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Ant-dispersed herbs (myrmecochores) can account for more than one-third of the stems in the temperate deciduous forests of eastern North America. Because many ant species have been observed collecting the seeds, this interaction is often described as a generalized mutualism. Here, we combine fieldwork and meta-analyses to test this assumption. Our meta-analysis demonstrated that *A. niger* ants (predominantly *A. niger*) collect approximately $74 \pm 26\%$ (mean \pm SD) of the myrmecochorous seeds in eastern North American forests where any encounters with *A. niger* were reported, and approximately $61 \pm 37\%$ of the seeds in all the eastern forests where any seed collection has been monitored. This remarkable monopolization of seeds is due to at least two factors: 1) *A. niger* are significantly more likely to collect the ant-adapted seeds they discover than are ten other ant genera found in these forests and 2) the densities of *A. niger* and myrmecochorous plants are positively correlated at three nested spatial scales (within 20×20 m patches, among patches within a forest, and among 41 forests in the eastern United States). Although other ants can collect seeds, our analyses demonstrate that *A. niger* is the primary seed dispersal vector for most of this rich temperate

of the eastern United States (Beattie and Culver 1981, Handel et al. 1981) and densities can be similar in comparable biomes in northern Europe and Japan. Richness can be even greater in drier biomes in South Africa and Australia. The morphological features associated with myrmecochory have evolved at least twenty times in the monocots (Dunn et al. 2007). As befits such diversity, myrmecochorous seeds vary in a number of ways (Giladi 2006), including 1) shape and weight, 2) food reward (caloric and nutritional content of elaiosomes), 3) presentation (e.g. diurnal and monthly phenologies, passively dropped vs ballistically dispersed) and 4) histological origin of the elaiosome. This variation does not distinguish myrmecochory from other mutualisms; that myrmecochory exhibits the same range of specialization, generalization and among-site heterogeneity in animal partners as other plant mutualisms is a reasonable null hypothesis.

Here, we describe the variation in these ant-plant mutualisms within the temperate deciduous forests of North America, complementing recent macro-ecological studies of myrmecochory that focused on the Mediterranean (Rey and Manzaneda 2007) and Australia (Gove et al. 2007). We test the hypothesis that one particular ant, *A. niger*, is a 'keystone mutualist' to myrmecochorous plants throughout the temperate deciduous forests of North America. Such a relationship has been implied by work in several sites in West Virginia (Beattie and Culver 1981), North Carolina (Zelikova et al. 2008) and Georgia, USA (Giladi 2004, Ness 2004). First, we contrast the likelihood of seed collection by *A. niger* with that by other North American ants. Second, we test the hypothesis that richness and density of myrmecochores in North American temperate deciduous forests are positively correlated with the distribution of *A. niger* ants within and among forests.

Last, we contrast the partner specialization reported for myrmecochory in North American temperate deciduous forests (the biome occupied by *A. niger*) with that in other well-studied plant-animal mutualisms including pollination and frugivory in temperate biomes, myrmecochory in sclerophyllous habitats, tropical ant-plants and extrafloral nectary-bearing plants. Intriguingly, no study of myrmecochory we are aware of takes a community-wide perspective, one that would facilitate a description of the network structure of the ant-seed interaction web for the myrmecochorous plant and ant communities at a particular site and permit comparisons with other mutualistic networks (Bascompte and Jordano 2007). Although such comparisons have been made in reference to ant gardens (the formation of which involve seed collection by ants, although perhaps without seed-associated rewards; Youngsteadt et al. 2008) and ants collecting seeds from fleshy, vertebrate-dispersed fruits or frugivore feces (Blüthgen et al. 2007, Guimarães et al. 2007), neither of these are myrmecochorous in the conventional sense. Here, we quantify plant partner diversity (i.e. the richness and relative frequency of prospective plant mutualists) to test the hypothesis that myrmecochory in temperate deciduous forests is more specialized than an analysis of fruit/seed dispersal (Wheelwright and Orians 1982, Blüthgen et al.

2007) or a characterization e

discoveries per patch, and richness (plant or ant) as the number of genera observed within the patch.

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The meta-analysis included studies performed in 41 forests in North America including North Carolina (Mitchell et al. 2002), West Virginia (Beattie and Culver 1981), Ohio (Heithaus and Humes 2003, S. Philpott pers. comm.), New York (Ellison et al. 2007), and Massachusetts and Vermont (Gottelli and Ellison 2002). These studies were chosen because they provide data on 1) the identity of ants attracted to tuna baits and 2) herbaceous plant communities, and we used these data to identify the richness of myrmecochores and percentage of plant species that were myrmecochores within study plots. We treated

Table 2. Comparisons of partner diversity for different plant–animal mutualisms. Partner diversity was described from the plant’s perspective, and estimated using Shannon’s diversity index (H'). Only studies and sites with at least five reported interactions with prospective partners for a species were included. The average among sites was calculated in instances where species had been studied in more than one location within a study. References are described in the Supplementary material Appendix 3.

Mutualism	Reference	H (avg \pm SD)	Plant species	Location
Myrmecochory in temperate deciduous forests	Beattie et al. (1979)	0.94 \pm 0.05	<i>Hepatica acutiloba</i> , <i>Sanguinaria canadensis</i>	West Virginia, USA
	Culver and Beattie (1978)	1.12	<i>Viola</i> spp.	West Virginia, USA
	Gibson (1993)	1.67	<i>Malanpyrum lineare</i>	Michigan, USA
	Giladi (2004)	0.76 \pm 0.06	<i>Hexastylis arifolio</i>	Georgia, USA (3 sites)
	Zelikova et al. (2008)	0.007	<i>Hexastylis arifolio</i>	Smoky Mountains, USA (sum of 7 sites)
	Heithaus (1986)	0.31 \pm 0.30	<i>Asarum canadense</i>	Georgia, USA (sum of 5 non- <i>Solenopsis</i>)

All of the patches included *A. ruginosus*. Myrmecochore species density was correlated with *A. ruginosus* density (simple linear regression, $F = 10.23$, $DF = 1,33$, $p = 0.003$, $R^2 = 0.24$; Fig. 2) and the proportion of ant-attended baits within each grid that attracted *A. ruginosus* (simple linear regression, $F = 5.6$, $DF = 1,33$, $p = 0.023$, $R^2 = 0.15$). Myrmecochore species richness was positively correlated with *A. ruginosus* density ($F = 5.3$, $DF = 1,33$, $p = 0.028$, $R^2 = 0.14$) and the proportion

of ant-attended baits within each grid that attracted *A. ruginosus* ($F = 3.99$, $DF = 1,33$, $p = 0.054$, $R^2 = 0.11$).

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The 41 forests included an average of 3.1 ± 3.9 (\pm SD) ant-dispersed plant species (Fig. 3a), and these species accounted for $13.1\% \pm 12.9$ of the herbaceous plant species

(Fig. 3b) within the study plots. The presence of both *A. mellificus* and at least one myrmecochore were recorded in 22 out of the 41 of the forests included in our analysis, 11 hosted *A. mellificus* but no myrmecochore, six hosted at least one myrmecochore and no *A. mellificus* and two had neither. This pattern of presence/absence of myrmecochores and *A. mellificus* was indistinguishable from a random distribution ($\chi^2 = 0.37$).

The 'myrmecochore-occupied' forests (n = 27) had an average of 4.7 ± 4.0 (\pm SD) ant-dispersed plant species in a plot, and these species accounted for $21\% \pm 9$ of the herbaceous plant species; these two measures were positively correlated in those forests (simple linear regression, $F = 15.3$, $DF = 1, 18$, $p = 0.0011$, $R^2 = 0.46$). Forests with myrmecochores included a greater proportion of baits that attracted *A. mellificus* than did forests without myrmecochores (mean proportions of baits that attracted ants \pm SD = 0.52 ± 0.40 , n = 27, and 0.33 ± 0.27 , n = 14, respectively; one-sided t = 0.33, values/F3 1 Tf3.03(stTm5D0)Tj/F8 1 Tf0.98-(stTm5D983 TD[(11)-3.8918.73myrmTJ/F3 1 Tf4.2793165

can provide great benefits without wholly excluding other prospective partners. Second, the solitary foragers typical of an *A. niger* colony quickly deliver resources to a nest rather than dissecting it on-site, thereby avoiding any damage to the seeds or 'elaiosome-robbing'.

The interaction between *A. niger* and seeds is the modal dispersal mechanism for these seeds for at least three reasons. First, *A. niger* is one of the most common and abundant epigenic ants in North American temperate deciduous forests (Culver 1974, Lynch 1981, Gotelli and Ellison 2002). It is inevitable that many prospective food items will be inspected by this ant. Second, the foraging ranges of *A. niger* colonies often overlap. Based on the even distribution of nests (Giladi 2004), estimates of colony density (>1 colony per m²; Headly 1952, Talbot 1957) and the mean and maximum distances that collected items are discovered from the nest (~50 cm and 1.5 m respectively, Ness et al. 2004), *A. niger* can provide more than 100% coverage of the forest floor. Based on the high frequency of *A. niger*-seed interactions, that ant might have a great effect on myrmecochores almost irrespective of their per-interaction effect (Vazquez et al. 2005). Third, because *A. niger* collects encountered seeds more readily than other ants, the proportions of seeds collected by that ant are even greater than would be predicted by encounter rate alone. The combination of high encounter rates, unusually high collection rates upon encountering seeds, and the benefit conferred to the seeds (above) qualifies *A. niger* as a keystone mutualist.

It is striking how many myrmecochore-ant interactions include *A. niger* rather than other more common and widespread omnivores in the Nearctic (e.g. *Formica*, *Lasius*, and *Pogonomyrmex* spp. in Ward 2000). If the interaction is specialized, how might plants filter prospective partners and target a particular taxon within an ant guild? One series of explanations focuses on the rewards associated with individual seeds. Elaiosomes have chemical cues that induce collection behaviors by *A. niger* (Marshall et al. 1979). However, similar responses can be elicited from a variety of ants (Skidmore and Heithaus 1988). Compositionally, the elaiosome requires no obvious morphological adaptations by a foragers to manipulate or nestmates to consume. Nonetheless, certain diaspores may be sufficiently small to be unrewarding for some ants to collect or sufficiently large that collection can be a challenge. If these distinctions are informed by the size of the ants (Beattie et al. 1979, Christian 2001) or their jaws, an intermediate-sized ant such as *A. niger* may be capable and willing to collect dia1 Tf.ru(upon)]TJ th375 uppreairtus

addition, from the plant's perspective, the interaction concludes once the seed is literally pulled into the ant colony's sphere of influence. In contrast, the interaction

- Lynch, J. F. 1981. Seasonal, successional and vertical segregation in a Maryland ant community. – *Oikos* 37: 183–198.
- Marshall, D. L. et al. 1979. Evidence for diglycerides as attractants in an ant–seed interaction. – *J. Chem. Ecol.* 5: 335–344.

Appendix 1. Responses of North American temperate deciduous ant species to seeds adapted for ant dispersal (myrmecochory). 'Seeds encountered' refers to observations of ants walking on cards with seeds. 'Seeds collected' refers to the subset of those encountered seeds that were removed from the cards (i.e. dispersed).

Appendix 2. Descriptions of the herbaceous plant community and the proportion of ant-discovered baits that were discovered by *Aphaenogaster*
