Myrmecological News	20	129-140	Online Earlier, for print 2014

Ant-mediated seed dispersal: A few ant species (Hymenoptera: Formicidae) benefit many plants

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Abstract

Ants are ecosystems engineers, keystone species and incredibly abundant worldwide. A major cosmopolitan interaction between ants and plants is ant-mediated seed dispersal (myrmecochory). The interaction involves more than 11,000 plant species, but far fewer ant species, possibly just a few dozen keystone species worldwide. Researchers only began recognizing this degree of asymmetry in ant-mediated seed dispersal in recent years, and we explore the ecological and evolutionary implications of the changed perspective. We review what makes ants effective dispersers, how plants coevolve with ant partners, and how the interaction may benefit both participants. We suggest that morphological adaptations for myrmecochory have evolved repeatedly and independently in many plants lineages worldwide, and these trait adaptations likely select for effective seed dispersing ants. We propose that myrmecochory evolves and spreads only in ecosystems where the ant community includes potentially effective seed dispersers in high abundance. Furthermore, we hypothesize that the evolution and maintenance of the interaction only is possible where the distribution of traits between beneficial and antagonistic ants can fall under plant selection for the best partners.

Key words: Elaiosome, mutualism, myrmecochory, review, species interaction.

Myrmecol. News 20: 129-140
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 25 March 2014; revision received 1 June 2014; accepted 4 June 2014
Subject Editor: Chris R. Smith

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Introduction

Ants exist in high abundance and diversity worldwide, and they exert considerable impacts – beneficial and antagonistic – on co-occurring organisms and ecosystems (Folgarait 1998, del Toro & al. 2012). The interactions between ants and plants vary from antagonistic (e.g., granivory) to mutualistic (e.g., seed dispersal) (Rico-Gray & Oliveira 2007), the latter interaction prompted by plant evolution targeting ants (Azcarate & Manzano 2011). A unique plant guild (myrmecochores) employs a distinct seed appendage (elaiosome) that mainly attracts solitary foraging, non-granivorous ants and induces them to carry seeds back to their colony. Successful dispersal requires that the ants remove the elaiosome without damaging the seed, which usually is discarded belowground in, or near, the ant nest.

Myrmecochory evolved in more than 11,000 plant species worldwide (Lengyel & al. 2010), but the number of ant species that effectively disperse myrmecochore seeds is considerably less, likely around 100, depending on how the interaction is defined (Gove & al. 2007, Ness & al. 2009). For this review, we consider myrmecochory in the narrow sense of a mutualistic exchange of a resource for a service (Jones & al. 2012) where plants produce elaiosomes as a food reward for ants that disperse seeds (Warren & al. 2014). Morphological adaptations for myrmecochory have evolved repeatedly and independently in many plants lineages worldwide (Lengyel & al. 2009), likely toward the end of the Eocene (Dunn & al. 2007). Most (> 50%) myrmecochorous plants originate and occur in Australia and South Africa in arid habitats with nutrient-poor soils that support sclerophyllous vegetation (Rico-Gray & Oliveira 2007, Lengyel & al. 2009, Lengyel & al. 2010), but we found that most myrmecochory research occurs in the temperate regions, particularly eastern North America (Tab. 1). Recently, considerably more myrmecochory research has occurred in understudied ecosystems (e.g., Pizo & Oliveira 2001, Christianini & al. 2007, Barroso & al. 2013), particularly in South America and in the Mediterranean basin (Fig. 1).

Whereas myrmecochory first was acknowledged as an important dispersal mode early in the 20th century, systematic research of myrmecochory as a biotic interaction began making considerable progress since the late 70s in North America (Culver & Beattie 1978, Beattie & al. 1979, Marshall & al. 1979, Culver & Beattie 1980, Heithaus & al. 1980, Pudlo & al. 1980, Beattie & Culver 1981, Culver & Beattie 1983, Hanzawa & al. 1988, Handel & Beattie 1990) and in Australia (Westoby & al. 1991, Hughes & Westoby 1992, Hughes & al. 1994). More recently, reviews on myrmecochory focused on the

Tab. 1: Myrmecochore research emphasis worldwide. [a]Estimated from publications used for this review, [b]estimated from LENGYEL & al. (2010) (Fig. 1).

Biogeographic region	Myrmecochore publications[a]	Myrmecochore genera[b]	Major habitat
Paleotropical	7%	18%	Arid
Australian	16%	32%	Arid
Palearctic	18%	25%	Temperate
Nearctic	50%	8%	Temperate
Neotropical	5%	18%	Tropical

evolutionary and phylogenetic origin of the interaction (DUNN & al. 2007, LENGYEL & al. 2009, LENGYEL & al. 2010) and on its ecology and evolution (GORB & GORB 2003, GILADI 2006, RICO-GRAY & OLIVEIRA 2007, GOMEZ & ESPADALER 2013). Since then, a major paradigm shift has occurred in myrmecochory from considering it a diffuse mutualism involving many plant and ant species to an emerging view that recognizes that only a few, specific ant species provide effective dispersal services (GOVE & al. 2007, NESS & al. 2009).

We examined literature for this review that is focused on recent insights and ideas about myrmecochory. We started with papers that we deemed important because of their insightful treatment of relevant topics (e.g., GARRIDO & al. 2002 – "geographic variation in diaspore traits", GILADI 2006 – "partner choice", GOVE & al. 2007 – "keystone disperser"). We then examined recent and historical studies that prompted or examined newer ideas we deemed relevant to the study of myrmecochory. We structure the review by first addressing the major shift in myrmecochory research from diffuse (many ants and plants) to specific (few ants and many plants). We include an analysis of seed bait station experiments that demonstrates how methodological approach might bias results to make specific ant-seed interactions appear diffuse. Secondly, the realization that myrmecochory is an asymmetric interaction refocuses myrmecochory research on several new research directions (GILADI 2006, GOVE & al. 2007, MANZANEDA & REY 2009, NESS & al. 2009), including: (a) Effective dispersers – which ecological, morphological and behavioral traits make an ant species a keystone disperser for myrmecochorous plants? Which of these traits are sufficiently variable (especially among ant species) and can be targeted by myrmecochorous plants? (b) Partner choice – Which plant traits increase the frequency and intensity of interactions with high-quality dispersers and reduce interactions with poor dispersers and enemies? (c) Asymmetrical benefits – how does the interaction between plants and seed-dispersing ants benefit each partner? Finally, we finish the review with summary conclusions and suggestions for future myrmecochory research.

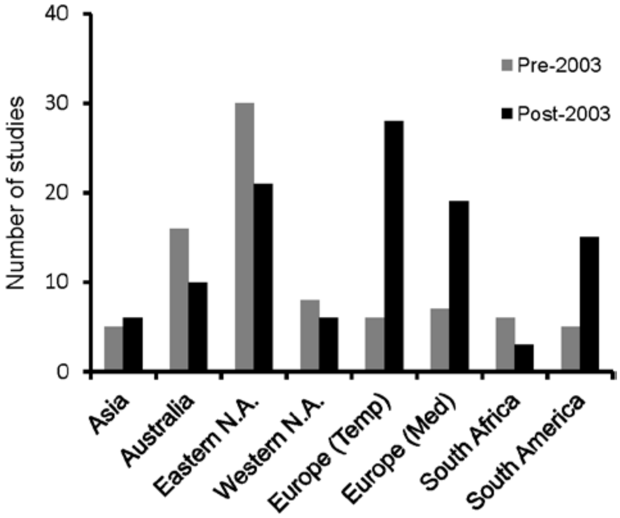

Fig. 1: Barplot showing the allocation of myrmecochory research effort by geographical region (number of published studies used for this review). Shifts in research emphasis are shown by presenting separately data for the last decade (post-2003) and for earlier publications (pre-2003). We used two categories for each of the most represented continents (North-America and Europe). Almost all the studies in eastern North America and temperate Europe were conducted in deciduous forest habitats, whereas studies in western North America and in Mediterranean Europe (mainly from the Iberian peninsula) were conducted in open habitats. The few studies included in the South-America category actually were conducted in tropical Central America.

The shift from diffuse to specific interaction in myrmecochory

"Obligate one-to-one mutualisms between species pairs are rare in practice and anomalous in theory." – HOWE (1984).

Species membership in ecological communities is (WALTHER & al. 2002), has been (ROOT & al. 2003) and will be (WILLIAMS & JACKSON 2007) largely transient. Spatial (THOMPSON 1994) and temporal (ROOT & al. 2003) instability in community compositions make nonsymbiotic, species-specific mutualisms unexpected and uncommon (HOWE 1984, JORDANO 1987, MORRIS 2003). Instead, animal-plant mutualisms often remain diffuse interactions with little specialization between specific species (HOWE 1984, JORDANO 1987). Myrmecochory long was considered a diffuse mutualism between scavenging ants and elaiosome-bearing plants (BERG 1966, HANDEL 1976, BEATTIE & al. 1979, BEATTIE & HUGHES 2002, GARRIDO & al. 2002) – the lack of pairwise specificity in ant-plant interactions presumably buffering it against environmental variability (BEATTIE & al. 1979). Worldwide, the number of plant species that utilize ant dispersal is, at least, an order

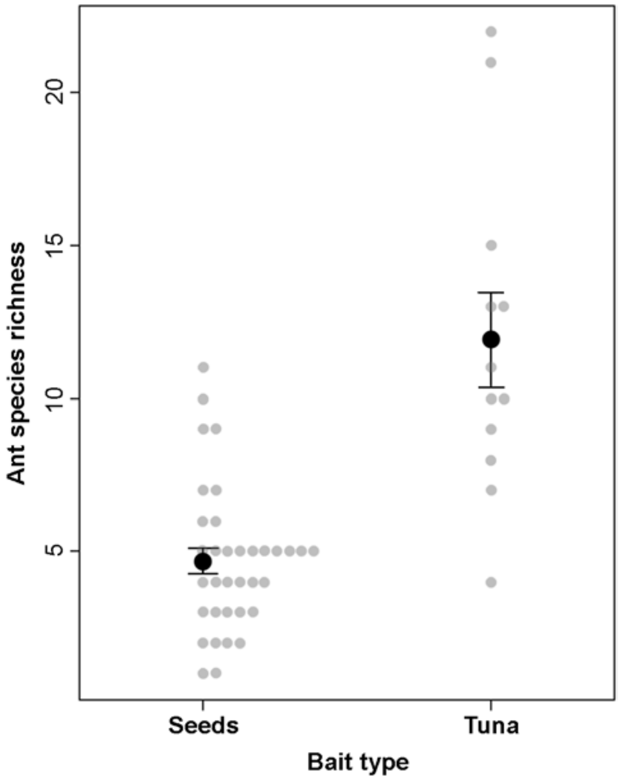

Fig. 2: Stripplot showing ant species richness (arithmetic mean ± standard deviation) at bait stations offering myrmecochore seeds with elaiosomes or tuna as an elaiosome proxy.

of magnitude higher than potential seed-dispersing ant species (see GORB & GORB 2003, RICO-GRAY & OLIVEIRA 2007 and references therein, LENGYEL & al. 2009). The great disparity between disperser ants and dispersed plants suggests little chance for the tight, pairwise coevolution that would create and maintain a specialized ant-plant seed mutualism (BEATTIE & HUGHES 2002). Still, spatial / geographic variation in the occurrence and strength of species interactions (SMITH & al. 1989a, b, BOULAY & al. 2006) could drive coevolutionary processes in diffuse mutualisms (THOMPSON 1994), as demonstrated in several well-studied myrmecochores (GARRIDO & al. 2002, FEDRIANI & al. 2004, MANZANEDA & al. 2005, BOULAY & al. 2006, 2007b, SERVIGNE & DETRAIN 2008).

Not all seed-dispersing ants are equally effective partners, however. Some ant species act as highly effective dispersers by rapidly finding and retrieving myrmecochore seeds to their nests without harming them; some ant species occasionally pick up seeds; and some species chew off the elaiosome without transporting the seed at all (ANDERSON 1988, ESPADALER & GOMEZ 1996, GARRIDO & al. 2002, BOULAY & al. 2007a). GOVE & al. (2007) and MANZANEDA & al. (2007) suggested that ant-mediated dispersal is only superficially diffuse, in contrast with much of the contemporary myrmecochory literature that considered ant-plant interactions non-specialized (HOWE & SMALLWOOD 1982, HANDEL & BEATTIE 1990, GARRIDO & al. 2002). GOVE & al. (2007) suggested that beneficial seed dispersal of myrmecochores might be dependent on specific ant taxa, "keystone dispersers". Subsequent research supports this perspective – many ant species may interact with myrmecochorous seeds, but only a small subset act as effective dispersers and dominate seed removal worldwide, such as Australia (GOVE & al. 2007, LUBERTAZZI & al. 2010, MAJER & al. 2011), North America (GILADI 2006, NESS & MORIN 2008, ZELIKOVA & al. 2008, NESS & al. 2009, WARREN & al. 2010), South America (YOUNGSTEADT & al. 2009, ARANDA-RICKERT & FRACCHIA 2011) and Europe (OOSTERMEIJER 1989, BARROSO & al. 2013) (Appendix S1, as digital supplementary material to this article, at the journal's web pages).

Whereas observational or conformational bias might overestimate diffusivity in myrmecochory interactions, we suggest that methodological approach also might introduce bias. For example, it is known that general methods for estimating ant species richness (e.g., pitfall traps) likely overestimate seed-dispersing ant richness by measuring general ant foraging frequency but not necessarily that of seed-dispersing ants (ALCANTARA & al. 2007). In order to focus on seed-dispersing ants only, many researchers use bait stations provisioned with elaiosomes, elaiosome proxies or other attractants (MARSHALL & al. 1979, SKIDMORE & HEITHAUS 1988, PIZO & OLIVEIRA 2001). Many myrmecochory studies employ tuna baits – relying on the fact that tuna contains chemical compounds similar to those in seed elaiosomes (see MARSHALL & al. 1979, BESTELMEYER & al. 2000).

We examined whether tuna baits may overestimate seed-dispersing ant richness by attracting competitive ants that generally overlook seeds. We evaluated papers used for this review and selected any that used seed and / or tuna bait stations to attract seed-dispersing ants. We did an additional ISI Web of Knowledge search using the terms "ant, tuna, seed dispersal and / or myrmecochory". We found 47 papers that investigated ant seed dispersers using myrmecochore seeds or tuna bait stations. We found that tuna bait studies attracted significantly more ant species than bait studies employing actual seeds (Fig. 2). SANDERS & GORDON (2000) noted that tuna baits create a much higher density and abundance of food than is found in the smaller, scattered elaiosome-bearing seeds in myrmecochore plant communities. Moreover, even when elaiosomes are used as baits, seed-dispersing ant richness may be overestimated if bait stations contain greater amounts of attractant than naturally occur (NESS & al. 2009).

New research directions

(a) Effective dispersers

Effective seed dispersers often are large scavenging or omnivorous ants that are attracted to elaiosomes. They typically forage individually and form small colonies. Effective dispersers benefit plant seed dispersal because they typically (1) are subordinate species that quickly discover and retrieve seeds before superior competitors interfere (MESLER & LU 1983, FELLERS 1987, ANDERSEN 1992, BOULAY & al. 2007a, NESS & al. 2009, ARANDA-RICKERT & FRACCHIA 2012), (2) exhibit predictable foraging schedules, either diurnally or annually, that correspond with myrmecochore seed release (BOULAY & al. 2007a, WARREN & al. 2011, ARANDA-RICKERT & FRACCHIA 2012) and (3) utilize the elaiosome without harming the seed – placing it in favorable conditions for germination and sur-

Fig. 3: Effective seed dispersers typically are highly abundant subordinate species that quickly discover and retrieve seeds before superior competitors interfere, they exhibit predictable foraging schedules that correspond with myrmecochore seed release, and they utilize the elaiosome without harming the seed. Shown here are two *Aphaenogaster fulva* ants with a *Sanguinaria canadensis* seed (eastern North America). Image © Alex Wild, used by permission.

vival (BEATTIE & CULVER 1982, HANZAWA & al. 1988). Ineffective seed dispersers often are (1) granivorous ants that forage in groups, recruit many workers to high quality resource patches and cache seeds in the nest or (2) elaiosome robbers that consume the elaiosome in place without providing any meaningful dispersal service (GILADI 2004, MANZANEDA & al. 2007, MANZANEDA & REY 2009).

Keystone seed dispersers such as *Rhytidoponera* spp. (Australia, GOVE & al. 2007), *Aphaenogaster* spp. (North America, NESS & al. 2009) and *Pogonomyrmex cunicularius* MAYR, 1887 (South America, ARANDA-RICKERT & FRACCHIA 2012) have all or most of the characteristics described above for effective dispersers (Fig. 3). Keystone dispersers generally remove > 75% of offered seeds (ZELIKOVA & al. 2008, NESS & al. 2009, WARREN & al. 2010) and provide dispersal services of high quality to the plant (HOWE & SMALLWOOD 1982, HANZAWA & al. 1988, GILADI 2006). In addition, keystone dispersers occur frequently (LYNCH & al. 1980, OOSTERMEIJER 1989, GOTELLI & ELLISON 2002, LUBERTAZZI 2012, KING & al. 2013), and often are among the most common ants in local communities (GOVE & al. 2007, NESS & al. 2009, LUBERTAZZI & al. 2010, ARANDA-RICKERT & FRACCHIA 2011, MAJER & al. 2011, KING & al. 2013).

Recent insights suggest some common traits in keystone dispersers that are frequently associated with efficient seed dispersal. Several important keystone dispersers relocate seeds after their initial arrival at the nest, such as, *Formica polyctena* FOERSTER, 1850 (Europe, GORB & al. 2000), *Aphaenogaster rudis* ENZMANN, 1947 (North America, CANNER & al. 2012), *Aphaenogaster senilis* MAYR, 1853 (Spain, BARROSO & al. 2013), *Rhytidoponera metallica* (F. SMITH, 1858) (Australia, WESTOBY & al. 1991, BEAUMONT & al. 2013), and *Rhytidoponera violacea* (FOREL, 1907) (Australia, LUBERTAZZI & al. 2010). Keystone dispersers are more likely to relocate seeds than non-effective seed dispersers (GORB & al. 2000, SERVIGNE & DETRAIN 2010, BEAUMONT & al. 2013). Relocation may be directed to specific or (apparently) random locations (GORB & al. 2000, LUBERTAZZI & al. 2010, CANNER & al. 2012, BARROSO & al. 2013, BEAUMONT & al. 2013). Relocation may reduce the probability that seeds benefit from ant nest placement, but it contributes to the reduction of negative density-dependence effects caused by the accumulation of seeds at an ant nest (SPIEGEL & NATHAN 2010, 2012).

Seed relocation also may occur within the nests of effective seed dispersers, such as *Pogonomyrmex cunicularius* (see ARANDA-RICKERT & FRACCHIA 2011) and *Myrmica rubra* (LINNAEUS, 1758) (SERVIGNE & DETRAIN 2010) after the elaiosomes are removed and fed to the larvae. The placement of discarded food items in refuse chambers is a nest hygiene behavior commonly observed in carnivorous ants (FOKUHL & al. 2007, SERVIGNE & DETRAIN 2010),

Fig. 4: In temperate North America and Europe, myrmecochorous species generally flower early in spring and set fruit in synchrony with early season ant foraging. Shown here is *Trillium vaseyi*, USA (photo by Robert Warren).

and the refuse chambers commonly occur at depths favorable for plant germination and survival.

Several studies suggest that the colony size of effective seed dispersing ants is small, around a few hundred workers (GILADI 2006, FOKUHL & al. 2007, MAJER & al. 2011, KING & al. 2013). Seed dispersing ants may build nests in very tiny structures, such as hickory nutshells (*A. rudis*, I. Giladi, unpubl.) or snail shells (*M. rubra*, see FOKUHL & al. 2007). The relatively small colonies are highly mobile as many keystone disperser ants frequently relocate their nests (WESTOBY & al. 1991), such as *A. rudis* (eastern North America, NESS & al. 2009), *A. senilis* (Spain, GALARZA & al. 2012), *Rhytidoponera* spp. (Australia, HUGHES 1990) and *P. cunicularius* (Argentina, ARANDA-RICKERT & FRACCHIA 2011), but not *Camponotus vagus* (SCOPOLI, 1763) (MANZANEDA & REY 2012). Ant colony transience may benefit plant fitness because the accumulation of seeds near a stationary ant nest can increase negative density-dependence effects (e.g., increasing interspecific competition and predation pressure) that may outweigh potential benefits from the nest environment (e.g., nutrient rich soil).

(b) Partner choice

The disproportional dependence of plants on a few, high quality, effective seed dispersing ants (GILADI 2006, GOVE & al. 2007, ZELIKOVA & al. 2008, BAS & al. 2009, NESS & al. 2009) should prompt coevolved mechanisms for attracting specific mutualist partners to plant seeds (HANZAWA & al. 1988, BURNS 2002, HERRERA 2002, PALMER & al. 2003, GILADI 2006, ARANDA-RICKERT & FRACCHIA 2011). Such a partner choice may evolve when variation in plant traits matches variation in the ant traits that differentiate effective from poor seed dispersing ants. ARANDA-RICKERT & FRACCHIA (2012) suggested that plant traits under selection by specific ants in a community might include seed and elaiosome size and chemistry (GARRIDO & al. 2002, BOULAY & al. 2006, 2007b), and seed phenology and presentation (HUGHES & WESTOBY 1992, OBERRATH & BOEHNING-GEASE 2002, GUITIAN & GARRIDO 2006, BOULAY & al. 2007a).

Seed removal rates and dispersal distances generally are positively correlated with seed size, elaiosome size and / or the elaiosome / seed ratio (DAVIDSON & MORTON 1981, GUNTHER & LANZA 1989, OOSTERMEIJER 1989, MARK & OLESEN 1996, RUHREN & DUDASH 1996, GORB & GORB 2003, PETERS & al. 2003, BAS & al. 2009, WARREN & al. 2014). Ants may disperse seeds that offer bigger rewards, and larger seeds can attract larger ants that carry seeds longer distances (LEAL & al. 2007). Seed size may facilitate effective dispersal if high-quality dispersers prefer seeds of a different size than poor seed dispersers (LEAL & al. 2014). In some regions, especially in myrmecochory hotspots, high-quality seed dispersers are relatively larger ants that prefer larger seeds, such as *Aphaenogaster* spp. (North America, NESS & al. 2009), *A. senilis* (Spain, BAS & al. 2009), *Camponotus cruentatus* (LATREILLE, 1802), *Formica lugubris* ZETTERSTEDT, 1838 (Spain, MANZANEDA & REY 2009), *A. famelica* (SMITH, 1874) (Japan, TAKAHASHI & ITINO 2012), and *F. poly-*

ctena (Europe, GORB & GORB 1995) [Appendix S1]. Where effective dispersers are larger, producing larger seeds may select for better partners.

Viewing large seed size as an adaptation toward improving seed dispersal may be too simplistic, however (BOULAY & al. 2007b). Ants may exert conflicting selection pressure on seed size, as the probability of being dispersed may be highest for large and small seeds, but successful plant establishment in the ant nest most likely for medium size seeds (MANZANEDA & al. 2009). Seed size in ant-dispersed species is limited by the jaw gape of the dispersing ants, as exemplified by the relatively narrow range of myrmecochore seed sizes worldwide (MOLES & al. 2005), and size-matching between ants and seeds occurs in several systems (SERVIGNE & DETRAIN 2008, BOIEIRO & al. 2012). Nevertheless, dispersal services by smaller ants often are quantitatively and qualitatively poorer than those provided by larger ants (GORB & GORB 1995, ALCANTARA & al. 2007). In general, larger ants provide relatively longer-distance dispersal for obligate myrmecochores, whereas small ants provide secondary dispersal for plants with other primary dispersal modes (GORB & GORB 1995, TAKAHASHI & ITINO 2012).

Plants also might target specific ants by matching seed release timing with foraging activity. Most research into possible synchrony between myrmecochorous seed release and ant foraging has occurred in North American and European temperate regions. Researchers have found that, across temperate continents, myrmecochorous species generally flower early in spring and set fruit weeks to months before non-myrmecochorous species (BEATTIE & CULVER 1981, HANDEL & al. 1981, THOMPSON 1981, TURNBULL & CULVER 1983, HEITHAUS 1986, HANDEL & BEATTIE 1990, GORB & GORB 1998, OBERRATH & BOEHNING-GEASE 2002, GORB & GORB 2003, GUITIAN & GARRIDO 2006, WARREN & al. 2014) (Fig. 4).

Elaiosomes may act as a dead insect analogue when resources are scarce (CARROLL & JANZEN 1973, HUGHES & al. 1994, RUHREN & DUDASH 1996, BOULAY & al. 2007a, CLARK & KING 2012) between late winter / early spring when temperatures begin to rise and ants break dormancy to forage (BEATTIE & CULVER 1981, GILADI 2006, WARREN & al. 2011, CLARK & KING 2012) and mid-to-late summer when the availability of alternate food sources (insect corpses and other scavenge) reduces ant interest in elaiosomes (CARROLL & JANZEN 1973, CULVER & BEATTIE 1978, GORB & GORB 2003, BOULAY & al. 2005, GUITIAN & GARRIDO 2006, WARREN & al. 2014). The myrmecochore seed set "window" also may be a balance between ant foraging abundance, which increases with the season, and seed predator abundance (rodents, beetles, granivorous ants), which also increases with the season, so that early seed release is a trade-off between available seed dispersers and seed predators (OHKAWARA & al. 1997).

Myrmecochore seed release appears synchronized with peak activity in effective (versus ineffective) seed-dispersing ants (TURNBULL & CULVER 1983, ESPADALER & GOMEZ 1996, OBERRATH & BOEHNING-GEASE 2002, GORB & GORB 2003, GUITIAN & GARRIDO 2006, BOULAY & al. 2007a but see RUHREN & DUDASH 1996). In temperate regions, early season seed set may be a mechanism by which plants synchronize seed release with specific, effective seed dispersing ant species (GILADI 2004). Seed-dispersing ants typically are subordinate species that tolerate suboptimal conditions (PARR & GIBB 2009), and in temperate regions, early spring and early in the day are the coldest periods for ant foraging, and seem to be when effective, subordinate seed dispersers are most active (TURNBULL & CULVER 1983, ZELIKOVA & al. 2008, NESS & al. 2009, WARREN & al. 2011). Alternately, subordinate species generally are scavengers, and scavengers may prefer extreme conditions as foraging success increases (CERDÁ & al. 2013). Similarly, the seed dispersing ant species of Australia forage early in the day when temperatures are cool to avoid competition with more competitive ants (GOVE & al. 2007, MAJER & al. 2011), though the seasonal foraging window is longer in Australia than in the temperate regions, and flowering phenology does not differ between myrmecochores and non-myrmecochores (MAJER & al. 2011).

WARREN & al. (2011) found that species-specific temperature cues prompted synchrony between myrmecochore seed release and spring foraging by keystone seed dispersers (*Aphaenogaster* spp.) in eastern North American forests. However, individual *Aphaenogaster* species have species-specific temperature limits and hence unique foraging cues (WARREN & al. 2011). Where early blooming myrmecochores set seed with an asynchronous *Aphaenogaster* sp., seed dispersal failed (WARREN & BRADFORD 2013). The failed dispersal coincided with failing plant populations at the species range edge (WARREN & BRADFORD 2013).

Specificity in partner choice is clearly disrupted by ant species replacement. Successful ant invaders generally are smaller than the native ants they displace (MCGLYNN 1999, HOLWAY & al. 2002). The loss of large ant species in invaded communities not only prevents the dispersal of large seeds, but also leaves the seeds exposed to the smaller exotic ants that consume the elaiosome without dispersal (ROWLES & O'DOWD 2009). Moreover, invasive ant species often possess a unique combination of traits that remove the selection pressure on partner choice between effective and ineffective dispersers (QUILICHINI & DEBUSSCHE 2000, GOMEZ & al. 2003, GUENARD & DUNN 2010, MAJER & al. 2011, RODRIGUEZ-CABAL & al. 2011). As a result, seed dispersal is significantly altered or even collapses in myrmecochore communities invaded by exotic ants (CHRISTIAN 2001, CARNEY & al. 2003, GOMEZ & al. 2003, NESS 2004, GUENARD & DUNN 2010, RODRIGUEZ-CABAL & al. 2011).

(c) Asymmetrical benefits

Ant dispersal benefits plants through the seed movement itself and / or by placing the seeds in establishment-friendly microhabitats (HOWE & SMALLWOOD 1982, HANZAWA & al. 1988, GILADI 2006). The most often reported benefit derived from myrmecochory is seed "predator avoidance" (e.g., HEITHAUS 1981, BOND & BREYTENBACH 1985, SMITH & al. 1986, OHKAWARA & al. 1997, NESS & BRESSMER 2005, KWIT & al. 2012), but many studies find no such protection (e.g., HORVITZ & SCHEMSKE 1986, RUHREN & DUDASH 1996, GILADI 2006). The "directed dispersal" hypothesis also considers safe nest placement the major plant benefit from ant-mediated dispersal (CULVER & BEATTIE 1983). Directed dispersal suggests that seed placement in nutrient enriched ant colony soil enhances seedling germination and survival, especially in low-nutrient habitats (but see RICE & WESTOBY 1986, BOND & STOCK 1989). "Distance dispersal" benefits plants by the movement of seeds itself, particularly away from parent plants (JANZEN 1970, CONNELL 1971) presumably reducing parent-offspring and sibling competition (HANDEL & BEATTIE 1990, GORB & GORB 2003, GILADI 2006, NESS & MORIN 2008), as well as providing other distance-dependent benefits such as escape from the accumulation of pathogens in proximity to parent plants (JANZEN 1970, CONNELL 1971). Such movement, often no more than 1 - 2 m (GOMEZ & ESPADALER 2013), also impacts gene flow (BEATTIE 1978, KALISZ & al. 1999, ZHOU & al. 2007). Whereas several authors suggest that plant benefits from ant dispersal appear geographic or habitat-specific (GILADI 2006, RICO-GRAY & OLIVEIRA 2007), we found the reported benefits spread rather evenly between continents, except for fire avoidance, which is primarily reported as beneficial in arid Australian and South African habitats (e.g., BOND & SLINGSBY 1983, HUGHES & WESTOBY 1992).

The ejection of myrmecochore seeds from apparently effective disperser nests and secondary dispersal (relocation) are not new observations (HEITHAUS 1986, GOMEZ & ESPADALER 1998), but most emphasis on plant benefits from myrmecochory focused on the nest environment as the final target of seeds dispersed by ants (RICE & WESTOBY 1981, BEATTIE & CULVER 1982, CULVER & BEATTIE 1983, HORVITZ & SCHEMSKE 1986, RICE & WESTOBY 1986, HANZAWA & al. 1988, WENNY 2001). The ubiquity of seed relocation by keystone dispersers only recently has been recognized (GORB & al. 2000, LUBERTAZZI & al. 2010, CANNER & al. 2012, BARROSO & al. 2013, BEAUMONT & al. 2013). That many seeds dispersed by keystone dispersers do not germinate within the ant nest or its vicinity should lead to a careful reassessment of ant nests as safe sites for germination (CANNER & al. 2012).

A growing consensus among researchers suggests that myrmecochore interactions are obligate for plants and facultative for ants (NESS & al. 2009, CLARK & KING 2012, BARROSO & al. 2013, CAUT & al. 2013). Whereas myrmecochores rely on ants for numerous benefits, and exhibit deleterious results when ants are lacking or excluded (WARREN & al. 2010, ZELIKOVA & al. 2011, WARREN & BRADFORD 2013), seed-dispersing ants exhibit no dependence on plants (MITCHELL & al. 2002, BRONSTEIN & al. 2006, NESS & al. 2009). Elaiosome retrieval does seem to impact ant colonies. Ants generally use elaiosomes as larval food, and ant colonies given supplemental elaiosomes may have higher brood size, larger larva and experience a shift in colony sex ratios toward female alates (MORALES & HEITHAUS 1998, BONO & HEITHAUS 2002, GAMMANS & al. 2005, FISCHER & al. 2008). However, almost as much work suggests this shift might not be a general pattern (BREW & al. 1989, MARUSSICH 2006, FOKUHL & al. 2007, CLARK & KING 2012, CAUT & al. 2013). Shifting sex ratios toward gynes may cause demographic changes in ant population structure (KELLER & PASSERA 1989), but data showing any effect of elaiosomes on ant colony fitness, persistence or distribution are lacking.

Supplementing ant diets with elaiosomes may just provide ants with additional food rather than providing a specific elaiosome-derived benefit (BONO & HEITHAUS 2002, DOS SANTOS FARNESE & al. 2011, CLARK & KING 2012, CAUT & al. 2013). Such supplementation might aid ant colonies when other food sources are scarce (CLARK & KING 2012), such as early spring in temperate forests (CARROLL & JANZEN 1973, GORB & GORB 2003, BOULAY & al. 2005, GUITIAN & GARRIDO 2006). Supplementing ant colonies with elaiosomes in laboratory conditions does not account for the foraging costs (e.g., energy spent in search and retrieval, mortality) incurred in natural settings (e.g., EDWARDS & al. 2006). Alternately, the chemicals in elaiosomes might just be attractants that change ant behavior (e.g., by mimicking dead insects) to provide dispersal services without delivering an appreciable benefit (MARSHALL & al. 1979, BREW & al. 1989, HUGHES & al. 1994, PFEIFFER & al. 2010). Indeed, PFEIFFER & al. (2010) found that myrmecochore "cheaters" can elicit seed dispersal by ants with no appreciable reward. Similarly, in comparing among several myrmecochores, TURNER & FREDERICKSON (2013) found that seed attractiveness to ants did not correlate with ant benefits, suggesting that some attractive myrmecochores do not provide any benefits at all to ants. Future research should assess ant colony health and demography to determine how elaiosome consumption impacts ant colony health and location under field conditions (CAUT & al. 2013).

Summary and suggested research directions

A relatively recent paradigm shift in myrmecochory changed the research perspective from viewing the interaction as a diffuse mutualism between a guild of plants and a group of seed dispersers to recognizing that a few keystone ant species perform most dispersal services (GOVE & al. 2007). As a result, linked myrmecological research areas emerged or re-emerged, and we highlighted three here: (a) effective dispersers, (b) partner choice and (c) asymmetrical benefits. We propose that myrmecochory evolves and spreads only in ecosystems where the ant community includes potentially effective seed dispersers in high abundance. Furthermore, we hypothesize that the evolution and maintenance of the interaction is only possible where the distribution of traits between beneficial and antagonistic ants can fall under plant selection for the best partners.

A key assumption in our hypotheses is that currently observed interactions – which themselves require additional empirical verification – reflect historical evolutionary pressures in shaping ant-plant relationships. Current ant and plant distributions, and their current abiotic and biotic contexts, may not accurately reflect past environmental conditions and distributions and hence may not accurately represent a map of the selection pressures that structured the evolution of this interaction. An immediate research focus should be toward how widespread and to what degree do plants exert selection pressure for protagonist ants and against antagonist ants. However, a second recent paradigm shift is the recognition that myrmecochory is necessary for the plants but not so much for ants. If so, then evolutionary pressure should be much greater on plants than ants. In that respect, it is interesting to note that many plant species invest in the production of the elaiosome, a structure whose main presumed function is the attraction of seed dispersing ants, but we know of no specific adaptation in ants that is targeted for specifically utilizing elaiosome-bearing seeds. For example, some authors suggest that the synchrony between seed release and peak beneficial ant activity is a pre-adaptation that allowed myrmecochory to evolve (BOULAY & al. 2007a, b). WARREN & al. (2014) showed that plants compete for ant dispersers, with small seeded plants on the losing end so that flowering phenology is staggered. We suggest that further research is needed on the interplay between ant and plant selection pressures on one another.

Moreover, given that myrmecochory research is heavily biased toward temperate ecosystems, we suggest that the field requires cosmopolitan research into ant and plant selection pressures focusing on less studied myrmecochory hot spots such as Australia and South Africa. Finally, while searching for universal patterns that define effective seed dispersers, researchers should assume that selection pressures and partner benefits might be contingent by system or geography and differences in effective seed dispersers may be as interesting as similarities (GARRIDO & al. 2002, FEDRIANI & al. 2004, BOULAY & al. 2006, ALCANTARA & al. 2007, BOULAY & al. 2007b). Researchers might also ask to what degree ant phylogeny explains dispersal efficiency and whether the strength in ant-plant interactions varies by species, geography and / or phylogeny.

Recent findings suggests some additional keystone ant characteristics worth research, such as a second phase of dispersal by ants that redistributes seeds within and outside the nest, frequent colony relocation and a high level of nest hygiene more typical of insectivorous ants (ARANDA-RICKERT & FRACCHIA 2012). BARROSO & al. (2013) proposed an interesting idea that links ant diet with seed dispersal efficiency. They noticed that unlike many other ant species, high-quality seed dispersers may be incapable of trophallaxis (i.e., the ability to carry liquid food) and thus they are "forced" to carry elaiosomes to their brood in the nest.

Elaiosomes generally attract carnivorous / scavenging ant species that consume the elaiosome without consuming the seed itself (CULVER & BEATTIE 1980, HUGHES & WESTOBY 1992, GIBSON 1993). Variation in elaiosome chemical composition, especially oleic acid content, may significantly increase seed dispersal by efficient seed dispersing ants (PIZO & OLIVEIRA 2001, BOULAY & al. 2006, 2007b, CHRISTIANINI & al. 2007, MANZANEDA & REY 2009), but not by granivorous ants (GAMMANS & al. 2006). Most studies linking variation in elaiosome chemistry with ant seed dispersal behavior focus on efficient dispersers or on the ant community as a whole, but do not include comparisons between efficient and potentially inefficient seed dispersers. Direct tests of the partner choice through elaiosome chemistry remain lacking (but see GAMMANS & al. 2006).

Plants commonly trick insects into self-serving behaviors (BRONSTEIN & al. 2006, EDWARDS & YU 2007), including behaviors that result in no appreciable benefit for the insects (SCHAFER & RUXTON 2009, URRU & al. 2011). Recent evidence suggests that classic ant-plant mutualisms are not as cooperative as once thought. *Pseudomyrmex ferrugineus* (F. SMITH, 1877) ants protect *Acacia* spp. in exchange for nutritive nectar; however, *Acacia* spp. manipulate *P. ferrugineus* into dependence (HEIL & al. 2014) – making the interaction as much exploitive as mutualistic. Overwhelmingly, mymecochory research focuses on plant benefits with far fewer studies examining ant benefits. Based on recent work (e.g., HEIL & al. 2014), we suggest that greater empirical research is needed to verify to what degree ants benefit from myrmecochory.

Acknowledgments

We thank Chris Smith, Brent Smith, Raphaël Boulay, Alexei Rowles and an anonymous reviewer for helpful comments that improved this manuscript. This is publication No. 839 of the Marco and Louise Mitrani Department of Desert Ecology.

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Digital supplementary material to

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Appendix S1: Ant species recognized (or proposed) as keystone seed dispersers. Support for keystone recognition is categorized as "overwhelming" (consistently confirmed by many studies at many sites and, usually, by several study groups); "intermediate" (several studies focus on the role of a specific ant species in seed dispersal/removal but more data are needed establishing dispersal effectiveness); and "limited" (keystone disperser role is suggested but limited geographically or only reported in a single study).

Disperser type is defined as "classic" when there is a substantial accumulation of support that an ant species is both the main seed remover of myrmecochorous seed and that the plant benefits from that interaction. Classic disperser ants typically have most traits associated with high quality seed dispersal. Some species appear keystone dispersers based on high removal rates, but the efficiency of the dispersal (i.e., it benefits the plant) is not confirmed ("effective seed removers"). Some authors use the term: "legitimate dispersers" to describe effective seed dispersers that have some traits suggesting a positive effect on seeds, but their status as keystone dispersers remains undetermined.

Ant species	**Ecosystem**	**References**	**Degree of support**	**Disperser type**	**Comments**
Aphaenogaster rudis complex	Deciduous forest, Eastern North America	NESS & al. (2009)	Overwhelming	"classic" seed disperser	
Formica polyctanea (FOERSTER, 1850)	Deciduous forest, Eastern Europe	GORB & GORB (1995, 2003)	Overwhelming	"classic" seed disperser	
Rhytidoponera metallica (F. SMITH, 1858)	Sandplain shrubland, Western Australia	GOVE & al. (2007)	Overwhelming	"classic" seed disperser	
Rhytidoponera violacea (FOREL, 1907)	Sandplain shrubland, Western Australia	GOVE & al. (2007), LUBERTAZZI & al. (2010)	Overwhelming	"classic" seed disperser	
Rhytidoponera inornata (CRAWLEY, 1922)	Sandplain shrubland, Western Australia	MAJER & al. (2011)	Overwhelming	"classic" seed disperser	
Anoplolepis custodiens (F. SMITH, 1858)	Fynbos, South-Africa	BOND & SLINGSBY (1983), CHRISTIAN (2001)	Overwhelming	"classic" seed disperser (?)	Many traits fit keystone disperser traits.
Melophorus turneri perthensis (W.M. WHEELER, 1934)	Sandplain shrubland, Western Australia	MAJER & al. (2011)	Intermediate	"classic" seed disperser	
Aphaenogaster longiceps (F. SMITH, 1858)	Open woodland, Newsouth Wales, Australia	ANDERSEN (1988), HUGHES (1991), HUGHES & WESTOBY (1992)	Intermediate	Effective seed remover	Some traits of classic keystone disperser.
Myrmica rubra (LINNAEUS, 1758)	Deciduous forest, Europe (invasive in NA)	SERVIGNE & DETRAIN (2008)	Intermediate	Legitimate disperser	Some traits of classic keystone disperser.
Pogonomyrmex cunicularius (MAYR, 1887)	Open semi-arid shrubland, Argentina	ARANDA-RICKERT & FRACCHIA (2011, 2012)	Limited	Effective seed remover	Studied over limited geographic extent. Some characters fit "classic" keystone disperser traits.
Formica lugubris (ZETTERSTEDT, 1838)	Temperate mountainous scrubland, North-Western Spain	BOULAY & al. (2006), MANZANEDA & REY (2009)	Limited	Legitimate disperser	Studied over limited geographical extent.
Camponotus vagus (SCOPOLI, 1763)	Temperate mountainous scrubland, North-Western Spain	MANZANEDA & REY (2012)	Limited	Legitimate disperser	Studied over limited geographical extent. High survival of seedlings around nest of this ant species.
Camponotus cruentatus (LATREILLE, 1802)	Mediterranean scrubland and mixed forest, Central-southern Spain	BOULAY & al. (2006), MANZANEDA & REY (2009)	Limited	Legitimate disperser	Studied over limited geographical extent.
Ectatomma brunneum (F. SMITH, 1858)	Tropical Savannah, French Guiana	RENARD & al. (2010)	Limited	Effective seed remover	Studied over limited geographical extent. Some traits that fit keystone disperser.

Pheidole capensis (MAYR, 1862)	Fynbos, South-Africa	BOND & SLINGSBY (1983), CHRISTIAN (2001), BOTES & al. (2006)	Limited	Effective seed remover	
Aphaenogaster senilis (MAYR, 1853)	Mediterranean scrubland, Spain	GOMEZ & ESPADALER (1998), BAS & al. (2009), BARROSO & al. (2013)	Contradictory	Effective seed remover	Remove seeds of both myrmecochores and non-myrmecochores. Some evidence for negative effect on seeds.

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