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Field experiments show contradictory short- and long-term myrmecochorous plant impacts on seed-dispersing ants

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Abstract. 1. Some interactions previously described as mutualistic were revealed to be commensal or parasitic in subsequent investigations. Ant-mediated seed dispersal has been described as a mutualism for more than a century; however, recent research suggests that it may be commensal or parasitic. Plants demonstrably benefit from ant-mediated seed dispersal, although there is little evidence available to demonstrate that the interaction benefits long-term ant fitness.

2. Field experiments were conducted in temperate North America focused on a key seed-dispersing ant. All herbaceous plants were removed from a forest understorey for 13 years, and supplemented ant colonies with large elaiosome-bearing seeds aiming to examine potential long- and short-term myrmecochorous plant benefits for the ants.

3. If elaiosome-bearing seeds benefit ants, suggesting a mutualistic relationship, it is expected that there would be greater worker and/or alate abundance and greater fat reserves (colony lipid content) with seed supplementation (short-term) and in areas with high understorey herb abundance.

4. Short-term seed supplementation of ant colonies did not result in an increase with respect to numbers or fat stores, although it did prompt the production of colony sexuals, which is a potential fitness benefit. In the long term, however, there was no positive effect on the ants and, instead, there were negative effects because the removal of elaiosome-bearing plants corresponded with greater colony health.

5. The data obtained in the present study suggest that the ant–plant interaction ranged from occasionally beneficial to neutral to overall negative for the ant partner. Such results did not support considering the interaction as a mutualism. Collectively, the data suggest the need to reconsider the nature of the relationship between these ants and plants.

Key words. Animal–plant interactions, *Aphaenogaster*, commensalism, dispersal, herbaceous, mutualism, species interactions, woodland.

Introduction

Observed species interactions in which cooperating partners appear to benefit mutually from the exchange of services and resources appear ubiquitous (Bertness & Callaway, 1994; Bruno *et al.*, 2003; Bronstein, 2009), although many of the described mutualisms are based on theory and observation without empirical backing (Bronstein, 2015). Indeed, empirical findings suggest that mutualisms are more complex than a simple ‘bartering’ of mutual services (Bronstein, 2001; Warren II *et al.*, 2014; Hoeksema & Bruna, 2015). For example, recent

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research reveals that many biotic interactions once considered as mutualistic are commensal, or even parasitic (Weeks, 2000; Freckleton & Cote, 2003; Wrege *et al.*, 2005; Heil *et al.*, 2014).

Ant-mediated seed dispersal (myrmecochory) is a cosmopolitan species interaction first described more than a century ago (Sernander, 1906) and is typically described as a mutualism (Rico-Gray & Oliveira, 2007). In myrmecochorous interactions (*sensu stricto*), plants produce a chemically-attractive seed appendage, known as an elaiosome, which prompts omnivorous foraging ants to retrieve the seeds to their nests. The elaiosome can be nutritive for ant larvae and often contains fatty acids that may mimic insect haemolymph, making it attractive to carnivorous and omnivorous ants that would otherwise ignore seeds (Marshall *et al.*, 1979; Hughes *et al.*, 1994; Fischer *et al.*, 2005, 2008). It is a diffuse, asymmetrical interaction in which thousands of plant species worldwide receive seed dispersal services from hundreds of ant species (Lengyel *et al.*, 2009; Warren II & Giladi, 2014). As a result, in any single system, a few 'effective' seed-dispersing ant taxa quickly retrieve seeds from many plant species and return the seeds undamaged to their nests (a full discussion of effective seed dispersers is provided in Warren II & Giladi, 2014).

For plants, the fitness gains are well documented. Seeds cached in ant nests may receive protection from fire in dry systems (Bond & Slingsby, 1983; Hughes & Westoby, 1992b) or protection from seed predators such as small rodents (Ness & Bressmer, 2005; Kwit *et al.*, 2012). The benefits of ant-mediated seed dispersal furthermore include the placement of seeds in establishment-friendly microhabitats (Hanzawa *et al.*, 1988; Tarsa *et al.*, 2018). Ant-mediated seed dispersal also alleviates inbreeding, pathogen accumulation and density-dependent competition through the movement of seeds away from adult conspecifics (Zhou *et al.*, 2007; Ness & Morin, 2008; Spiegel & Nathan, 2010, 2012). Overall, ant-mediated seed dispersal provides clear benefits for myrmecochore plant populations and is a major determinant of their spatial structure and local-scale distributions (Mitchell *et al.*, 2002; Gorb & Gorb, 2003; Ness *et al.*, 2009). Specifically, myrmecochore plant populations decline and plant distribution becomes aggregated where seed-dispersing ants have been excluded experimentally (Zelikova *et al.*, 2011). The same effects are observed where microclimate limits ants (Warren II *et al.*, 2010; Warren II & Bradford, 2013) and where invasive ants displace native seed dispersers (Christian, 2001; Rodriguez-Cabal *et al.*, 2012; Warren II *et al.*, 2015a).

For ants, the fitness benefits are less obvious. Ant interest in myrmecochorous seeds depends greatly on elaiosome size and chemistry, which is highly contingent upon plant species and location (Alcantara *et al.*, 2007; Boieiro *et al.*, 2012; Warren II *et al.*, 2014). In general, ants prefer larger seeds, which typically have larger elaiosomes (Garrido *et al.*, 2002; Bas *et al.*, 2009; Warren II *et al.*, 2014). Presumably, ants choose elaiosomes with greater nutritional quality (e.g. a higher lipid content), although they also retrieve elaiosomes with little or no nutritive content (Pfeiffer *et al.*, 2010; Turner & Frederickson, 2013). Some studies report that supplementing ant colonies with elaiosomes over short time periods can increase larval size, brood numbers and/or female alate abundance (Gammans *et al.*, 2005; Fischer *et al.*, 2008; Turner & Frederickson, 2013), as well as maintain colony lipid content (Clark & King, 2012). Whole colony lipid content of workers provides a time-integrated estimate of colony energetic reserves, in addition to indicating nutritional status and, indirectly, the reproductive potential of the colony (Tschinkel, 1999). However, it is not yet clear whether these effects are long lasting and whether they manifest in field settings, potentially for example by providing unique value to ant diets (Fokuhl *et al.*, 2007; Clark & King, 2012; Caut *et al.*, 2013).

One expectation is that elaiosomes provide nutrition during early spring when other food resources, such as insect prey or carrion, are scarce (Carroll & Janzen, 1973; Clark & King, 2012). Clark and King (2012) described the relationship as a probable 'facultative mutualism' as a result of a lack of evidence indicating that seeds were crucial for ant colony growth. However, more recent work shows that seeds do not appear to be particularly important to ants during this early spring period (Warren II *et al.*, 2014, 2015b). Moreover, conclusions that are based on supplementation of ant colonies with elaiosomes under laboratory conditions (Clark & King 2012) do not account for foraging and retrieval costs that might be substantial in an ecologically realistic setting (Caut *et al.*, 2013; Warren II & Giladi, 2014). As such, it remains uncertain as to whether seed retrieval and the consumption of elaiosomes by ants significantly contributes to long-term fitness of the ants (Brew *et al.*, 1989; Marussich, 2006; Fokuhl *et al.*, 2007; Clark & King, 2012; Caut *et al.*, 2013; Warren II *et al.*, 2014). More importantly, although ants strongly affect the population-level fitness of myrmecochorous plants, there is no evidence that plants influence the long-term fitness of seed-dispersing ant populations (Mitchell *et al.*, 2002; Ness *et al.*, 2009).

Previous attempts to discern ant benefits from myrmecochorus plants seeds lacked long-term data combined with field experimentation. We have conducted two field experiments, one long-term and one short-term, in a North American system where the interaction has focused on the keystone seed-dispersing ant [*Aphaenogaster picea* (of the *Aphaenogaster rudis* complex)]. In this system, the only myrmecochorous plants are understorey herbs (Warren II *et al.*, 2014) and the only ant–seed interaction comprises elaiosome-mediated seed dispersal (myrmecochory *sensu* stricto). For the long-term experiment, we annually removed all herbaceous plants from the forest understorey for 13 years and compared the fitness of *A. picea* ants in these removal plots with those in adjacent control plots where the high herb abundance (including many myrmecochorous plant species) was left intact. If the ant–plant interaction is mutualistic, we expected (i) greater worker and alate abundance for *A. picea* in the control plots and (ii) higher colony lipid content (as an indicator of current and potential fitness) in the control plots. Alternately, if elaiosome-bearing seeds provide little to no benefit for ants, the ants should be unaffected by the long-term herb removal. For the short-term experiment, we supplemented ant colonies in the long-term plots with large elaiosome-bearing seeds. If elaiosome-bearing seeds are beneficial for ants, suggesting a mutualistic relationship, we expected greater worker and alate abundance and greater fat reserves (colony lipid content) with seed supplementation. Alternately, if elaiosome-bearing seeds are neutral for ants, they should be unaffected by elaiosome-bearing seed supplementation.

Materials and methods

Study species and sites

Ants in the *A. rudis* 'complex' (hereafter '*A. rudis*'), which includes *A. picea* (Wheeler, W.M., 1908), dominate understorey habitats in eastern North American forests (Lubertazzi, 2012; King *et al.*, 2013), where they are the main dispersers of myrmecochore seeds (aproximately 75% of seeds removed, Ness *et al.*, 2009; Warren II *et al.*, 2010, 2014). *Aphaenogaster rudis* ants generally forage aproximately 60–120 cm from their nests, which are usually located under rocks or in coarse woody material (Smallwood & Culver, 1979; Giladi, 2004; Lubertazzi, 2012). Colony relocation can be somewhat frequent for *A. rudis*, with 60–70% of the colonies relocating one to three times per season; however, the relocation distance (aproximately 40 cm) generally is localised (Smallwood & Culver, 1979). Thus, foraging and colony movement occurs at scales much smaller than the dimensions of our experimental plots. *Aphaenogaster rudis* colonies are monogyne and monodomous (i.e. single queen colonies, not sharing workers or queens between colonies).

Southern Appalachian Mountain cove forests in the Eastern U.S.A. are relatively mesic with rich and relatively deep soils. The forests contain dense canopies with mesophytic tree species such as *Liriodendron tulipifera* L., *Tilia americana* Miller, *Aesculus flava* Aiton ex Hope, *Betula lenta* L., *Magnolia acuminata* L., *Prunus serotina* Ehrhart and *Fraxinus americana* L., although most plant diversity (70–90%) is contained in the herbaceous layer (Whigham, 2004; Elliott *et al.*, 2014) with aproximately 40 forb species adapted for ant dispersal (Cain *et al.*, 1998; Mitchell *et al.*, 2002; Warren II *et al.*, 2014). The present study was conducted in a rich mesophytic cove forest within the Coweeta Hydrologic Laboratory watershed (Coweeta) in Macon County, North Carolina, U.S.A. (35°02′N, 83°27′W; 885–902 m elevation).

Experiment 1: long-term removal of herbaceous plants

Aphaenogaster rudis ants only occur in forested habitat in North America, although they will occupy fragmented patches and can re-colonise after canopy disturbance within one to two decades (Mitchell *et al.*, 2002; Wike *et al.*, 2010; Warren II *et al.*, 2015b). However, no research exists that has examined the response of *A. rudis* to understorey disturbance with an intact overstorey with the aim of disentangling the effects of removing herbs on ants from the multiple other factors that change during forest disturbances such as tree harvest. Twelve plots (20 × 20 m) were established at Coweeta, in 1999, and all aboveground herbaceous plant materials (myrmecochorous and non-myrmecochorous) were hand-removed from the same six, randomly chosen plots, each year in May to June throughout 2011 (hereafter, 'removal plots') and the other six plots received no treatment and were used as controls (hereafter, 'control plots') (Appendix S1). The plot size assured that there were multiple colonies per plot and colonies were unlikely to relocate or forage outside of plots over the course of multiple years given the known colony foraging and relocation distances. The plots were separated by distances ranging from 20 to 100 m, although the paired control and treatment plots were approximately 10 m apart. We evaluated the impact of herbaceous removal at the cessation of herbaceous removal in 2012 and then again in 2016. Myrmecochorous and non-myrmecochorous herbaceous plant density and cover in the control and treatment plots were measured in 20 subplots (1 m^2) that bisected the plots in a '+' shape (two linear transects) with 1 m between each subplot. All plants were counted and identified to species.

Soil temperature and moisture were measured in April, May and June 2012 in eight locations within each plot (2 and 7 m from each side). Soil temperature was measured using a wide-range thermometer (Taylor Precision Produces, Las Cruces, New Mexico) at a depth of 5 cm; soil moisture was measured using a Hydrosense soil moisture sensor with 12-cm stainless steel rods (Campbell Scientific, Logan, Utah) at three points per measurement and the values obtained were averaged.

Five *A. picea* colonies were collected randomly from beneath stones, downed wood and leaf litter throughout each plot in August 2012 ($n = 60$ colonies). Once discovered, the colonies were collected with a 20 V cordless wet-dry vacuum (DC500; DeWalt, Baltimore, Maryland), placed on ice for transport and freeze killed in the laboratory. This method is effective for whole-colony collection in forest settings (King *et al.*, 2013). The colonies were processed to determine the fresh and dry (65 °C) biomass, queen and female alate (winged queen) mass, and fat content of colony members. Colony lipid content was measured by determining queen, alate and colony dry biomass before and after lipid removal using Soxhlet extraction (Smith & Tschinkel, 2009), modified for whole colony extraction.

Experiment 2: short-term seed supplementation

To monitor ant colonies and induce predictable colony locations for seed augmentation experiments, eight artificial ant nests were placed in each plot, 2 and 7 m in from each side in August 2012 ($n = 96$ total in the 12 plots). Each nest consisted of a wooden pine board (12 × 14 × 1.7 cm) with a 'G'-shaped chamber (25 × 2 × 1 cm) routed out and opening to the outside. The chamber was topped with Plexiglas and a ceramic tile, in accordance with established protocols (Warren II & Bradford, 2012; Bradford *et al.*, 2014; Warren II *et al.*, 2015b). The nests were checked for colonisation by *A. picea* in May 2013 and, subsequently, in May 2016, the artificial ant nests were checked and all occupied nests were inspected for seed supplementation. From those that were occupied ($n = 44$), 22 were randomly selected for seed addition and these were stratified evenly across the herb removal treatments. Seed bait stations were placed 30 cm from the nests in July 2016 and 12 *Sanguinaria canadensis* seeds were added to each tray every other day for 24 days ($n = 12$ bait days; 3168 total seeds) and monitored for 1 h to confirm seed removal by ants. We chose *S. canadensis* as one of the more preferred, larger myrmecochore seeds in eastern deciduous forests (Warren II *et al.*, 2014). Fruit production is low in woodland myrmecochores and, when it occurs, plants usually produce one fruit with approximately 24 seeds (Harris, 1910; Giladi, 2004). Hence, our seed baits mimicked six fruits maturing per day, which is plausible in high-diversity myrmecochore communities in eastern deciduous forests (Beattie & Culver, 1981; Handel *et al.*, 1981; Rico-Gray & Oliveira, 2007). The nests were collected (with ant colonies) in August 2016 after the seed addition experiment.

Soil temperature and moisture were measured as described above at each bait station in April, May and June 2016. All ant colonies were retrieved in August 2016 and freeze-killed. Ants and seeds were removed from the nests, and whole colony (except pupae and eggs) lipid content was assessed. We also counted workers, larvae and male and female alates.

Statistical analysis

We used mixed models in the *lme4* package (Bates *et al.*, 2015) in R software, version 3.5.0 (R Core Team, 2016) to evaluate colony lipid content, worker and alate abundance, and nest occupancy in 2012. We used linear mixed models assuming a Gaussian error distribution for colony lipid percentage, and we used generalised linear mixed models (GLMM) assuming a Poisson error distribution for worker and alate abundance and a binomial distribution for nest occupation. We included plot as a random effect to account for potential autocorrelation within the clustered subplots, and herbaceous removal was the fixed effect. We used analysis of deviance (ANODEV) to fit the mixed models and type II Wald χ^2 tests to determine whether likelihoods of compared models are significantly different. We also used mixed ANODEV models to evaluate colony lipid content, worker and alate abundance, alate sex ratio (female : male) and nest occupancy in 2016. We used the same error distributions as in the 2012 models, and a binomial error distribution for the alate sex ratio (binomial proportion). We included plots as a random effect, with herbaceous removal and seed addition comprising the fixed effects. We included a herbaceous (removal × seed addition) interaction term.

To investigate whether herbaceous removal was a reasonable predictor of myrmecochore cover, we analysed model fit [based on a difference in Akaike's information criterion (ΔAIC) > 2] between myrmecochore cover and herbaceous cover for all variables affected by the herbaceous removal treatment (2012 colony lipid content, 2016 colony lipid content, alate abundance and nest occupancy).

Given the expected relationship between colony lipid content and reproduction, as well as a discrepancy in herbaceous removal and seed addition treatment correlation with alate abundance, we used GLMMs to evaluate alate abundance (Poisson) and alate sex ratios (binomial) as a function of colony lipid content with plot as a random effect.

We included an observation-level random effect to model extra-Poisson or extra-binomial variation (Harrison, 2014) in the generalised models where overdispersion was > 2.0. We tested for collinearity in the 2016 models using the *car* package (Fox & Weisberg, 2011).

Results

Thirteen years of manual herbaceous plant removal reduced myrmecochore plant density (stems m^{-2}) by 83% and cover (%) by 88% compared with that observed in control plots (Appendix S2). Although the manual removal of herbaceous species ceased in 2012, the impacts remained apparent for another 4 years because, in 2016, myrmecochore density remained 83% lower, and cover 80% lower, compared with that in control plots (2012 non-myrmecochorous stems were reduced by 74% and non-myrmecochorous cover by 82%). Except for 2016 nest occupancy (ΔAIC < 2), all ant responses (2012 lipid content, 2016 colony lipid content and 2016 alate abundance) were better predicted by

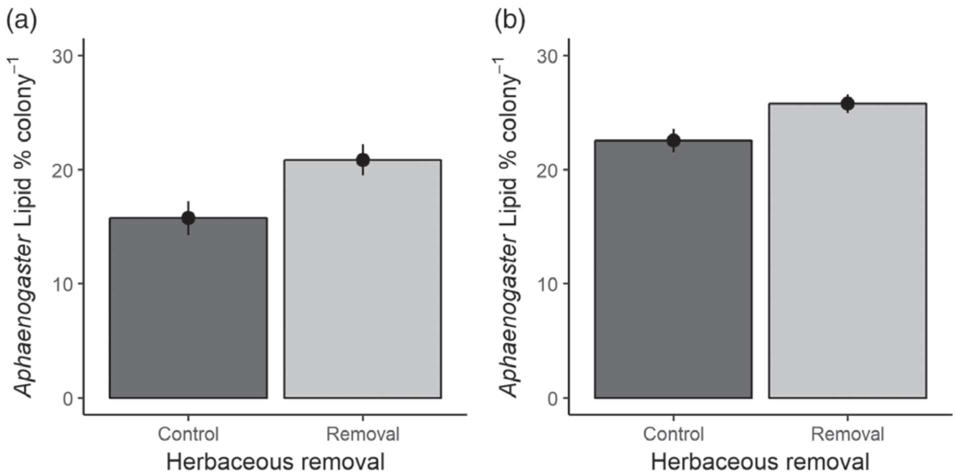

Fig. 1. *Aphaenogaster picea* fat stores (colony lipid content) were higher (d.f. = 1, χ^2 = 5.980, P = 0.014) in temperate deciduous forest plots where all understorey plants were removed for 13 years than in control plots in 2012 (a) and this treatment effect remained significant (d.f. = 1, χ^2 = 5.545, P = 0.018) 4 years later in 2016 (b).

Table 1. Analysis of deviance results for 2012 *Aphaenogaster picea* colony lipid content (Gaussian), worker abundance (Poisson), alate abundance (Poisson), and nest occupancy (binomial) mixed models.

Coefficient	d.f.	χ^2	P
Colony lipid content			
Herbaceous removal	1	5.980	0.014
Worker abundance			
Herbaceous removal	1	1.059	0.303
Alate abundance			
Herbaceous removal	1	0.025	0.872
Nest occupancy (2013)			
Herbaceous removal	1	0.858	0.354

Plot was included as a random effect in all models. *P*-values were calculated using Type II Wald χ^2 tests.

myrmecochore abundance than overall herbaceous abundance (ΔAIC > 2).

Of the 3168 total seeds added to the 22 baits stations in July 2016, 48% were removed by foraging ants in the 1-h time window after offering. The vast majority of ants observed visiting seed bait stations (95%) and occupying artificial nests (90%) were *A. picea*. The other ants occasionally observed at bait stations and in artificial nests were *Lasius alienus* (Foerster, 1850), *Prenolepis imparis* (Say, 1836), and *Crematogaster ashmeadi* (Mayr, 1886).

In 2012, after 13 years of understorey removal, colony lipid content was higher in plots with herbaceous removal than in control plots (Fig. 1a), although worker and alate abundance, as well as nest occupancy, were unaffected by the treatment (Table 1). In 2016, colony lipid content again was higher in plots where herbs were removed (Fig. 1b), although it was not affected by seed addition (Table 2). Worker abundance was unaffected by herbaceous removal and seed addition (Table 2). A significant interaction term indicated that alate abundance was unaffected by seed addition in herbaceous control plots, although it increased with herbaceous removal (Fig. 2a); however, alate sex ratios were unaffected by herbaceous removal and seed addition. A significant interaction term indicated that nest occupancy was unaffected by seed addition in herbaceous control plots but decreased with seed addition in plots with herbaceous removal (Table 2).

Alate abundance increased with colony lipid content in 2016 (coefficient = 0.175, SE = 0.953, $z = 9.100$, $P < 0.001$) (Fig. 3), although alate sex ratios were unaffected (coefficient = −0.093, SE = 0.091, $z = -1.0280$, $P = 0.304$). Alate production increased greatly from zero when colony lipid content > 27%, suggesting a threshold for reproduction, and, for colonies with a lipid content > 27%, alate abundance was higher with seed supplementation (Fig. 3).

Table 2. Analysis of deviance results for 2016 *Aphaenogaster picea* colony lipid content (Gaussian), worker abundance (Poisson), alate abundance (Poisson), alate sex ratio (binomial proportion), and nest occupancy (binomial) mixed models.

Coefficient	d.f.	χ^2	P
Colony lipid content			
Herbaceous removal	1	5.545	0.018
Seed addition	1	0.255	0.613
Herbaceous × Seed	1	0.140	0.707
Worker abundance			
Herbaceous removal	1	1.120	0.289
Seed addition	1	0.058	0.808
Herbaceous × Seed	1	0.403	0.525
Alate abundance			
Herbaceous removal	1	1 996 443	< 0.001
Seed addition	1	456 003	< 0.001
Herbaceous × Seed	1	91 609	< 0.001
Alate sex ratio			
Herbaceous removal	1	0.144	0.703
Seed addition	1	0.044	0.832
Herbaceous × Seed	1	0.029	0.864
Nest occupancy (2016)			
Herbaceous removal	1	0.280	0.596
Seed addition	1	0.649	0.420
Herbaceous × Seed	1	3.381	0.065

Plot was included as a random effect in all models. the parameters for the reduced models are shown. *P*-values were calculated using type II Wald χ^2 tests.

Discussion

A successful mutualism requires that both partners receive net benefits. The results of the present study (Table 1) and those of previous studies (Caut *et al.*, 2013) suggest that the short-term benefits for ants from elaiosome-bearing plant seeds are equivocal. In the present study, seed supplementation prompted an increased production of alates in healthy colonies, comprising a potential benefit, although ant colonies did not increase in numbers or fat stores with this short-term seed supplementation. In the long term, the results showed that removing elaiosome-bearing plants for 13 years did not impact ant colony abundance (neutral effect) and the presence of myrmecochorous plants corresponded with greater colony fat stores and alate abundance (negative effect).

The contradiction between the short-term benefits of seed supplementation and long-term neutral to negative effects of seed removal (i.e. myrmecochorous plant removal) obviously requires explanation. First, it may be related to retrieval costs. We offered seeds with elaiosomes, which are some of the largest available in eastern deciduous forests (Warren II *et al.*, 2014), in very close proximity to the ant colonies and this approach, as with other laboratory studies, does not account for foraging and retrieval costs, which would be embedded in the long-term study.

A second possibility is that the ants foraged or migrated outside the herbaceous removal zones and accessed myrmecochorous seeds. However, given that the plots were 20 × 20 m and the mean foraging distance for *A. rudis* foraging is 57 cm, the plot size should have provided adequate treatment for the majority of ant colonies. The mean distance for *A. rudis* colony relocation is 40 cm and approximately 60–70% of colonies move one to three times per year (Smallwood & Culver, 1979; Herbers, 1985; Lubertazzi, 2012). In the present study, 44 nests were found occupied in May 2016 and 70% remained occupied in August 2016 (regardless of herb-removal treatment) compared with 61% as reported by Smallwood and Culver (1979). The

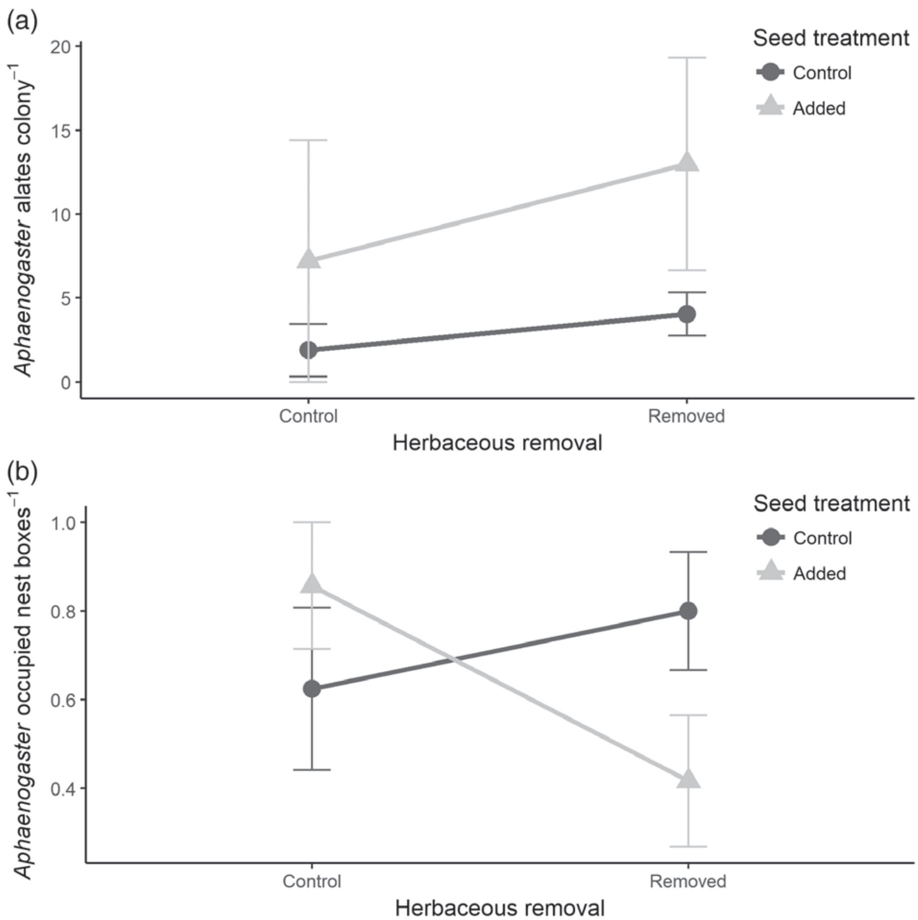

Fig. 2. . Interaction plots (mean ± SE) for *Aphaenogaster picea* alate production and nest occupancy. A significant interaction term (d.f. = 1, $\chi^2 = 91\ 609$, $P < 0.001$) indicated that seed addition did not impact alate abundance in control plots with intact herbaceous vegetation but alate abundance increased with seed addition in colonies located in herbaceous removal plots (a). A marginally significant (d.f. = 1, $\chi^2 = 3.381$, $P = 0.065$) interaction term also indicated that nest occupancy was unaffected by seed addition in herbaceous control plots but was lower with seed addition in plots with herbaceous removal (b).

long-term removal of all herbaceous plants may have altered plot dynamics other than elaiosome availability, such as reducing arthropod prey or altering microhabitats. We note, however, that myrmecochore-only cover was a better fit for ant responses than overall herbaceous cover, and there was little difference in soil moisture and temperature between control and removal plots.

Our findings appear to be consistent with those of previous studies that failed to connect *A. rudis* seed retrieval with colony-level fitness benefits (Caut *et al.*, 2013; Turner & Frederickson, 2013). Warren II *et al.* (2015b) found that colony lipid content increased with arthropod remains but decreased with the number of myrmecochorous seeds found in ant nest midden. These results suggested that seed retrieval may impose a cost on ant colonies, particularly if the ants spend time retrieving seeds that could be spent foraging for more nutritive foods. Our results are consistent with the possibility that the cost of seed retrieval might not be worth the benefit. We only found a positive impact when colonies were supplemented with seeds near the nest, although there was no indication of benefit when ants had to forage for the seeds. Indeed, colony lipid content was higher in ant colonies where plants were removed. Arthropod prey (live or carrion) likely is a more important food source for colonies than seeds (Clark & King, 2012; Warren II *et al.*, 2015b) and retrieving seeds may reduce the foraging efficiency for these foods.

We did find a short-term increase in the production of alates with seed supplementation. We found that only colonies with colony lipid content > 27% produced alates. This finding is consistent with the results of a study by Lubertazzi (2012) who suggested that *Aphaenogaster* alate production may be resource limited. It is possible that elaiosomes mainly benefit colonies already in a poor nutritive state (Warren II *et al.*, 2015b), although we found that seed supplementation only prompted alate production in already healthy (higher colony lipid content) colonies and did not appear to initiate alate production itself. Seed supplementation altered ant sex ratios in other studies (Morales & Heithaus, 1998; Bono & Heithaus, 2002); however, we found no change in sex ratios, suggesting that elaiosomes were not limiting.

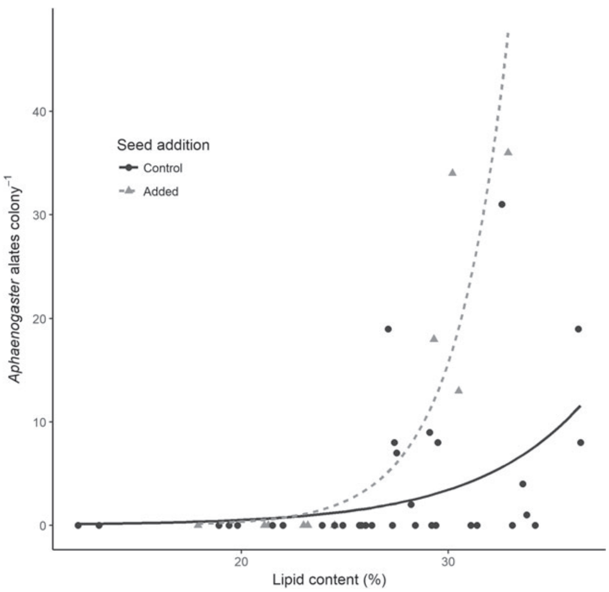

Fig. 3. . Scatterplot with fitted lines (generalised linear mixed models assuming a Poisson distribution) showing 2016 *Aphaenogaster rudis* alate abundance as a function of colony lipid content and seed addition (seeds added, grey dashed line and triangles; control, black solid line and circles). Alate abundance increased with colony lipid content (coefficient = 0.175, SE = 0.953, $P < 0.001$). Alate production initiated when colony lipid content > 27%, and alate abundance was higher with seed supplementation (Fig. 3).

Overall, our data, suggest that it is feasible that some myrmecochores exploit ants for seed dispersal, without providing any long-term fitness benefits. For example, plants evolved traits (e.g. elaiosomes) specifically targeted toward attracting seed dispersing ants (Giladi, 2006; Warren II & Giladi, 2014; Warren II *et al.*, 2014), whereas no reciprocal coevolved traits are known to occur in ants. Furthermore, ants are susceptible to manipulation by plants (Pfeiffer *et al.*, 2010; Heil *et al.*, 2014; Hojo *et al.*, 2015; Warren II *et al.*, 2015b). For example, some plants trick ants with seeds with the chemical signature of a false elaiosome (Pfeiffer *et al.*, 2010; Vereecken & McNeil, 2010). Indeed, the chemical content of elaiosomes (oleic acids, lipids) may create 'sensory traps' that exploit ants more than they provide nutrition (Edwards & Yu, 2007; Pfeiffer *et al.*, 2010; Turner & Frederickson, 2013). Similarly, at least two insect taxa parasitise ant foraging in a manner similar to plant seeds: *Phasmatodea* (stick insects) and (*Cynipidae*) gall wasps produce eggs with elaiosome-like appendages that induce egg retrieval to colony nests by ants with no apparent benefit for the ants (Hughes & Westoby, 1992a; Stanton *et al.*, 2015; Warren II *et al.*, 2015b). Accordingly, although ants might engage in a a certain behaviour (i.e. specifically seed retrieval), it is plausible that such behaviour may not equate to enhanced colony fitness. Additional research is needed to clarify the long-term benefits and costs of myrmecochory for ants, including the consideration of geography and history, with the aim of understanding the evolution and maintenance of an interaction that may not provide a clear benefit. Future work may refine the present study with a better targeted myrmecochore (as opposed to all herbaceous cover) removal, as well as evaluation of food switching with removal (e.g. insects, fungi, etc.) and microhabitat changes.

It is unlikely that the ant–plant interaction could persist without some mutual benefit at the population level of the ant behaviour because exploitative relationships can persist only if the costs do not outweigh the benefits of the behaviour being exploited (Bronstein, 2009). Specifically, plants can take advantage of stereotyped ant foraging behaviours. Evolutionary changes that possibly diminishing ant attraction to elaiosomes might also diminish their attraction to important food items that elaiosomes mimic, such as arthropod carcasses; in addition, at least for some plants, providing ants nutritive elaiosomes may offset their foraging costs (Clark & King, 2012). Where those costs are not offset, there is some experimental bait-station evidence suggesting that seed satiation can occur (Smith *et al.*, 1989a,b; Heithaus *et al.*, 2005; Bologna & Detrain, 2015); hence, ants may have a mechanism for lessening seed exploitation. Even in the absence of satiation, seed retrieval costs are not imposed on one or two solitary individuals but, instead, they are amortised across an entire social colony, which typically comprise large, common ant colonies (Warren II & Giladi, 2014). As such, the costs of seed retrieval may be relatively minor at the colony level. Our data are consistent with the idea of neutral costs, with no net loss or gain to the ants of seed retrieval.

Species interactions are context-dependent (Thompson, 1988; Bradford *et al.*, 2014; Fraterrigo *et al.*, 2014) and the repertoire of interactions between species may vary among mutualistic, commensalistic, and parasitic (Bronstein, 1994; Chamberlain *et al.*, 2014; Hoeksema & Bruna, 2015). Previous attempts to demonstrate a positive effect of elaiosome-bearing seeds on ants generally were laboratory-based and short-term. Collectively, our data suggest that the impact of myrmecochores plants on *A. picea* ranged from occasionally beneficial (facultatively mutualistic) to neutral (commensalistic) to negative (parasitic) for the ant partner. Seed-dispersing ants occur in the absence of myrmecochorous plants (Mitchell *et al.*, 2002; Ness *et al.*, 2009) and our long-term myrmecochorous plant removal indicated that the ants were healthier without them. Myrmecochory is a long-described interaction (Sernander, 1906) that is assumed to be mutualistic; however, more recent empirical studies suggest that it is at best commensal for the ants (Weeks, 2000; Freckleton & Cote, 2003; Wrege *et al.*, 2005; Caut *et al.*, 2013; Heil *et al.*, 2014; Warren II *et al.*, 2015b). The research efforts aiming to understand plant benefits from ant-mediated seed dispersal far exceed those with respect to ant benefits (Warren II & Giladi, 2014). Our data suggest that the default assumption of the interaction being mutualist needs rethinking, and attention should shift toward a better understanding of ant costs and benefits from the interaction.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. All ground-layer vegetation was hand removed annually from temperate forest plots at the Coweeta Hydrologic Laboratory in Otto, North Carolina, U.S.A. This photo shows the edge between the treatment plot (left) and control (right) (photograph by R. Warren).

Appendix S2. Mean ± SE myrmecochorous (a) and non-myrmecochorous (b) plant abundance and cover, microclimate (c) and *Aphaenogaster rudis* demographics (d) for herbaceous removal plots.

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