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“Redirecting” the Study of Mutualistic Benefits To Plants In Myrmecochory

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“Redirecting” the study of mutualistic benefits to plants
in myrmecochoery

By Mariah Patton

Mentor: Dr. Charles Kwit
Abstract

Myrmecochory is typically cast as a mutualistic relationship in which seed dispersal of plants with elaiosome-bearing seeds is performed by ants. Benefits of this mutualism may seem simple at first: ants gain a nutritive reward via elaiosomes, while plant propagules gain protection and a more suitable microsite for establishment and growth. However, there is growing literature suggesting that ants may not consistently receive benefits from elaiosome-based diets, and studies depicting plant benefits are constrained by the “ideal” model framework, by temporal limitations, and by limitations of sources of mortality that have typically been investigated. Furthermore, from the plant perspective, many key parts as well as inconsistencies within this more complex process have not been well explored. Here, I provide a more realistic guiding framework and identify where research needs to be further conducted and what questions should be answered to better address the positive mechanistic role ants may play in this quintessential mutualism.

Introduction

Mutualisms are defined and cast as involving positive outcomes for both partners. In this relationship, each partner benefits from the other in a positive fashion, often through the provision of services. Mutualistic interactions among organisms have been described and quantified in a variety of ways, with specific benefits gained from each partner being easily recognizable. In mutualisms involving plant-animal interactions, each partner gains a fitness advantage from the other’s involvement (Bronstein 1994).
Quintessential examples of mutualisms involving plants and animals include pollination (Fenster et al. 2004), ants and extra-floral nectaries (Bentley 1976), and animal-mediated seed dispersal (Howe and Smallwood 1982). While each of these general interactions is cast as a mutualism, their coevolutionary nature invokes complexities. Thus, the notion that both partners typically benefit belies the mutualistic assertion. In pollination, there is a clear view of gains from both partners— the pollinator gains food and the plant gains the benefit of spreading its genetic material. In the mutualistic relationship between ants and extra-floral nectaries, ants benefit from the food gained by these nectaries while the plants benefit from protection by their ant partners from herbivorous predators. In animal-mediated seed dispersal, the disperser often gains food while the plant gains advantage by obtaining distance from the parent plant (Janzen 1970; Connell 1971; Cheplick 1992). Despite numerous examples of mutualistic animal-mediated seed dispersal, one of the best-supported examples is that of myrmecochory (Howe and Smallwood 1982; Hanzawa et al. 1988; Wenny 2001; Wang and Smith 2002). As with other coevolutionary relationships, though, myrmecochory may not be a perfect mutualism, and is arguably a poorly conceived mutualistic process.

**Myrmecochory**

Myrmecochory, seed dispersal by ants of plants with elaiosome-bearing seeds, is a widespread phenomenon, pertaining to over 11,000 plant species in over 77 plant families (Lengyel et al. 2009) as well as at least 71 different species of omnivorous and carnivorous ants (Christianini et al. 2012). Not only has this
mutualism become widespread among types of plants, but myrmecochory has also been shown to independently evolve somewhere from 101 to 147 times (Lengyel et al. 2009). This mutualistic relationship can be found in a variety of sites, including nutrient-poor soil areas of sclerophyllous Australia (Berg 1975; Rice and Westoby 1986; Orians and Milewski 2007) and South Africa (Milewski and Bond 1982), Mediterranean climates (Espadaler & Gómez 1996), a mix of dry forest patches and more semi-arid sclerophyllous areas of the Caatinga ecosystem in Brazil (Leal et al. 2007), and north temperate meadows and forests (Beattie and Culver 1981; Handel et al. 1981; Beattie 1983).

One identifying feature that defines myrmecochory is the presence of a seed-attached elaiosome. The elaiosome is a lipid- and protein-rich appendage that attracts ants to carry away the plant’s diaspor (dispersal unit of seed and elaiosome) (Giladi 2006) and provides nutritional reward primarily to developing brood in the nest (Boulay et al. 2005). Elaiosomes vary in physical and chemical structure from plant to plant and place to place (Beattie 1985; Turner and Frederickson 2013; Reifenrath et al. 2012). The morphology of these elaiosomes, along with that of the ants involved (especially size and shape of mandibles) determines diaspor movement success (Gunther and Lanza 1989; Oostermeijer 1989; Hughes and Westoby 1992). The variation of chemical makeup of elaiosomes influence movement as well. To attract ants, a diglyceride component called diolene 1:2 has been shown to be very effective (Marshall et al. 1979). However, it has been shown that an increased expression of a different compound, oleic acid, can be used as a competitive advantage to attract even
more ants to retrieve seeds (Turner and Frederickson 2013). Oleic acid in nature often induces what is known as corpse-carrying behavior, wherein ants carry their dead to a midden pile (Skidmore and Heithaus 1988). This acid is also similar to insects’ haemolymph, which also incites a prey-carrying behavior as well among carnivorous ants (Skidmore and Heithaus, 1988; Hughes et al. 1994; Boulay et al. 2006; Gammans et al. 2006; Fischer et al. 2008). Nutritional makeup of elaiosomes differs among myrmecochores as well, especially in lipid composition (Pizo and Oliveira 2001). While their presence is important for diaspore detection and movement to nest locations, ramifications of elaiosome consumption and removal are in need of further and better-formulated studies, as well as better integration into mutualistic models of myrmecochoary.

**Benefits of Myrmecochoary**

**Benefits to ants**

The putative benefits ants derive from elaiosomes are dietary in nature, yet the fitness consequences of engaging in the mutualism (i.e., incorporating elaiosomes into the diet) have not been well explored. Beattie (1985) emphasizes that the food needed to support ants is dependent on the state of the colony. Different castes of the ant colony have different energetic needs. Ant workers, for example, need quick sugar sources or carbohydrates to sustain their more active roles in the colony (Wilson and Eisner 1957). Thus, food sources other than elaiosomes that contain mostly fatty acids and other lipids as well as essential amino acid and less sugar and protein may be more preferential (Fischer et al. 2005).
This being said, elaiosomes may serve as an important food source for a colony that may be comprised of a high density of larvae whose nutritional requirements consist of proteins and fats (Vinson 1968; Hölldobler and Wilson 1990). Elaiosomes could also potentially serve as a vital resource when other foods may not be available (Hughes et al. 1994; Clark and King 2012). Morales and Heithanus (1998) claim that not only do ants use these elaiosomes as a food source, but also these elaiosomes can alter sex ratios in colonies in producing more reproductive females. Other than the work of Gammans et al. (2005), there is little support for the fitness benefits conferred to ants via elaiosomes of myrmecochoorous plants.

Some recent studies have suggested that feeding on elaiosomes may not always be of benefit to ant populations. For example, Turner and Frederickson (2013) showed that while Trillium grandiflorum diaspores attracted more seed dispersers with higher oleic acid content, more ant worker death were reported compared to ants that dispersed diaspores of other myrmecochores. This study shows a significant detrimental effect to the ant in this relationship, and corroborates other work showing that signaling outweighs nutritional benefit when seeds are dispersed by ants (Pfeiffer et al. 2012). An isotope study form Clark and King (2012) also show that nutrition from elaiosomes is more facultative in nature; ants benefit more from elaiosomes when insect prey is not as abundant. An additional isotopic study revealed similar results, in that pupae production in Aphaenogaster senilis was not enhanced by supplementation of elaiosomes (Caut et al. 2013). While the benefits conferred to ants do not
constitute the main subject of this review, as these studies suggest, it is clear that the direct benefit gained from ants in the mutualism of myrmecochory remain unsolved.

**Benefits to plants**

In a much better fashion than for ants, plants have been shown to benefit in a number of ways through the mutualism of myrmecochory. Indeed, a thorough review of the topic describes the advantages gained by plants as the placement of seeds in an appropriate germination site: below ground, away from predators, and probably in enriched soil (Rico-Gray and Oliveira 2007). An overlooked portion of this model is the assumed importance and removal of elaiosomes, often by larvae within ant nests. When combined, the model depicted in Fig. 1 exemplifies the positive benefits gained by plants in this relationship. In short, foraging worker ants detect diasporpes (an intact seed with elaiosome attached), pick them up and carry them to the nest, where elaiosomes are consumed by larvae. Afterwards, seeds remain in the nest or are redispersed out of the nest to nearby midden piles (Beattie 1985; Hughes and Westoby 1992; Gomez and Espadaler 1998; Gorb *et al.* 2000), where they subsequently germinate and establish in nutrient-rich microsites. While numerous empirical and experimental studies attest to various facets of these ant-mediated advantages (see below), the advantages in this framework (1) are not consistent across all systems, and are sometimes ephemeral, (2) lack explicit mention of physical or chemical seed treatment, and (3) rarely if ever incorporate multiple participants, including not only multiple ant species (and ramifications thereof), but also involvement of
other taxa (e.g., microbes). As cast, the “perfect picture” of myrmecochory for plants posed in Fig. 1 has rarely been documented in its entirety; some examples come close (Aranda-Rickert and Fracchia 2011), while others fail to meet the standards (see Bas et al. 2007; Leal et al. 2007; Martins et al. 2009). Here, we confront the three aforementioned issues and in the process, pose a new framework to consider this classic coevolutionary relationship, in particular from the plant perspective.

**Figure 1.** The more commonly viewed and simple process of myrmecochory where ants take diaspores (seeds + elaiosomes) back to the nest, where elaiosomes are consumed by developing larvae, followed by subsequent seed germination in nutrient-rich environments.
The plant advantages of myrmecochory meet at the nexus of the 'directed dispersal' hypothesis and the 'nutrient enrichment' hypothesis. These hypotheses have been developed independently, and have been considered together in some vertebrate-mediated seed dispersal processes (Andresen 1999; Brewer and Rejmánek 1999; Chapman 1989; Chapman et al. 1992; Chavez-Ramirez and Slack 1994; Davidar 1983; Janzen 1986), though their intermingling is regularly posed in descriptions of myrmecochory. Howe and Smallwood (1982) first proposed the directed dispersal hypothesis as a phenomenon where adaptations of a diaspore ensure that the seed is taken to a more suitable site for establishment. The nutrient enrichment hypothesis was first developed in a myrmecochorous system by Beattie and Culver (1982), stating that seeds are placed in microsites that may be dense in available nutrients which allows for successful establishment as opposed to areas elsewhere. The primary advantages of ants moving seeds in this relationship include burial, escape from predators (which may or may not be tied to burial), and placement in enriched soil conferring higher germination success. Each of these has substantial backing in the literature.

Seed burial in myrmecochory is often intertwined with escape from dangers such as predators and fire. Positive effects of seed burial on seed survival have been determined experimentally in a number of systems, including a variety of forest and non-forest habitats in Spain (Manzaneda et al. 2005), deciduous forests of eastern North America (Kwit et al. 2012), and fire-prone fynbos in South Africa (Christian and Stanton 2004). In the latter case, deeper-buried
*Leucospermum truncatulum* seeds experienced less predation by granivorous rodents; however, this came with the caveat of remaining dormant in the seedbank (Christian and Stanton 2004). So even though burial within ant nests may translate into short-term escape from fire and predators, it may prove detrimental without redispersal (Renard *et al.* 2010).

Ants disperse seeds of myrmecochorous plants short distances, but these distances may be enough to escape distance-dependent predation. Based on 7889 observations from multiple studies, the mean ant-mediated seed dispersal distance currently ranks at 2.24 +/- 7.19 m, with variation depending on the vegetation found in the area studied and the ants observed in the relationship (Gomez and Espalder 2013). Andersen (1988) related observed seed dispersal distances and % frequency of the seeds found in ant nests. Since fitted models in Andersen (1988) resemble those of known optimal dispersal curves shown by Green (1983), and distances agree with scales that were shown by Antonovics *et al.* (1987) to respond well to environmental heterogeneity, dispersal away from the parent plants would be expected to be beneficial. The short dispersal distances provided by ants may also be complemented by enough integration of non-sib individuals such that distance- or frequency-dependent seed mortality may be offset (Kalisz *et al.* 1999).

Last, locations of ant seed dispersal have been documented as being nutrient-rich. The seed without its elaiosome is often assumed to be abandoned in the nest or a midden or pile in the immediate vicinity: a nutrient-rich environment, where probabilities of emergence and establishment are enhanced
(Beattie and Culver 1982, 1983; Beattie 1985; Smith et al. 1989; Woodell and King 1991; Hughes and Westoby 1992; McGinley et al. 1994). Being placed in a nutrient-rich microsite, can lead to some crucial benefits gained by the dispersed seed. For example, a study by Prior et al. (2014) showed that the longer that *Chelidonium majus* seeds remained in *Aphaenogaster rudis* nests, the more seedlings emerged. Seeds that remain in these nests have a longer time frame to take advantage of absorbing essential nutrients in such a nutrient enriched microsite. Emerging seedlings from these microsites have also been considered more numerous, healthy, and having a longer longevity (Beattie 1985). This has been exemplified by some studies, including those of the invasive *Euphorbia esula*, which was found in higher densities on *Formica obscuripes* ant mound soils, which contained higher levels of nitrogen and phosphorous than surrounding non-mound soils (Berg-Binder et al. 2012). Aside from being nutrient-rich, these ant nests may also provide preferred moist microhabitat conditions that are more suitable to germination. While some work has been done to clarify the exact benefits of the two players of this relationship, the exact benefits or whether these services always remain beneficial remains unclear.

**Inconsistencies in the Mutualism of Myrmecochoy**

While many of the cases above illustrate the utility of ants dispersing seeds of myrmecochores, they do not provide a consistent, all-encompassing view of plant benefits. Each of the aforementioned advantages conferred by ants can be thrown into suspicion when one considers that (1) benefits from seed burial are, in some cases, detrimental, and in many cases, ephemeral; (2) benefits from the
direct seed treatment of elaiosome removal are overstated; and (3) ants may involve other taxa into the equation for plant fitness.

**Seed burial**

Though ant-dispersed seed burial can lower probabilities of seed depredation, the locations of nest chambers can make any short-term benefits null and void. Many destinations may be too far underground for germination to ever take place. One study conducted by Renard *et al.* (2010) showed that *Ectatomma brunneum* ants in French Guinea would carry diaspores from *Manihot esculenta* subsp. *flabellifolia* 14 to 40 cm deep within chambers of the nest, where elaiosomes are consumed by their brood. Such depths are considered much too deep for successful germination to occur for this plant species. In addition to this, the microsites of nests of numerous seed-dispersing ant species are not conducive to seed germination and subsequent seedling establishment. In addition to nesting in leaf litter, the most prominent seed-dispersing ant genus in North America, *Aphaenogaster*, is known to nest in rotting logs and under rocks (Canner *et al.* 2012), both of which are inhospitable to establishment. This emphasizes the importance of ants redispersing the elaiosome-removed seeds to more favorable depths and/or microsites outside the nest. Very few studies, with the exception of Renard *et al.* 2010 and Servigne and Detrain 2010, actually follow seed destination into the nest, emphasizing the need for further empirical or experimental work on burial depths and their effects on seed germination.

The time ant-dispersed seeds remain in ant nests may be short in a number of cases. While redispersal of seeds out of ant nests and into middens or piles
has been documented (see above), new evidence points towards isotropic redispersal at short distances from the nest. Canner et al. (2012) showed that the keystone ant partner in myrmecochory in eastern North America, *Aphaenogaster rudis*, redisperses around 93% of handled seeds outside of the nest and into the surrounding leaf litter within one week of the primary dispersal event. Hence, ant-dispersed seeds may not gain a long- assumed, long-term benefit of remaining hidden below-ground in ant nest chambers, or the even longer-term, long-assumed advantage of nutrient-rich ant nest sites that would be advantageous post-germination. Short-distance isotropic redispersal from ant nests may still result in advantageous circumstances. Canner et al. (2012) emphasized that such redispersal away from ant nests can widen the spatial density of myrmecochorous seeds, which may lower the probability of seed predation by density-dependent predators, particularly mammals (see Heithaus 1981).

**Elaiosome removal**

Removal of elaiosomes is often posed as the most important direct treatment seed-dispersing ants provide to seeds. Indeed, a number of myrmecochorous plants, though not all, have been shown to benefit from the removal of elaiosomes (Table 1). Advantages include increased probabilities of seed germination, and the hastening of seed germination. In addition, seeds not having elaiosomes removed are exposed to higher predation risks, especially by mammals (Heithaus 1981; Garrido et al. 2009; Kwit et al. 2012). Much of the evidence therefore hints towards the importance of elaiosome removal, which is often assumed to take place in the nest of seed-dispersing ants. It should be
noted, however, that with the exception of the work conducted by Boyd (2001), the vast majority of the work on benefits of elaiosome removal have all involved experimental removal of elaiosomes by humans. Hence, there is little information known about the specific benefits of the direct physical handling of myrmecochore seeds by ants.

**Table 1.** Various studies showing the effects of ants “handling” seeds. (G = germination, SP = seed predation, E= emergence, + = advantageous to plant, - = disadvantageous to plant).

<table>
<thead>
<tr>
<th>Paper</th>
<th>Location</th>
<th>Plant Species</th>
<th>Ant Species Observed Handling</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prior et al. 2014</td>
<td>Deciduous forest southern Ontario</td>
<td>Chelidonium majus</td>
<td>Aphaenogaster rudies &amp; Myrmica rubra</td>
<td>G(+)</td>
</tr>
<tr>
<td>Cumberland &amp; Kirkman 2013</td>
<td>SW Georgia</td>
<td>common ground cover sp.</td>
<td>Solenopsis invicta</td>
<td>G(NS)</td>
</tr>
<tr>
<td>Kwit et al. 2012</td>
<td>Ohio, USA</td>
<td>Asarum canadense</td>
<td>Most likely Aphaenogaster rudis</td>
<td>SP(+)</td>
</tr>
<tr>
<td>Salazar-Rojas et al. 2012</td>
<td>CICOLMA Mexico</td>
<td>Turnera ulmifolia L.</td>
<td>Forelius analis</td>
<td>E(+)</td>
</tr>
<tr>
<td>Soriano et al. 2012</td>
<td>Central Apennine (Mediterranean, Euro-Siberian regions)</td>
<td>Moehringia papulosa</td>
<td>N/A</td>
<td>G(+)</td>
</tr>
<tr>
<td>Garrido et al. 2009</td>
<td>Iberian Peninsula</td>
<td>Helleborus foetidus</td>
<td>36 species mostly from Aphaenogaster, Camponotus, and Lasius</td>
<td>E(+),SP(+)</td>
</tr>
<tr>
<td>Cassaza et al. 2008</td>
<td>Italy, Argentina</td>
<td>Moehringia trinervia L., M. mucosa L., M. sedoideis, M. lebrunii</td>
<td>Lasius emarginatus, Pheidole pallidula, Crematogaster scutellaris</td>
<td>G(+)</td>
</tr>
<tr>
<td>Leal et al. 2007</td>
<td>Caatinga ecosystem (north-east Brazil)</td>
<td>Euphorbiaceae</td>
<td>Cyphomyrmex, Crematogaster, Dorymyrmex, Pheidole and Trachymyrmex species</td>
<td>G(+)</td>
</tr>
<tr>
<td>Imbert 2006</td>
<td>Massif de la Cape, near Narbonne (S of France)</td>
<td>Euphorbia characias,Centaurea corymbosa</td>
<td>Pheidole pallidula, Crematogaster scutellaris</td>
<td>G(-)</td>
</tr>
<tr>
<td>Christian &amp; Stanton 2004</td>
<td>fynbos shrublands of South Africa.</td>
<td>Leucospermum trancatulum</td>
<td>Anoplolepis custodiens, A. steingroveri, Pheidole capensis</td>
<td>E(NS), SP(+)</td>
</tr>
<tr>
<td>Passos and Ferreira 1996</td>
<td>semideciduous forest in S.E. Brazil</td>
<td>Croton priscus (Euphorbiaceae)</td>
<td>Atta sexdens and Pheidole</td>
<td>G(NS)</td>
</tr>
<tr>
<td>Espadaler &amp; Gómez 1996</td>
<td>Barcelona, Spain</td>
<td>Euphorbia characias</td>
<td>Pheidole pallidula, Aphaenogaster senilis, Tapinoma nigerrimum, Messor barbarus</td>
<td>SP(+)</td>
</tr>
<tr>
<td>Boyd 2001</td>
<td>central California</td>
<td>Fremontodendron decumbens</td>
<td>Messor andrei</td>
<td>G(NS), SP(+)</td>
</tr>
<tr>
<td>Castro et al. 2010</td>
<td>Alta Garroxa, Girona (Catalunya, Spain)</td>
<td>Polygala vayredae</td>
<td>Crematogaster scutellaris, Formica gagates</td>
<td>G(NS), SP(NS)</td>
</tr>
</tbody>
</table>
Other predators and participants

Mammals are cast as the primary seed predators of myrmecochores, but they may not be the only sources of mortality. The vast majority of studies addressing seed predation of myrmecochores emphasize that mammals, especially small rodents, are the primary sources of seed mortality (Reichman 1980; Heithaus 1981; Smith et al. 1989; Auld and Denham 1999; Fuchs et al. 2000). However, much like fruits and arils, elaiosomes likely attract fungi and bacteria that could cause issues with seed survival, especially in cases where diaspires are not dispersed (and elaiosomes are not removed). Dispersed and redispersed seeds will encounter soil microbes during the long time period (often > 6 months; Baskin and Baskin 2001) prior to germination. Rarely have pathogenic factors such as microbes been considered seed predators of myrmecochore seeds; this oversight is curious given their ubiquity as seed predators in a number of systems (Bell et al. 2006; Mangan et al. 2010; Tewksbury et al. 2008). It (see Fricke et al. 2014) has been suggested that gastropods may play an even more important role in myrmecochory than ants (Turke et al. 2012).
Little is known about what occurs to ant-dispersed seeds within ant nests, which has led to ant nests being referred to as “black boxes” (Servigne and Detrain 2010). Escape from predation may have more to do with ant seed-handling than previously thought. Numerous ant species have a paired set of glands called the metapleural glands, which have been shown to store a variety of antimicrobial compounds (Brown 1968; Beattie et al. 1986; Hölldobler and Wilson 1990; Veal et al. 1992; Mackintosh et al. 1995; Nascimento et al. 1996; Bot et al. 2002). While these glands are constantly secreting these antimicrobial compounds, ants have been shown to actively spread these secretions especially when there is a threat to fungal infection (Fernández-Marín 2006) and in instances of general nest and brood cleaning (Tranter et al. 2014). This being said, it is reasonable to question whether secretions from metapleural or venom glands poses any effect on the likelihood of handled seeds gaining resistance to microbial pathogens. If exposed to these secretions, seeds may have more of a chance to resists the many soil pathogens that may result in decreased livelihood of the seed or death altogether.

**Benefits of Myrmecochory Revisited**

Despite seed burial being ephemeral, elaiosome removal being inconclusive and not adequately tested, and seeds being subject to predators besides vertebrates, the importance of ants in myrmecochory may still be unequivocal. To better address the potential positive role of ants in myrmecochory, a shift in approaches is necessary (Fig. 2).
**Figure 2.** The less commonly understood and complex process of myrmecochory where seeds may be subjected to granivory and microbial/fungal predation, cleaned by ants through metapleural secretions and abandoned within the nest or redispersed elsewhere.

Elaiosomes provide a starting point for a new viewpoint of myrmecochory, and specifically the benefits ants provide myrmecochorous plants. While the chemical composition of elaiosome is known to be involved in attracting foraging ants to diaspores and enhance dispersal to ant nests, it may attract microbial predators as well. Appendages such as arils, which technically are a type of elaiosome (Lengyel *et al.* 2010), and fruits in general, are known to harbor microbes (see Oliveira *et al.* 1995) that may well inflict considerable mortality to
seeds (Augspurger 1990). Indeed, fungus-culturing ants that remove fruit pulp and arils from fallen fruits have been shown to significantly increase seed germination probabilities (Leal and Oliveira 1998), presumably by deterring fungal infection. Whether elaiosomes of myrmecochorous plants harbor microbes harmful or beneficial to the seeds they are attached to is unknown. Hence, the need to have elaiosomes quickly removed (e.g. consumed by larvae in nests) is the first test of ants’ important roles in myrmecochoory.

The framework to test the importance of elaiosome removal by ants, and the importance of ant seed dispersal for plants in general, needs to be cast in a series of steps, reflective of the pathways that seeds follow (Table 2). Once the diaspore is brought to the nest, the elaiosome portion is consumed by developing larvae. Historically, this act of elaiosome removal has been viewed as a critical step for subsequent germination; yet other possibilities involving ant ‘treatment’ of seeds during this process within ant nests have been neglected. This includes possible seed “cleaning” in cases where workers secrete antimicrobial compounds in nests (and in seed-dispersing ant cases, onto seeds) to protect the brood from fungal parasites (Tranter et al. 2014). The benefits of such “double duty” have not been adequately tested, and present the next series of tests of ants’ important roles in myrmecochoory.
Table 2. Areas to further research to better understand myrmecochory.

<table>
<thead>
<tr>
<th>Questions in need of future addressing in terms of plant benefits in myrmecochorous systems</th>
</tr>
</thead>
<tbody>
<tr>
<td>What are the chances that pathogens will kill the seed if left behind by the ant?</td>
</tr>
<tr>
<td>Are the ants providing anti-pathogenic properties to the seeds when handling diasporas?</td>
</tr>
<tr>
<td>Do plants benefit more from being left in the nest or moved outside?</td>
</tr>
<tr>
<td>Are seeds being redispersed in random/non-special areas or midden piles or are they nutrient dense?</td>
</tr>
<tr>
<td>What are specific effects of elaiosome being removed by ants rather than experimentally removed by researchers?</td>
</tr>
</tbody>
</table>

The relevance of elaiosome removal could well differ for seeds that remain in nests versus those that are redispersed to middens are random locations near ant nests. Elaiosome-removed seeds that remain in nests are less likely to be subject to vertebrate seed predation than those that are redispersed. As such, consumptive removal of elaiosomes and/or any seed treatment may be imperative for escape from microbial pathogens for seeds remaining in nests. For those that are redispersed, elaiosome removal and/or seed treatment may be important for escape from previously mentioned microbes as well as vertebrate predators.

Ultimately, any seed dispersal treatment a seed-dispersing ant provides that enhances seed survival will need to be followed by adequate seedling establishment. As ant nests continue to be documented as ephemeral locations for seeds, in particular for those that are redispersed (e.g. Canner et al. 2012),
the locations to examine for advantageous microsites needs to shift ever so slightly to areas near ant nests, rather than ant nests themselves. In cases where redispersal has been documented, it remains unclear if such locations are either more nutrient-rich or relatively freer of microbial pathogens than other areas in the systems where myrmecochores are found.

It may indeed be necessary to question myrmecochory as an ideal example of mutualism. There are still sections of this story not yet known and it is imperative to further delve into these questions. It is probable that this relationship is more of an evolved dependence (Mazancourt et al. 2005), with plants gaining more of a benefit from this relationship. By delving further into the details of myrmecochory, we may be able to further understand the phenomenon of coevolution. We hope that imminent knowledge gained can be applied to other systems where effects of seed treatment by dispersers are currently being pursued (e.g. Fricke et al. 2013).

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(Euphorbiaceae), a pioneer tree species in Brazil. *Sociobiology* **42**:597-603.


