Multiphase myrmecochory: the roles of different ant species and effects of fire

Kieren P. Beaumont · Duncan A. Mackay · Molly A. Whalen

Abstract Seed dispersal by ants (myrmecochory) can be influenced by changes to ant assemblages resulting from habitat disturbance as well as by differences in disperser behaviour. We investigated the effect of habitat disturbance by fire on the dispersal of seeds of a myrmecochorous shrub, *Pultenaea daphnoides*. We also investigated the consequence of the seed relocation behaviours of two common dispersers (*Pheidole* sp. A and *Rhytidoponera metallica*) for the redispersal of seeds. *Pheidole* sp. A colonies did not relocate seeds outside their nests. In contrast, *R. metallica* colonies relocated 43.6 % of seeds fed to them, of which 96.9 % had residual elaiosome that remained attached. On average, *R. metallica* relocated seeds 78.9 and 60.7 cm from the nest entrances in burned and unburned habitat, respectively. Seeds were removed faster in burned than in unburned habitat, and seeds previously relocated by *R. metallica* were removed at similar rates to seeds with intact elaiosomes, but faster than seeds with detached elaiosomes. Dispersal distances were not significantly different between burned (51.3 cm) and unburned (70.9 cm) habitat or between seeds with different elaiosome conditions. Differences between habitat types in the frequency of seed removal, the shape of the seed dispersal curve, and the relative contribution of *R. metallica* and *Pheidole* sp. A to seed dispersal were largely due to the effect of recent fire on the abundance of *Pheidole* sp. A. Across habitat types, the number of seeds removed from depots and during dispersal trials most strongly related to the combined abundances of *R. metallica* and *Pheidole*. Our findings show that myrmecochory can involve more than one dispersal phase and that fire indirectly influences myrmecochory by altering the abundances of seed-dispersing ants.

Keywords Ant · Disturbance · Dispersal distance · Prescribed burn · *Rhytidoponera*

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Introduction

By dispersing seeds, animals influence the conditions that seeds and seedlings experience and hence can affect plant recruitment (Wang and Smith 2002). Globally, ants play an important role in seed dispersal (Rico-Gray and Oliveira 2007), and approximately 11,000 plant species have seeds with a specialized appendage called the elaiosome (Lengyel et al. 2010) that is attractive to ants and facilitates seed dispersal by them (myrmecochory), (Beattie 1985). Myrmecochory is considered to be a mutualism because seed-dispersing ant colonies benefit from the lipid-rich elaiosomes (Morales and Heithaus 1998; Gammans et al. 2005), and plants can benefit in several ways by having their seeds dispersed (Beattie 1985; Giladi 2006; Rico-Gray and Oliveira 2007). By burying seeds within their nests, ants can protect myrmecochorous seeds from predators (predator avoidance hypothesis; e.g. Bond and Slingsby 1984; Smith et al. 1989; Auld and Denham 1999), and from lethal soil surface temperatures that occur during fires (escape from fire hypothesis; e.g. Shea et al. 1979; Majer 1982; Hughes and Westoby 1992a). The soil

associated with ant nests can have greater levels of nutrients than other locations which can result in increased seedling growth and survival (directed dispersal hypothesis; e.g. Davidson and Morton 1981; Beattie and Culver 1983). The greater dispersion of seeds resulting from myrmecochory can reduce parent–offspring and seedling–seedling competition (Boyd 2001), and may also facilitate the arrival of seeds at favourable but rare microsites required for successful seed germination and seedling establishment (Andersen 1988a), (distance dispersal hypothesis).

The relative importance of the ways in which plants can benefit from myrmecochory varies between ecosystems, and such variation may arise from differences in behaviours of seed-dispersing ants (Giladi 2006). At a local scale, plants often have their seeds collected by several species which can differ greatly in the distance that they disperse the seeds (Hughes and Westoby 1992a; Andersen and Morrison 1998; Gomez and Espadaler 1998a; Parr et al. 2007) and in the seed fates that they facilitate (Hughes and Westoby 1992a). The quality of dispersal services provided by ants may be strongly dependent on the fate of seeds once they reach ant nests. Ant species retain seeds within their nests to varying degrees (Gomez et al. 2005; Servigne and Detrain 2010), while seeds taken out of nests can be placed on nest mounds (e.g. Davidson and Morton 1981), or relocated to sites some distance away from nest entrances (Berg 1975; Kjellsson 1985; Hughes and Westoby 1992a; Gorb and Gorb 2003; Lubertazzi et al. 2010; Canner et al. 2012). In addition, seeds discarded from nests often have their elaiosomes removed (Hughes and Westoby 1992a; Gorb and Gorb 2003; Canner et al. 2012), although some ant species discard seeds that still have residual elaiosome attached (Berg 1975; Lopez-Vila and Garcia-Fayos 2005; Servigne and Detrain 2010). The relocation of seeds by ants from within nests to sites away from nest entrances may strongly affect the benefits, as well as the costs associated with myrmecochory. For example, seed relocation removes seeds from the nest negating any benefits provided by the nest environment (Canner et al. 2012), and may re-expose seeds to risks associated with being on the soil surface (Gomez and Espadaler 1998b). However, seed relocation represents a secondary phase of dispersal (Gorb and Gorb 2003; Canner et al. 2012) and may also facilitate the subsequent redispersal of seeds to other ant nests (Hughes and Westoby 1992a). Seed relocation by ants has received little attention, despite the important implications it can have for the distribution and fate of myrmecochorous seeds (Hughes and Westoby 1992a; Gorb and Gorb 2003; Canner et al. 2012).

Due to variation in the behaviour of seed dispersers and the seed fates that they facilitate, the fitness outcomes of myrmecochory are likely to depend on the composition of the local disperser assemblage. This composition, in turn, can be altered by environmental fluctuations, and changes to aspects of myrmecochory such as seed removal rates and dispersal distances can be particularly prominent in environments subjected to disturbance (Pudlo et al. 1980; Andersen and Morrison 1998; Zelikova and Breed 2008). In Australia, fire is a widespread cause of disturbance in sclerophyll forest and woodlands where myrmecochorous plants are most common (Berg 1975). Fire cues are often required for the germination of myrmecochorous seeds (Shea et al. 1979; Majer 1982; Auld 1986; Hughes and Westoby 1992a), while post-fire changes in habitat conditions can alter the composition of ant assemblages (Andersen 1991; York 2000; Beaumont et al. 2012). Consequently, the dynamics of myrmecochory may be closely linked to fire events and fire history. Indeed, previous studies have found that recent fire can affect seed dispersal distances (Parr et al. 2007), the rate of seed removal and the contribution that different ant species make to dispersal (Parr et al. 2007; Beaumont et al. 2011). These changes were attributed to the effect of fire on the activity and/or abundances of seed-dispersing ants (Parr et al. 2007; Beaumont et al. 2011). While these studies provide important insights into the effect of fire on myrmecochory, the influence of fire on multiple phases of seed dispersal by ants has not previously been considered.

The aim of this study was to investigate the influence of fire history (i.e. recently burned and long unburned habitat) on the dispersal, relocation and redispersal of seeds of a myrmecochorous shrub, *Pultenaea daphnoides* J. C. Wendl. (Fabaceae). Seed 'relocation' and 'redispersal' are terms that have both been used to describe the transportation of seeds from within the nest to sites some distance from the nest entrance, but given that multiple phases of myrmecochory are considered here, we restrict the term seed 'relocation' to describe the transport of seeds away from ant nest entrances, and seed 'redispersal' to describe the dispersal phase in which relocated seeds are discovered by ants and further transported. Our study was prompted by our observations that a common seed-dispersing ant, *Rhytidoponera metallica* Smith, frequently relocated previously collected seeds away from their nests even though the seeds often had at least partial elaiosomes that remained attached (e.g. Online resource 1). Since the elaiosomes of such seeds have usually been at least partially consumed in the nest, the elaiosome condition of relocated seeds differed from that of seeds primarily available to ants.

In this context, we conducted a series of experiments to address the following questions.

1. Do fire history and elaiosome condition affect the removal, dispersal and redispersal of seeds by ants?
2. Does fire history affect seed removal and dispersal by altering the abundance of seed-dispersing ants?

3. Does fire history affect the distance that *R. metallica* relocate seeds away from their nests?

   Lastly, we investigated the seed discarding behaviour of the two common dispersers, *R. metallica* and *Pheidole* sp. A., to determine their potential contribution to the relocation and redispersal of seeds. Specifically we asked;

4. Does the proportion of seeds discarded from nests, and the elaiosome mass of discarded seeds, differ between two seed-dispersing ant species?

Materials and methods

Study sites and species

Field work was conducted in Belair National Park (35°00′20″S, 138°39′50″E) and Cleland Conservation Park (34°58′S, 138°42′E) located in the Mount Lofty Ranges of South Australia. The climate is temperate, with an average annual rainfall of 778 and 991 mm for Belair and Cleland, respectively. The study sites were located in *Eucalyptus obliqua* L'Hér. forest/woodland, with ground cover vegetation dominated by *Lepidosperma semiteres* F.Muell. ex Boeckeler and *Hibbertia* species under a mid-story shrub layer variably co-dominated by *Pultenaea daphnoides*, *Hakea rostrata* F.Muell. ex Meisn., *Acacia myrtifolia* (Sm.) Willd. and *Leptospermum myrsinoides* Schltdl. *Pultenaea daphnoides* is a 1 to 3-m-high myrmecochorous shrub that is distributed throughout southern and southeastern Australia and is common in *E. obliqua* forest of the Mount Lofty Ranges. Diaspores of this species weigh an average of 6.5 ± 0.16 mg (mean $\pm$ 1SE) and each seed has a white elaiosome that on average accounts for 9.86 ± 0.36 % of the diaspore mass ($n = 30$). Following fire, *P. daphnoides* regenerates from soil stored seeds. In addition, plants in the Mount Lofty Ranges can resprout from basal buds (Jianmin and Sinclair 1993) and begin to produce seed following two winter seasons after fire (personal observation).

Seed removal and seed dispersal experiments, as well as pitfall trap sampling of the associated ant communities, were conducted at four sites within Cleland Conservation Park, while observations of seed relocation distances facilitated by *R. metallica* were conducted at two of the four sites. Observations of seed discarding by colonies of *Pheidole* sp. A and *R. metallica* were conducted at a site within Belair National Park. Each site within Cleland contained one long-unburned plot ('unburned') and one recently burned plot ('burned') separated by a distance of approximately 50 m. All sites were previously burned by a single bushfire in 1983 and only burned plots were additionally subjected to prescribed fires that were conducted separately in the spring seasons of 2004 ($n = 1$), 2005 ($n = 2$) and 2006 ($n = 1$). The four sites were spaced over a distance of nearly 2 km, with a minimum and maximum distance between sites of 360 and 900 m, respectively. Study plots were 15×35 m in area, with grid points marked at 5-m intervals, totalling 32 grid points per plot.

Elaiosome condition, seed removal rate and dispersal distances

Seed removal and seed dispersal experiments were carried out over 3 months (January–March 2009), following the peak seedfall period of *P. daphnoides* and other myrmecochorous shrubs. Fruiting *P. daphnoides* plants were present on all plots, except for the plot burned in 2006. The duration between the last fire and these experiments ranged from approximately 2.3–4.3 years for burned plots and 26 years for unburned plots.

Seed depot experiments were conducted to assess the influence of fire history and four elaiosome conditions on the rate at which *P. daphnoides* seeds are removed by ants. The four elaiosome conditions were:

Natural: seeds with natural elaiosomes are the condition of diaspores that ants encounter following seedfall and the dispersal of such seeds represents the primary dispersal phase. The elaiosomes of these seeds accounted for an average of 9.86 ± 0.34 % (mean $\pm$ SE; $n = 30$) of diaspore weight.

Handled: seeds with handled elaiosomes represent a condition of diaspores that ants may encounter if seeds are discovered after being relocated outside of ant nests. The redispersal of seeds with handled elaiosomes represents a tertiary phase of myrmecochory. To obtain handled diaspores, 16 *Rhytidoponera metallica* colonies were located on Flinders University campus and enclosures were placed around their nest entrances. On two separate occasions, each colony was offered 50 *P. daphnoides* seeds and monitored to confirm that all were taken into their nests. Seeds that were subsequently discarded on the soil surface were collected daily for 10 days. On average, elaiosomes constituted 5.01 ± 0.43 % ($n = 30$) of the weight of handled diaspores, with 10 % having the elaiosome completely detached. All seeds discarded by *R. metallica* colonies were deemed handled, regardless of the state of the elaiosomes.

Detached: seeds with the elaiosomes detached represents a condition of seeds that ants may encounter if elaiosomes are completely consumed within nests and seeds are then relocated outside of ant nests. The redispersal of seeds with the elaiosomes detached would also represent a tertiary phase of myrmecochory. The elaiosomes were detached from seeds using forceps.

Cut: seeds with approximately 50 % of the elaiosome removed with a scalpel. The elaiosomes of this treatment group accounted for an average of 6.33 ± 0.29 % ($n = 30$) of the diaspore weight. It was noted that, in addition to having reduced elaiosome mass, handled elaiosomes often appeared more yellow than natural elaiosomes, possibly signifying a deterioration of elaiosome attractiveness. Also, there may be other handling effects on elaiosome condition that influence seed removal rates independent of a reduction in elaiosome mass. An effect of seed handling by *R. metallica* on removal rates, independent of a reduction in elaiosome mass, was investigated by comparing removal rates of seeds with cut and handled elaiosomes. Also, an effect of a reduction in elaiosome size independent of potential seed handling effects was tested by comparing removal rates of seeds with cut and natural elaiosomes.

Seed removal experiments were conducted consecutively at each study site between January and February 2009. In each plot, depots were positioned next to the 32 marked grid points and each depot was randomly assigned to one of the four elaiosome conditions (i.e. 8 depots/elaiosome condition/plot). Depots consisted of plastic Petri dishes (9 cm in diameter) with four 2-cm-wide holes cut into the lid and base to allow access by ants. Ten seeds were placed in each depot at 0800 hours and the numbers of seeds that remained were recorded 3, 6, 9, 12, 24, 36 and 48 h later.

During February and March 2009, direct observations of seed dispersal by ants were conducted in burned and unburned plots for seeds with natural, handled and detached elaiosomes. In each observation trial, five seeds of the three elaiosome treatments were placed within a 0.5×0.5-m quadrat, at 15 randomly selected quadrat points (out of a possible 25) with a minimum spacing of 10 cm between each point. The seeds were placed on small pieces of corrugated cardboard, held in place with a wooden skewer, to prevent seeds being lost in the leaf litter. Each observation trial ran for 40 min, during which seed dispersal distances, final seed locations (i.e. nest site or dropped in transit) and the disperser species were recorded. Dispersed seeds were replaced with new seeds with the same elaiosome condition. Seed dispersal trials were conducted between 0730 and 1300 hours, which is a period that covers a high to decreasing rate of seed removal in this vegetation (see Beaumont et al. 2011). Twelve trials were conducted at each plot on two separate days, totalling 96 trials.

Ant abundances

The ant communities at each study plot were sampled using pitfall traps in February 2009 to quantify the abundance of seed-dispersing ant species. Pitfall traps consisted of plastic jars (4.5 cm in diameter) that were half filled with saturated salt solution and a drop of detergent to reduce the surface tension of the solution. For each plot, 20 traps were positioned within 1 m of 20 randomly selected grid points (out of 32 grid points) and left open for 4 days. Ants were extracted from traps and identified to genus using Shattuck (1999) and to lower taxonomic levels where possible.

Seed discarding and elaiosome condition

Seed feeding experiments were carried out to investigate the proportion of *P. daphnoides* seeds discarded outside nests by colonies of *Pheidole* sp. A (referred to as *Pheidole* hereafter) and *R. metallica*, and to determine the condition of the elaiosomes of discarded seeds. Ant nests were located at the site in Belair National Park that had been burned 1 year previously and at which, consequently, resident *P. daphnoides* plants had not yet started to produce seeds. Plastic cylinders (10.5 cm diameter) were installed around the entrances of 6 *Pheidole* and 18 *R. metallica* nests so that discarded seed could be located and so that they were not available to other ants. A strip of Tangle-Trap gel (Tanglefoot, Grand Rapids, MI, USA) was applied to the inner and outer surface of the enclosures, and fine sand was placed at the base of the enclosures to hinder any attempts by ants to tunnel out. Each colony was offered 25 *P. daphnoides* seeds, all of which were taken into nests. Each colony was additionally fed with 1 cricket (*Acheta domesticus*) every 6–8 days. Whether elaiosomes were completely detached or not was scored for discarded seeds. Also, the mass of each elaiosome that remained attached to discarded seeds was obtained by calculating the differences in mass between seeds with and without their elaiosomes. The average elaiosome mass of discarded seeds was then compared with the average elaiosome mass of seeds from the same seed lot, but that were not fed to ant nests ($n = 60$). Measurements were made to the nearest 0.001 mg using a micro-balance (Mettler Toledo MX5).

Seed relocation distances

We have previously observed that seeds placed close to the nest entrances of *R. metallica* colonies can be carried away from, rather than taken into, nests. This behaviour of *R. metallica* was used to estimate the distances that they relocate seeds away from their nests. Observations were made from December 2009 to February 2010 on four colonies in each of two burned (burned in 2004 and 2005) and two unburned plots. Observations were conducted between 1700 and 2000 hours when colonies were most active during the afternoon period. For each nest, a *P. daphnoides* seed with an intact elaiosome was placed within 1 cm of the nest entrance. If an ant relocated the

seed away from its nest, the direction and distance of seed relocation was measured. Up to 15 seeds were offered to each colony, with a minimum interval of 5 min between each offering.

Data analysis

The effects of fire history and elaiosome conditions on the proportion of seeds remaining within depots were tested using a generalized linear mixed model with the error modelled as a binomial distribution. Fire history and elaiosome condition were treated as fixed factors, site was treated as a random factor and repeated observations of seed depots were treated as repeated measures. Tests of significance were based on likelihood ratios. The analysis was conducted using the lme4 package (Bates and Maechler 2010) in the R statistical software system, v.2.11.1 (R Development Core Team 2010).

The effects of fire history, elaiosome condition and site on seed dispersal distances facilitated by all ants were tested using a linear mixed model. Dispersal distances were log-transformed so that the distribution of these values was more normally distributed and so that the variance was not significantly different among groups. Fire history and elaiosome condition were treated as fixed factors and site was treated as a random factor. Differences in shape of the frequency distribution of seed dispersal distances (including seeds with all elaiosome conditions) between burned and unburned habitat were investigated using a two-sample Kolmogorov–Smirnov test.

Differences between burned ($n = 4$ plots) and unburned ($n = 4$ plots) habitat in the frequency of seed dispersals facilitated by *Pheidole* and *R. metallica*, as well as by all seed-dispersing ants and by seed-dispersing ants other than *Pheidole* and *R. metallica*, were investigated using Mann–Whitney U tests. The effect of fire history on the relative contribution of *Pheidole*, *R. metallica* and other seed-dispersing ant species to seed dispersal (expressed as a percentage of the total number of seed dispersal events) was also tested using Mann–Whitney U tests.

The effect of fire history on the abundance of seed-dispersing ant species was analysed in a similar way as described for the frequency of seed dispersal. The frequency of pitfall occurrences of an ant species was used as a measure of its abundance. The abundance of ant species groups (i.e. all seed-dispersing ant species and seed-dispersing ant species other than *Pheidole* and *R. metallica*) was defined as the sum of pitfall occurrences of the component ant species. The relative abundance of *Pheidole*, *R. metallica* and other seed-dispersing ant species was defined as the sum of their pitfall occurrences divided by the sum of pitfall occurrences of all seed-dispersing ant species, expressed as a percentage.

Non-parametric correlations (Spearman's rho) were used to investigate the relationships between seed removal (i.e. the number of seeds removed from depots after 24 h and the number of seeds removed during seed dispersal trials) and the abundance of particular ant species and species groups. Plots were treated as replicates and the analyses included both burned and unburned plots (i.e. $n = 8$). Only seeds with natural elaiosomes were used in these analyses and the frequency of pitfall occurrences was used as a measure of ant abundance. The total number of seeds removed was correlated with the abundance of *Pheidole* and of *R. metallica*, the combined abundance of *Pheidole* and *R. metallica* and, lastly, the combined abundance of all seed-dispersing ant species other than *Pheidole* and *R. metallica*.

An independent samples t test was used to investigate whether fire history affects the average distance that *R. metallica* colonies relocate seeds from nests (i.e. ant colonies were used as replicates). Three colonies, two in burned habitat and one in unburned habitat, took all seeds offered into their nests and thus were not included in the analysis. Rayleigh tests were used to test whether the directions that colonies relocated seeds away from their nests deviated significantly from uniformity. Tests were conducted for nine colonies that discarded ≥5 seeds using the Circular package (Lund and Agostinelli 2011) in the R statistical software system, v.2.11.1 (R Development Core Team 2010).

Results

Elaiosome condition, seed removal rate and dispersal distances

The proportion of seeds that remained in depots was significantly higher in unburned vegetation compared to burned vegetation ($Z = 2.863$, $P = 0.004$; Fig. 1). Significantly more seeds with detached elaiosomes remained in depots compared to seeds with natural elaiosomes ($Z = 2.645$, $P = 0.008$); however, seeds with cut and handled elaiosomes were removed at a similar rate to seeds with natural elaiosomes ($Z = -1.514$, $P = 0.130$; $Z = -0.404$, $P = 0.686$, respectively). No significant interactions between fire history and elaiosome conditions were observed. The estimated standard deviations of the random effects of depots, time and site were 0.267, 0.093 and 0.703, respectively. Seed removal rate was rapid over the first 24 h and then slowed over the last 24 h of the experiment (Fig. 1).

During seed dispersal trials, six ant species facilitated a total of 136 seed dispersal events (Table 1), of which 51.5, 40.4 and 8.1 % were seeds that had natural, handled and
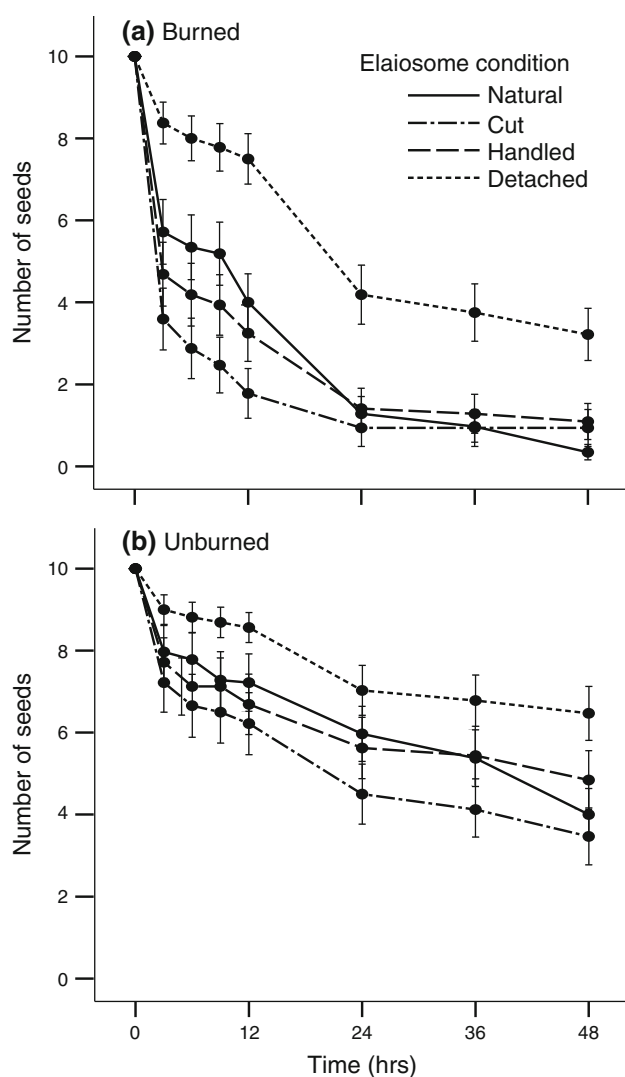
Fig. 1 Mean number of seeds remaining in seed depots located in **a** burned and **b** unburned habitat overtime. *Symbols* represent four elaiosome conditions of *P. daphnoides* seeds: *Natural*—seeds with non-manipulated elaiosomes; *Cut*—seeds with ca. 50 % of each elaiosome removed; *Handled*—seeds with residual elaiosomes that were handled within nests of *R. metallica* and then discarded outside nests; *Detached*—seeds with the elaiosomes completely detached. Values are means ± 1SE ($n = 32$)

detached elaiosomes, respectively. Average seed dispersal distance (log-transformed) was not significantly affected by fire history ($F_{1,12} = 3.546$; $P = 0.084$), elaiosome condition ($F_{2,12} = 0.860$; $P = 0.448$), or by the interaction between fire history and elaiosome condition ($F_{2,12} = 1.051$; $P = 0.380$). Most seeds (95.6 %) were taken into ant nests and were dispersed an average distance (mean ± 1SE) of 51.3 ± 5.8 cm (maximum 280 cm) and 70.9 ± 10.9 cm (maximum 377 cm) in burned and unburned habitat, respectively. The frequency distribution of seed dispersal distances (data pooled over elaiosome conditions) was significantly different between habitat types,

($Z = 4.594$, $P = 0.012$), being more skewed in burned habitat (Fig. 2a) than in unburned habitat (Fig. 2b). *Pheidole* dispersed seeds shorter distances than *R. metallica* (Table 1; Fig. 2a, b) and, together, these species facilitated 83.8 % of all seed dispersal events.

On average, more dispersals per plot occurred in burned vegetation than in unburned vegetation, although this trend was not significant (Table 2). *Pheidole* ants dispersed significantly more seeds in burned than in unburned vegetation. A similar but non-significant trend was observed for *R. metallica* (Table 2). In relative terms, *Pheidole* ants facilitated a significantly greater proportion of the dispersal events in burned habitat (32.2 %) than in unburned (3.7 %), while *R. metallica* ants facilitated a significantly larger proportion of the dispersal events in unburned habitat (77.6 %) than in burned habitat (48.7 %), (Table 2).

Ant abundance and seed removal

A total of 32 ant species were detected (Online resource 2) with an average of 13.3 ± 0.95 and 11.3 ± 0.85 found on burned and unburned plots, respectively. On average, 4.5 ± 0.29 and 4.3 ± 0.25 seed-dispersing species occurred per burned and unburned plots, respectively. The total abundance of the six seed-dispersing ant species was significantly higher in burned habitat (Table 3). The abundance of the two common seed-dispersing ant species (*R. metallica* and *Pheidole*) tended to be higher in burned habitat than in unburned; however this trend was only significant for *Pheidole* (Table 3). In addition, *Pheidole* ants accounted for a larger proportion of the seed-dispersing ant community in burned habitat than in unburned habitat, although this trend was marginally non-significant (Table 3).

The total number of seeds (with natural elaiosomes) removed from depots over 24 h was significantly correlated with the abundance of *Pheidole* ants (Spearman rank order correlation; $\rho = 0.826$, $P = 0.011$), but not with the abundance of *R. metallica* ants ($\rho = 0.455$, $P = 0.257$). However, the combined abundance of both *Pheidole* and *R. metallica* ants appears to explain more variation in seed removal ($\rho = 0.929$, $P = 0.001$; Fig. 3a) than either species alone. Seed removal from depots was not correlated with the combined abundance of the remaining seed-dispersing ant species ($\rho = -0.595$, $P = 0.120$).

On the other hand, the total number of seeds removed (with natural elaiosomes) during seed dispersal trials was correlated with the abundance of *R. metallica* ($\rho = 0.801$, $P = 0.017$), not with the abundance of *Pheidole* ($\rho = 0.500$, $P = 0.207$), but, similarly, not with the combined abundance of other seed-dispersing ants ($\rho = -0.108$, $P = 0.799$). Again, the combined abundance of *R. metallica* and *Pheidole* appears to explain slightly more

Table 1 Number of seed dispersal events facilitated by ants in burned and unburned habitat for seeds with three elaiosome conditions. Seed dispersal distances (mean $\pm$ 1SE) facilitated by each ant species and for each elaiosome condition in burned and unburned habitat are also shown

	Burned					Unburned				
	No. of dispersal events					No. of dispersal events				
	N	H	D	Total	Dispersal distance (cm)[a]	N	H	D	Total	Dispersal distance (cm)[a]
Rhytidoponera metallica	26	20	2	48	82 $\pm$ 9.3	17	12	3	32	82 $\pm$ 12.9
Pheidole sp. A	16	10	6	32	13 $\pm$ 1.2	1	1	–	2	8 $\pm$ 1.0
Pheidole ampla perthensis	1	1	–	2	17 $\pm$ 9.0	–	1	–	1	45
Iridomyrmex mattiroloi splendens	4	5	–	9	49 $\pm$ 9.7	–	–	–	–	–
Anonychomyrma sp. nr. *nitidiceps*	2	–	–	2	17 $\pm$ 0.5	2	3	–	5	33 $\pm$ 9.6
Anonychomyrma sp. A	1	2	–	3	22 $\pm$ 6.7		–	–	–	–
Total	50	38	8	96		20	17	3	40	
Dispersal distance (cm)[b]	49 $\pm$ 8.9	59 $\pm$ 8.5	25 $\pm$ 6.5	51.3 $\pm$ 5.8		87 $\pm$ 20	55 $\pm$ 8.7	49 $\pm$ 20.4	70.9 $\pm$ 10.9	

Elaiosome conditions: *N* natural, *H* handled, *D* detached

[a] Mean dispersal distances for each species are based on data pooled over three elaiosome conditions

[b] Mean dispersal distances for each elaiosome condition are based on data pooled over all ant species

variation in the number of seeds removed ($\rho = 0.826$, $P = 0.011$; Fig. 3b) than either species alone.

Seed discarding and elaiosome condition

Pheidole colonies did not discard any seeds. On average, *Rhytidoponera metallica* colonies discarded 43.6 $\pm$ 7.6 % (range 0–100 %) of the seeds fed to them, of which 3.1 % had the elaiosomes completely detached and the other 96.9 % had at least some elaiosome that remained attached. It was estimated that the elaiosome mass of seeds discarded by *R. metallica* colonies was reduced by an average ca. 50 %. That is, the average elaiosome mass of seeds that were not fed to ants was 0.616 $\pm$ 0.020 mg, whereas the average elaiosome mass of discarded seeds (not including the 3.1 % which had their elaiosome completely detached) was 0.312 $\pm$ 0.010 mg.

Seed relocation distances

Of 182 seeds offered to *R. metallica* colonies, 71 seeds were relocated away from nests and the remaining 111 were taken into nests. The majority of seeds either taken into or away from nests were carried by workers coming from the nests (94 %) rather than by returning foragers

(6 %). Hence, most seed relocations (86 %) were facilitated by workers coming out of their nests. The directions that colonies relocated seeds did not differ significantly from uniformity (Rayleigh tests, $P > 0.273$ for all cases tested). Colonies in burned and unburned habitats relocated seeds an average distance of 78.9 $\pm$ 11.1 cm ($n = 6$ colonies) and 60.7 $\pm$ 7.8 cm ($n = 7$ colonies) from their nest entrances, respectively. Relocation distances did not differ significantly between burned and unburned habitat ($t = 1.374$; $df = 11$; $P = 0.197$). The frequency distribution of distances appears to be somewhat skewed towards shorter distances (Fig. 4). The maximum distances that ants relocated seeds were 230 and 145 cm in burned and unburned habitat, respectively.

Discussion

The results of this study highlight two factors that influence the removal and dispersal of *P. daphnoides* seeds by ants and that have more general implications for the study of myrmecochory and the effectiveness of dispersal services provided by ants. First, *R. metallica* ants may facilitate additional dispersal phases by relocating some seeds, typically with residual elaiosomes, away from their nests after
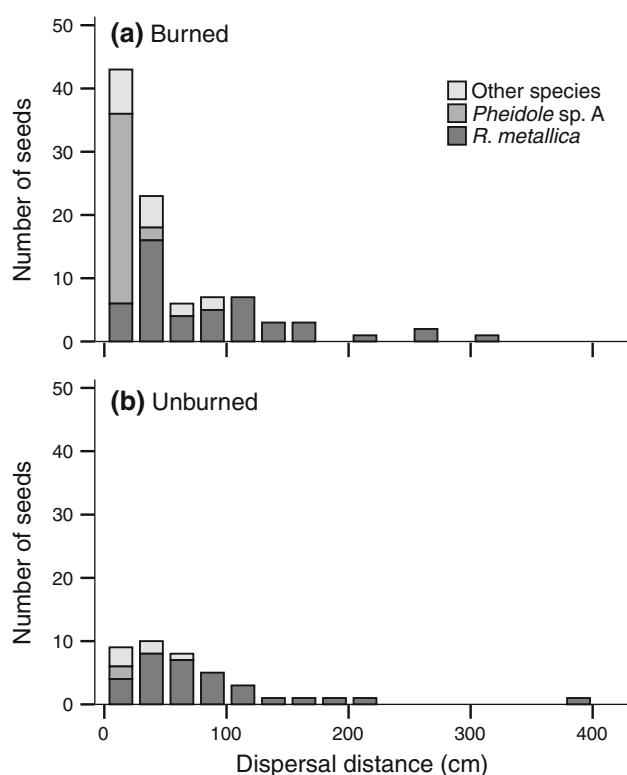
Fig. 2 Frequency distribution of seed dispersal distances of *P. daphnoides* facilitated by ants in **a** burned ($n = 96$ seeds) and **b** unburned ($n = 40$ seeds) habitat. *Shaded segments* of *bars* show the number of dispersal events facilitated by *R. metallica*, *Pheidole* sp. A, and four other species. Data for three elaiosome conditions (natural, handled, and detached elaiosomes) are pooled because elaiosome condition did not affect dispersal distance

first transporting them into their nests. Such seeds are then potentially available for further dispersal by ants (multiphase myrmecochory). Second, recent fire altered aspects of seed dispersal including seed removal rate (Fig. 1), the relative contribution of *R. metallica* and *Pheidole* to seed dispersal (Table 2) and the shape of the seed dispersal curve (Fig. 2). These effects appeared to be primarily due to fire-driven changes in the abundance of *Pheidole*, and, to a lesser extent, *R. metallica* ants (Table 3).

Multiple phases of myrmecochory and the influence of *Rhytidoponera metallica*

Of the two main dispersers in this study, only *R. metallica* facilitated potential multiple phases of dispersal by relocating seeds away from their nest entrances. In contrast, seeds dispersed by *Pheidole* ants remained buried within their nests. Other species of *Rhytidoponera* have been observed to relocate seeds (Berg 1975) and seed analogues (Lubertazzi et al. 2010) from within their nests for distances of up to, and more than, 2 m, respectively, which is similar to those facilitated by *R. metallica* (Fig. 4). In this study, relocation distances were estimated by placing seeds with elaiosomes attached near nest entrances and then following ants that carried seeds away from their nests. This behaviour has been observed for other ant species (O'Dowd and Hay 1980; Gomez and Espadaler 1998b; Bas et al. 2009), but the extent to which it accurately estimates seed relocation distances of seeds that have previously been manipulated within *R. metallica* nests requires confirmation, perhaps by using recent techniques for marking seeds (e.g. Canner and Spence 2011) and by controlling for worker age (Gomez and Espadaler 1998b).

R. metallica is expected to facilitate the redispersal of seeds that they relocate because some elaiosome remained attached on the majority of seed they discarded. This is perhaps surprising given that myrmecochory is commonly thought to involve seeds being discarded by ants only after the complete removal of elaiosomes. Even so, Berg (1975) noted that 'some' seeds of *Dillwinia juniperina* that were

Table 2 Number of seed dispersal events (mean $\pm$ 1SE) and the relative contribution (%) of ants to seed dispersal in burned and unburned habitats

|	Burned	Unburned	P
Number of dispersals			
R. metallica	12.0 ± 2.80	8.0 ± 2.12	0.243
Pheidole sp. A	8.0 ± 1.91	0.5 ± 0.29	0.019
Other species	4.0 ± 1.47	1.5 ± 0.65	0.144
All species	24.0 ± 4.56	10.0 ± 2.04	0.083
Relative contribution to dispersals (%)			
R. metallica	48.7 ± 7.02	77.6 ± 7.55	0.043
Pheidole sp. A	32.2 ± 2.84	3.7 ± 2.14	0.020
Other species	19.0 ± 7.25	18.7 ± 8.89	1.000

Values are presented for two common seed dispersers (*R. metallica* and *Pheidole* sp. A) and for the four uncommon seed-dispersing ant species (other species). Values are means $\pm$ 1SE and are pooled over elaiosome conditions. *P* values are derived from Mann–Whitney *U* tests indicating the significance of differences in rank values between burned ($n = 4$) and unburned ($n = 4$) plots

Table 3 Number of pitfall occurrences (mean ± 1SE) and relative pitfall occurrences (%) of seed-dispersing ants in burned and unburned habitats
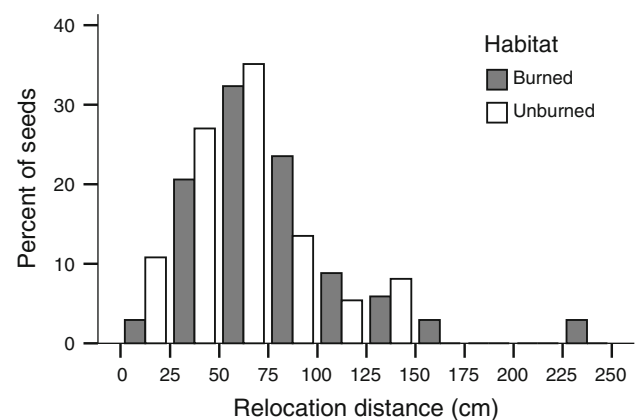
	Burned	Unburned	P
Pitfall occurrence			
R. metallica	12.3 ± 3.17	7.5 ± 1.32	0.309
Pheidole sp. A	12.5 ± 2.25	3.5 ± 1.19	0.020
Other species	10.5 ± 3.93	10.3 ± 0.85	0.386
All species	35.3 ± 4.59	21.3 ± 1.44	0.020
Relative pitfall occurrence (%)			
R. metallica	35.2 ± 8.88	34.8 ± 4.27	1.000
Pheidole sp. A	36.5 ± 8.14	15.9 ± 5.61	0.081
Other species	28.3 ± 7.17	49.3 ± 6.60	0.083

Values are presented for two common seed dispersers (*R. metallica* and *Pheidole* sp. A) and for the four uncommon seed-dispersing ant species (other species). Values are means ± 1SE and *P* values are derived from Mann–Whitney *U* tests indicating the significance of differences in rank values between burned (*n* = 4) and unburned (*n* = 4) plots
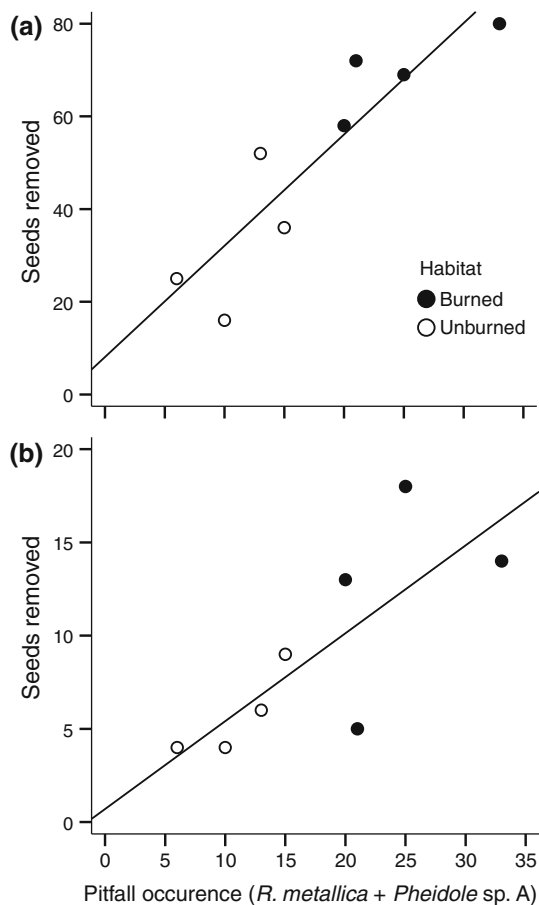
Fig. 3 Relationship between the summed pitfall occurrences of two common seed dispersers (*R. metallica* and *Pheidole*) and **a** total numbers of seeds with natural elaiosomes removed from depots after 24 h and **b** total numbers of seeds with natural elaiosomes removed during dispersal trials. Data from burned and unburned plots are indicated

Fig. 4 Frequency distributions of the distances that *R. metallica* ants relocated *P. daphnoides* seeds from their nest entrances in burned (*n* = 34 seeds) and unburned (*n* = 37 seeds) habitat

scattered around a *R. tasmaniensis* nest had residual elaiosomes, and Servigne and Detrain (2010) found that a proportion of seeds with elaiosomes can be discarded from nests because seed discarding rates were not strongly coupled with rates of elaiosome detachment. The discarding of seeds with residual elaiosomes by *R. metallica* and other species may be due to a number of factors that require further examination. For example, an uneven distribution of nutrients within elaiosomes (Bresinsky 1963) may result in incomplete elaiosome consumption (Servigne and Detrain 2010) or the toughness of elaiosome tissue may affect the ability of ants to completely remove elaiosomes. Finally, oleic acid in elaiosomes can elicit the collection of myrmecochorous seeds by ants (Marshall et al. 1979; Brew et al. 1989), but is also known to trigger necrophoric behaviours (Wilson et al. 1958; Gordon 1983). Furthermore, whether objects treated with oleic acid are taken into nests or to refuse piles outside of nests can depend on the predominant task being carried out by ant colonies (i.e. foraging or nest cleaning) (Gordon 1983). The discarding and relocation of seeds, including those with elaiosomes, may be a hygiene-related behaviour akin to necrophory, but

whether oleic acid triggers the relocation of elaiosome bearing seeds by dispersers is unknown.

Seeds discarded by *R. metallica* (i.e. seeds with handled elaiosomes) were found to be removed by ants at a similar rate to seeds with natural elaiosomes (Fig. 1). This indicates that the rate of redispersal is similar to that of seeds initially removed following seedfall. Furthermore, the reduced elaiosome mass of seeds discarded by *R. metallica* and the previous handling of elaiosomes within *R. metallica* nests did not significantly reduce the attractiveness of discarded diaspores. Dispersal distances were also not significantly different for seeds with natural, handled and detached elaiosomes, and a similar set of species were involved in their transportation. Therefore, redispersal of seed with residual elaiosomes following their relocation from ant nests appears similar to the initial or primary dispersal phase in terms of the ant species involved, the rates of seed removal and the seed transportation distances. An important difference, however, is that, under natural circumstances, seeds would be redispersed from sites determined by the relocation behaviour of *R. metallica*, whereas seeds initially dispersed would be transported from under adult plants. More generally, the structural firmness and persistent attractiveness typical of elaiosomes of Australian plants (Berg 1975; Hughes and Westoby 1990) appear to be essential in facilitating multiple phases of myrmecochory.

Given that only a small proportion (3.1 %) of seeds discarded by *R. metallica* colonies had the elaiosomes completely detached, the redispersal of such seeds would be uncommon. As in other studies (Auld 1986; Brew et al. 1989; Hughes and Westoby 1992b), seeds without elaiosomes were removed at a significantly slower rate than seeds with elaiosomes. During dispersal trials, the only species observed to remove seeds with detached elaiosomes were *Pheidole* and *R. metallica* (Table 1). Residual elaiosome odour may have elicited removal; however, species of *Pheidole* and *Rhytidoponera* are known to collect myrmecochorous seeds without elaiosomes (Hughes and Westoby 1992b) as well as seeds of non-myrmecochorous plants (Drake 1981; Andersen 1988b). *Pheidole* ants removed seeds with detached elaiosomes by grasping seeds at the elaiosome attachment point. *R. metallica* ants were able to carry seeds with detached elaiosomes by holding the seeds at their smallest width, although their ability to rapidly grasp such seeds appeared to be diminished (personal observation).

The overall mean dispersal distance observed here (0.57 m, n = 136) is short compared to the world average (0.96 m; Gomez and Espadaler 1998c) and is substantially shorter than average dispersal distances of Australian myrmecochore seeds generated by other ant communities (see Andersen 1988a; Hughes and Westoby 1992a;

Andersen and Morrison 1998; Parr et al. 2007; Beaumont et al. 2009). While the short dispersal distances facilitated by *Pheidole* are comparable to those generated by other *Pheidole* species (Hughes and Westoby 1992a; Andersen and Morrison 1998), *R. metallica* dispersed seeds considerably shorter distances than the averages of between 1 and 2 m observed in other vegetation types (Hughes and Westoby 1992a; Beaumont et al. 2009; Gove et al. 2007), perhaps due to habitat-specific differences in their nest densities and/or foraging distances. Dispersal trials were conducted over part of the day, and, hence, extended sampling may have detected additional seed dispersers, although it is not known if this would affect estimates of average dispersal distances.

Multiple phases of myrmecochory and the influence of disturbance by fire

Average seed dispersal, seed relocation and seed redispersal distances were not significantly different between burned and unburned habitats. However, seed removal rates, the relative contribution of ant species to seed dispersal, and the shapes of the dispersal curves were different between habitat types. We attribute these changes to the effect of recent fire on the abundance of seed dispersers. As has previously been found (Parr et al. 2007; Beaumont et al. 2011), seed removal rates can be higher in burned compared to unburned habitat. The abundances of *Rhytidoponera* species in Australia, including *R. metallica*, are typically higher in recently or frequently burned vegetation (Hoffmann and Andersen 2003), and so there is potential for them to facilitate more seed dispersal in such habitats (Gove et al. 2007). Although not significant, the greater number of seed dispersals facilitated by *R. metallica* (Table 2) and their higher pitfall occurrences (Table 3) in burned habitat are trends that support such a proposition. More apparent, however, was the greater abundance of *Pheidole* in burned habitat (see also Beaumont et al. 2012), which led to this species being a major contributor to the greater number of seed dispersal events in burned compared to unburned habitat. In addition, the greater contribution of *Pheidole* to seed dispersal in burned habitat significantly altered the shape of the seed dispersal curve (Fig. 2), although average seed dispersal distance was not significantly affected by fire. The latter finding differs from that of Parr et al. (2007), where recent fire in savanna vegetation significantly increased dispersal distance, due to the increased activity and expanded foraging range of a seed-dispersing ant.

The importance of the abundances of different seed dispersers in affecting the frequency of seed removal was further demonstrated by the finding that the numbers of seeds removed from depots and during dispersal trials were

best related to the combined abundances of *R. metallica* and *Pheidole* (Fig. 3a, b). Interestingly, the individual abundances of *R. metallica* and *Pheidole* were only related to the number of seeds removed from depots and the number of seeds removed during dispersal trials, respectively. This may have resulted from differences between the two experiments in trial duration, or in seed presentation (i.e. clumped versus scattered) which can affect rates of seed removal by individual species (Hughes and Westoby 1992b). Previous studies highlight the importance of disperser abundance, with seed removal rate often dependent on the abundance of a single or restricted number of ant species (Gove et al. 2007; Zelikova et al. 2008; Manzaneda and Rey 2009; Ness et al. 2009; Aranda-Rickert and Fracchia 2011). Our finding that *R. metallica* was the main seed disperser here and elsewhere in the Mount Lofty Ranges (Beaumont et al. 2011) accords with *Rhytidoponera* species being keystone seed dispersers of Australian myrmecochorous plants (Gove et al. 2007). Notwithstanding this, the abundance of *Pheidole* also appeared to influence the frequency of seed removal across sites, and its response to recent fire resulted in differences between habitat types in several aspects of myrmecochory.

Potential consequences of multiple phases of myrmecochory and disturbance by fire

Any net benefit of myrmecochory may accumulate via different avenues and can depend upon a series of cost-benefit tradeoffs (Boyd 2001; Christian and Stanton 2004; Giladi 2006). Therefore, understanding the fates of seeds is an important step in identifying potential benefits gained by myrmecochorous plants. For example, in eastern temperate forests of North America, the relocation of seeds by a common disperser, *Aphaenogaster rudis*, may benefit plants by increasing overall seed dispersal distances; however, seed relocation may also negate benefits potentially gained from seeds remaining buried within nests (Canner et al. 2012). Here, the relocation of a proportion of seeds by *R. metallica* and their subsequent redispersal is expected to reduce the number of seeds within nests of *R. metallica*, decrease seed density, and result in a proportion of seeds being dispersed greater distances than could be achieved from a single dispersal phase. The question remains as to how multiple phases of dispersal by ants, and fire-driven changes to disperser abundance, may affect dispersal-related benefits gained by *P. daphnoides*.

As is the case for seeds of many Australian myrmecochorous plants (Hughes and Westoby 1992a), buried seeds of *P. daphnoides* require heat shock, such as is received during bushfire, to break their physical dormancy (Auld and O'Connell 1991). The level of soil heating during fire can vary greatly both vertically within the soil profile (Bradstock and Auld 1995) and horizontally at a scale of metres (Hobbs and Atkins 1988; Perez and Moreno 1998; Gimeno-Garcia et al. 2004). Similarly, patchiness in the distribution of post-fire microhabitats suitable for seedling establishment can also occur at a scale relevant to seed dispersal by ants (Arnan et al. 2010). Thus, a greater scattering of seeds due to multiple dispersal phases, in addition to their burial within nests, may facilitate seeds reaching a greater number of microsites favourable for breaking seed dormancy during fire and for seedling establishment after fire. In addition, lower post-fire densities of seedlings may result in reduced competition among seedlings (Hughes and Westoby 1992a) and between seedlings and resprouting adult plants (e.g. Boyd 2001).

The benefits of myrmecochory, including those potentially accrued via multiple dispersal phases, should be influenced by differences in the fates of seeds that are finally deposited in the nests of different ant species. Here, the proportion of seeds dispersed more than once and the final location of seeds are expected to depend on fire history due to significant differences between burned and unburned habitat in the relative contribution of *R. metallica* and *Pheidole* to seed dispersal (Table 2). Thus, the seed dispersal effectiveness (sensu Schupp et al. 2010) of *P. daphnoides* may differ between habitat types. The magnitude of such a difference may depend largely on the quality of *R. metallica* and *Pheidole* nests as seed deposition sites. While *Pheidole* species and *R. metallica* can both facilitate post-fire plant recruitment (Hughes and Westoby 1992a), *Pheidole* ants are generally considered to facilitate less desirable seed fates because they can bury large numbers of myrmecochorous seeds too deep for successful germination (Auld 1986; Harrington and Driver 1995) and can produce highly clumped seedling distributions (Hughes and Westoby 1992a). They can also predate some myrmecochorous seeds (Hughes and Westoby 1992a); however, the hard seed coats of *P. daphnoides* likely protect them (Rodgerson 1998). Conversely, *R. metallica* is generally considered to provide higher quality dispersal because they disperse seed greater distances, are less likely to predate seeds and produce lower seedling densities (Hughes and Westoby 1992a). Even so, *R. metallica* may limit its contribution to plant recruitment by frequently nesting under rocks (personal observation), by re-exposing seed to potential risks associated with being on the soil surface or by facilitating the redispersal of seeds to nests of less favourable ant species (Hughes and Westoby 1992a).

Conclusion

The results of this study demonstrate that processes of myrmecochory can be influenced by habitat disturbance by

fire via its effect on the abundances of ant species as well as by the differential dispersal and post-dispersal behaviours of ant species. Further study is needed to determine whether the interplay between the effects of fire (including a greater range of fire histories than examined here) on the species composition and behavioural diversity of seed-dispersing ant communities results in predictable changes to the recruitment of myrmecochorous plants. Also, given the importance of *Rhytidoponera* species as dispersers of Australian myrmecochores (Gove et al. 2007), the frequency with which they relocate seeds and facilitate seed redispersal, as reported here for *R. metallica*, requires further investigation. The potential benefits of increased dissemination of seeds via multiple dispersal phases may be particularly important for myrmecochorous plants that develop persistent seed banks during inter-fire periods and that recruit on mass following fire.

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