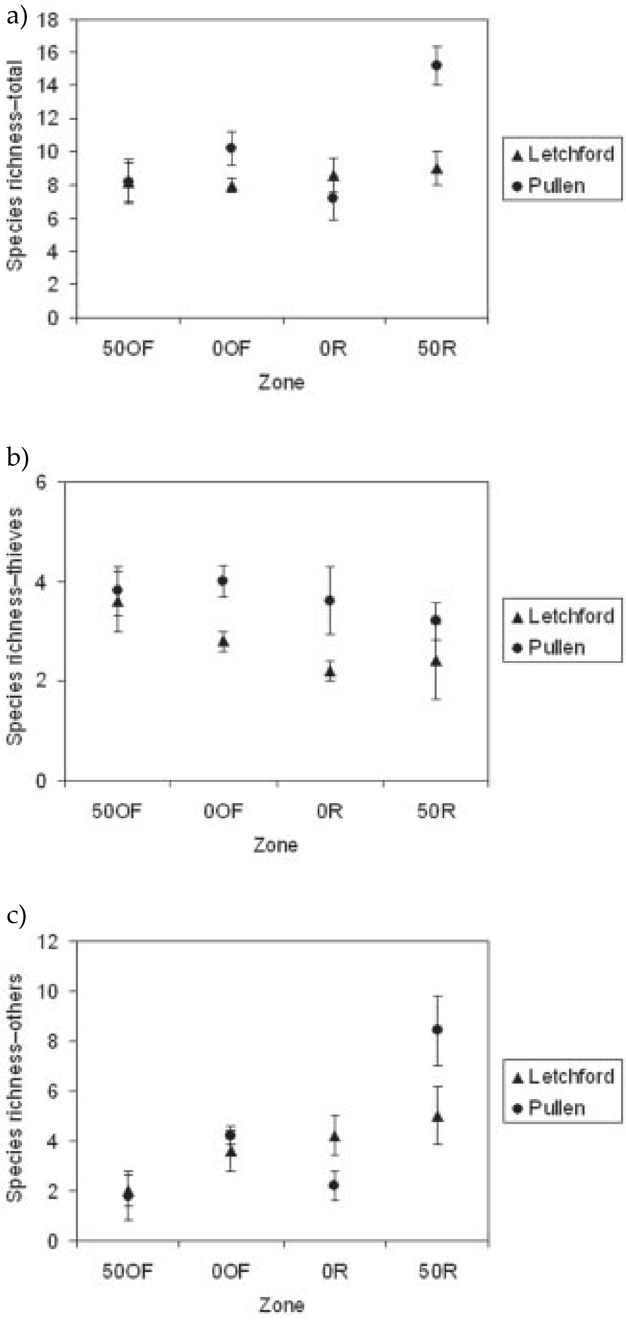


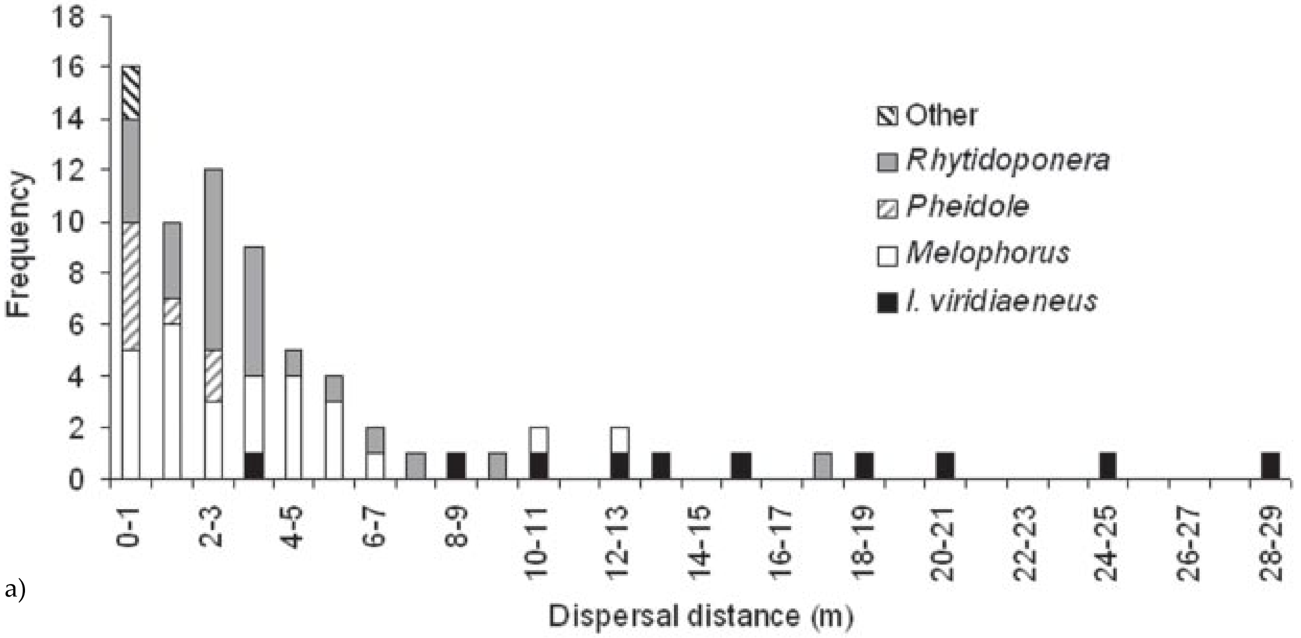
Figure 3. Comparison of species richness of ants sampled using pitfall traps: a) all ants b) elaiosome thieves and c) other ants not associated with seeds. Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field. Values are means ± SE; n = 5.

Pullen. Functionally, these two species are likely to be similar.

Ant-mediated seed dispersal

Of the 576 *Acacia* seeds offered, 76.7 % were dispersed, 11.6 % had their elaiosome removed *in situ* while the remainder (11.7 %) were unmoved at the end of the observation period. A total of 74 dispersal events were observed, of which 70 resulted in the seed entering a nest. Some ant colonies were responsible for more than one dispersal event. Thirteen species were recorded dispersing seeds (Table 1), but most dispersal events were by various species of *Melophorus* (28 observations) *Rhytidoponera violacea* (22), or *Iridomyrmex viridiaeneus* (10). Foragers of *Melophorus* were only active when it was too hot for the other species.

Most (78%) dispersal events were < 6 m (mean 4.83 ± 0.66 m), but foragers of *R. violacea, I. viridiaeneus, Melophorus bruneus* complex JDM791 and *Melophorus wheeleri* dispersed seeds over greater distances (Fig. 4a). Dispersal distances were similar within each habitat (Fig. 4b). There were no seeds dispersed from the remnants into the old-fields. However, seeds were taken from a site on the edge of the old-field over a distance of 28.1 m into the remnant by workers from a large *I. viridiaeneus* colony.



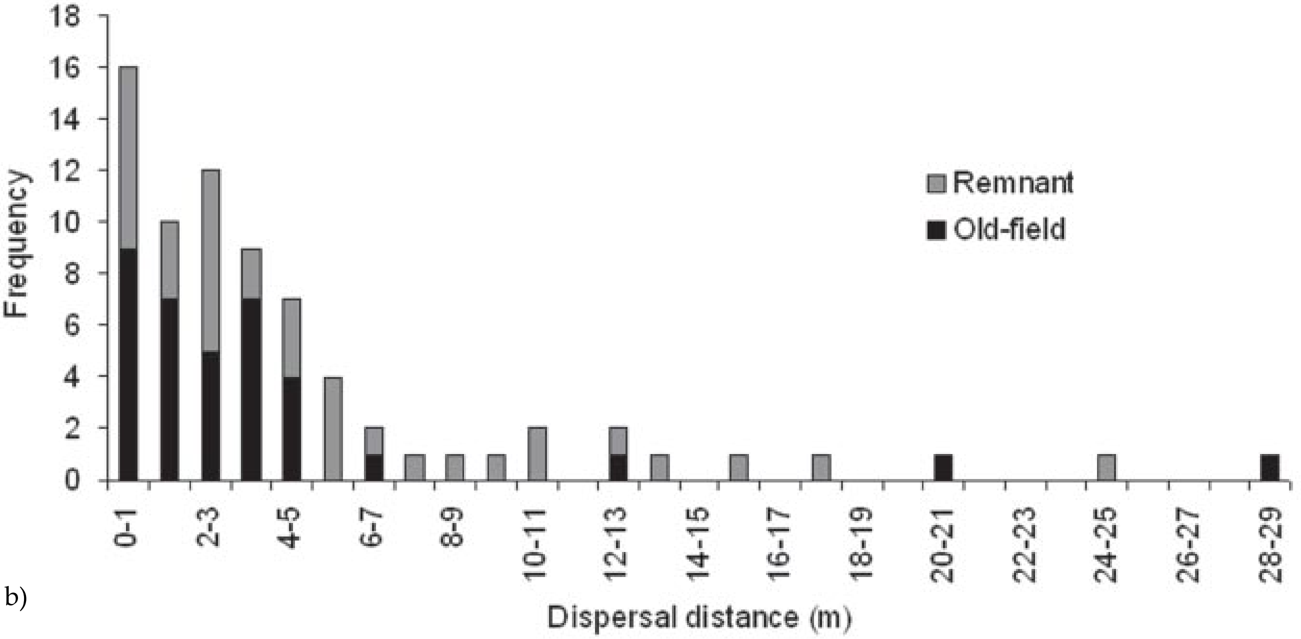


Figure 4. Dispersal distances (m) of *Acacia* seeds from filter paper discs according to: a) ant species and b) habitat.

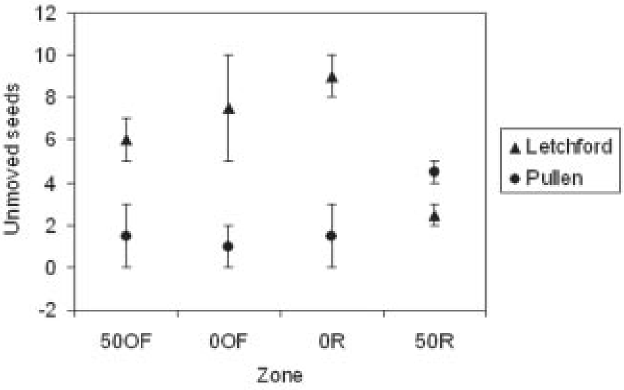


Figure 5. The mean number (± SE) of *Acacia* seeds, of 36 offered, that were unmoved at the end of the three hour periods of observation (*n* = 2). Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field.

The *Acacia* seeds that had their elaiosome removed became unattractive to ants dispersing seeds. Twelve taxa were recorded thieving elaiosomes (Table 1). Of the 39 thieves collected, 20 (51%) were one or other of five species of *Monomorium* and 14 (36%) were the numerically abundant *Iridomyrmex* (*I. chasei* and *I. chasei concolour*). None of the *Monomorium* or *Iridomyrmex* species dispersed seeds.

There were more unmoved seeds at Letchford than at Pullen, except in the 50R zone where there were more unmoved seeds at Pullen (Fig. 5; MS (site) = 68.06; d.f. = 1,8; $P = 0.002$; MS (zone) = 2.40 ; d.f. = 3,8; $P = 0.59$; MS (site x zone) = 18.23; d.f. = 3,8; $P = 0.03$). The frequency of seed dispersal and eliaosome thieving was similar among zones and between sites ($P > 0.05$ for all).

Seed predation by ants

At Pullen, seeds had disappeared from 10 feeding stations (35 % of total seeds offered) from within all zones. The stations were restocked and seeds continued to disappear. Foragers of *Pheidole ampla* and *Monomorium aithoderum* were observed collecting seeds from two stations. Seeds were also missing from four non-feeding stations (12.5% of total). Also, *Pheidole ampla* and *Pheidole* JDM177 were observed removing seeds on dishes at Pullen prior to the study.

At Letchford, seeds had disappeared from one feeding station (1.5 % of total seeds offered). The station was restocked and there was no evidence that ants were feeding at the station as these seeds remained in the station. Seeds were also missing from two of the non-feeding stations (11.25% of total).

Discussion

We found that ant-mediated seed dispersal onto old-fields was rare: none of the *Acacia* seeds that we offered were dispersed from either remnant into the adjacent old-field. Instead, the majority of dispersal events were less than 3.6 m from the seed source. We found that the relative proportions of seed dispersers, elaiosome thieves and seed harvesters were similar across zones, despite differences in the species composition between sites and a reduction in species richness in the old-fields. Moreover, rates of elaiosome thieving and seed predation were not elevated in the old-fields compared with their rates in the other zones. Lastly, there were differences in ant assemblages and ant-seed interactions between sites despite their proximity.

Ant assemblages

The ant assemblages in the woodlands and the old-fields were different; however, the species that were observed interacting with seeds were present in both habitats. The species richness of ants unassociated with seeds was highest in the woodlands. Although these taxa were not associated with seeds in this study, it is likely that some of the omnivorous *Melophorus* species collect seeds (Briese & Macauley 1981).

The Pullen woodland had more leaf and twig litter compared with the Letchford woodland, which could explain the higher species richness at this site. Secondly, pitfall traps are likely to sample active foragers, whose activity will be modified by the ground cover surrounding the trap; trapping efficiency increases with increasing simplification of the ground cover (Majer 1980a). This may account for the very high abundance of *I. chasei* in the Letchford woodland. Surveying nest densities may give a more accurate picture of relative abundance between habitats, and would be an easy task for those species with large visible nests, such as *Melophorus wheeleri* complex (which includes *M. wheeleri*, *M. turneri* and *M. turneri perthensis*), *Rhytidoponera* spp. and *I. viridiaeneus*, all common seed dispersers in this study (Table 1). We recognise too, that we have probably missed sampling some ants that are active at other times of the year. Similarly, our observations of ant-seed interactions may or may not be typical of these interactions at other times of the year (*e.g.* December, when *Acacia* seeds fall).

Ant-mediated seed dispersal

We did not record any ant-mediated seed dispersal from the remnants into the adjacent old-fields. However, it is likely to occur occasionally, as the main seed-dispersing species are present in both habitats, their nests are near to the boundary and the maximum dispersal distances are sufficient to affect dispersal between habitats. In particular, *Rhytidoponera* is one of most important seed dispersers in Australia (Gove *et al*. 2007; Dunn *et al*. 2008). Also, they do not have specific habitat preferences (Bisevac & Majer 1999; May & Heterick 2000) which suggests that the boundary would not represent a barrier to dispersal by ants belonging to this genus.

Field-based studies of ant-mediated seed dispersal typically generate a dispersal curve similar to the one in this study, with most seeds dispersed short distances (*i.e.* < 1m; Gomez & Espadaler 1998). Dispersal distance has been shown to increase with worker body size (Gomez & Espadaler 1998, Ness *et al*. 2004), and this was the case in our study. *Iridomyrmex viridiaeneus* and *R. violacea,* the largest species recorded taking seed, were the only taxa to disperse seeds beyond 13 m. However, small *Melophorus* workers were a notable exception; they dragged seeds much larger than themselves over large distances to their nest (up to 12 m). The maximum dispersal distance recorded in the literature is 180 m (Whitney 2002), compared with 28.1 m recorded here. However, well-worn foraging trails of *I. viridiaeneus* extended from the colony well beyond the zone where seed dispersal was recorded in the old-field at Pullen, so it is likely that seed would have been taken greater distances by this species if seeds were placed at greater distances from their nests.

Generally, not all seeds that are carried reach a nest. In our study, four seeds were dropped *en route* to a nest. On one occasion, a *Melophorus* forager was disturbed by a predatory spider and abandoned the seed. In another case, an I. v*iridiaeneus* forager dropped a seed on a well-formed *I. viridiaeneus* foraging trail, and the seed remained there, ignored by the stream of foragers that passed during the observation period. Such seeds can potentially be picked up by other ants and taken to their nests.

Typically, the elaiosome thieves are small ants that appear as though they would have difficulty dragging the seed to their nest. Elaiosome thieving usually occurs near to the seed source and prevents further dispersal by myrmechorous species. Where elaiosome thieving occurs away from the parent plant, it can increase the likelihood of seed germination (Pizo & Oliveira 2001; Passos & Oliveira 2002). In most cases, however, the seed will remain on the soil surface or it may be taken by a seed predator.

The old-field and woodland habitats were floristically and structurally distinct (Standish *et al.* 2007), yet *Acacia*-seed removal rates were similar as was the abundance of ant seed dispersers. This result contrasts with that of Grimbacher & Hughes (2002), who found seed removal rates of both native and exotic seeds were significantly lower in weedy sites than in undamaged bushland. In our study, removal rates across both habitats (76.7% within 3 hours) were high compared with rates reported in other studies (Majer 1980b and references cited). This suggests that seeds were in short supply.

Seed predation by ants

The percentage of York gum seeds removed from the feeding stations was low, whereas there was a higher than expected loss of seeds from the non-feeding stations. Yates *et al.* (1995) found 21% of seeds were removed from feeding stations within 24 hrs and only 0.25% of seeds were missing from non-feeding stations in the same period; they also found that seed removal was patchy–depending on whether or not ants recruited to the feeding stations. It is unclear why we had high rates of seed loss from the non-feeding stations. It is possible that the Tac-gel had lost its effectiveness as a barrier, allowing ants to enter and remove seeds.

Three species were observed predating seed at Pullen and none were observed at Letchford. However, the three species recorded predating seeds at Pullen were sampled at Letchford, but at lower relative abundance (mean = 2.0 ± 1.3 workers/pitfall at Letchford compared with 9.3 ± 6.2 at Pullen). The three seed harvesters were recorded in both the remnant and old-field habitats, but they were sampled too infrequently to compare their abundance between these habitats. It is likely that some of the other *Pheidole* and *Monomorium* taxa sampled in the pitfall traps at the two sites would also predate eucalypt and other seeds. The availability of eucalypt seeds in Pullen and Letchford old-fields is limited; instead the seed supply is dominated by native and exotic grasses such as *Avena barbata* (Standish *et al.* 2007). No doubt the seeds of these species are attractive to some ants, for example, the husks of *A. barbata* seeds were found discarded around the entrances to *Melophorus wheeleri* nests on these old-fields.

Ants feed on eucalypt seeds *in situ* (Wellington 1989) or store them in their nests (Andersen & Yen 1985; Wellington & Noble 1985; Hughes & Westoby 1992). Some of the stored seeds can geminate (Andersen & Yen 1985; Hughes 1991), although small seeds such as those of salmon gum are unlikely to germinate if they are buried more than a few centimetres below the soil surface (Yates *et al.* 1995; Grant *et al.* 1996). Eucalypt recruitment generally occurs after a large-scale disturbance event, such as fire, when ant harvesters are satiated and safe sites for germination are abundant (Wellington & Noble 1985; Andersen 1987; Yates *et al.* 1995). However, it is conceivable that predation could limit recruitment after fire on old-fields where the local seed supply is limited.

Implications for old-field recolonisation

Ant-mediated long-distance dispersal events are rare, so these are unlikely to be significant for returning native plants to old-fields (Cain *et al.* 2000; this study). The majority of ant-mediated seed dispersal events were less than 3.6 m from the seed source, so we might expect a gradual spread of ant-dispersed woodland species into the old-field as seen elsewhere (*e.g.* Bossuyt *et al.* 1999). On the other hand, it has recently been suggested that kangaroos and emus can act as non-standard dispersers of myrmechorous seeds, which means that long-distance dispersal events remain a possibility (Calviño-Cancela *et al*. 2008). However, in our case there was no evidence of the spread of woodland species into the old-fields. There are several possible reasons for this. First, recruitment can be limited by competition with exotic grasses (Standish *et al*. 2008). Moreover, recruitment is inherently rare because for most species it is contingent upon the unusual coincidence of large-scale disturbance events, such as wildfire, to trigger seed fall and germination, followed by summer rainfall to ensure seedling establishment (Yates *et al.* 1994b; Ruthrof *et al.* 2003; Yates *et al.* 2003; Standish *et al.* 2007). Taken together, the evidence suggests that we should expect the return of native woodland species to old-fields to be slow or non-existent.

For old-fields such as Pullen and Letchford, woodland species may not return without assistance. The removal of the exotic grasses followed by direct seeding will be necessary to ensure their restoration (Standish *et al.* 2007; Standish *et al*. 2008). There are no quantitative data on the success of grass removal and direct seeding for the restoration of old-fields, but the factors that effect the recruitment of broadcast seeds onto rehabilitated mine-sites are likely to be similar, and seed predation by ants is among these (Majer 1980b; Majer & Abbott 1989; Majer *et al.* 2007). In this context, ant predation is likely to play a more significant role in the availability of seeds for old-field recolonisation.

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