

An invasive slug exploits an ant-seed dispersal mutualism

Shannon A. Meadley Dunphy¹ · Kirsten M. Prior^{1,2} · Megan E. Frederickson¹

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Abstract Plant–animal mutualisms, such as seed dispersal, are often vulnerable to disruption by invasive species. Here, we show for the first time how a non-ant invasive species negatively affects seed dispersal by ants. We examined the effects of several animal species that co-occur in a temperate deciduous forest—including native and invasive seed-dispersing ants (*Aphaenogaster rudis* and *Myrmica rubra*, respectively), an invasive slug (*Arion subfuscus*), and native rodents—on a native myrmecochorous plant, *Asarum canadense*. We experimentally manipulated ant, slug, and rodent access to seed depots and measured seed removal. We also video-recorded depots to determine which other taxa interact with seeds. We found that *A. rudis* was the main disperser of seeds and that *A. subfuscus* consumed elaiosomes without dispersing seeds. Rodent visitation was rare, and rodent exclusion had no significant effect on seed or elaiosome removal. We then used data obtained from laboratory and field mesocosm experiments to determine how elaiosome robbing by *A. subfuscus* affects seed dispersal by *A. rudis* and *M. rubra*. We found that elaiosome robbing by slugs reduced seed dispersal by

ants, especially in mesocosms with *A. rudis*, which picks up seeds more slowly than *M. rubra*. Taken together, our results show that elaiosome robbing by an invasive slug reduces seed dispersal by ants, suggesting that invasive slugs can have profound negative effects on seed dispersal mutualisms.

Keywords Invasion · Myrmecochory · Mutualism · *Aphaenogaster rudis* · *Arion subfuscus*

Introduction

Invasive species often integrate easily into existing plant–animal mutualistic networks, with varied effects. Plant–animal mutualisms are frequently disrupted by the introduction of a novel partner, such as a new plant, seed disperser, or pollinator (Traveset and Richardson 2006, 2014). However, mutualisms can also be indirectly affected by the introduction of a third-party species that does not replace either mutualistic partner but instead acts as a predator or competitor of one of the partners (e.g., Christian 2001; Traveset and Riera 2005; Traveset and Richardson 2006; Rodriguez-Cabal et al. 2011; Riginos et al. 2015). Here, we report our study of a third-party invasive species that has the potential to disrupt a plant–animal mutualism because it “robs” the reward offered by plants to attract beneficial animals. This occurs because the invasive species consumes the food reward (here, elaiosomes) intended for “legitimate” mutualists, without offering any beneficial service (in this context, seed dispersal) in return. Plants have had less opportunity to evolve defenses against invasive exploiters compared to native ones and, consequently, exploitation by invasive species may be especially detrimental. For example, in Hawaii, where all ant species are introduced

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✉ Shannon A. Meadley Dunphy
shannon.meadleydunphy@mail.utoronto.ca

¹ Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada

² Present Address: Department of Biology, University of Florida, 411 Carr Hall, Gainesville, FL 32611, USA

species, native plants have no floral defenses against ants and are exploited by nectar-robbing ants more than invasive plants that have evolved alongside ants (Junker et al. 2011). In seed dispersal mutualisms, the effects of reward robbing by invasive species have received very little attention relative to the effects of novel partners (e.g., Prior et al. 2015).

Although the presence of a fleshy, nutrient-rich elaiosome on a seed typically signifies seed dispersal by ants (myrmecochory), elaiosomes can attract a diversity of native and invasive insects, gastropods, and mammals that may pick up and move seeds to sites suitable for germination (seed dispersal), eat seeds plus elaiosomes in their entirety (seed predation), or consume only elaiosomes without dispersing seeds (elaiosome robbing). While the fine line between seed dispersal and seed predation has received some attention in the literature, elaiosome robbing is poorly understood, even though it may be a widespread phenomenon (e.g., Ohara and Higashi 1987; Kalisz et al. 1999; Boulay et al. 2009; Beaumont et al. 2011). Worldwide, the seeds of an estimated 11,000 plant species have elaiosomes (Lengyel et al. 2009), and in the deciduous forests of northeastern North America, as many as 30 % of herbaceous plants produce elaiosome-bearing seeds (Beattie and Culver 1981; Handel et al. 1981). Ants generally pick up seeds with their elaiosomes attached and bring them to their nest where they remove and feed the elaiosomes to their larvae prior to depositing seeds in a midden, thereby affecting seed dispersal (Servigne and Detrain 2010). Various signaling compounds in elaiosomes, such as oleic acid, are thought to be important factors which stimulate ants to pick up and move diaspores (Turner and Frederickson 2013), but even ants, especially invasive ants, sometimes “rob” elaiosomes without dispersing seeds (Horvitz and Schemske 1986; Ness 2004). This latter behavior may negatively impact seed fates because elaiosome robbing does not result in seed removal from beneath parent plants, and elaiosome-robbed seeds may experience reduced dispersal rates by other seed-dispersing ants (Horvitz and Schemske 1986). To date, experiments have assessed the effects of elaiosome robbing by invasive species only for invasive ants; in the study reported here, we investigated whether an invasive slug robs elaiosomes and thereby decreases the likelihood that ants disperse seeds.

Türke et al. (2010, 2012) recently showed that in ant-limited European forests, gastropods can consume entire diaspores (i.e., seeds plus elaiosomes) and internally disperse viable seeds. In these studies, slugs also occasionally consumed only the elaiosomes, leaving the seeds behind. There are also scattered reports of elaiosome robbing (Mesler and Lu 1983; Gunther and Lanza 1989; Kalisz et al. 1999) as well as the consumption of developing fruits and seeds (Muir 1997) by slugs in North America, but our study is the first in North America to experimentally

exclude slugs from seed depots with the aim to quantify their effects on seed fates. Invasive slugs, such as *Arion subfuscus*, are becoming an increasing problem in North America, not only as agricultural and urban pests, but also by threatening endangered plant species (Cowie and Robinson 2003; Joe and Daehler 2007; Hahn et al. 2011). Many invasive slugs, including *A. subfuscus*, arrived in North America from Europe where they historically co-occurred with myrmecochorous herbs; thus they may be adapted to consuming diaspores or elaiosomes.

In our study, we examined the effects of invasive slugs, invasive and native seed-dispersing ants, and native rodents on seed dispersal, seed predation, and elaiosome robbing of a spring ephemeral, *Asarum canadense*. Myrmecochorous seeds in eastern North America are principally dispersed by the ant *Aphaenogaster rudis* s.l., which is considered to be a keystone mutualist because it disperses as many as 70 % of the seeds it encounters (Ness et al. 2009). Prior et al. (2015) found that seed dispersal by *A. rudis* increased recruitment of native seedlings, including *A. canadense*, relative to the no-ant controls, thereby demonstrating that *A. rudis* is an effective seed disperser of *A. canadense* and other myrmecochorous herbs. Although many invasive ants are ineffective seed dispersers (e.g., Christian 2001; Carney et al. 2003; Ness 2004; Rodriguez-Cabal et al. 2011; Warren et al. 2015), some invasive ants can be high-quality seed dispersers in their introduced ranges. For example, the European fire ant, *Myrmica rubra*, is an important seed disperser in its native range (Gorb and Gorb 1999; Fokuhl et al. 2007) and has recently been shown to disperse seeds in its introduced range in North America (Prior et al. 2015).

Plants can benefit from ant dispersal in multiple ways, including through directed dispersal to favorable microhabitats (Gibson 1993), reduced parent–offspring competition (Kalisz et al. 1999; Boyd 2001), or reduced seed predation rates (O’Dowd and Hay 1980; Heithaus 1981). Although escape from predation, particularly by granivorous rodents, is often considered to be a major benefit and driver of the evolution of myrmecochory (O’Dowd and Hay 1980; Heithaus 1981), rodent predation is frequently low or spatially variable in many systems (e.g., Smith et al. 1989). Thus, we experimentally manipulated rodent access to seed depots across several sites to determine whether rodents consume significant numbers of *A. canadense* seeds. We also video-recorded seed depots to determine which other taxa interact with *A. canadense* diaspores besides ants, slugs, and rodents. In some systems, vespid wasps (Jules 1996; Zettler et al. 2001) and Opiliones (Kalisz et al. 1999; Chlumsky et al. 2012) can be effective seed dispersers; to the contrary, carabid beetles or, occasionally, springtails, spiders, or ticks consume seeds or elaiosomes without moving seeds (Ohara and Higashi 1987; Ohkawara et al. 1996; Giladi 2006).

Our study is divided into four parts. First, in a field experiment, we excluded ants, slugs, and rodents from seed depots to ask: do these taxa remove seeds or simply consume elaiosomes, and what are their interactive effects on seed removal rates? Second, animal activity at seed depots was monitored by video recordings to ask: which other non-focal organisms are attracted to seeds and is there any evidence of interference competition? Third, ant preferences for seeds with and without elaiosomes were tested in the laboratory to ask: does elaiosome robbing by slugs prevent ants from picking up seeds? Fourth, slug densities in mesocosms with ant colonies in the field were manipulated to ask: what effect does slug density have on seed removal by native and invasive seed-dispersing ant species?

Methods

Study system and site

We conducted this study at the Koffler Scientific Reserve at Joker's Hill (KSR, 44°02'N, 79°32'W) near King City, Ontario, Canada. The 350-ha property is composed of deciduous and mixed old growth and secondary forests in addition to old fields and wetlands. Canadian wild ginger, *Asarum canadense* (Aristolochiaceae), is highly abundant at KSR, often forming large clonal patches. Fruits of *A. canadense* develop at the base of the plant in the leaf litter and release seeds with large, fleshy, oleic-acid rich elaiosomes that are attractive to ants (Turner and Frederickson 2013). Diaspores of *A. canadense* are large (11.6 mg) with a relatively high elaiosome: seed mass ratio (KM Prior, unpublished data). We collected *A. canadense* diaspores when fruits dehisced (mid-to-late June, 2013) and stored them at -21°C until use. Ants do not prefer fresh over previously frozen diaspores (Zelikova et al. 2008).

We offered *A. canadense* diaspores to ants in depots, where they were principally dispersed by *Aphaenogaster rudis* s.l. (see Results). The taxonomy of the *Aphaenogaster rudis-fulva-texanus* species complex is under consideration; species in this group are difficult to distinguish morphologically (Umphrey 1996) and differ in their distributions and climate preferences (Warren et al. 2011). We follow previous studies (Lubertazzi 2012; Prior et al. 2014, 2015) in referring to our study species as *A. rudis*, but recognize that it is likely *Aphaenogaster picea* or an undescribed species in this complex. *A. rudis* is abundant at KSR and has been called a "keystone mutualist" because it disperses up to 70 % of the myrmecochorous diaspores it encounters (Ness et al. 2009). These ants nest mainly in rotting wood, but also in soil, forming monogynous colonies with several hundred workers (Lubertazzi 2012).

Arion subfuscus (Draparnaud), an invasive slug native to Europe, also visited the depots in large numbers. *A. subfuscus* is a member of the *Arion subfuscus-fuscus* species complex in Europe (Pinceel et al. 2004), and both of these species have been recorded in North America (Pinceel et al. 2005; Barr et al. 2009). Because *A. subfuscus* is the more widespread of the two species in North America (Pinceel et al. 2005), we refer to this dominant slug as *A. subfuscus*. This slug measures up to 5–8 cm long when fully extended and occurs in a variety of habitats, predominately forested areas, where it feeds chiefly on plant and fungal material (Chichester and Getz 1973; Beyer and Saari 1978). The first record of *A. subfuscus* in Ontario dates to 1966 (Pinceel et al. 2005), and it currently occurs at high densities in many parts of its introduced range, which covers eastern North America, reaching up to 30 individuals/m² at KSR. Numerous rodent species at KSR may also interact with the diaspores of myrmecochorous plants; video footage (see Results section) captured *Napaeozapus insignis*, the woodland jumping mouse, visiting depots.

Finally, in the mesocosm experiment, we studied the effects of several slug densities on seed removal by *A. rudis* and by the invasive European fire ant, *Myrmica rubra*. Although *M. rubra* did not visit the field depots and has not yet invaded forests at KSR, it occurs in old fields and grasslands at KSR. *M. rubra* is also abundant at nearby forested sites, where it co-occurs with *A. rudis*, *A. subfuscus*, and myrmecochorous plants. Although *A. rudis* and *M. rubra* likely have different habitat preferences, with *A. rudis* preferring drier, upland forest patches and *M. rubra* preferring riparian forest patches, in the study region, these species coexist in forests that contain both habitat types (KM Prior, unpublished data). *M. rubra* disperses seeds of many myrmecochorous plants in both its native (Gorb and Gorb 1999; Fokuhl et al. 2007) and introduced ranges (Prior et al. 2014, 2015). This ant species was introduced to North America over 100 years ago and has been in Ontario since at least 1975 (Groden et al. 2005). *M. rubra* workers are approximately the same size as *A. rudis* workers, but they live in large colonies with multiple queens (polygyny) and multiple nests (polydomy) (Groden et al. 2005).

Ant, slug, and rodent exclusion experiment

From 15 July 2013 to 27 July 2013, we conducted a field experiment in maple–beech forests in which we excluded ants, slugs, or rodents from depots in a full factorial design and monitored diaspore removal and elaiosome consumption. We created eight treatments: (1) all access; (2) ant exclusion; (3) rodent exclusion; (4) slug exclusion; (5) rodent and ant exclusion; (6) rodent and slug exclusion; (7) ant and slug exclusion; (8) rodent, slug, and ant exclusion. In each replicate, we put ten *A. canadense* diaspores

in a 10 × 10-cm plastic petri dish lid (the “depot”) that was affixed to a 25 × 25-cm plywood platform. We built metal mesh cages to exclude rodents; the cages measured 26 × 26 × 10 cm, with a mesh size of 1.3 cm. A cage was placed over each depot assigned to a rodent exclusion treatment and anchored to the ground. To exclude ants, we applied a 0.75-cm-wide band of Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) directly to the plywood platform around the petri dish. The application of Tanglefoot did not deter slugs from depots, as they were able to arch over the barrier and easily access the petri dish. Tanglefoot may also exclude other crawling arthropods; however, this likely had negligible effects on seed dispersal given that we did not observe any non-focal taxa removing seeds in our video recordings (see below and the [Results](#) section). To exclude gastropods, we first tried using a 2.5-cm-wide copper barrier around the petri dish, as previous studies found that slugs are reluctant to cross copper (Türke et al. 2010); however, laboratory trials with *A. subfuscus* revealed that copper alone did not keep slugs from reaching depots. When we added a 4-cm-wide strip of Fluon (Insect-a-Slip; BioQuip Products, Inc., Compton, CA; more commonly used to keep ants from crawling up vertical surfaces), the combined copper and Fluon were effective at excluding slugs from depots in almost all trials, while ants were still able to cross the horizontal strip of Fluon (see [Results](#) section). The effectiveness of all treatments was confirmed with video-recording trials (see below).

We carried out the experiment at five old-growth forest sites at KSR, each separated by at least 140 m. Each site comprised six blocks spaced 10 m apart in a 3-by-2 grid. In five of the blocks, we put out eight depots (one in each treatment) 50 cm apart and arranged in a 2-by-4 grid. The sixth block contained the video setup (see below). Treatments were randomly assigned to depots within each block, and the location of sixth block (video) was randomly assigned at each site. We conducted this experiment at sites on different days within the 2-week period and randomly chose the order of sites. We put out the depots at 0900 hours and left them out for 24 h. The trials were conducted only on warm, sunny days with zero precipitation (as rain ruined the effectiveness of the slug barriers). We observed ants or slugs breach the exclusion treatments around a few depots (2 and 10 %, respectively) and therefore removed these from analyses. We analyzed the numbers of seeds and elaiosomes removed from depots after 24 h using generalized linear mixed models (GLMMs) fitted to a negative binomial distribution, with site as a random factor, and ant, slug, and rodent exclusion and all interactions as fixed effects. All statistical analyses were carried out in R v. 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria).

Video-recording of depots

We video-recorded animal activity at a subset of the depots to identify all taxa that interacted with diaspores, including ants, slugs, and rodents, as well as more occasional visitors, such as Vespidae (wasps), Carabidae (ground beetles), Diptera (flies), and Opiliones (Harvestmen), and to look for evidence of direct interactions between species visiting the depots. Preliminary video trials were also set up once for each exclusion treatment (i.e., ant, rodent, or slug) prior to the main experiment to confirm the effectiveness of each type of exclusion treatment and to confirm that exclusion treatments did not negatively impact any other focal taxa. At each of our five sites, one of the six blocks contained the video camera setup to record all activity over 24 h on an all-access depot with 30 diaspores. We put 30 diaspores (instead of 10, as in our main experiment) in each video-recorded depot so that the animals which discovered the depot first were less likely to remove all of the diaspores before other animals could visit, thus increasing our chances of observing a greater diversity of visitors. We used a D-Link Cloud Camera model 2300 (D-Link Corp., Tapei, Taiwan, ROC) with infrared night vision powered by a portable power source and suspended 75 cm directly above the depot. We analyzed the video footage on fast-forward speed and recorded the identities of all visitors to the depots, the time each visitor spent in the petri dish, and how the visitors interacted with the diaspores. All animals which entered the petri dish were considered to be “visitors.” So long as the animal remained on the plywood platform, we recorded it as a single visit, even if the visitor left the petri dish; however if an animal left the wooden platform or video frame and later returned, it was considered to be a new visitor. The number of seeds or elaiosomes removed after 24 h was regressed against the number of ant or slug visits (log-transformed after adding 1), respectively.

Ant preferences for seeds with and without elaiosomes

We tested whether elaiosome removal by slugs makes *A. canadense* diaspores less attractive to ants in a bioassay. We used ten laboratory *A. rudis* colonies previously collected at KSR; colonies were fed an artificial diet every 2–3 days [modified from the Bhatkar–Whitcomb diet as described by Dussutour and Simpson (2008)], but starved for 5 days before the experiment. We standardized the size of the ant colonies in order to have ten colonies, each with one queen, 200 workers, and 50 brood (larvae and pupae). We housed ant colonies in plastic containers (7 × 14 × 14 cm) attached by plastic tubing to arenas (42.9 × 34 × 13.7 cm). Ants could access the arenas only during the bioassays. For each of our ten replicates, we removed ten intact diaspores

from the freezer, held five in reserve at ambient temperature and collectively offered the other five to 20 *A. subfuscus* individuals, which removed elaiosomes from all of the diaspores. We then put the five diaspores with elaiosomes removed by slugs and the five intact diaspores in two separate petri dishes (diameter 4 cm) in the center of each arena and allowed ants access to the seeds. We counted the numbers of seeds remaining in the petri dishes 24 h later and compared the numbers of seeds removed between treatments using a paired *t* test.

Ant and slug mesocosm experiment

To investigate how slug density affects diaspore retrieval by ants, in July 2014 we built 60 mesocosms in a red pine plantation at KSR that provided even shading. Mesocosms were made out of 8.7-L plant pots encased in fine mesh netting (625 holes per square inch; No-see-um netting; Skeeta, Bradenton, FL), half-filled with woodchips, and buried so that the woodchips were flush with the ground. We coated the inside top margin of the containers with Fluon to help prevent ants and slugs from escaping.

Thirty mesocosms received one *A. rudis* colony (collected at KSR) and 30 mesocosms received one *M. rubra* colony (collected from forested areas in nearby Toronto). In early July, we transferred each ant colony into a mesocosm in a 10-cm piece of vinyl tubing with one end filled with a moist cloth. We loosely buried each nest tube such that the open end was sticking out of the woodchips. Colonies were previously standardized for another experiment to 250 workers, 60 larvae, and one (*A. rudis*) or two (*M. rubra*) queens, but between colony standardization and the initiation of this experiment, most colonies lost a large portion of their workers. For this reason, at the conclusion of this experiment we extracted all ant colonies and counted queen and worker numbers to measure colony size; colonies with 0–50 workers were excluded from the analysis. Prior to this experiment, ant colonies were fed half a cricket and cotton soaked in honey-water twice a week. Some colonies were initially fed diaspores of two myrmecochorous species as part of a different study, so we starved the ant colonies for 2 weeks prior to the start of this experiment to diminish any effects of previous feeding treatments.

We randomly assigned ant colonies to one of three treatments: no slugs, two slugs (low density), or six slugs (high density) per mesocosm, with each treatment replicated 10 times per ant species. Two and six slugs were chosen to represent low and high slug densities, respectively, because this reflects the natural variation in slug density that we observed at KSR. In our field experiment, we often observed two to six slugs feeding at the same depot, and on video, we observed up to 12 slugs on a depot at the same

time (see [Results](#) section). Furthermore, *A. subfuscus* densities of 11 individuals/m² have been reported from New York (Beyer and Saari 1978). We added slugs, collected at KSR, to mesocosms on 29 July 2014 and allowed them to acclimatize for 1 day. On 30 July 2014, we put 15 *A. canadense* diaspores in a petri dish in each mesocosm; 24 h later we counted the numbers of seeds with and without elaiosomes remaining in the petri dishes. Two replicates in the no slug treatment were excluded from the analysis because they were found to contain a slug that had consumed some elaiosomes. We analyzed the numbers of diaspores and elaiosomes removed from depots using generalized linear models (GLM) fitted to a negative binomial distribution; the final models included ant species, slug density, ant colony size, and an ant species × slug density interaction term as fixed effects.

Results

Ant, slug, and rodent exclusion experiment

Only ants, and not slugs or rodents, removed large numbers of diaspores from the depots. There was a highly significant effect of ant exclusion (GLMM: $z = -3.29$, $p = 0.001$; Fig. 1a), and no effect of slug exclusion ($z = 0.50$, $p = 0.62$), rodent exclusion ($z = -0.06$, $p = 0.95$), or any interaction terms (ants × slugs: $z = 0.23$, $p = 0.82$; ants × rodents: $z = 0.53$, $p = 0.59$; slugs × rodents: $z = -1.64$, $p = 0.10$; ants × slugs × rodents: $z = -0.11$, $p = 0.91$) on diaspore removal. When they had access to depots, ants removed 21.3 % ± 15.1 % [mean ± 1 standard error (SE)] of diaspores, although there was substantial variation among sites [Electronic Supplementary Material (ESM) Fig. S1a].

Slugs consumed elaiosomes without dispersing seeds. Slug exclusion significantly reduced the numbers of seeds that lost elaiosomes (GLMM: $z = -5.48$, $p < 0.001$; Fig. 1b), while ant and rodent exclusion and all interactions had no effect on elaiosome damage (ants: $z = 0.03$, $p = 0.98$; rodents: $z = -0.46$, $p = 0.64$; ants × slugs: $z = 0.32$, $p = 0.75$; ants × rodents: $z = -0.76$, $p = 0.45$; slugs × rodents: $z = -1.69$, $p = 0.09$; ants × slugs × rodents: $z = 0.00$, $p = 1.00$). Slugs consumed 39.4 ± 28.2 % of elaiosomes, although again there was substantial variation among sites (ESM Fig. S1b).

Rodent visitation was rare. We observed one rodent on camera (see [Video recording of depots](#) section), and we inferred that a second rodent consumed seeds at three adjacent depots because we observed scat and footprints on the depots. Rodents visiting depots left only seed coats, consuming both seeds and elaiosomes.

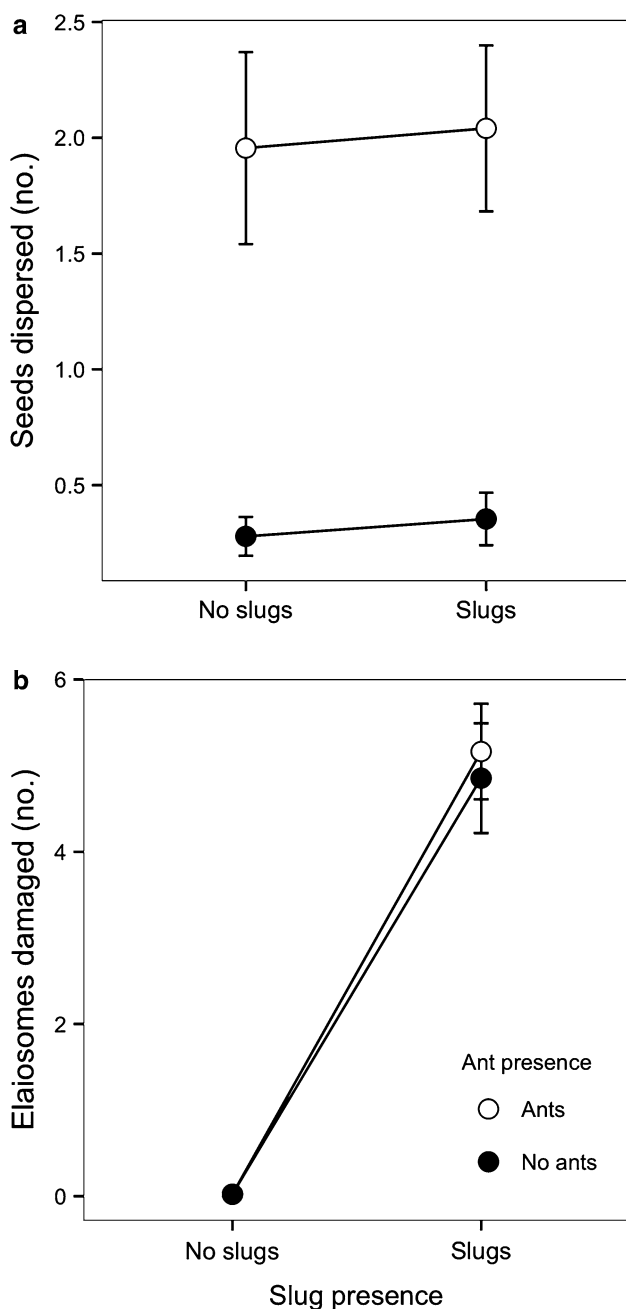


Fig. 1 Fates of Canadian wild ginger (*Asarum canadense*) diaspores in the presence or absence of slugs and ants. Data are presented as the mean (circles) ± 1 standard error (SE; whiskers) number of seeds dispersed (a) and elaiosomes damaged (b) per depot. Each depot initially had 10 seeds. Means are calculated from all treatment levels across all sites

Video recording of depots

Video monitoring confirmed that ants and slugs were the main visitors to the depots. *Aphaenogaster rudis* was the dominant ant species visiting depots, accounting for 97 % of all ant visits; *A. rudis* was also the only ant

species to move or disperse diaspores. The number of *A. rudis* visits was positively correlated with the number of seeds removed from the video-recorded depots (adjusted $R^2 = 0.88$, $p = 0.01$; ESM Fig. S2a); workers of this species removed 28.7 ± 10.0 % of diaspores present in the five video-recorded depots.

There was a high level of variation among sites (ESM Fig. S1). The video-recorded depot at site B had 73 slug visits (Fig. 2; ESM video 1) and only three ant visits, whereas the video-recorded depot at site C had over 130 ant visits (Fig. 2; ESM video 2) but only one slug visit. At slug-dominated site B, slugs passively removed nine of the 30 diaspores without their elaiosomes from the video-recorded depot after 24 h; these seeds were stuck to slug bodies or mucus and were often scraped off their bodies on the edge of the wooden depot. The number of *Arion subfuscus* visits was not correlated with the number of elaiosomes damaged in the video-recorded depots (adjusted $R^2 = 0.20$, $p = 0.25$; ESM Fig. 2b), even though slugs consumed 55.3 ± 15.4 % of the elaiosomes and passively removed 6 % of seeds present in the five video-recorded depots.

Harvestmen were also frequent visitors to the seed depots; we observed them feeding on elaiosomes on at least 12 occasions and sometimes picking up seeds while eating. However, they were never observed carrying seeds out of the petri dishes. Furthermore, we were not able to attribute any elaiosome removal directly to harvestmen, as they were often present alongside slugs; any elaiosome damage they may have inflicted was probably only partial. Large calyptrate flies occasionally visited depots and were observed trying to pick up seeds and possibly feeding on elaiosomes. We observed no interactions among focal taxa at the depots; specifically, we noticed no direct or aggressive interactions between ants and slugs when they were both present. A single rodent visit (*Napaeozapus insignis*, the woodland jumping mouse) was caught on camera; it consumed 26 diaspores in less than 5 min (Fig. 2; ESM video 3).

Ant preferences for seeds with and without elaiosomes

Over 24 h, *A. rudis* colonies removed 19-fold more seeds with elaiosomes (38 ± 11 %, mean ± 1 SE) than without elaiosomes (2 ± 2 %; $t_9 = 3.25$, $p = 0.01$).

Ant-slug mesocosm experiment

As slug density increased, ants dispersed fewer seeds (Fig. 3a) because slugs removed more elaiosomes (Fig. 3b). Slug density negatively affected seed removal from the depots (GLM; slug density: $z = -1.98$, $p = 0.048$; Fig. 3a); ants removed more diaspores when slugs were absent than when they were present at high densities. Slugs consumed



Fig. 2 Stills from the video monitoring. *Left still* shows a high density of the invasive slug *Arion subfuscus* at site B, with 9 individuals, *center still* shows individuals of the ant *Aphaenogaster rudis* removing diaspores at site C (*arrows* locations of 3 *A. rudis* workers carry-

ing diaspores, *dots* locations of 2 other ants), *right still* shows *Napaeozapus insignis*, the woodland jumping mouse, feeding on diaspores at site E (recording was made at night under infrared light)

the most elaiosomes when they occurred at high density in the presence of *A. rudis* (Fig. 3b), although there was no significant effect of ant species or an ant species by slug density interaction on seed removal (ant species: $z = 0.95$, $p = 0.34$; ants \times slugs: $z = 0.87$, $p = 0.38$). However, larger ant colonies of both species removed more seeds ($z = 2.30$, $p = 0.02$). Elaiosome removal increased significantly with increasing slug density (GLM; slug density: $z = 3.78$, $p < 0.001$), while ant species, colony size, and an ant species by slug density interaction had no effect on elaiosome removal (ant species: $z = 0.03$, $p = 0.97$; colony size: $z = -1.61$, $p = 0.11$; ants \times slugs: $z = -0.79$, $p = 0.43$; Fig. 3b). At high slug densities, all diaspores were either dispersed by ants or had their elaiosomes robbed by slugs. Thus, slug presence, and the resulting elaiosome removal, limited the number of diaspores dispersed by ants.

Discussion

Many mutualisms, including seed dispersal, are vulnerable to disruption by invasive species (Bond and Slingsby 1984; Christian 2001; Traveset and Richardson 2006; Prior et al. 2015). Here, we show for the first time how a non-ant invasive species affects seed dispersal by ants, with a potential for cascading effects on forest plant communities. At KSR, the invasive slug, *Arion subfuscus*, “robbed” diaspores of their elaiosomes. In our main field experiment and on video recordings, *Aphaenogaster rudis* ants were the primary dispersers of Canadian wild ginger, *Asarum canadense*, diaspores (and the number of *A. rudis* visits to video-recorded depots was a good predictor of the number of seeds removed), while slugs consumed elaiosomes without dispersing seeds. Laboratory trials showed that elaiosome consumption by *A. subfuscus* drastically reduced seed removal by *A. rudis*. Although the number of slug

visits to video-recorded depots did not significantly predict the number of elaiosomes damaged, in a field mesocosm experiment with greater statistical power, the number of elaiosomes robbed increased with increasing slug density and higher densities of slugs significantly reduced seed removal by ants. Thus, our results show that invasive slugs rob elaiosomes, which results in reduced seed dispersal by ants when slugs are at high densities, suggesting that invasive slugs can have profound negative effects on seed dispersal mutualisms.

We did not find an effect of elaiosome robbing on seed removal by ants in our main field experiment (i.e., no significant ant \times slug interaction effect on seed removal; $p = 0.10$). However, the results from our laboratory and mesocosm experiments showed that ants did not disperse seeds with their elaiosomes removed via slug feeding, suggesting that this interaction can have significant effects on seed dispersal. We believe that this lack of interaction in the field may be a result of ants and slugs not co-occurring at sufficiently high densities at our sites (ESM Fig. S1). The patchy visitation rates by ants and slugs could be a result of spatial or temporal variation among sites because each site was tested for seed removal on a separate day over the 2-week period. The strong negative effect of elaiosome robbing by slugs on seed removal by ants in laboratory and field mesocosms is likely diminished by the natural spatiotemporal variation of visitation rates in the field.

In the five video-recorded depots, the number of *A. subfuscus* visits was not significantly correlated with the number of elaiosomes damaged, likely because we had low power to detect a correlation. Furthermore, just a few slugs could consume all of the elaiosomes available in a depot, but slugs continued to visit depots (sometimes in large numbers) even after all elaiosomes were removed. Nonetheless, our field mesocosm results show how the effect of elaiosome robbing by slugs on seed dispersal by ants depends

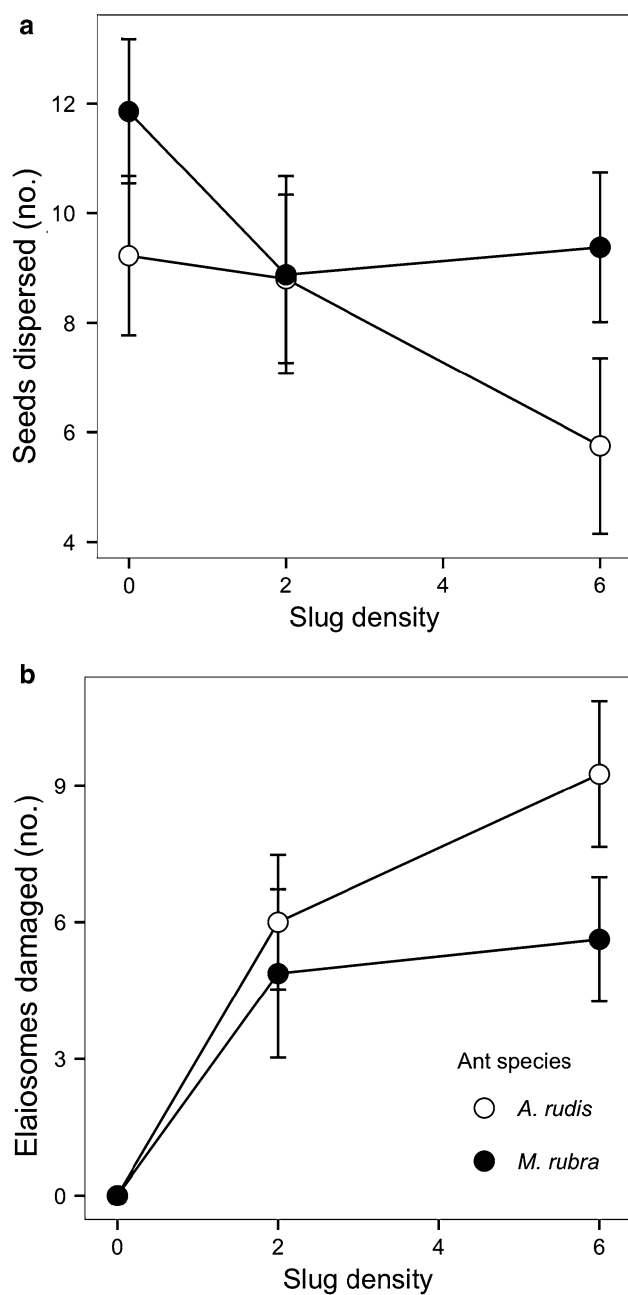


Fig. 3 *Asarum canadense* diaspore fates by *Arion subfuscus* slug density and ant species (*Aphaenogaster rudis* or *Myrmica rubra*). Data are presented as the mean (circles) \pm 1 SE (whiskers) number of seeds dispersed (a) and elaiosomes damaged (b) per mesocosm. Each depot initially had 15 seeds

on slug density, suggesting that this effect may vary among locations that differ in invasion history. For example, wherever *A. subfuscus* has been present long enough to establish in large numbers, we might expect plant populations to experience strong negative effects of elaiosome robbing on seed dispersal. The timing of the introduction of *A. subfuscus* at KSR is unknown. Many factors could have produced

the variation we observed in slug activity among sites at KSR (ESM Figs. 1, 2). In particular, since we could maintain the effectiveness of our slug exclusion treatment only on warm, dry days, we may have inadvertently selected for days with low slug activity. Our mesocosm results also suggest that the timing of visits could be important because if ants are able to disperse seeds first, there is no opportunity for slugs to rob elaiosomes. In the field experiment, we put seeds out in the morning and left them for 24 h. Alternatively, it is possible that if they were left out longer we may have seen higher removal rates; however, *A. canadense* elaiosomes dry out quickly and become unattractive to ants and slugs. In addition to daily activity patterns, slug activity also has seasonal patterns, which could affect plant species differently depending on when fruits release seeds (S. Gordon and S. A. Meadley Dunphy, unpublished data). Therefore, the magnitude of the negative effect of slugs on seed dispersal depends on the seasonal and daily timing of slug activity, as well as the density of co-occurring ants and slugs.

At our field sites, rodent seed predation is probably unimportant to *A. canadense* populations, as rodent exclusion had no effect on seed or elaiosome removal. Predator avoidance is often considered to be a major selective advantage of myrmecochory for plants (e.g., Heithaus 1981), and a meta-analysis by Giladi (2006) found support for the predator avoidance hypothesis in 82 % of studies that were tested for it. However, Smith et al. (1989) found that rodent consumption of myrmecochorous seeds in some systems can be very patchy and rare, varying from site to site, or even nonexistent. Of all non-focal taxa, harvestmen interacted with diaspores most frequently in our video monitoring. There have been scant reports of harvestmen interacting with myrmecochorous seeds, either feeding on elaiosomes or picking up and carrying diaspores (Gunther and Lanza 1989; Kalisz et al. 1999; Chlumsky et al. 2012). However, we did not observe harvestmen removing diaspores from depots, and any elaiosome consumption was likely only partial. Additionally, we did not observe any wasps, beetles, or spiders, which have been reported to act as either important dispersers or predators of myrmecochorous seeds in other studies (e.g., Ohara and Higashi 1987; Jules 1996; Zettler et al. 2001b).

One important caveat of our study is that we measured only seed removal, and we assumed that higher seed removal rates lead to better seed dispersal and plant recruitment. Although the removal of seeds by ants from beneath adult plants does not necessarily add up to effective seed dispersal and subsequent plant recruitment (Prior et al. 2015), it often confers various long-term benefits to plants (e.g., Kjellsson 1991; Kalisz et al. 1999). Similarly, elaiosome robbing by slugs may have several effects on seedling recruitment. Our results show that ants do not remove

diaspores with elaiosomes consumed by slugs. Other studies have shown that elaiosome robbing by ants or ground beetles reduces seed dispersal by “legitimate” ant partners and increases seed predation by rodents (Boulay et al. 2009) or seedling clumping around adult plants (Ohara and Higashi 1987). Conversely, removal of elaiosomes can also decrease detection and thereby seed predation by rodents (Boyd 2001; Christian and Stanton 2004). We did not test whether elaiosome removal by slugs affects germination, but elaiosome removal by slugs can sometimes increase germination rates (Calvino-Cancela and Rubido-Bará 2012). However, in our system, if elaiosome-robbled seeds do germinate, they would do so only under parent plants. For *A. canadense*, this would be especially detrimental, since seeds are released directly onto the ground at the base of the adult plant, and seedling mortality is significantly higher inside an *Asarum* clone than outside of it (Gorb and Gorb 2003).

It is interesting to compare the effects of elaiosome robbing on myrmecochory to the much better studied effects of nectar robbing on pollination (Irwin et al. 2010). Floral visitors that remove nectar without pollinating can have various direct and indirect effects on plant reproduction, such as by damaging plant reproductive organs or causing pollinators to avoid nectar-robbled flowers (Maloof and Inouye 2000; Irwin et al. 2010). While we do not know whether slugs damage seeds when removing elaiosomes, our results show that ants avoid elaiosome-robbled seeds; consequently, elaiosome robbing can be detrimental to seed dispersal. The timing of visits is important; much as nectar robbers may have larger negative effects on plant reproduction when they visit before—rather than after—legitimate pollinators (e.g., Morris 1996), slugs may affect seed dispersal only if they reach seeds before ants. Although we put diaspores out at 0900 hours and monitored them for 24 h, *A. canadense* is thought to release seeds slowly throughout the day and night. Future work could determine whether the timing of seed release in *A. canadense* and the daily activity patterns of slugs and ants influence which animal gets to a seed first. Our previous work has shown that *A. rudis* disperses seeds more slowly than *Myrmica rubra* (Prior et al. 2015), which could provide slugs with more opportunity to rob elaiosomes in the presence of *A. rudis* compared to *M. rubra*, with concomitant effects on seed dispersal, although we did not find a significant ant species \times slug density interaction in our mesocosm experiment. Finally, some floral traits are thought to be defenses against nectar robbers (Irwin et al. 2010), and thus it is interesting to consider whether slugs could be selecting for seed or elaiosome traits that reduce elaiosome robbing in our system.

Recent work has shown that native and invasive slugs internally disperse elaiosome-bearing seeds in temperate

deciduous forests in Europe (Türke et al. 2010, 2012), although many seeds are damaged by passage through the gut of an invasive slug (Blattmann et al. 2013). Our results show, however, that slugs at our North American field site typically rob elaiosomes without moving seeds, thereby making the latter less attractive to legitimate seed dispersers such as *A. rudis* and *M. rubra*. Whether slugs ingest whole diaspores or just elaiosomes appears to be determined by body size and seed size (Türke and Weisser 2013), and thus in our system, *A. subfuscus* might internally disperse plant species with smaller seeds. The invasive slug *A. subfuscus* occurs at high densities in forests in and around our study site, and in our field experiment we found that slugs consumed elaiosomes in 64 % of the depots that they had access to. *A. subfuscus* also exerts strong herbivory pressures in its introduced range (Cardina et al. 1996; Fritz et al. 2001), and a congener with a similar invasion history, *A. fasciatus*, is a major predator of *A. canadense* flowers, fruits, and developing seeds, resulting in decreased seedling emergence (Muir 1997). Given the high densities of *A. subfuscus* and its potential to act as a herbivore on *A. canadense* fruits, developing seeds, and seedlings, in addition to the consumption of elaiosomes, this slug may significantly impact forest ecosystems. Our study has important implications for understanding the impacts of invasive slugs on natural ecosystems and also how anthropogenic change influences eastern North American forest ecosystems.

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Author contribution statement SAMD, KMP, and MEF conceived and designed the experiments. SAMD and KMP implemented the experiments. SAMD, KMP, and MEF analyzed the data and wrote the manuscript.

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