

A keystone ant species promotes seed dispersal in a “diffuse” mutualism

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Abstract In order to understand the dynamics of co-evolution it is important to consider spatial variation in interaction dynamics. We examined the relative importance of ant activity, diversity and species identity in an ant seed dispersal mutualism at local, regional and continental scales. We also studied the determinants of seed dispersal rates and dispersal distances at eight sites in the Eneabba sandplain (29.63 S, 115.22 E), western Australia to understand local variation in seed dispersal rate and distance. To test the generality of the conclusions derived from the eight local sites, we established 16 sites along a 1650-km transect in western Australia, covering 11° of latitude and a six-fold increase in rainfall, at which we sampled the ant assemblage, estimated ant species richness and ant activity and observed the removal rate of myrmecochorous seeds. We also assessed the importance of ant species identity at a continental scale via a review of studies carried out throughout Australia which examined ant seed dispersal. Among the eight sandplain shrubland sites, ant species identity, in particular the presence of one genus, *Rhytidoponera*, was associated with the most dispersal and above average dispersal distances. At the landscape scale, *Rhyti-*

doponera presence was the most important determinant of seed removal rate, while seed removal rate was negatively correlated with ant species richness and latitude. Most ant seed removal studies carried out throughout Australia reinforce our observations that *Rhytidoponera* species were particularly important seed dispersers. It is suggested that superficially diffuse mutualisms may depend greatly on the identity of particular partners. Even at large biogeographic scales, temporal and spatial variation in what are considered to be diffuse mutualisms may often be linked to variation in the abundance of particular partners, and be only weakly – or negatively – associated with the diversity of partners.

Keywords Diversity · Ecosystem function · Functional redundancy · Myrmecochory · *Rhytidoponera*

Introduction

Recent emphasis on the study of positive interactions among species has centred on apparently diffuse mutualisms, such as seed dispersal, pollination and plant protection (e.g. Rico-Gray 1993; Zamora 2000; Stanton 2003). In diffuse mutualisms, the focal species is dependent on multiple partners. Imagine, as an example, a case where a plant species depends on many animal species for pollination. In truly diffuse mutualisms, many of the species that function as partners (pollinators in our example) are similar in terms of the frequency and consequences of their interactions (Zamora 2000). We term this first type of mutualism “evenly diffuse”, because multiple partners are evenly represented. A more poorly explored possibility is that one or a few species are particularly important, even though the total number of partner species is high (Jordano

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1987), such as if there were many pollinator species, but one that was disproportionately important. We term this type of mutualism “unevenly diffuse” and call the mutualist which plays a more fundamental role than its density would suggest, the “keystone mutualist” (Gilbert 1980), while the other mutualists could be considered functionally redundant. Depending on which form of diffuse mutualism prevails, the consequences of temporal and spatial variation in mutualist communities may be very different for the focal species. If, in our example of the plant and its pollinator, the mutualism is evenly diffuse, then the expectation is that pollination rate will either decline or remain invariant with reductions in pollinator diversity. If, on the other hand, one or a few species are keystone mutualists, then the effects of reductions in the diversity of the pollinator species depend on which species are lost. If the non-keystone species are lost, species loss could actually improve pollination rates by reducing interference competition among pollinator species (Huston 1997; Symstad et al. 1998).

Myrmecochory, the dispersal of seeds by ants, represents an ideal mutualism in which to consider the functioning of diffuse mutualisms and the consequences of variation in mutualist communities. Myrmecochory is successful for the plant when ants take the entire seed back to the nest, where they remove the elaiosome (a fatty body attached to the seed which serves as a food reward for the ants) and discard the seed in a midden. Myrmecochorous seed removal and dispersal is more readily observed and tracked than vertebrate seed dispersal and so can potentially be related to aspects of the abiotic or biotic environment. Myrmecochory has evolved independently in Mediterranean habitats, temperate forest understories, tropical forest understories and tropical forest canopies (e.g. Dunn et al. 2007a, b) and is common where present. Total ant species diversity, in regions where myrmecochory occurs, ranges from two to 20 species in temperate forest understories (J. Zeilakova, personal communication; Dunn et al. 2007a) to hundreds of species in tropical forest understories (e.g. Longino et al. 2002).

Ant-mediated dispersal is typically considered to be an evenly diffuse mutualism, with multiple ant species offering similar benefits in a given site (e.g. Garrido et al. 2002). Although several studies have emphasised the importance of particular species groups (e.g. large-bodied species, Horvitz and Schemske 1986; Ness et al. 2004), these groups in themselves tend to be relatively diverse. Gorb and Gorb (1999), however, suggest seed dispersal by ants may be most effective where one or a few effective seed-dispersing ant species dominate, which is to say where seed dispersal mutualisms are unevenly diffuse. To our knowledge, no studies have systematically explored the evenness of seed dispersal

mutualisms or tested the consequences of that evenness for seed dispersal.

Here, we test two hypotheses regarding the dispersal of seeds by ants. First, we test the hypothesis that dispersal is evenly diffuse; that is, that dispersal is carried out by many functionally similar ant species. If the mutualism is evenly diffuse, the seed removal rate should remain constant under changing levels of diversity, or it may increase (if there is synergism among ant species), providing ant density remains constant. In the second hypothesis, if the mutualism is unevenly diffuse, the removal rate will depend entirely upon the presence of a given species and may decrease with increasing diversity, if interference competition amongst species increases with increasing diversity.

Because variation in space or among spatial scales in the mutualist communities can mediate co-evolution (Thompson 2005), we also examine the consistency of the mutualism over several spatial scales. At local scales, we examine the roles of species diversity, ant activity and the presence of a potential keystone ant genus (*Rhytidoponera*) in the variation of seed removal rates and dispersal distances at several sites in the western Australian Kwongan. At 16 sites spanning 1650 km and strong environmental gradients (which may alter the ant activity or assemblage composition), we then examine the importance of ant diversity, abundance and keystone (*Rhytidoponera*) presence. Finally, we compare our results to those of 29 other studies of ant seed dispersal in Australia and examine the extent to which our conclusions regarding the importance of the diffuseness of mutualisms are supported at a continental scale.

Materials and methods

Sites and design

Within habitat analysis of seed removal and dispersal distance

Eight quadrats were established in sandplain shrubland (‘Kwongan’), approximately 300 km north of Perth (29.7 S, 115.25 W). This location was chosen as it is an area of particularly high plant diversity, where more than one third of the plant species are ant-dispersed (Lamont et al. 1977). Each quadrat was 10 × 10 m and was subdivided at 2-m intervals. To account for important features of local topography (Hnatiuk and Hopkins 1981), we paired quadrats to sample both sand dune crests and swales. Paired sites were at least 100 m apart, while each pair was no less than 400 m from another pair.

Throughout the study we used the seed of *Acacia blakeyi*, a species indigenous to western Australia. It is considered

to be myrmecochorous as it possesses an off-white eliasome smaller than the seed itself. Seeds fall to the ground soon after maturity. The seeds weigh approximately 22 mg, which is perhaps heavier than average amongst *ant-dispersed* seeds, but not extreme (e.g. Moles and Westoby 2003). We chose to use this species as it is the most abundant myrmecochorous plant species at our focal study site, was readily harvestable as a fresh seed and is morphologically similar to the seeds of other ant-dispersed *Acacia*. Importantly, *Acacia* is Australia's most speciose genus and, consequently, is probably the most frequently ant-dispersed group of plants on the Australian continent.

At each site we placed a seed at each of 36 points in each quadrat. The seeds were then observed from approximately 0600 to 1400 hours in an attempt to maximise observed dispersal events. When a dispersal event was observed, we followed the ant to its nest, measured the dispersal distance and identified the ant to genus/species. We replaced all removed seeds whether or not we observed the dispersal event. We recorded each unique dispersal event and the number of total depots from which seed removal occurred. A dispersal event was considered unique if it involved a new depot or a new nest (i.e. no matter how many times a single colony exploited a particular depot, only a single dispersal event was recorded). Our aim in replenishing depots was to increase the opportunity to observe new, unique dispersal events.

To sample the local ant fauna at each site more generally, we collected leaf litter in 0.5×1 -m plots on either side of the depot grid. At each of ten plots, we sorted all litter, including sticks and logs (Bestelmeyer et al. 2000). Ant activity was defined as the total number of ants found in the litter samples. Western Australia does not possess a particularly specialised litter ant assemblage, so the ants we sampled were ground-foraging species that could potentially interact with seeds. All ants were removed, preserved and identified to species wherever possible. Final identifications were provided by Dr. Brian Heterick at Curtin University, Perth, western Australia.

Landscape level analysis of dispersal rate

We established a latitudinal transect spanning 1650 km, representing approximately 11° of latitude and a strong rainfall gradient (approx. 200–1200 mm; Bureau of Meteorology 2000) in western Australia (Fig. 1). The range in yearly mean minimum and maximum temperatures was 9.8 – 20.4°C in the south to 17.7 – 31.6°C in the north. Sixteen sites were established along the gradient to reflect the major vegetation types of the region.

At each site, we established a 3×6 grid of seed depots, with depots separated by 5 m. We placed three seeds at each of the 18 depots. We then recorded the number of

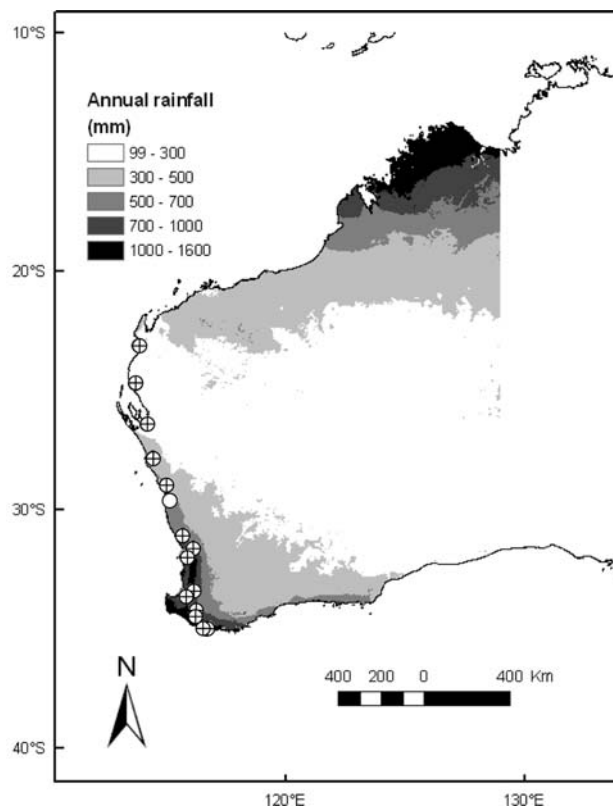


Fig. 1 Map of western Australia, showing sample sites. The focal study site, Eneabba, is shown as an open circle. Background shading represents average annual precipitation

remaining seeds each hour. Here we compare the number of seeds remaining after 5 h – which is generally the time at which dispersal had subsided. Each trial began at approximately 0800 hours and covered the range of daily temperatures (from high teens to high 30s). We noted all observations of dispersal events, and ants dispersing seeds were collected and later identified. The ant assemblage was sampled at each site as described above for the within-habitat studies.

Continental review of ant seed dispersers and dispersal distance

We surveyed all research articles in which ant seed dispersal was examined in Australia. Formis (a database of all ant-related papers published up until 2001) and Web of Science were searched for all articles with Australia and either eliasome, myrmecochory or ant (seed dispersal) in their keywords or abstract. We did not include studies which focussed exclusively on granivory, as the ants involved generally interact with a subset of available seed species which they consume (e.g. Gross et al. 1991). We recorded the frequency with which dispersal by *Rhytidoponera* species was observed and compared the recorded

dispersal distance with that of other species. Where a paper spanned several regions, we treated each region as an independent sample. Where papers used multiple species of seeds, we combined data to provide single measure of dispersal for each ant species.

Analyses

Within-habitat analysis of seed removal and dispersal distance

At a local scale, we examined the influence of the same three variables on seed removal rate: ant species richness, ant activity and the presence of *Rhytidoponera* species. Species richness was estimated using the CHAO2 estimator based on species sampled in the litter plots with each quadrat as the sample unit (Colwell 2000). Because of the smaller sample size at the local scale, we used three separate non-parametric tests in lieu of a single parametric test, such as a linear model. We used the Mann–Whitney *U*-test to examine the effect of *Rhytidoponera* presence and Pearson's correlation to examine the effect of ant activity and species richness on seed removal rate.

Landscape level analysis of dispersal rate

A generalised linear model, with Poisson distribution, was used to examine the relationship between numbers of seeds removed and ant activity, species richness, *Rhytidoponera* presence and latitude. The best statistical model was arrived at by manual stepwise model reduction (Crawley 2002).

Continental review of ant seed dispersers and dispersal distance

Using the 14 studies from nine publications in which seed-removing genera and/or species were quantified, we compared the observed dominance (proportion of seeds removed by the most active genus) to that expected were seed removals to be performed evenly by the observed seed-removing ant assemblage. Within each study, we analysed the number of study sites in which each genus was recorded and the total number of seeds removed by each genus and species. We created our null distribution, to which we compared our observed dominance using EcoSIM 7 (Gotelli and Entsminger 2004). Our null distribution was created by randomly distributing the same number of removed seed within the study over all genera and/or species which were observed removing seed in the given study. For each study, we performed this randomisation and calculated a dominance index 1000 times in order to establish 95% confidence limits with which to compare our observed dominance index.

Results

Within-habitat analysis of seed removal and dispersal distance

In the focal study region, dispersal rates varied among sites. No dispersal events were recorded at three sites, while one site had more than sixfold the dispersal rate of any other site. Of the observed seed removal events, 72% were carried out by ants of one genus, *Rhytidoponera* (*R. metallica*, 16%; *R. violacea*, 57%). However, only 2% of individual ants were *Rhytidoponera* species. The presence of *Rhytidoponera* in each plot was associated with numbers of seed being removed to nests (Mann–Whitney $U = 2.5$, $n = 8$, $P = 0.051$). Seed removal was not a consequence of *Rhytidoponera* presence alone, as sites where *Rhytidoponera* was present did not uniformly exhibit high rates of seed dispersal (Fig. 2). Species richness ($r = 0.192$, $n = 8$, $P = 0.649$) and ant activity ($r = -0.303$, $n = 8$, $P = 0.466$) were not associated with seed removal rates. Like removal rate, dispersal distance was also a function of species identity. Mean dispersal distances for *Rhytidoponera* dispersals were: *R. metallica* = 1.83 m ($n = 7$) and *R. violacea* = 3.80 m ($n = 25$). All other species combined had an average dispersal distance of 0.22 m ($n = 11$), and all of these resulted in a seed being dropped on the soil surface, with the exception of one dispersal event by *Iridomyrmex greensladei*.

Landscape level analysis of dispersal rate

Latitude, species richness and composition of the ant assemblage were all associated with seed removal rate (Table 1). Removal rates were greater where *Rhytidoponera* spp. were present and were negatively correlated with ant species diversity and latitude (Fig. 2). Latitude and species richness were not correlated ($n = 16$, $\rho_s = 0.254$, $P = 0.343$). Of 912 ant individuals sampled, only 8% were *Rhytidoponera* species. The four *Rhytidoponera* species sampled (and the percentage of all individuals sampled) were *R. inornata* (2%), *R. metallica* (3%), *R. rufonigra* (1%) and *R. violacea* (2%). All of these species, except for *R. rufonigra* (which has not been studied), have been shown to disperse seeds, either at our main study site (herein) or elsewhere in Australia (Table 2).

Continental review of ant seed dispersers and dispersal distance

We surveyed 29 study sites from 23 published papers that included the identity of ant seed dispersers in Australia (Table 2). A total of 20 seed-removing ant genera were recorded (Table 3). Of the 29 study sites, 23 had at least

Fig. 2 *Top* Seed removal at eight sites within a single western Australian sandplain shrubland region, showing the relationship with ant activity and estimated species richness. *Bottom* Total numbers of seed removed at each of 16 transect sites in relation to latitude and estimated species richness. *Open and closed points* represent absence and presence of *Rhytidoponera*, respectively. Species richness is based on the CHAO2 estimator

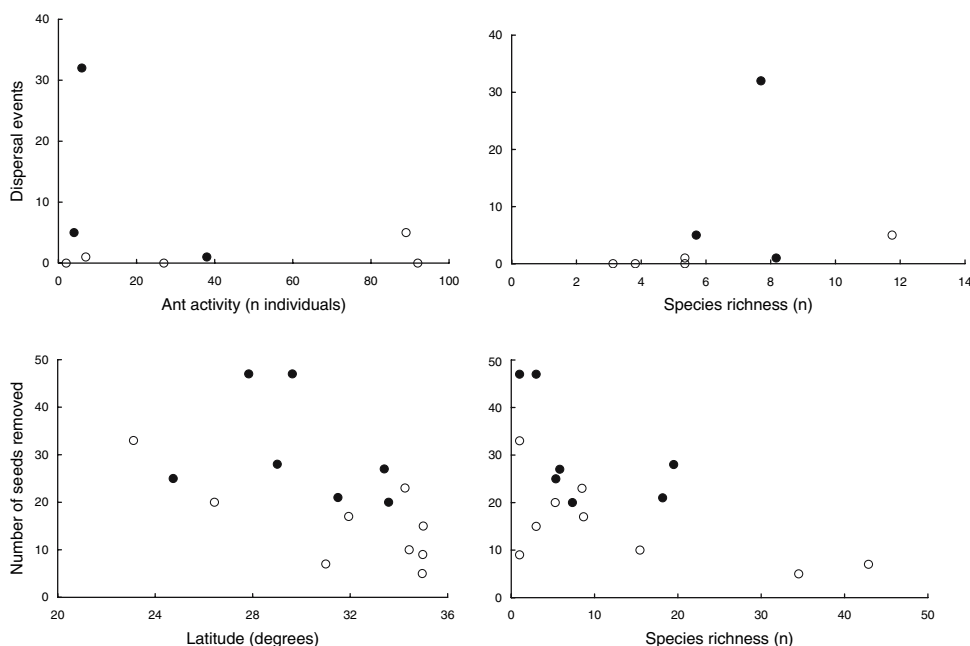


Table 1 Results of the Generalised Linear Model reduction. The response variable is the total number of seed left at a site after approximately 5 h

	<i>df</i>	Deviance	Residual <i>df</i>	Residual deviance	<i>F</i>	<i>P</i>
Species richness	1	23.38	14	85.73	23.38	<0.001
<i>Rhytidoponera</i> presence	1	23.96	13	61.77	23.96	<0.001
Latitude	1	10.85	12	50.92	10.85	0.001

one *Rhytidoponera* species as a seed disperser. Of the 23 studies where *Rhytidoponera* was a seed disperser, 14 offered some comparison of frequency of seed dispersal by different species. Of these 14 studies, ten found that *Rhytidoponera* species were the most common seed-removing ants.

Overall, *Rhytidoponera* species removed seed in more studies than would be expected by chance (Table 4). *Rhytidoponera* was also the most common seed-removing genus in 6/13 studies that contained data on seed removal rates. In 6/10 studies in which a genus was found to be significantly dominant, that genus was *Rhytidoponera*. At the species level, one of five different *Rhytidoponera* species dominated 7/10 studies (Table 4).

Of the four studies in which *Rhytidoponera* was present, but was not the most important seed remover, “seed removal” events may have actually been seed parasitism rather than dispersal in two cases (*Pheidole* and *Monomorium*, Majer and Lamont 1985; Mossop 1989). In the other two studies, the primary ants removing seeds were actually seed dispersers (*Melophorus* and *Iridomyrmex*, Schatral et al. 1994; Hughes and Westoby 1990). Overall, in those studies that provided information on the number of dispersal events by different ant taxa, 45% of individual events were carried out by *Rhytidoponera* species, 13% by *Pheidole*

species, 12% by *Iridomyrmex* species, 9% by *Melophorus* species and 6% by *Monomorium* species (Table 3).

Global dispersal distances of seeds taken by ants average 0.96 m (Gomez and Espadaler 1998). All four Australian studies which measured dispersal distances recorded *Rhytidoponera* providing above the global average dispersal distance, as did our own data from the sandplains site for *R. ‘metallica’* and *R. violacea*. Further, in three of four studies, dispersal distances by *Rhytidoponera* species were above the average distance calculated for Australia by Gomez and Espadaler (1998).

Discussion

Based on our results, we find that the mutualism of dispersal of seeds by ants is unevenly diffuse in terms of the ant partners. Locally, regionally and continentally, seed dispersal by ants is generally dominated by one keystone mutualist genus, *Rhytidoponera*. Along our transect in western Australia, the presence of species of *Rhytidoponera* was the best predictor of the rate of seed removal. Our results stand in contrast to frequent statements in the literature on seed dispersal by ants, which emphasise the diversity of ant partners (e.g. Garrido et al. 2002). Other

Table 2 Summary of ant seed dispersal studies carried out in Australia (ND not determined; NA not available)

Author	Regions	<i>Rhytidoponera</i> as seed remover?	<i>Rhytidoponera</i> most frequent remover?	Plant species	Percentage of seeds dispersed & <i>Rhytidoponera</i> spp.	Dispersal distance by <i>R. species</i> , Overall
Andersen 1988a	Wilson's Promontory, Victoria	Yes	Yes	<i>Acacia suaveolens</i>	91%, <i>R. tasmaniensis</i>	2.0 m, 2.1 m
Andersen and Ashton 1985	Wilson's Promontory, Victoria	Yes	Yes	16 plant species	<i>R. victoriarum</i> & <i>R. tasmaniensis</i> "most important"	ND
Andersen and Morrison 1998	Kakadu, Northern Territory	Yes	Yes	<i>Acacia holosericea</i>	34%, <i>R. aurata</i>	<i>R. aurata</i> 3.48 m, other <i>R. spp</i> 1.89, overall 2.61 m
Ashton 1979	Wallaby Creek, Victoria	No	No	<i>Eucalyptus regnans</i>	NA	NA
Auld 1986	Near Sydney, New South Wales	No	No	<i>Acacia suaveolens</i>	NA	NA
Auld and Denham 1999	Sydney, New South Wales	Yes	ND	<i>Grevillea</i> spp.	ND	ND
Berg 1975	Australian Capital Territory	Yes	ND	Approx. 100 species	<i>R. victoriarum</i> , <i>R. tasmaniensis</i> , <i>R. metallica</i>	ND
Berg 1975	New South Wales	Yes	ND		<i>R. tasmaniensis</i>	ND
Brew et al. 1989	Gembrook State Forest, Victoria	Yes	Yes	<i>Acacia myrtifolia</i> , <i>Tetratheca stenocarpa</i>	63% (<i>A. myrtifolia</i>), 55% (<i>T. stenocarpa</i>) by <i>R. victoriarum</i>	ND
Briese and Macauley 1981	Deniliquin, New South Wales	No	No	Based on material going to nests	NA	NA
Clifford and Monteith 1989	Chinchilla, Queensland	Yes	Yes	<i>Petalostigma pubescens</i>	100%, <i>R. metallica</i>	ND
Clifford and Monteith 1989	Brisbane, Queensland	Yes	ND	<i>Petalostigma pubescens</i>	¼ ant species; <i>R. metallica</i>	ND
Davidson and Morton 1981	Central South Australia	Yes	Yes	<i>Sclerolaena diacantha</i> & <i>Dissocapus biflorus</i> var. <i>Biflorus</i>	<i>R. spp</i> "principal agent"	Up to 9 m (sp. B), up to 4 m (sp. D)
Davidson and Morton 1984	Central Australia (13 sites)	Yes (8/13 sites)	ND	18 <i>Acacia</i> species	<i>R. mayri</i>	ND
Drake 1981	North Stradbroke Island, Queensland	Yes	Yes	15 species	50%, <i>R. metallica</i>	ND
Gibb and Hochuli 2003	Near Sydney, New South Wales	Yes	ND	<i>Acacia botrycephalus</i>	<i>R. metallica</i>	ND
Hughes and Westoby 1990	Kuringai Chase N.P. New South Wales	Yes	No	<i>Acacia linifolia</i> & <i>Bossiaea obcordata</i>	17%, <i>R. metallica</i>	ND
Hughes and Westoby 1992	Kuringai Chase N.P. New South Wales	Yes	Yes	<i>Acacia terminalis</i> & <i>Dillwynia retorta</i>	57%, <i>R. 'metallica'</i>	1.57 m
Ireland and Andrew 1995	Middleback, South Australia	Yes	ND	<i>Acacia papyrocarpa</i>	<i>R. 'metallica'</i>	ND
Majer 1982	Darling Botanical District, Western Australia	Yes	ND	<i>Acacia extensa</i>	<i>R. violacea</i> , <i>R. inornata</i>	ND
Majer 1985	North Stradbroke Island, Queensland	Yes	ND	<i>Acacia concurrens</i>	<i>R. 'metallica'</i>	ND

Table 2 continued

Author	Regions	<i>Rhytidoponera</i> as seed remover?	<i>Rhytidoponera</i> most frequent remover?	Plant species	Percentage of seeds dispersed & <i>Rhytidoponera</i> spp.	Dispersal distance by <i>R. species</i> , Overall
Majer and Lamont 1985	Groote Eylandt, Northern Territory	No	No	<i>Grevillea pteridifolia</i> <i>Acacia aulacocarpa</i>	NA	NA
Majer and Lamont 1985	Grove, Northern Territory	No	No	<i>Grevillea pteridifolia</i> <i>Acacia aulacocarpa</i>	NA	NA
Majer and Lamont 1985	Weipa, Queensland	Yes	No	<i>Grevillea pteridifolia</i> <i>Acacia aulacocarpa</i>	6.25%, <i>R. 'metallica'</i> .	ND
Mossop 1989	Royal N.P. New South Wales	Yes	No	<i>Acacia terminalis</i> & <i>Bossiaea obcordata</i>	5%, <i>R. metallica</i>	ND
Schatral et al. 1994	Kings Park, Western Australia	Yes	No	<i>Hibbertia hypericoides</i>	5%, <i>R. violacea</i>	ND
Schatral et al. 1994	Wireless Hill, Western Australia	No	No	<i>Hibbertia hypericoides</i>	NA	ND
Schatral et al. 1994	Cooljarloo, Western Australia	Yes	Yes	<i>Hibbertia hypericoides</i>	70%, <i>R. violacea</i>	ND
Whitney 2005	Kinchega N.P., New South Wales	Yes	Yes	<i>Acacia ligulata</i>	91% (approximately), <i>R. mayri</i> & <i>R. metallica</i>	ND

Table 3 Ant genera observed removing seed in Australian myrmecochory studies

Genus	Seed removal		
	Number of sites	Number of seeds	Mean % of seeds ^a
<i>Rhytidoponera</i>	11	461	33
<i>Pheidole</i> ^b	7	134	16
<i>Iridomyrmex</i>	10	127	13
<i>Melophorus</i>	2	89	15
<i>Monomorium</i>	5	63	11
<i>Notoncus</i>	2	31	2
<i>Aphaenogaster</i>	2	28	2
<i>Crematogaster</i>	3	25	2
<i>Meranoplus</i> ^b	4	11	1
<i>Tetramorium</i> ^b	2	11	1
<i>Camponotus</i>	3	9	1
<i>Paratrechina</i>	3	8	1
<i>Solenopsis</i>	2	5	1
<i>Prolasius</i>	2	4	<1
<i>Papyrius</i>	1	4	<1
<i>Technomyrmex</i>	1	4	<1
<i>Polyrhachis</i>	2	4	<1
<i>Opisthopsis</i>	1	1	<1
<i>Oecophylla</i>	1	1	<1
<i>Bothroponera</i>	1	1	<1

^a Mean % of seeds: the percentage of seeds taken by each genus, averaged over all studies

^b Likely seed predators

cases of keystone dispersal agents exist, including cases of saurochory (Traveset and Reira 2005) and dispersal by functionally unique bird species such as rattites (Stocker and Irvine 1983; Cancela et al. 2006), but the example documented here is among the most general in that it could potentially apply across many plant species and broad spatial scales, including an entire continent.

Is myrmecochory an unevenly diffuse mutualism?

In the study region, myrmecochory appears to be an unevenly diffuse mutualism at all scales. At the local scale, removal of seeds was almost entirely due to two species of *Rhytidoponera*: *R. metallica* and *R. violacea*. Although several other ant genera removed seed, in most cases, these seeds were dropped after a short distance or represented rare events. Similarly, in other studies in Australia, seed dispersal tends to be dominated by *Rhytidoponera* species to a greater extent than would be expected based on the number of ant genera known to take seeds. Uneven mutualisms with ants may be relatively common. For example,

Table 4 Analysis of dominant seed-removing genera and species

	Genus level dominance ^a			Species level dominance ^a		
	Observed	95% Confidence interval	Dominant genus	Observed	95% Confidence interval	Dominant species
Andersen 1988	90.6	34.4–42.7	<i>Rhytidoponera</i>	90.6	34.4–42.7	<i>R. tasmaniensis</i>
Andersen and Morrison 1998	47.4	11.7–16.8	<i>Rhytidoponera</i>	34.4	8.4–12.3	<i>R. aurata</i>
Brew et al. 1989	61	21.3–27.9	<i>Rhytidoponera</i>	61	21.3–27.9	<i>R. victoriae</i>
Drake 1981	68.6	25.7–34.3	<i>Rhytidoponera</i>	68.2	20.3–21.9	<i>R. metallica</i>
Hughes and Westoby 1990	45.7	16.3–23.9	<i>Iridomyrmex</i>	18.3	8.6–14	<i>R. metallica</i>
Hughes and Westoby 1992	56.9	20.8–26.9	<i>Rhytidoponera</i>	56.9	10.2–14.2	<i>R. metallica</i>
Majer and Lamont 1985	70	27.5–40	<i>Monomorium</i>	Genera only		
Majer and Lamont 1985	35.7	21.4–39.3	<i>Pheidole</i>	Genera only		
Majer and Lamont 1985	37.5	20.8–37.5	<i>Monomorium/ Pheidole</i>	Genera only		
Mossop 1989	63.2	15.8–26.3	<i>Pheidole</i>	33.3	10.3–20.5	<i>Pheidole</i> sp. 4
Schatral and Fox 1994	90.4	34.9–46	<i>Melophorus</i>	69.8	27–36.5	<i>Melophorus</i> sp. JDM 358
Schatral and Fox 1994	100	~	<i>Melophorus</i> ^c	100	~	<i>Melophorus</i> sp. JDM 358
Schatral and Fox 1994	68.8	50–68.8	<i>Rhytidoponera</i>	68.8	50–68.8	<i>R. violacea</i>
All (no. of studies) ^b	16.9	7.6–13.8	<i>Rhytidoponera</i>			

^a Dominance is defined as the fraction of seed removed by the most common seed remover. This dominance is compared with a null model which assumes an even number of seed removals over the genera/species observed. Genera or species which are significantly dominant ($P < 0.05$) are in bold

^b Tests whether *Rhytidoponera* appears in more studies than expected by chance

^c Only one genus observed, hence no statistical test possible

since the submission of this manuscript, Beattie (2006) has suggested a small guild of ant species may be selected for their effectiveness in plant pollination.

Rhytidoponera species were not the only dispersers of seeds. We also recorded dispersal of seeds by *Iridomyrmex* species and have seen dispersal of seeds by a *Melophorus* species at our main field sites in the Eneabba sandplains. In a separate investigation at our main study landscape (Eneabba), Neil McCoy (personal communication) found that a species other than a species of *Rhytidoponera*, *I. greensladei*, was the most important seed disperser at one of the 17 sites. Our continental analysis of myrmecochory also suggests that a range of other ant genera are sometimes effective seed dispersers, particularly ants of these two genera as well as species of *Pheidole*. However, at all scales of analysis, *Rhytidoponera* appears to play a disproportionate role in seed removal.

Our results concerning the unevenness of myrmecochory may also extend beyond Australia. Globally, just a handful of ant genera disperse most of the seeds. In temperate forests, species of *Formica*, *Aphaenogaster* and *Myrmica* take almost all seeds. In the Fynbos, most seeds are taken by species of *Anoplolepis* and *Pheidole*. Thus, although many species do occasionally take seeds (Beattie 1985), most are taken by only a subset of the species present in a community.

What governs spatial variation in the rate of seed removal?

We considered seed removal across a large (1650 km) spatial gradient, in part because we suspected that the strong environmental gradient along the transect would influence seed removal through changes to ant activity or assemblage structure. We did observe a correlation between seed removal with latitude. However, the presence of the keystone mutualist *Rhytidoponera* explained more variation in removal rate than did latitude per se. The presence of species of the genus *Rhytidoponera* appear to be main determinants of the rate at which seeds are removed.

In contrast to the pattern for other regions (e.g. Kaspari et al. 2003), ant diversity was not strongly correlated with latitude. Understanding why latitude and ant diversity are not correlated in western Australia is beyond the scope of the present study, but the lack of correlation has the advantage that it allows us to disentangle the effect of diversity and the other potential correlates of latitude (such as climate). Ant diversity played some role in the removal rate of seeds, but not in the direction we might predict if myrmecochory were an evenly diffuse mutualism and certainly not if species diversity acts synergistically (e.g. Loreau et al. 2001). Removal rates were lower where ant diversity was higher. We suspect that the higher removal rates of seeds in

lower diversity ant communities were due to reduced competition of *Rhytidoponera* with behaviourally dominant species. Andersen (1993) demonstrated a negative association between ant species density and *Rhytidoponera* presence. Anecdotally, we noted that where diversity was higher, seeds were more likely to be behaviourally dominated by small, aggressive seed parasites, such as *Iridomyrmex chasei* and *Crematogaster* species. Although some authors have linked myrmecochory to higher ant activity (see Beattie and Culver 1981 for a site in eastern North America), we found no advantage of increased ant activity to seed removal across space. Sites with many individual ants tended to be dominated by small seed parasites rather than by individuals of *Rhytidoponera* or other seed-dispersing ants.

What makes *Rhytidoponera* special?

Rhytidoponera species are behaviourally subordinate (Andersen 1990, 1992), avoid competition by foraging at relatively cool temperatures (Andersen 1986) and take advantage of disturbed sites (Andersen 1986, 1991; Andersen and McKaige 1987; reviewed in Hoffmann and Andersen 2003), which means that *Rhytidoponera* species may be more likely than other ant genera to rapidly remove seeds, rather than feed on seed in situ and risk interference competition (Messler and Lu 1983). Globally, the behaviour of behaviourally subordinate species appears to be integral to successful myrmecochory (e.g. Messler and Lu 1983). Howe (1979) suggested a similarly important behaviour of “fearful frugivores” responding to predation pressure around abundantly fruiting trees. Behavioural subordination may be important for seed dispersers in many regions. The important seed-dispersing ant genus in temperate forests in Asia, North America and Mediterranean Europe, *Aphaenogaster*, is also behaviourally subordinate where it has been studied (e.g. Fellers 1987). One of the two ant genera that are important to the dispersal of seeds in Europe, *Myrmica*, but not the other, *Formica*, is typically considered to be behaviourally subordinate (Vepsäläinen and Savolainen 1990). Perhaps the most general statement we can make at this time is that effective seed removers are those that need to remove seeds to the nest rapidly. One factor that encourages such rapid removal is behavioural subordination.

Our conclusion that *Rhytidoponera* species are keystone dispersers may not generalize to all groups of ant-dispersed plant species in Australia. *Rhytidoponera* species are relatively large (Shattuck 1999) and could be disproportionately effective as dispersers of large-seeded plant species. Such large-seeded species would include not only *Acacia*, which is widespread and particularly speciose, but most likely most of the peas as well (Papilionaceae, Table 2). We can not entirely exclude the possibility that smaller seeds might favour a more diffuse assemblage of ants or simply a

different keystone group of ants which are unable to disperse large seeds. However, smaller ants, such as some of the smaller *Iridomyrmex* species, were able to remove *Acacia blakeleyi* seed individually, while smaller ants co-operatively transport larger items to the nest (e.g. Pfeiffer et al. 2006). In addition, when we repeated the local seed dispersal trials with a seed a quarter the mass of *A. blakeleyi* (*A. neurophylla*), *Rhytidoponera* species were still the most important seed dispersers at those sites. We also noted, anecdotally, that seed parasitism (in situ ‘aril robbing’) tended to be an innate behaviour rather than a consequence of seeds being too difficult to transport, such that our results may actually generalize to smaller seeds; such generalization will await further tests.

Consequences of an unevenly diffuse mutualism

If *Rhytidoponera* species are the key to seed dispersal in Australia, a remaining question is what governs the distribution of *Rhytidoponera*? At the largest scale, *Rhytidoponera* species can be found throughout Australia, from the wettest forests to the driest deserts (e.g. Shattuck 1999). At a landscape scale, however, our results show that *Rhytidoponera* species are patchily distributed. One explanation for patchiness in *Rhytidoponera* presence in space may be the disturbance history of the sites. Species of the genus *Rhytidoponera* are recognised as disturbance specialists in functional group classifications (e.g. Hoffman and Andersen 2003) and are common both in urban environments (May and Heterick 2000) and in relatively large disturbances such as restored minesites (Majer 1982). Historically, and across much of modern Australia, the most common disturbance would have been fire (Gill et al. 1981). In studies of the relationship between ants and fire in Australia, species of *Rhytidoponera*, including *R. metallica* (Andersen 1991; York 2000; Hoffmann and Andersen 2003), *R. (turneri) sp.3* (Andersen 1991), *R. trachypyx* (Andersen 1991), *R. aurata* (Andersen 1991) and *R. victoriae* (York 2000), are all more common in recently burned sites than in either unburned sites or sites that burn less frequently. Some variation among plots in our study and, more generally, in seed removal rates may thus be due to the time since fire or another type of disturbance has occurred at the study sites. Disturbance would then be the over-riding mechanism creating a shifting mosaic (see Thompson 2005) in which the strength and outcomes of the ant-plant mutualism vary.

If *Rhytidoponera* is most common after fires, it suggests to us the following testable scenario. After fires, *Rhytidoponera* species recruit into plots. In the years following fires, plants begin to produce seeds, and those seeds are dispersed primarily by *Rhytidoponera* species. As the canopy closes, the environment becomes less suitable for *Rhytidoponera* species, and seed dispersal rates decrease (as documented

for one site by Parr et al. 2007), such that more seeds are abandoned and consequently parasitized or predated. We offer this scenario as a hypothesis for further testing.

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References

- Andersen AN (1986) Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in south-eastern Australia. *Aust J Zool* 34:53–64
- Andersen AN (1988) Dispersal distance as a benefit of myrmecochory. *Oecologia* 75:507–511
- Andersen AN (1990) The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proc Ecol Soc Aust* 16:347–357
- Andersen AN (1991) Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* 23:575–585
- Andersen AN (1992) Regulation of “momentary” diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *Am Nat* 140:401–420
- Andersen AN (1993) Ant communities in the Gulf Region of Australia’s semi-arid tropics: species composition, patterns of organisation, and biogeography. *Aust J Zool* 41:399–414
- Andersen AN, Ashton DH (1985) Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Aust J Ecol* 10:381–390
- Andersen AN, McKaige ME (1987) Ant communities at Rotamah Island Victoria, with particular reference to disturbance and *Rhytidoponera tasmaniensis*. *Proc Roy Soc Victoria* 99:141–146
- Andersen AN, Morrison SC (1998) Myrmecochory in Australia’s seasonal tropics: Effects of disturbance on distance dispersal. *Aust J Ecol* 23:483–491
- Ashton DH (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell in central Victoria. *Aust J Ecol* 4:265–277
- Auld TD (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Dispersal and the dynamics of the soil seed-bank. *Aust J Ecol* 11:235–254
- Auld TD, Denham AJ (1999) The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecol* 144:201–213
- Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms, 1st edn. Cambridge University Press, Cambridge
- Beattie AJ (2006) The evolution of ant pollination systems. *Bot Jahrb* 127:43–55
- Beattie AJ, Culver DC (1981) The guild of myrmecochores in the herbaceous flora of West Virginia forests. *Ecology* 62:107–115
- Berg RY (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Aust J Bot* 23:475–508
- Bestelmeyer BT et al (2000) Field techniques for the study of ground-dwelling ants. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington D.C., pp 122–144
- Brew CR, O’Dowd DJ, Rae ID (1989) Seed dispersal by ants: behaviour-releasing compounds in elaiosomes. *Oecologia* 80:490–497
- Briese DT, Macauley BJ (1981) Food collection within an ant community in semi-arid Australia, with special reference to seed harvesters. *Aust J Ecol* 6:1–19
- Calviño-Cancela M, Dunn RR, van Etten EJB, Lamont BB (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. *Ecography* 29:632–640
- Clifford HT, Monteith GB (1989) A three phase seed dispersal mechanism in Australian Quinine Bush (*Petalostigma pubescens* Domin). *Biotropica* 21:284–286
- Colwell RK (2000) User’s guide to ESTIMATE S 6. In: <http://viceroy-eeb.uconn.edu/estimates>
- Crawley MJ (2002) *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley & Sons, London
- Davidson DW, Morton SR (1981) Myrmecochory in some plants (F. *Chenopodiaceae*) of the Australian arid zone. *Oecologia* 50:357–366
- Davidson DW, Morton SR (1984) Dispersal adaptations of some *Acacia* species in the Australian arid zone. *Ecology* 65:1038–1051
- Drake WE (1981) Ant-seed interaction in dry sclerophyll forest on North Stradbroke Island, Queensland. *Aust J Bot* 29:293–309
- Dunn RR, Parker CR, Sanders NJ (2007a) Disentangling the roles of competition and the environment as drivers of phenological patterns of ant diversity. *Biol J Linn Soc* (in press)
- Dunn RR, Parker CR, Gerhaghty M, Sanders NJ (2007b) Reproductive phenologies in a diverse temperate ant fauna. *Ecol Entomol* 32:135–142
- Fellers JH (1987) Interference and exploitation in a guild of woodland ants. *Ecology* 68:1466–1478
- Garrido JL, Rey PJ, Cerdá X, Herrera CM (2002) Geographical variation in diaspore traits of an ant-dispersed plant (*Helleborus foetidus*): are ant community composition and diaspore traits correlated? *J Ecol* 90:446–455
- Gibb H, Hochuli DF (2003) Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. *Oikos* 103:469–478
- Gilbert LE (1980) Food web organization and the conservation of neotropical diversity. In: Soulé ME, Wilcox BA (eds) *Conservation biology: an evolutionary-ecological perspective*. Sinauer, Sunderland, pp 11–33
- Gill AM, Groves RH, Noble IR (eds) (1981) *Fire and the Australian biota*. Australian Academy of Science, Canberra
- Gómez C, Espadaler X (1998) Myrmecochorous dispersal distances: a world survey. *J Biogeogr* 25:573–580
- Gorb SN, Gorb EV (1999) Effects of ant species composition on seed removal in deciduous forest in eastern Europe. *Oikos* 84:110–118
- Gotelli NJ, Entsminger GL (2004) *EcoSIM: Null models software for ecology*. Version 7. Acquired Intelligence Inc/Kesey-Bear, Jericho (<http://garyentsminger.com/ecosim/index.htm>)
- Gross CL, Whalen MA, Andrew MH (1991) Seed selection and removal by ants in a tropical savanna woodland in northern Australia. *J Trop Ecol* 7:99–112
- Hnatiuk RJ, Hopkins AJM (1981) An ecological analysis of kwongan vegetation south of Eneabba, Western Australia. *Aust J Ecol* 6:423–438
- Hoffmann BD, Andersen AN (2003) Response of ants to disturbance in Australia, with particular reference to functional groups. *Aust Ecol* 28:444–464
- Horvitz CC, Schemske DW (1986) Seed dispersal of a neotropical myrmecochore: Variation in removal rates and dispersal distance. *Biotropica* 18:319–323
- Howe HF (1979) Fear and frugivory. *Am Nat* 114:925–931
- Hughes L, Westoby M (1990) Removal rates of seed adapted for dispersal by ants. *Ecology* 71:138–148
- Hughes L, Westoby M (1992) Fates of seed adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* 73:1285–1299

- Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460
- Ireland C, Andrew MH (1995) Ants remove virtually all western myall (*Acacia papyrocarpa* Benth.) seeds at Middleback, South Australia. *Aust J Ecol* 20:565–570
- Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am Nat* 129:657–677
- Kaspari M, Yuan M, Alonso L (2003) Spatial grain and the causes of regional diversity gradients in ants. *Am Nat* 161:459–477
- Lamont BB, Downes S, Fox JED (1977) Importance-value curves and diversity indices applied to species-rich heathland in Western Australia. *Nature* 265:438–441
- Longino JT, Coddington J, Colwell RK (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology* 83:689–702
- Loreau M et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808
- Majer JD (1982) Ant-plant interactions in the Darling Botanical District of Western Australia. In: Buckley RC (ed) Ant-plant interactions in Australia. Dr W. Junk Publ, The Hague, pp 45–61
- Majer JD (1985) Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Aust J Ecol* 10:31–48
- Majer JD, Lamont BB (1985) Removal of seed of *Grevillea pteridifolia* (Proteaceae) by ants. *Aust J Bot* 33:611–618
- May JE, Heterick BE (2000) Effects of the costal brown ant, *Pheidole megacephala* (Fabricius), on the ant fauna of the Perth metropolitan region, western Australia. *Pac Conserv Biol* 6:81–85
- Mesler MR, Lu KL (1983) Seed dispersal of *Trillium ovatum* (Liliaceae) in second-growth Redwood forests. *Am J Bot* 70:1460–1467
- Moles AT, Westoby M. (2003) Latitude, seed predation and seed mass. *J Biogeogr* 30: 105–128
- Mossop MK (1989) Comparison of seed removal by ants in vegetation on fertile and infertile soils. *Aust J Ecol* 14:367–374
- Ness JN, Bronstein JL, Andersen AN, Holland JN (2004) Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology* 85:1244–1250
- Parr CL, Andersen AN, Chastagnol C, Duffaud C (2007) Savanna fires increase rate and distances of seed dispersal by ants. *Oecologia* 151: 33–41
- Pfeiffer M, Nais J, Linsenmair KE (2006) Worker size and seed size selection in ‘seed’-collecting ant ensembles (Hymenoptera: Formicidae) in primary rain forests on Borneo. *J Trop Ecol* 22: 685–693
- Rico-Gray V (1993) Use of plant-derived food resources by ants in the dry tropical lowlands of coastal Veracruz, Mexico. *Biotropica* 25:301–315
- Schatral A, Kailis SG, Fox JED (1994) Seed dispersal by *Hibbertia hypericoides* (Dilleniaceae) by ants. *J R Soc West Aust* 77:81–85
- Shattuck SO (1999) Australian ants: their biology and identification. CSIRO, Collingwood
- Stanton ML (2003) Interacting guilds: Moving beyond the pairwise perspective on mutualisms. *Am Nat* 162:S10–S23
- Stocker GC, Irvine AK (1983) Seed dispersal by Cassowaries (*Casuaris casuaris*) in North Queensland’s rainforests. *Biotropica* 15:170–176
- Symstad AJ, Tilman D, Willson J, Knops JMH (1998) Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos* 81:389–397
- Thompson JN (2005) The geographical mosaic of coevolution. University of Chicago Press, Chicago
- Traveset A, Riera N (2005) Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conserv Biol* 19:421–431
- Vepsäläinen K, Savolainen R (1990) The effect of interference by formicine ants on the foraging of *Myrmica*. *J Anim Ecol* 59:643–654
- Whitney KD (2005) Linking frugivores to the dynamics of a fruit color polymorphism. *Am J Bot* 92:859–867
- York A (2000) Long-term effects of frequent low-intensity burning on ant communities in coastal blackbutt forests of southeastern Australia. *Aust Ecol* 25:83–98
- Zamora R (2000) Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. *Oikos* 88:442–447