

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory

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Myrmecochory, or seed dispersal by ants, is a dispersal syndrome found among several thousand plant species occupying different ecosystems and geographical regions. Typically, ants benefit from consuming a lipid-rich appendage on the seed and in return provide seed dispersal service to the plant. Several hypotheses have been proposed to explain the selective advantage for plants resulting from myrmecochory, including directed dispersal, dispersal for distance and escape from seed predators. I contrast the evidence available in the literature for these hypotheses and distinguish the studies on the basis of ecosystem and plant growth forms. The predator-avoidance and the distance dispersal hypotheses were supported in most studies that addressed them, and the directed dispersal hypothesis was supported in about half of the studies that tested it. Multiple hypotheses were supported in most studies that tested more than one hypothesis, suggesting that the various selective advantages conferred from myrmecochory are seldom exclusive. I also review evidence for the hypothesis that plants have evolved adaptations both for selecting seed dispersers and for manipulating the behavior of those dispersers. Based on this evidence, I argue that focusing future research on the evolution of partner choice by myrmecochores and its effects on the overall plant fitness will be more fruitful than putting an emphasis on classifying the selective advantage to plants into distinct categories and test for their existence separately.

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Myrmecochory, or seed dispersal by ants, is often regarded as a diffuse mutualism between a guild of plants and a guild of ants. It has been reported in over 3000 plant species and in more than eighty plant families, and the interaction is common across a variety

of ecosystems (Berg 1975, Bond and Slingsby 1983, Beattie 1985). It is particularly common among herbs in temperate deciduous forests of the Northern Hemisphere (Culver and Beattie 1978, Beattie et al. 1979, Beattie and Culver 1981, Handel et al. 1981), and sclerophyll shrubs

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on low-nutrient soils in Australia and South Africa (Berg 1975, Milewski 1982, Bond and Slingsby 1983, Slingsby and Bond 1985, Andersen and Morrison 1998, Whitney 2002). The geographical and taxonomic distributions of myrmecochory among plants suggest that it has independently evolved many times, possibly as a response to different selection pressures operating in different ecological circumstance (Westoby et al. 1991). In this paper, I summarize the evidence in the literature for three major hypotheses (Beattie 1985) on the evolution of myrmecochory. I review the evidence for different strategies adopted by myrmecochores that may improve their fitness through efficient seed dispersal.

The diaspore of myrmecochorous plants consists of a seed and a lipid-rich appendage called elaiosome. The elaiosome acts as an attractant and may elicit seed collection by ants (Marshall et al. 1979, Kusmenoglu et al. 1989, Lanza et al. 1992, but see Sheridan et al. 1996, Espadaler and Gomez 1997a). Typically, ants transfer the diaspore to their nest, remove the elaiosome, and then deposit the intact seed in a shallow chamber within the nest or in a refuse pile outside (Beattie 1985). The consumption of the elaiosome, which in many myrmecochores contains high concentrations of essential fatty acids (Hughes et al. 1994), may contribute to an increase in ant colony fitness (Morales and Heithaus 1998, Bono and Heithaus 2002).

Plants may attain selective advantage from myrmecochory in several ways: a) directed dispersal – ants disperse seeds to sites where the plant fitness is higher than it would be in a random location, most likely due to nutrient enrichment at or near the ant nest (Hanzawa et al. 1988), b) predator-avoidance – dispersal and burial of seeds by ants reduce the ability of seed predators to locate and obtain seeds (Heithaus 1981, Higashi et al. 1989, Smith et al. 1989, Ohkawara and Higashi 1994, Ohkawara et al. 1997), c) distance dispersal – seed dispersal reduces parent-offspring conflict and sibling competition (Higashi et al. 1989, Boyd 2001), d) fire-avoidance – seed burial by ants increases survival through fire, and/or post-fire performance of seeds, seedlings and adults (Hughes and Westoby 1992b, Boyd 2001), and e) nutrient limitation – the production of elaiosome, which has a low potassium content, may be favored in environments such as the extremely nutrient-poor regions of Australia and South Africa, where production of potassium-rich dispersal units (e.g. fleshy fruits) is prohibitively costly (Westoby et al. 1991, Hughes et al. 1993). While some of these hypotheses, such as the fire-avoidance and the nutrient-limitation have been evoked to explain the evolution of myrmecochory in specific ecosystems, the other hypotheses have often been treated as more general hypotheses (Beattie 1985). There may also be an overlap among these hypotheses; for example, long distance dispersal may decrease seed densities and thus facilitate escape

from density-dependent natural enemies. The main aim of this paper is to evaluate the support for the various hypotheses in the literature.

Based on the evidence available at the time, Beattie (1985) argued that the directed dispersal hypothesis was the best supported hypothesis, and it is still perceived as the leading hypothesis on the evolution of myrmecochory (Wenny 2001) even though it has been frequently challenged (Bond et al. 1990, Westoby et al. 1990). Beattie (1985) has also argued that evidence supporting the predator-avoidance hypothesis will be found mainly where seed predation by small mammals, which are assumed to be the main competitors of seed-dispersing ants, is dominant. I test this assertion by comparing the evidence for this hypothesis across different ecosystems with varying degrees of seed predation by small mammals. The distance dispersal hypothesis was challenged by the argument that ants are unlikely to disperse seeds sufficiently far to reduce parent–offspring competition, and may actually intensify among-sibling competition by aggregating seeds in or around their nest (Culver and Beattie 1980, Horvitz 1981). However, these claims are based on the rarely tested assumptions that a) the scale of negative parent–offspring interaction is larger than dispersal distances, and b) as a result of myrmecochory, seeds in or around ant nests are more clumped than undispersed seeds. Because the scale of parent–offspring interaction might be positively correlated with plant stature and growth form, I hypothesized that distance dispersal by ants, which typically includes very short distances, may benefit mainly myrmecochores of small stature.

Seed dispersal is an extremely important life transition (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000), and plant traits that affect seed dispersal are likely to be under strong selection pressure. I argue that the overall fitness gain for plants resulting from myrmecochory significantly depends on the identity and behavior of the seed disperser. To support this argument, I review the evidence in the literature for different traits of myrmecochores that may affect the identity and behavior of their main seed dispersers, and I discuss the evolutionary implications of this partner choice.

Literature search

I used the ISI Web of Science database to search for published studies on the evolution of myrmecochory. First, I searched for articles that contained the terms “myrmecochory” and “evolution” or keywords related to the various hypotheses. I also used the references cited by the articles found by the initial search, and the forward citation option of Web of Science to look for other relevant publications. I mainly included studies that used observational or experimental data to test one

or more of the hypotheses on the evolution of myrmecochory that are listed above. Studies that were mainly designed to test other hypotheses, but which contained information pertaining to a test of any of the aforementioned hypotheses were also included. In addition, I also included a few theoretical studies that made strong mathematical, graphical, or verbal arguments in favor or in contrary to one or more of the hypotheses. For each of the published studies included in that summary, I noted the hypotheses tested, the plant species, the plant's growth form, the habitat type, and whether the hypotheses were supported or refuted. As the approaches and methods for testing any of the hypotheses differed markedly among published studies, incorporating the results into one statistical framework such as meta-analysis was impractical. Instead, I used a simple tally of the number of studies that supported or refuted each of the hypotheses and I elaborated on the significance and weight of the evidence in a qualitative manner. Though I originally sought only to test whether support for the predator-avoidance and the distance dispersal hypotheses depended on ecosystem-specific seed predation and plant stature, respectively, sorting the evidence for all the hypotheses by ecosystem and plant stature was both insightful and interesting. Thus, the results for all hypotheses were arranged in two tables classified by ecosystem or plant stature.

Support for the various hypotheses in the literature

Sixty-two published studies tested one or more of the main hypotheses on the evolution of myrmecochory (Appendix 1). I found considerable evidence that myrmecochory is advantageous to plants. The directed dispersal and the predator-avoidance hypothesis were

each tested in about half of the published studies included in this review, while the distance dispersal hypothesis was tested less frequently (Table 1). Contrary to an earlier review (Beattie 1985), which favored the directed dispersal hypothesis, I found that the support in the literature for the predator-avoidance and the distance dispersal hypotheses was just as compelling as that for the directed dispersal hypothesis.

Directed dispersal hypothesis

The directed dispersal hypothesis was supported in about half of the studies (12 of 26) that tested it (Table 1). About half of the studies that were conducted in sclerophyll vegetation or in temperate open habitats supported the directed dispersal hypothesis. However, the directed dispersal hypothesis was only supported in two of eight studies conducted in deciduous forests. Gibson (1993b) and Gorb et al. (2000) reported an increase in plant fitness resulting from directed dispersal. However, that benefit was not attributed to nutrient enrichment at the ant nest (the most frequently proposed mechanism underlying this hypothesis). Gibson (1993b) found that improvement in seedling germination and survival near ant nests resulted from conditions which have already existed in these sites before they were colonized by ants. Gorb et al. (2000) found that seeds deposited outside the ant territory borders performed better than seeds located at the ant nest vicinity, which actually provides a poor environment for establishment. The only ecosystem where the directed dispersal was consistently supported was the tropical forest, although there are too few studies in this ecosystem to justify strong conclusions (Table 1). The only growth form for which the directed dispersal hypothesis got unequivocal support was trees (Table 2). The evidence from the tropics suggests that ants are often secondary dispersers

Table 1. Summary of studies that tested three hypotheses on the evolution of myrmecochory. Results are sorted by ecosystem.

Hypothesis tested	Conclusion	Habitat				Total
		Sclerophyll	Temperate open	Temperate forest	Tropical forest	
Directed dispersal	supported	4	3	2	3	12
	not supported	3	3	5	1	12
	non conclusive	0	1	1	0	2
	total	7	7	8	4	26
	% support	57	43	25	75	46
Distance dispersal	supported	3	2	6	2	13
	not supported	0	1	0	0	1
	non conclusive	1	0	2	0	3
	total	4	3	8	2	17
	% support	75	67	75	100	76
Predator avoidance	supported	6	8	8	0	22
	not supported	0	0	0	1	1
	non conclusive	1	1	2	0	4
	total	7	9	10	1	27
	% support	86	89	80	0	81
Total		18	19	26	7	70

Table 2. Summary of studies that tested three hypotheses on the evolution of myrmecochory. Results are sorted by plant growth form.

Hypothesis tested	Conclusion	Habitat				
		Herb	Shrub	Tree	Unspecified	Total
Directed dispersal	supported	6	2	4	0	12
	not supported	7	3	0	2	12
	non conclusive	1	0	0	1	2
	total	14	5	4	3	26
	% supported	43	40	100	0	46
Distance dispersal	supported	9	1	3	0	13
	not supported	1	0	0	0	1
	non conclusive	2	0	0	1	3
	total	12	1	3	1	17
	% supported	75	100	100	0	76
Predator avoidance	supported	12	10	0	1	23
	not supported	1	0	0	0	1
	non conclusive	3	1	0	0	4
	total	16	11	0	1	28
	% supported	75	91	–	100	82
Total		42	17	7	5	71

of trees and shrubs, which are primarily dispersed by vertebrates. More studies are needed to ascertain whether dispersal by ants in these ecosystems is mainly a “fine tuning” directed dispersal following distance dispersal by vertebrates. It should be emphasized here that in the analysis presented above the directed dispersal hypothesis is treated in a rather narrow sense where the benefits associated with myrmecochory are mainly attributed to the physical and chemical alteration of the nest site by the seed-dispersing ant. An alternative, broader, definition of the directed dispersal hypothesis is discussed in the conclusion section of this paper.

Distance dispersal hypothesis

The distance dispersal hypothesis was supported in 13 of the 17 studies that tested it. The distance dispersal hypothesis was most frequently tested, and supported, using temperate forest herbs, and this seems to support my original hypothesis that myrmecochory may mainly benefit plants of small stature. However, only a handful of studies addressed the distance dispersal hypothesis for shrubs and trees, so a thorough comparison can not be done. One possible explanation for the lack of such studies is that most myrmecochorous shrubs are found in the southern hemisphere where dispersal distances of seeds by some ant species are close to the order of seed dispersal by vertebrates, and may even assist plant to colonize new habitat patches (Davidson and Morton 1981, Smith 1989, Whitney 2002). Therefore, the question of whether ants disperse seeds sufficiently far from the mother plant to provide any selective advantage might seem too trivial in these ecosystems.

A major expectation stemming from the distance dispersal hypothesis is that myrmecochory is likely to evolve where the range of seed dispersal by ants exceeds

the spatial scale of parent–offspring conflict. The dispersal distances of myrmecochores are strongly influenced by ant communities and may thus be constrained by the habitat- or ecosystem-specific ant community (Gomez and Espadaler 1998b). The spatial scale where parent–offspring conflict is intense is expected to increase with plant size. Therefore, plant size for which myrmecochory may provide an advantage through distance dispersal may be constrained by the distances traveled by the seed-dispersing ant species typical for an ecosystem or a habitat. In concordance with this expectation is the fact that seeds of myrmecochores in the Southern Hemisphere, which are mainly shrubs and small trees, disperse significantly farther than seeds of temperate forest myrmecochores, which are mainly herbs (Gomez and Espadaler 1998b). Similarly, within Australia, myrmecochory is common on infertile soils, where plants are also smaller. In contrast, myrmecochory is rare and large plants are common on more fertile soils. Most (84%) of the difference among soil types in the incidence of myrmecochory was explained by plant stature (Westoby et al. 1991). However, the differences in both plant stature and dispersal distances between ecosystems and among habitats within ecosystems could be attributed to factors that are unrelated to myrmecochory. Ant body size is positively correlated with dispersal distance (Gomez and Espadaler 1998a, Ness et al. 2004), and larger ants are likely to carry larger seeds with larger elaiosomes (Beattie et al. 1979, Davidson and Morton 1981, Gorb and Gorb 1999). Therefore seed size and elaiosome size are traits that can potentially influence dispersal distances even within the constraints specified by the available ensembles of potential seed dispersers in any specific ecosystem. However, whether these traits are under selection pressure related to myrmecochory is still an open question (Garrido et al. 2002).

Predator-avoidance hypothesis

The predator-avoidance hypothesis was supported in a majority of studies that tested it regardless of the ecosystem or the growth form. Much of the evidence supporting this hypothesis came from ecosystems where small mammals were not the main seed predators (e.g. sclerophyll vegetation in Australia, deciduous forests in Japan). Seed predation by spiders, ticks, and mainly ground beetles or granivorous ants seem to exert similar selection pressure as seed predation by rodents does (Ohara and Higashi 1987, Hughes and Westoby 1990, Ohkawara et al. 1996, 1997). The predator-avoidance hypothesis was rarely tested in tropical forests or with trees. Further, the interpretation of what constitutes a test and/or support of this hypothesis varied greatly among studies (Appendix 1). Nevertheless, I included studies with various test and degrees of support for this hypothesis, and I discuss the implications of that inclusive approach by contrasting the strength of the different tests and support for the predator-avoidance hypothesis.

The classical test of the predator-avoidance hypothesis involves estimating the relative contribution of seed dispersers (ants) and seed predators (rodents) to seed removal rates using pairwise exclusion experiments. In most of these studies ants were extremely efficient in locating and rapidly removing seeds. Rodents removed a considerable number of seeds in some studies (Heithaus 1981, Smith et al. 1986), but few in others (Horvitz and Schemske 1986, Hughes and Westoby 1990, Gibson 1993a, Ruhren and Dudash 1996, Guitian et al. 2003), and large spatio-temporal variation in seed predation by rodents was often reported within studies (Smith et al. 1989, Fedriani et al. 2004). Rapid removal of vulnerable seeds by non-granivorous ants clearly supports the predator-avoidance hypothesis, but the interpretation is more ambiguous when seed predation pressures are weaker. That interaction could reflect the absence of selection pressures from predators, spatio-temporal heterogeneity in those selection pressures, or a plant trait that evolved as a response to intense seed predation in the evolutionary past (Heithaus et al. 1980, Gibson 1993a). Another concern is that experimental treatments that are designed to mainly exclude seed dispersers (i.e. ant mutualists) also exclude antagonist invertebrates such as spiders, ticks, ground beetles (Ohara and Higashi 1987, Ohkawara et al. 1996, 1997) and granivorous ants.

If seed predation pressure is a main force selecting for myrmecochory, one should expect that the presence of the elaiosome, a specialized structure that characterizes this interaction, would decrease predation pressure. Intriguingly, the presence of an elaiosome typically promotes seed predation in the absence of ant mutualists (Heithaus 1981, Bond and Breytenbach 1985, Gibson 1993a, Espadaler and Gomez 1997b, Boyd 2001, Christian and Stanton 2004, but see Hanzawa et al. 1985).

Nevertheless, as long as the benefits in attracting seed dispersers outweigh the costs associated with an increasing attraction of seed predators, natural selection will favor elaiosome production (Hughes and Westoby 1990). Some evidence in support of this assertion comes from a comparative study of many species from the genus *Gravillea* that found that the probability of a seed being taken by seed-dispersing ant species and not by a seed predator was augmented by the presence of elaiosome (Auld and Denham 1999). Similarly, Hughes and Westoby (1992a) found that the probability of a seed being taken by seed-dispersing ant species and not by a seed predator increased with an increase in the elaiosome/seed ratio. The different means by which plants may affect the probability of a seed being taken by efficient seed dispersers rather than by a seed predator or a poor seed disperser are discussed in detail in the partner choice section below. Evidence in support of the predator-avoidance hypothesis also comes from the finding that the replacement of native seed-dispersing ants by an invasive ant is associated with an increase in seed predation by native seed predators, whose abundance was most likely unaffected by the invasion itself (Bond and Slingsby 1983, Carney et al. 2003).

Caveats

Like any metaanalysis, this study may be prone to a publication bias where studies that did not find a support for their declared hypothesis are less likely to be published and are thus underrepresented. I minimized the effect of any such biases on the conclusions drawn in this review in two ways. First, about quarter of the studies I have included tested several hypotheses simultaneously and reported the evidence for all of them. Second, I included a significant number of articles whose main goal was not testing hypotheses on the evolution of myrmecochory, yet they contained information regarding these hypotheses (Appendix 1). In both cases, the publication of results that are unlikely to be published alone (statistically non-significant or contradictory to the main hypotheses), is facilitated by their inclusion in the same paper with more “publishable” results.

The amount of support for each of the hypotheses as reflected in the literature survey may be affected by the relative difficulties in demonstrating a link between an increase in plant fitness and the specific selective advantage proposed by the hypothesis tested. Establishing such a link is a difficult task because the effect of seed dispersal on the plant fitness may come much later in the plant life (Hanzawa et al. 1988), and because the various advantages conveyed by myrmecochory may be hard to separate, and their effects may be interdependent. While these problems may complicate the test of each of the hypotheses, they are especially pronounced

with regard to testing the directed dispersal hypothesis. Seed may be placed at various depths within a nest, near its entrance, or away from the nest. Any of these sites may count as a safe site if it's physical, chemical and/or biological attributes improves plant performance. Many studies that tested the directed dispersal hypothesis employed multiple comparisons of a large set of variables measured around the nest and at control sites rather than relying on an a priori identification of the attributes which render a putative deposition site as a safe site. The inference that can be made by these studies is weak, even when differences are found.

As I show in the second part of this article, many of the traits of myrmecochores, which are suggested as evidence supporting the predator-avoidance hypothesis, may also be seen as adaptation for "choosing" seed disperser among many possible options. This is consistent with the hypothesized evolution of myrmecochory from granivory (Rissing 1986, Levey and Byrne 1993), wherein different seed dispersers represent transitions along a continuum from seed predation to mutualism. While counting adaptations for a partner choice as adaptations for predator-avoidance may inflate the apparent support of the predator-avoidance hypothesis, a distinction between the two may be more semantic than real. This is especially true since that distinction depends largely on the intensity of seed-predation pressure, which exhibits high spatio-temporal heterogeneity (Fedriani et al. 2004, Manzaneda et al. 2005).

The uneven representation of studies of myrmecochory across ecosystems and plant growth forms may also affect the comparison of the weight of evidence for each of the various hypotheses, especially if the importance of each selective advantage varies across categories. This unevenness may represent the distribution of myrmecochorous species among these categories, an unbalanced research effort among ecosystems and plants growth forms, or both. In a review of dispersal distances by ants, Gomez and Espadaler (1998b) reported a similar problem and suggested concentrating future research effort studying dispersal distance by ants in habitats and geographic regions where it was seldom studied. Similarly, our understanding of the evolution of myrmecochory will be advanced if future work addresses the gaps in knowledge identified in this contribution.

Partner choice and its effect on plant fitness

The outcomes of interspecific interactions are often conditioned on the abiotic and biotic contexts of the interaction and on the identities and behaviors of the participating species (Cushman and Whitham 1989, Cushman and Beattie 1991, Bronstein 1994a). The selection for or against mutualism may vary greatly across space and time if the context within which the

interaction occurs vary as well (Bronstein 1994a, Thompson 1999). While plants may have little direct effect on the broader ecological context in which they interact with potential seed dispersers, myrmecochores may have adopted strategies for selecting seed dispersers and for modifying their behavior. An ideal partner, one that simultaneously disperses seeds rapidly enough to reduce predation risk, far enough to reduce distance-related and density-dependent costs, and to a site disproportionately suitable for establishment, might not be available in every setting. However, these benefits are not necessarily contradictory and a high-quality seed disperser may simultaneously offer several benefits to its plant partner. Fourteen of the eighteen studies that tested multiple hypotheses found support for more than one hypothesis. Thus, the selective advantages conferred from myrmecochory appear to seldom be exclusive. Furthermore, the contributions of several means of selective advantage for plant fitness may positively interact. For example, O'Dowd and Hay (1980) found that protection from predators increases with distance from the parent plant, and Boyd (2001) found that the positive effects of escape from predator and distance dispersal were apparent only in post-fire conditions. Being blind to the means by which fitness increases, selection pressure may have lead plants to select for partner(s) that provide the highest total increase in fitness, regardless of the avenue by which it is achieved. Below I review the different means by which myrmecochores may "choose" their seed dispersers or influence their behaviors, and discuss how these modifications could improve plant fitness.

Guilds of seed collecting ants

Seed-collecting ants have been classified into two behavioral guilds (Bullock 1989, Hughes and Westoby 1992b, Espadaler and Gomez 1996). Guild 1 ("poor quality dispersers") is characterized by granivorous ants that forage in groups, recruit many workers to seed source, and cache seeds in the nest. Guild 2 ("high quality dispersers" or "removalists") is characterized by scavenging or omnivorous ants that forage individually, carry diaspores to the nest, and successively consume only the elaiosomes and discard the intact seeds outside the nest. Seed removal of myrmecochores is done chiefly by ant species from guild 2, which take seeds much faster than species from guild 1 (Hughes and Westoby 1992a, Hughes et al. 1994). The chemical composition of the elaiosomes of many myrmecochores resembles that of the insect prey in the diets of ant species from guild 2 (Hughes et al. 1994), and may play an important role in specifically attracting ants from this guild (Marshall et al. 1979, Kusmenoglu et al. 1989, Lanza et al. 1992, but see Sheridan et al. 1996, Espadaler and Gomez 1997a).

Variation in diaspore traits and partner choice

An association between variation in elaiosome size and in elaiosome chemistry and variation in seed removal rates has been shown by many studies (Hughes and Westoby 1992a, Lanza et al. 1992, Gorb and Gorb 1995, Mark and Olesen 1996, Pizo and Oliveira 2001, Peters et al. 2003). As most of these studies investigated the response of a single ant species or of the seed-dispersing ant community as a whole to variation in elaiosome traits, the possible effects of these traits on partner choice has not been evaluated (Mark and Olesen 1996, Garrido et al. 2002, Peters et al. 2003). Nevertheless, when the responses of various partners were compared, a higher representation of high-quality seed-dispersing species was correlated with an increase in elaiosome size (Hughes and Westoby 1992a), indicating that elaiosome traits may be associated with partner choice.

Satiation of ants by seeds

There is some evidence, mainly from studies in deciduous forests, that ants may be satiated by seeds of an abundant myrmecochore and prefer seeds of species they encounter less frequently (Smith et al. 1986, 1989, Ruhren and Dudash 1996). In deciduous forests of North America and Japan, seed-dispersing ants occupy transient nests, have small colony size, and often forage in small, overlapping territories (Culver and Beattie 1978, Smallwood and Culver 1979, Higashi et al. 1989). Because these foraging territories overlap, the satiation of one colony may promote the distribution of seeds into several ant nests, thereby reducing competition among siblings. I am not aware of any study that suggested or tested any possible mechanism underlying this satiation behavior or that addressed the ecological consequences of this behavior.

Timing of seed release and its effect on partner choice

The timing of seed release is perhaps jointly constrained by factors that affect flowering and fruit phenology (i.e. climate, pollinator activity). However, if there is temporal partitioning in the activity of seed dispersers and seed predators, the timing of seed release may be under selection to coincide with the peak activity of “high quality” disperser. For example, Oberrath and Bohning-Gaese (2002) found that myrmecochores fruited significantly earlier than non-myrmecochores and that this early fruiting coincides with the peak in ant activity and increases the probability for seed removal. On a shorter time scale, some myrmecochores release a disproportionate number of seeds in the morning, thus improving the likelihood that seed will be removed by diurnal seed

dispersers rather than nocturnal seed predators (Turnbull and Culver 1983, Gibson 1993a, Ohkawara et al. 1997). Daily and seasonal activity of ants are species-specific (Fellers 1989), and temporal partitioning of ants activity (Herbers 1989) may be exploited by plants to improve the probability of a seed to be taken by “high quality” disperser. The time of seed release of *Hexastylis arifolia* coincides with the seasonal peak in activity of *Aphaenogaster* spp., a “high quality” seed-dispersing ant, and with the decline in activity of *Prenolepis imparis*, a “low quality” seed-dispersing ant (Giladi 2004).

Spatial patterns of seed presentation affect partner choice

Ants encounter seeds on the ground after the seeds fell from the mother plant. These seeds can be passively dropped (i.e. ‘gravity dispersed’) or ejected ballistically, a mechanism that produces an overdispersed pattern of seeds (Culver and Beattie 1978, Ohkawara and Higashi 1994, Espadaler and Gomez 1996). The scattered pattern of seeds on the ground prior to dispersal by ants favors the collection of seeds by solitary foraging ants (i.e. “high quality” dispersers from guild 2) over collection by mass recruiters (i.e. ants from guild 1) (Crist and Haefner 1994). The overdispersion of seeds may also reduce seed predation (Hughes and Westoby 1990, 1992b, Ohkawara and Higashi 1994, Ohkawara et al. 1996). Additionally, scattered presentation of seeds improves the odds that seeds from a single parent may be carried to several nests, thus reducing competition among siblings. Slow release of seeds as opposed to mass release of many seeds also favors the removal of seeds by solitary foraging ants, which are often “high quality” dispersers and reduces seed predation (Ohara and Higashi 1987, Ohkawara et al. 1996).

Plants may exploit dominance hierarchies in the ant community to increase seed dispersal efficiency

In some ant communities, dominant species that monopolize food resources coexist with subordinate ants that are more efficient in locating new resources (Fellers 1989). In deciduous forests with high diversity and density of ants, “high quality” dispersers are often subordinate ants (Ohkawara et al. 1996, Ruhren and Dudash 1996, Giladi 2004). Subordinate ants may have been under selection pressure to minimize the risk of being “robbed” by dominant species, thus deferring seed handling and elaiosome consumption to the nest. This behavior is advantageous to the plant because it guarantees that ants are rewarded for their dispersal service only after it was done. Mesler and Lu (1983)

found that in a second growth redwood forest the only species of seed-carrying ant consumed the elaiosomes of *Trillium ovatum* next to the parent plant without providing any dispersal service. Mesler and Lu (1983) suggested that the low diversity ant community in redwood forests provides no selection pressure to defer the elaiosome removal to the nest. They further speculated that *Trillium ovatum* and other redwood forests myrmecochores evolved their myrmecochorous adaptations outside their current habitat in ant-rich environments where this selection pressure is strong (Higashi et al. 1989, Lanza et al. 1992, Kalisz et al. 1999).

Partner choice and support for the hypotheses on evolution of dispersal

Different seed-dispersing ants may contribute to plants fitness via different avenues, so that partner choice, while mainly selected if it increases overall fitness, may also affect the means by which selective advantage is gained. In some ecosystems, dispersal by ants is preceded by gravity dispersal, ballistic dispersal, or dispersal by vertebrates. In systems where ants are secondary seed dispersers, if dispersal distances by ants are dwarfed by distances seeds traveled earlier (Levey and Byrne 1993, Passos and Oliveira 2002), then ants may benefit plants by providing directed dispersal and/or escape from natural enemies. However, when the primary and secondary (ants) dispersal mechanisms generate similar or greater dispersal distances, ants contribution to distance dispersal cannot be simply dismissed (Culver and Beattie 1978, Ohkawara and Higashi 1994, Passos and Ferreira 1996).

The commonly used narrow-sense interpretation of the directed dispersal hypothesis is based on the premise that alteration of the nest environment by ants (most likely by nutrient enrichment, but changes in soil structure, and edaphic conditions may be considered too) affect plant fitness. This effect, which might be positive or negative (Appendix 1), is likely to be more significant for mound-building ants which occupy the same site for many years (Culver and Beattie 1983, Higashi et al. 1989). However, many seed-dispersing ants occupy nests that are frequently relocated (Culver and Beattie 1978, Smallwood and Culver 1979, Higashi et al. 1989, Hughes 1990) so a significant build up of nutrients near these nests environment is less likely. The frequent relocation of nests may prevent an aggregation of many seeds in one location, thus reducing the potential for intraspecific and interspecific competition. In addition, seeds that are deposited outside the nest may not experience the nest environment, especially when the nest is located in a very small cavity (folded leaf, twig, etc.), as is the case with some important seed-dispersing ants.

The dispersal curve of many myrmecochores is leptokurtic where most seeds are dispersed over short distances by one or two seed-dispersing ant species and only a few seeds are dispersed over long distance by other ant species (Horvitz and Schemske 1986, Gomez and Espadaler 1998a, Giladi 2004). Whitney (2002) suggested a partner-specific advantage where short-distance seed-dispersing ants move seeds to safe sites, while long-distance dispersers provide distance-related advantages and allow the plant to colonize new areas.

Myrmecochory has not been considered a species-specific mutualism. However, it is probably not as diffuse as it is frequently presented. In most of the ecosystems where myrmecochory is common, many species of ants may remove seeds, but efficient seed dispersal of many plant species is provided by small subset of the local ant community (often at the order of two to three species). Only few studies demonstrated benefits to the ant partner (Morales and Heithaus 1998, Bono and Heithaus 2002), and only one study found some evidence that ants, at least for some period, strongly relied on seeds of one species of myrmecochore for food (Oostermeijer 1989). This apparent asymmetry in that interaction may be biologically meaningful or reflect an asymmetry in research effort as in the investigation of other plant–animal mutualisms (Cushman and Beattie 1991, Bronstein 1994b). Anyway, the dependency of plant species on a small suit of seed-dispersing ants may make populations and communities of myrmecochores systems sensitive to changes in the ant community. The collapse of this mutualism when native ants are replaced by invasive exotic ants (Bond and Slingsby 1983, Carney et al. 2003), or when the ant community is otherwise altered (Mesler and Lu 1983, Pudlo et al. 1990) provide powerful examples of this dependency.

Conclusions and future directions

There is an ample support in the literature for each of the three main hypotheses on the selective advantage of myrmecochory for plants. While the relative contribution of each of the selective advantages to the evolution of myrmecochory may vary with the plant species, the ant species, and the ecosystem, our view on the evolution of myrmecochory depends also on the way by which we define hypotheses and set experiments to test for the possible effects of the various selective advantages on plant fitness. For example, some advantages of the directed dispersal, mainly those associate with the burial of seeds, are often attributed to other hypotheses such as the predator- and fire-avoidance hypotheses (Beattie and Culver 1982). The apparent weaker support for the directed dispersal hypothesis in the current review compared to that in Beattie (1985) may be a consequence of the inclusion of new information in the current review

(44 out of 62 studies included here were published later than 1985), but the difference may also result from the rather restrictive definition of that hypothesis I used in the evaluation of the evidence in the literature. If we consider directed dispersal *sensu lato*, as including both seed burial (with all the associated benefits), and horizontal directed dispersal, the support for this hypothesis in the literature is solid. Nevertheless, I have decided to evaluate the support for the directed dispersal *sensu strictu* (i.e. improved conditions around the ant nest) because it is in that sense that it is frequently cited as the main selective advantage for the evolution of myrmecochory. The interpretation of future studies' results will significantly improve if the specific aspects and predictions of the hypotheses that are being tested will be clearly defined. As two or more of the selective advantages are often conveyed as a package, their isolation is experimentally challenging and their separate ecological and evolutionary significance is not always clear. Plants have probably been selected to attract one or a few partners that offer the best packages of benefits rather than choosing among specific benefits.

The traditional pairwise perspective on mutualism has been recently shifted to admit a network of multiple interacting species, and whose evolution and maintenance are influenced by the biotic and abiotic contexts in which the interaction occurs (Stanton 2003, Thomson 2003). Myrmecochory, which has long been considered as a diffuse mutualism between a guild of plants and a guild of ants, fits very well into this new framework. However, the ample evidence presented in this paper regarding partner choice by myrmecochorous plants indicates that myrmecochory, from the plant point of view, is less diffuse than it has frequently been perceived. Although many ant species are often selective in their food choice, we know virtually nothing about the possible effects that these choices may have on the fitness of any myrmecochorous ants. A phylogenetic approach, which has been successfully used to study other mutualistic ant–plant interactions (Itino et al. 2001) may be used for exploring the mutual diffuseness (or specificity) in myrmecochory and its evolutionary significance.

Investigation of full demographic analysis of myrmecochory is rare (Hanzawa et al. 1988), possibly due to the fact that most myrmecochores are long-lived plants. Nevertheless, in order to determine the potential of partner choice to affect the evolution of myrmecochory, comparisons of the consequences of treatment by different ant species on the major life-cycle transitions are required. More studies exploring the association between diaspore traits and the composition of seed-dispersing ant species, coupled with the investigation of the effects of various seed-dispersing ants on plant fitness are necessary for evaluating the importance of partner choice for the evolution of myrmecochory.

The problem of attracting beneficial partners (i.e. seed-dispersing ants) while avoiding antagonists (here, seed predators or low quality dispersers) is a common one for prospective mutualists (Irwin et al. 2004 for interactions between flowering plants, pollinators, and nectar robbers), and the diversity of “solutions” to this problem might be similarly great. There is ample evidence to suggest that plants have evolved various means for selecting seed-dispersers which probably contribute most to their fitness. In addition, an efficient seed-disperser may simultaneously contribute to plant fitness via several avenues. Therefore, I believe that focusing future research on the evolution of partner choice by myrmecochores will be more insightful than following the classification of selective advantages in myrmecochory to the hypotheses that were reviewed in the first part of this article.

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Appendix A can be found at: www.oikos.ekol.lu.se

References

- Andersen, A. N. 1988a. Dispersal distance as a benefit of myrmecochory. – *Oecologia* 75: 507–511.
- Andersen, A. N. 1988b. Soil of nest-mounds of the seed-dispersing ant, *Aphaenogaster longiceps*, enhances seedling growth. – *Aust. J. Ecol.* 13: 469–471.
- Andersen, A. N. and Morrison, S. C. 1998. Myrmecochory in Australia's seasonal tropics: effects of disturbance on distance dispersal. – *Aust. J. Ecol.* 23: 483–491.
- Auld, T. D. and Denham, A. J. 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, A. J. 1985. The evolutionary ecology of ant–plant mutualism. – Cambridge Univ. Press.
- Beattie, A. J. and Culver, D. C. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. – *Ecology* 62: 107–115.
- Beattie, A. J. and Culver, D. C. 1982. Inhumation: how ants and other invertebrates help seeds. – *Nature* 297: 627.
- Beattie, A. J. and Culver, D. C. 1983. The nest chemistry of two seed-dispersing ant species. – *Oecologia* 56: 99–103.
- Beattie, A. J., Culver, D. C. and Pudlo, R. C. 1979. Interaction between ants and the diaspores of some common spring-flowering herbs in West Virginia. – *Castanea* 44: 177–186.
- Berg, R. Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. – *Aust. J. Bot.* 23: 475–508.
- Bond, W. and Breytenbach, G. J. 1985. Ants, rodents and seed predation in Proteaceae. – *S. Afr. J. Zool.* 20.
- Bond, W. J. and Slingsby, P. 1983. Seed dispersal by ants in shrublands of the Cape province and its evolutionary implications. – *S. Afr. J. Sci.* 79: 231–233.

- Bond, W. and Slingsby, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. – *Ecology* 65: 1031–1037.
- Bond, W. J. and Stock, W. D. 1989. The costs of leaving home: ants disperse myrmecochorous seeds to low nutrient sites. – *Oecologia* 81: 412–417.
- Bond, W. J., Yeaton, R. and Stock, W. D. 1990. Myrmecochory in the cape fynbos. – In: Huxley, C. R. and Cutler, D. F. (eds), *Ant-plant interactions*. Oxford Univ. Press, pp. 448–462.
- Bono, J. M. and Heithaus, E. R. 2002. Sex ratios and the distribution of elaiosomes in colonies of the ant, *Aphaenogaster rudis*. – *Insectes Soc.* 49: 320–325.
- Boyd, R. S. 2001. Ecological benefits of myrmecochory for the endangered chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). – *Am. J. Bot.* 88: 234–241.
- Bronstein, J. L. 1994a. Conditional outcomes in mutualistic interactions. – *Trends Ecol. Evol.* 9: 214–217.
- Bronstein, J. L. 1994b. Our current understanding of mutualism. – *Q. Rev. Biol.* 69: 31–51.
- Bullock, S. H. 1989. Life history and seed dispersal of a short-lived Chaparral shrub, *Dendromecon rigida* (Papaveraceae). – *Am. J. Bot.* 76: 1506–1517.
- Carney, S. E., Byerley, M. B. and Holway, D. A. 2003. Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. – *Oecologia* 135: 577–582.
- Christian, C. E. and Stanton, M. L. 2004. Cryptic consequences of a dispersal mutualism: seed burial, elaiosome removal, and seed-bank dynamics. – *Ecology* 85: 1101–1110.
- Crist, T. O. and Haefner, J. W. 1994. Spatial model of movement and foraging in harvester ants (*Pogonomyrmex*), (ii): the roles of environment and seed dispersion. – *J. Theor. Biol.* 166: 315–323.
- Culver, D. C. and Beattie, A. J. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. – *J. Ecol.* 66: 53–72.
- Culver, D. C. and Beattie, A. J. 1980. The fate of *Viola* seeds dispersed by ants. – *Am. J. Bot.* 67: 710–714.
- Culver, D. C. and Beattie, A. J. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in Colorado Montane meadow. – *Ecology* 64: 485–492.
- Cushman, J. H. and Whitham, T. G. 1989. Conditional mutualism in a membracid ant association-temporal, age-specific, and density-dependent effects. – *Ecology* 70: 1040–1047.
- Cushman, J. H. and Beattie, A. J. 1991. Mutualisms – assessing the benefits to hosts and visitors. – *Trends Ecol. Evol.* 6: 193–195.
- Davidson, D. W. and Morton, S. R. 1981. Myrmecochory in some plants (Chenopodiaceae) of the Australian arid zone. – *Oecologia* 50: 357–366.
- Davidson, D. W. and Morton, S. R. 1984. Dispersal adaptations of some *Acacia* species in the Australian arid zone. – *Ecology* 65: 1038–1051.
- Espadaler, X. and Gomez, C. 1996. Seed production, predation and dispersal in the Mediterranean myrmecochore *Euphorbia characias* (Euphorbiaceae). – *Ecography* 19: 7–15.
- Espadaler, X. and Gomez, C. 1997a. Falling or movement of seeds and the presence of an elaiosome: its effect on ant reaction (Hymenoptera: Formicidae) in a myrmecochorous species, *Euphorbia characias* (Euphorbiaceae). – *Sociobiology* 30: 175–183.
- Espadaler, X. and Gomez, C. 1997b. Soil surface searching and transport of *Euphorbia characias* seeds by ants. – *Acta Oecol.* 18: 39–46.
- Fedriani, J. M., Rey, P. J., Garrido, J. L. et al. 2004. Geographical variation in the potential of mice to constrain an ant-seed dispersal mutualism. – *Oikos* 105: 181–191.
- Fellers, J. H. 1989. Daily and seasonal activity in woodland ants. – *Oecologia* 78: 69–76.
- Garrido, J. L., Rey, P. J., Cerda, X. et al. 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.
- Gibson, W. 1993a. Selective advantages to hemi-parasitic annuals, genus *Melampyrum*, of a seed dispersal mutualism involving ants. 2. Seed-predator avoidance. – *Oikos* 67: 345–350.
- Gibson, W. 1993b. Selective advantages to hemi-parasitic annuals, genus *Melampyrum*, of a seed dispersal mutualism involving ants. 1. Favorable nest sites. – *Oikos* 67: 334–344.
- Giladi, I. 2004. The role of habitat-specific demography, habitat-specific dispersal, and the evolution of dispersal distances in determining current and future distributions of the ant-dispersed forest herb, *Hexastylis arifolia*. – *Inst. Ecol., Athens, GA, Univ. of Georgia*: 175.
- Gomez, C. and Espadaler, X. 1998a. Seed dispersal curve of a Mediterranean myrmecochore: Influence of ant size and the distance to nests. – *Ecol. Res.* 13: 347–354.
- Gomez, C. and Espadaler, X. 1998b. Myrmecochorous dispersal distances: a world survey. – *J. Biogeogr.* 25: 573–580.
- Gorb, E. V. and Gorb, S. N. 1995. Influence of myrmecochory on spatial pattern and seedlings mortality in *Asarum europaeum* L (Aristolochiaceae). – *Zhurnal Obshechi Biol.* 56: 470–476.
- Gorb, E. V. and Gorb, S. N. 1996. Ant nests as the habitats of myrmecochores: do the nest mounds of *Formica polyctena* Fabr provide the advantageous microsites for the violet *Viola odorata* L.? – *Zhurnal Obshechi Biol.* 57: 452–456.
- Gorb, E. V. and Gorb, S. N. 1997. Decrease of seedlings density as an adaptive advantage of myrmecochory in *Corydalis solida* (L.) Clairv (Fumariceae). – *Zhurnal Obshechi Biol.* 58: 89–96.
- Gorb, S. N. and Gorb, E. V. 1999. Dropping rates of elaiosome-bearing seeds during transport by ants (*Formica polyctena* Foerst.): implications for distance dispersal. – *Acta Oecol.* 20: 509–518.
- Gorb, S. N., Gorb, E. V. and Punttila, P. 2000. Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: a case study. – *Acta Oecol.* 21: 293–301.
- Guitian, P., Medrano, M. and Guitian, J. 2003. Seed dispersal in *Erythronium dens-canis* L. (Liliaceae): variation among habitats in myrmecochorous plant. – *Plant Ecol.* 169: 171–177.
- Handel, S. N., Fisch, S. B. and Schatz, G. E. 1981. Ants disperse a majority of herbs in a mesic forest community in New-York state. – *Bull. Torrey Bot. Club* 108: 430–437.
- Hanzawa, F. M., Beattie, A. J. and Holmes, A. 1985. Dual function of the elaiosome of *Corydalis aurea* (Fumariaceae) – attraction of dispersal agents and repulsion of *Peromyscus maniculatus*, a seed predator. – *Am. J. Bot.* 72: 1707–1711.
- Hanzawa, F. M., Beattie, A. J. and Culver, D. C. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. – *Am. Nat.* 131: 1–13.
- Heithaus, E. R. 1981. Seed predation by rodents on 3 ant-dispersed plants. – *Ecology* 62: 136–145.
- Heithaus, E. R., Culver, D. C. and Beattie, A. J. 1980. Models of some ant-plant mutualisms. – *Am. Nat.* 116: 347–361.
- Herbers, J. M. 1989. Community structure in north temperate ants: temporal and spatial variation. – *Oecologia* 81: 201–211.
- Higashi, S., Tsuyuzaki, S., Ohara, M. et al. 1989. Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). – *Oikos* 54: 389–394.
- Horvitz, C. C. 1981. Analysis of how ant behaviors affect germination in a tropical Myrmecochore *Calathea microcephala* (P and E) Koernicke (Marantaceae): microsite selection and aril removal by Neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). – *Oecologia* 51: 47–52.
- Horvitz, C. C. and Beattie, A. J. 1980. Ant dispersal of *Calathea* (Marantaceae) seeds by carnivorous Ponerines (Formicidae) in a tropical rain-forest. – *Am. J. Bot.* 67: 321–326.

- Horvitz, C. C. and Schemske, D. W. 1986. Seed dispersal of a Neotropical myrmecochore: variation in removal rates and dispersal distance. – *Biotropica* 18: 319–323.
- Horvitz, C. C. and Schemske, D. W. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. – *Ecology* 75: 1949–1958.
- Hughes, L. 1990. The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. – *Aust. J. Ecol.* 16: 207–214.
- Hughes, L. and Westoby, M. 1990. Removal rates of seeds adapted for dispersal by ants. – *Ecology* 71: 138–148.
- Hughes, L. and Westoby, M. 1992a. Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. – *Ecology* 73: 1300–1312.
- Hughes, L. and Westoby, M. 1992b. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. – *Ecology* 73: 1285–1299.
- Hughes, L., Westoby, M. and Johnson, A. D. 1993. Nutrient costs of vertebrate-dispersed and ant-dispersed fruits. – *Funct. Ecol.* 7: 54–62.
- Hughes, L., Westoby, M. and Jurado, E. 1994. Convergence of elaiosomes and insect prey-evidence from ant foraging behavior and fatty-acid composition. – *Funct. Ecol.* 8: 358–365.
- Irwin, R. E., Adler, L. S. and Brody, A. K. 2004. The dual role of floral traits: pollinator attraction and plant defense. – *Ecology* 85: 1503–1511.
- Itino, T., Davies, S. J., Tada, H. et al. 2001. Cospeciation of ants and plants. – *Ecol. Res.* 16: 787–793.
- Kalisz, S., Hanzawa, F. M., Tonsor, S. J. et al. 1999. Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. – *Ecology* 80: 2620–2634.
- Kjellsson, G. 1985a. Seed fate in a population of *Carex pilulifera* L. 1. Seed dispersal and ant-seed mutualism. – *Oecologia* 67: 416–423.
- Kjellsson, G. 1985b. Seed fate in a population of *Carex pilulifera* L. 2. Seed predation and its consequences for dispersal and seed bank. – *Oecologia* 67: 424–429.
- Kjellsson, G. 1991. Seed fate in an ant-dispersed sedge, *Carex pilulifera* L-recruitment and seedling survival in tests of models for spatial-dispersion. – *Oecologia* 88: 435–443.
- Kusmenoglu, S., Rockwood, L. L. and Gretz, M. R. 1989. Fatty acids and diacylglycerols from elaiosomes of some ant-dispersed seeds. – *Phytochemistry* 28: 2601–2602.
- Lanza, J., Schmitt, M. A. and Awad, A. B. 1992. Comparative chemistry of elaiosomes of 3 species of *Trillium*. – *J. Chem. Ecol.* 18: 209–221.
- Levey, D. J. and Byrne, M. M. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. – *Ecology* 74: 1802–1812.
- Lisci, M., Bianchini, M. and Pacini, E. 1996. Structure and function of the elaiosome in some angiosperm species. – *Flora* 191: 131–141.
- Lobstein, M. B. and Rockwood, L. L. 1993. Influence of elaiosome removal on germination in five ant-dispersed plant species. – *Virginia J. Sci.* 44: 59–72.
- Manzaneda, A. J., Fedriani, J. M. and Rey, P. J. 2005. Adaptive advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographical range. – *Ecography* 28: 1–10.
- Mark, S. and Olesen, J. M. 1996. Importance of elaiosome size to removal of ant-dispersed seeds. – *Oecologia* 107: 95–101.
- Marshall, D. L., Beattie, A. J. and Bollenbacher, W. E. 1979. Evidence for diglycerides as attractants in an ant-seed interaction. – *J. Chem. Ecol.* 5: 335–344.
- Mesler, M. R. and Lu, K. L. 1983. Seed dispersal of *Trillium ovatum* (Liliaceae) in 2nd-growth redwood forests. – *Am. J. Bot.* 70: 1460–1467.
- Milewski, A. V. 1982. The occurrence of seeds and fruits taken by ants versus birds in Mediterranean Australia and Southern-Africa, in relation to the availability of soil potassium. – *J. Biogeogr.* 9: 505–516.
- Morales, M. A. and Heithaus, E. R. 1998. Food from seed dispersal mutualism shifts sex ratios in colonies of the ant *Aphaenogaster rudis*. – *Ecology* 79: 734–739.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – *Trends Ecol. Evol.* 15: 278–285.
- Ness, J. H., Bronstein, J. L., Andersen, A. N. et al. 2004. Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. – *Ecology* 85: 1244–1250.
- Oberrath, R. and Bohning-Gaese, K. 2002. Phenological adaptation of ant-dispersed plants to seasonal variation in ant activity. – *Ecology* 83: 1412–1420.
- O'Dowd, D. J. and Hay, M. E. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. – *Ecology* 6: 531–540.
- Ohara, M. and Higashi, S. 1987. Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). – *J. Ecol.* 75: 1091–1098.
- Ohkawara, K. and Higashi, S. 1994. Relative importance of ballistic and ant dispersal in two diplochorous *Viola* species (Violaceae). – *Oecologia* 100: 135–140.
- Ohkawara, K., Higashi, S. and Ohara, M. 1996. Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne (Liliaceae). – *Oecologia* 106: 500–506.
- Ohkawara, K., Ohara, M. and Higashi, S. 1997. The evolution of ant-dispersal in a spring-ephemeral *Corydalis ambigua* (Papaveraceae): timing of seed-fall and effects of ants and ground beetles. – *Ecography* 20: 217–223.
- Oostermeijer, J. G. B. 1989. Myrmecochory in *Polygala vulgaris* L., *Luzula campestris* (L) Dc and *Viola curtisii* Forster in a Dutch dune area. – *Oecologia* 78: 302–311.
- Passos, L. and Ferreira, S. O. 1996. Ant dispersal of *Croton priscus* (Euphorbiaceae) seeds in a tropical semideciduous forest in southeastern Brazil. – *Biotropica* 28: 697–700.
- Passos, L. and Oliveira, P. S. 2002. Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. – *J. Ecol.* 90: 517–528.
- Peters, M., Oberrath, R. and Bohning-Gaese, K. 2003. Seed dispersal by ants: are seed preferences influenced by foraging strategies or historical constraints? – *Flora* 198: 413–420.
- Pizo, M. A. and Oliveira, P. S. 2001. Size and lipid content of nonmyrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. – *Plant Ecol.* 157: 37–52.
- Pudro, R. J., Beattie, A. J. and Culver, D. C. 1990. Population consequences of changed in ant seed mutualism in *Sanguinaria canadensis*. – *Oecologia* 46: 32–37.
- Rice, B. and Westoby, M. 1986. Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. – *Ecology* 67: 1270–1274.
- Rissing, S. W. 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. – *Oecologia* 68: 231–234.
- Ruhren, S. and Dudash, M. R. 1996. Consequences of the timing of seed release of *Erythronium americanum* (Liliaceae), a deciduous forest myrmecochore. – *Am. J. Bot.* 83: 633–640.
- Schupp, E. W. and Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. – *Ecoscience* 2: 267–275.
- Sheridan, S. L., Iversen, K. A. and Itagaki, H. 1996. The role of chemical senses in seed-carrying behavior by ants: a behavioral, physiological, and morphological study. – *J. Insect Physiol.* 42: 149–159.
- Slingsby, P. and Bond, W. J. 1985. The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L) Buek (Proteaceae). – *S. Afr. J. Bot.* 51: 30–34.

- Smallwood, J. and Culver, D. C. 1979. Colony movements of some North American ants. – *J. Anim. Ecol.* 48: 373–382.
- Smith, B. H., Rosenheim, M. L. and Swartz, K. R. 1986. Reproductive ecology of *Jeffersonia diphylla* (Berberidaceae). – *Am. J. Bot.* 73: 1416–1426.
- Smith, B. H., Forman, P. D. and Boyd, A. E. 1989. Spatial patterns of seed dispersal and predation of 2 myrmecochorous forest herbs. – *Ecology* 70: 1649–1656.
- Smith, J. N. B. 1989. An example of ant-assisted plant invasion. – *Aust. J. Ecol.* 14: 247–250.
- Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualism. – *Am. Nat.* 162: S10–S23.
- Thompson, J. N. 1999. Specific hypotheses on the geographic mosaic of coevolution. – *Am. Nat.* 153: S1–S14.
- Thomson, J. 2003. When is it mutualism? – *Am. Nat.* 162: S1–S9.
- Turnbull, C. L. and Culver, D. C. 1983. The timing of seed dispersal in *Viola nuttallii*: attraction of dispersers and avoidance of predators. – *Oecologia* 59: 360–365.
- Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. – *Evol. Ecol. Res.* 3: 51–74.
- Westoby, M., Hughes, L. and Rice, B. 1990. Seed dispersal by ants; comparing infertile and fertile soils. – In: Huxley, C. R. and Cutler, D. F. (eds), *Ant–plant interactions*. Oxford Univ. Press, pp. 431–447.
- Westoby, M., French, K., Hughes, L. et al. 1991. Why do more plant species use ants for dispersal on infertile compared with fertile soils. – *Aust. J. Ecol.* 16: 445–455.
- Whitney, K. D. 2002. Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*. – *Aust. Ecol.* 27: 589–595.

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