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Redispersal of seeds by a keystone ant augments the spread of common wildflowers

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ABSTRACT

Myrmecochory (dispersal of seeds by ants) is an evolutionarily and ecologically common mutualism. Most of the research on the costs and benefits of myrmecochory in North America assumes that ant-dispersed seeds are taken to, and left in, the ant nest. Here, we use a novel seed-tracking technique to quantify secondary dispersal of seeds from the nest into the surrounding leaf litter by the keystone seed-dispersing ant, *Aphaenogaster rudis*. We found that *A. rudis* redispersed >90% of the seeds it took into its nest an average distance of 51.5 cm. A mathematical model shows redispersal increases the rate of population spread of the myrmecochores *Hexastylis arifolia* and *Asarum canadense* by 22.5%, and increases the expected cumulative dispersal distance away from the parent plant by 24%. Our results suggest myrmecochory benefits plants in eastern North American forests by increasing the distance between the seed and parent plant and reducing competition among siblings.

1. Introduction

Much of ecology seeks to understand interactions among species and their consequences. Evidence continues to grow that facilitation, and more specifically mutualism, increases biological diversity and shapes the structure of ecological communities (Gross, 2008; Lengyel et al., 2009). In particular, ant-seed dispersal mutualisms (myrmecochory) are both geographically widespread and ecologically important (Giladi, 2006; Lengyel et al., 2010). Myrmecochorous seeds have a small, lipid-rich appendage called an elaiosome that ants remove and consume after dispersal. Elaiosomes have evolved tens of times in the monocots (Dunn et al., 2007) and over a hundred times in the angiosperms more generally (Lengyel et al., 2009, 2010). Over 11,000 species and 77 families of angiosperms participate in myrmecochorous relationships across a variety of ecosystems that span arid, tropical, and temperate regions (Giladi, 2006; Lengyel et al., 2010). To date, our understanding of the benefits of myrmecochory to plants (reviewed in Giladi, 2006) focus on dispersal distance of the seed away from its parent (e.g., Andersen, 1988), reduction in seed predation due to dispersal (e.g., Culver and Beattie, 1978; Heithaus, 1981) and movement of the seed to a favorable germination site (e.g., Beattie and Culver, 1983; Hanzawa et al., 1988). The importance of each proposed benefit is ecosystem-specific, linked to differences in behavior of the main seed-dispersing ant species (Giladi, 2006). However, despite the numerous advances in our understanding of myrmecochory, key observations relevant to each mechanism are missing, such as the fate of seeds once in ant nests (Servigne and Detrain, 2010).

Servigne and Detrain (2010) classify seed dispersal by ants into three stages: the collection of seeds and movement to a nest or central location (stage I), the removal of elaiosomes within the nest (stage II) and the abandonment of seeds either inside the nest or rejected outwards from the nest (stage III). In eastern North American temperate forests, most studies of myrmecochory focus on stage I of dispersal, with little research having been done and an implicit assumption in many studies that stage III generally consists of only abandonment inside the nest. The validity of this assumption has mainly been tested in European temperate deciduous forests where seeds are frequently observed being taken away from the nest (e.g., Gorb et al., 2000; Gorb and Gorb, 2003). However, to our knowledge, although redispersal has been described in eastern North American forests (Heithaus, 1986), it has not been well-quantified, particularly with regard to the

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distances seeds are redispersed. Redispersal has the potential to increase dispersal distances away from the parent plant, with consequent effects on the population spread rate of the plant. In addition, frequent redispersal would make several of the proposed benefits (and costs) of myrmecochory largely irrelevant (beneficial effects of being in a nest, for example, are unimportant if seeds aren't actually in nests). As the consequences of redispersal may be ecosystem-specific and depend on the behavior of the main seed-dispersing ant species, it is important to study redispersal with careful attention to the identity and behavior of the seed-dispersing ant species. This is especially true in ecosystems where seed dispersal service is predominately provided by a few keystone seed dispersers (Ness et al., 2009). Here, we explore further the redispersal of seeds by ants and the effect that it may have on the spatial population dynamics of plants in eastern North American forests.

Our study focuses on the ant species complex *Aphaenogaster rudis*. These ants are widespread and common where they occur (Giladi, 2004; Heithaus and Humes, 2003; Ness et al., 2009). They are also the most frequently cited seed-dispersing species in eastern North America (Beattie and Culver, 1981; Culver and Beattie, 1978; Heithaus, 1981; Gaddy, 1986; Warren et al., 2010; Zelikova et al., 2008) and considered the keystone seed disperser of myrmecochores in eastern North America (Ness et al., 2009). The reported average distances of primary dispersal distance of seeds by *A. rudis* range from 50 to 100 cm (Culver and Beattie, 1978; Giladi, 2004; Gómez and Espadaler, 1998; Kalisz et al., 1999; Zelikova et al., 2008). In temperate deciduous forests in eastern North America, ants, in particular *A. rudis*, disperse the seeds of 20%–70% of the total herbaceous flora (Beattie and Culver, 1981; Gaddy, 1986; Handel et al., 1981; Pudlo et al., 1980) depending on the geographic location. Consequently, if *A. rudis* tends to avoid disposal of seeds inside its nests, the effects may be relevant to a broad suite of plant species across a large geographic region, because seed rejection from the nest tends to be ant-specific (Servigne and Detrain, 2010). In addition, the specialization of eastern North American myrmecochores on *A. rudis* for dispersal may lead to significant effects on the population spread rate of myrmecochores due to the sensitivity of *A. rudis* to the effects of climate change (Warren et al., 2011) and invasive species (Rodriguez-Cabal et al., 2011).

To better understand the effects of redispersal on myrmecochore populations in eastern North America, we conducted both an empirical and mathematical exploration of redispersal. First, we documented redispersal frequency and distance of *Asarum canadense* by *A. rudis* using a novel seed-tagging technique for small seeds (Canner and Spence, 2011). Second, we modeled the consequences of redispersal on population spread rate for two related local myrmecochores, *Hexastylis arifolia* and *A. canadense*. Although the ranges of *H. arifolia* and *A. canadense* are not actively expanding, their ability to spread to new, suitable habitats may play a role in their future survival given the potential threats to their current ranges (e.g., climate change, habitat destruction and invasive species). We discuss the effects of redispersal on our current understanding of the benefits of myrmecochory to plants based on our empirical and model results.

2. Materials and methods

2.1. Study location

We conducted our study of seed redispersal in Lake Raleigh (Quay) Woods, a mixed pine-hardwood forest located on ∼97 acres of Centennial Campus, North Carolina State University, Raleigh, NC,

USA. The Lake Raleigh Woods understory includes many myrmecochorous plant species, but to measure redispersal, we use the seeds from a species in the family Aristolochiaceae (Birthwort), *A. canadense* L.

2.2. Study species

A. canadense (Canadian wild ginger) is a small, evergreen, herbaceous perennial, common in deciduous and occasionally mixed forests in eastern North America as far south as North Carolina and north into Canada (Cain and Damman, 1997; Heithaus, 1986; Offer, 1992). Reproduction occurs through seed production, with approximately 10–30 seeds per reproductive plant, and clonal reproduction (Cain and Damman, 1997; Offer, 1992). Flowering begins in late March and early April and fruiting occurs late May and early June in North Carolina (Smith et al., 1989; personal observation). The fruit grows from the base of the stem from a short prostrate peduncle (Beattie and Culver, 1981) and seed dehiscence occurs when the fruit opens to display the seeds. We collected *A. canadense* seeds for the study just prior to full fruit dehiscence. Seeds were promptly stored at −18 °C to prevent decomposition and oxidation of the elaiosome. The seeds of *A. canadense* are about 3–5 mm in length, narrowly ovate, with an elaiosome running the entire length of the seed, and a mean dry mass of 6.8 mg (mean fresh mass of 14.2 mg) (Smith et al., 1989). All redispersal measurements were of *A. canadense* seeds.

In a pilot study, in the summer 2007, we also observed the redispersal of *H. arifolia* from *A. rudis* nests. We were unable to acquire enough *H. arifolia* seeds to include this species in the experimental portion of our current study. However, we did extend our model analysis to include *H. arifolia* to examine the effect of redispersal on its population spread rate and we therefore include a description of the species here. *H. arifolia* (little brown jug) is a small, evergreen, herbaceous perennial and its range extends throughout the southeastern United States in deciduous and mixed forests (Gonzalez, 1972). Reproduction occurs through seed production, with approximately 20 seeds per reproductive plant (Giladi, 2004), with no clonal growth. Flowering begins in late March and early April and fruiting occurs in late May and June (Gonzalez, 1972), though *H. arifolia* tends to fruit later than *A. canadense* in our study location (personal observation). The seeds of *H. arifolia* are similar in both size and shape to *A. canadense*; they are ovate with a length of 2–4 mm and a weight of 8–12 mg (Giladi, 2004).

We focused our study on the ant species *A. rudis* because of its importance to understory seed dispersal in eastern North America. *A. rudis* nests are small and temporary (Culver and Beattie, 1978; Smallwood, 1982a, 1982b) and are in logs, under rocks, in the leaf litter, or below ground in temperate deciduous forests (Talbot, 1951). *A. rudis* hibernate underground until early spring, emerge, move the entire colony to temporary dwellings within the leaf litter, and then seek more established nest sites (Talbot, 1951; Smallwood, 1982b). The density of *A. rudis* nests in eastern North American forests is estimated to be greater than 1 colony per meter^2 in suitable habitat (see references in Ness et al., 2009). *A. rudis* are omnivorous, indiscriminant foragers. They forage individually with modest recruitment when they find a food cache. The density of *A. rudis* colonies combined with an average foraging distance of 50 cm or greater and overlapping territories makes it possible for *A. rudis* to cover 100% of the forest floor (Ness et al., 2009). *A. rudis* is a keystone mutualist (Ness et al., 2009; Zelikova et al., 2008) on which many understory herb species exclusively or nearly exclusively depend for seed dispersal. For our two species of interest, *A. rudis* is the primary disperser of *A. canadense*

(70–100% of dispersals; Heithaus, 1986) and *H. arifolia* (60–80% of dispersals; Giladi, 2004).

2.3. Seed preparation and detection

We used a new technique to mark and recover small seeds in the leaf litter using Coded Wire Tags (CWTs) (Northwest Marine Technologies, Inc., Shaw Island, WA) developed by Canner and Spence (2011). We injected small metal tags into the top of the seeds and we marked the seeds with yellow enamel paint to increase visibility within the leaf litter after initial detection. Preliminary studies showed that *A. rudis* and other ant species had no preference for tagged versus untagged seeds, nor did the paint or tag influence redispersal from the nest after elaiosome consumption (Canner and Spence, 2011). At the conclusion of each trial, we used the Handheld Wand Detector (NMT, Inc.) to detect the tagged seeds in the nest area and surrounding leaf litter. In addition, we could detect marked seeds artificially buried up to several centimeters in the leaf litter or soil.

2.4. Data collection and experimental design

We fed 20 *A. rudis* colonies between late May and early July 2008, to coincide with peak fruiting time and peak ant activity. Nests were located with baits one to two days prior to feeding and were at least 10 m apart. In a similar manner to other studies of seed fate within the nest (see Culver and Beattie, 1980; Hanzawa et al., 1988; Heithaus et al., 2005; Hughes and Westoby, 1992), we placed up to 50 marked *A. canadense* seeds near the nest entrance and observed the seeds' removal by *A. rudis* to be sure all seeds went into the same nest. Feedings occurred between 0900 and 1400 h, when daily ant activity peaked, until the colony removed all 50 seeds or until 30 min had passed since the last removal. The number of seeds fed to each nest is consistent with the average number of seeds a single *A. rudis* colony may consume in a day (Heithaus et al., 2005) and the number of seeds that may be naturally available near a colony (Gonzalez, 1972; Heithaus et al., 2005). After approximately 7 days, we excavated each nest and scanned all the leaf litter surrounding the nest within a 150 cm radius. We assume redispersal would not be greater than typical foraging distances of *A. rudis* colonies. Therefore, a 150 cm radius would be sufficient to recover most seeds because previous studies all reported an average seed dispersal distance by *A. rudis* of less than 100 cm (e.g., Culver and Beattie, 1978; Giladi, 2004; Pudlo et al., 1980; Zelikova et al., 2008).

We began the excavation at the outer edge of the 150 cm circle and systematically scanned the area with the detector until we reached the nest entrance. We marked detections with a flag, and then removed the leaf litter within a 2.5 cm radius of the detection point and searched for the seed or tag within the litter. If we found the seed(s) or tag(s), we then recorded the radial distance and direction from the seed location to the original nest entrance. In addition to the surrounding leaf litter, we also excavated the nest in 1–2 cm layers. We scanned each layer and recorded the depth of each recovered seed or tag. Excavation continued as long as we found ants or nest cavities within the log and/or leaf litter. We collected each colony and recorded the total number of workers, brood and alates. If a colony moved ($n = 3$; a common occurrence for *A. rudis*; see Culver and Beattie, 1978; Smallwood, 1982a, b), we marked the new nest location of any colony that contained tagged seeds, but we measured redispersal distance from the original location of the nest. In doing so, we adhered to the definition of redispersal as any movement of the seeds away from the endpoint of initial dispersal. We recorded seeds found in the original nest as a radial distance of 0 cm. We analyzed our data to determine if there were relationships between redispersal distance and frequency, colony size, nest type, and recovery rate of seeds. In addition, we conducted a Kruskal–Wallis Test to determine if there was a statistically significant difference between the distributions of redispersal distances between the nests. We used R Statistical Software (R Development Core Team, 2009) for all analysis.

2.5. Modeling spatial population dynamics

Redispersal has the potential to augment both a population's rate of spatial spread and its ability to reach a new, more suitable habitat. To compare population spread rate both with and without redispersal, we used a spatially explicit model of stage-structured population dynamics (Neubert and Caswell, 2000). The model is a discrete-time, continuous-space model that uses an integrodifference equation to incorporate movement at each demographic transition. To build such a model for our study system, two components are necessary. First, the model requires the annual demographic transitions among stages for the myrmecochore. Second, the model requires specifying the dispersal kernels that define the movement of the myrmecochore at each demographic transition. If we assume that the dispersal kernels are similar for each species, we can then use the model to calculate population spread rate and compare spread rate under different dispersal scenarios for both *A. canadense* and *H. arifolia*. We describe the model in brief here and provide details in Appendix A.

2.5.1. Demography of A. canadense

We estimate the annual transitions (e.g., survival, growth, and fecundity) for *A. canadense* by using the average population projection matrix for multiple years (1990–1995) between 2 plots from Cain and Damman's (1997) demographic study of the same species in late successional forest habitat. Life history stages were classified by Cain and Damman (1997) as seedling, yearling, lateral shoot (reproductive), and mature ramets (reproductive) (Table B.1, Appendix B). There is no documented seed bank for *A. canadense*. Dispersal can only occur between the lateral shoot and seedling stages and the mature ramets and seedling stages and does not vary with stage.

2.5.2. Demography of H. arifolia

We estimated the annual transitions for *H. arifolia*, a closely related species to *A. canadense*, by using the average population projection matrix for three populations from Giladi's (2004) demographic study of the same species (Table B.2, Appendix B). Giladi (2004) classified life history stages by leaf size and reproductive ability. In contrast to *A. canadense*, there is no clonal reproduction in *H. arifolia* populations. The stages are seedlings (stage 1), sub-adult (stage 2), non-reproductive adult (stage 3), reproductive adults with a small leaf size (stage 4), medium leaf size (stage 5), and large leaf size (stage 6), and dormant adult (stage 7). There is no known seed bank for *H. arifolia* (Giladi, 2004). Dispersal can only occur between the reproductive adult (4–6) and seedling stage (1) and does not vary with stage.

2.5.3. Movement of seeds

To evaluate the effect of redispersal on plant population spread rate, we consider three dispersal scenarios to contrast the differences in spatial dynamics with the addition of each new dispersal event. The first scenario considers only autochorous dispersal (i.e., no ant dispersal) in which dispersal distances follow a half-Gaussian distribution with a mean of 0.53 cm and

a standard deviation of 0.44 cm. We chose a conservative estimate of the parameters for the autochorous dispersal kernel based on the assumption that most seeds may disperse up to 2 cm on average from the parent plant in the absence of an ant disperser. The assumed distance is based on the observed lengths of the prostrate peduncle attached to the fruit. The second scenario is primary dispersal, which incorporates initial dispersal to the nest by ants. The dispersal kernel for primary dispersal is the convolution of the autochorous dispersal kernel and the measured initial dispersal kernel of seed dispersal from the parent to the nest (Neubert and Parker, 2004). We quantified the initial dispersal kernel based on data collected in collaboration with Zelikova et al. (2008) detailing site to nest dispersal distances of *H. arifolia* (mean = 73.85 cm, sd = 42.64 cm, n = 146). We assume that a fraction p_1 of seeds undergo primary dispersal by ants and fix p_1 at 74%, which is the average removal rate for *A. rudis* when *A. rudis* is present (Ness et al., 2009). The third scenario includes autochorous dispersal, initial dispersal and redispersal away from the nest. The dispersal kernel for the secondary-dispersal scenario is the convolution of the primary dispersal kernel (autochorous and initial dispersal) and the measured dispersal kernel for redispersal from the nest, with the fraction p_2 fixed at 93% of seeds redispersed based on data presented herein (rounded from 93.2%; see Section 4.1). We assumed that dispersal is isotropic (same in all directions) and we used a nonparametric method to fit the measured dispersal kernels to *A. rudis* dispersal and redispersal distance data (see Appendix A for details). Nonparametric methods allow us to avoid assumptions about the underlying distribution of the dispersal kernel (Clark et al., 2001; Lewis et al., 2006).

We also explored how changes in *A. rudis* density affect population spread rate by varying the removal rate p_1, because the removal rate of seeds depends on both the presence and abundance of *A. rudis* (Ness et al., 2009; Zelikova et al., 2008; Warren et al., 2010). Our data only account for dispersal by *A. rudis*, so our overall invasion speed may be an underestimate because it does not account for dispersal by other ant species and other dispersal vectors (e.g., Vellend et al., 2003).

3. Results

3.1. Redispersal frequency and distances

In total, we fed 20 colonies 864 seeds and we recovered, in total, 539 (63.3%) seeds and tags from the excavations. All recovered seeds were intact and without elaiosomes. The recovery rate for individual nests ranged from 26.5% to 98% of seeds fed to the colony. The pooled overall mean redispersal distance for individual seeds dispersed from all nests, including those found in the nest, is 51.5 cm (n = 539, sd = 32.5 cm) with a maximum observed distance of 148 cm (Fig. 1). We found redispersed seeds within the leaf litter surrounding the nest, not in obvious middens. We recovered seeds in the nest in 9 out of 20 nests. Thirty-seven seeds and loose tags were found within the nests (6.8% of all recovered), a result comparable with the observations of Heithaus (1986). We assume (perhaps conservatively) that redispersed and non-redispersed seeds were equally likely to be recovered. We then estimate that 93.2% of seeds were redispersed. We found no seeds in the nests deeper than 2 cm in the ground, most (64% of seeds found in nests) within a log or leaf litter. We recovered 48 tags (8.9% of total seeds and tags) unattached to seeds. In rare cases, we found a marked seed without a tag with a loose tag in the excavated leaf litter. Therefore, it is likely that some tags came loose from their seeds during excavation.
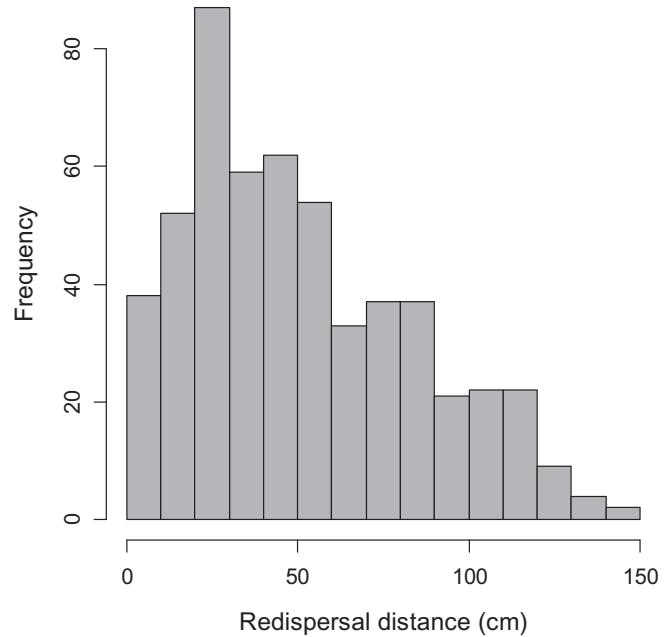

Fig. 1. Histogram of redispersal distances for all sampled nests. Data include seeds that remained in the nest (measured as 0 cm).

3.2. Variability of redispersal distances and frequency for individual nests

The distribution of redispersal distances for each nest was highly variable between nests (Fig. 2; Appendix C). The mean redispersal distances for individual nests ranged from 28.3 to 106.1 cm and the median redispersal distances for individual nests ranged from 11.8 cm to 111.8 cm. The proportion of seeds redispersed for individual nests ranged from 86% to 100% of seeds found.
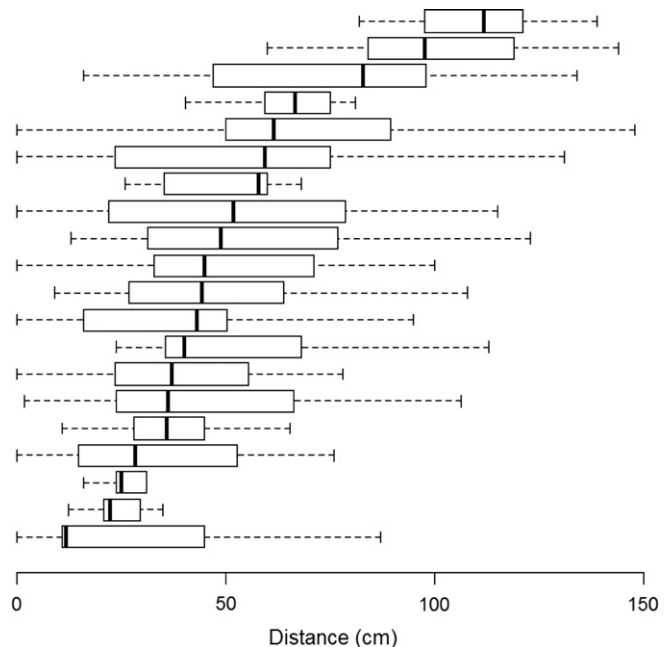

Fig. 2. Box-plots for individual nest redispersal distances ordered bottom to top by the median redispersal distance (smallest to largest) for each nest. Redispersal distances include seeds that remained in the nest (0 cm).

We recovered colonies for 16 of the 20 nests. Of the 16 recovered nests, 3 were collected from locations different from the original nest and were identified based on the recovery of tagged seeds from within the nests. The number of workers captured ranged from 14 to 285 ($n = 16$, mean $= 111.88$ cm, sd $= 63.91$ cm). The nest types varied among logs ($n = 7$), leaf litter ($n = 11$), and log and leaf litter mixed nests ($n = 2$).

We found no significant difference among the median dispersal distances for the three nest types (ANOVA $F_{2,17} = 1.41$, $p = 0.271$). In addition, we found that colony size (Regression ANOVA $F_{1,14} = 1.57$, $p = 0.231$) and recovery rate (Regression ANOVA $F_{1,18} = 1.59$, $p = 0.224$) were not significant predictors of the median dispersal distance. There was no relationship between colony size and redispersal frequency (Regression ANOVA $F_{1,14} = 0.40$, $p = 0.532$).

There was a statistically significant difference between the distributions of the redispersal distances among the individual nests (Kruskal–Wallis Test, $\chi^2 = 132.8$, df $= 19$, $p < 0.0001$). The variability among the nests could not be attributed to a single factor measured in our study. Original colonies could not be located for two of the extreme nest redispersal distributions (nest 18 and 19) so it may be possible that nest movement added to redispersal distance from the original location. Because redispersal distances were pooled in our model, the difference in redispersal distances between nests will not significantly affect the overall estimates of population spread rate.

3.3. Population spread rate

Our model results found that redispersal increases the invasion speed of *H. arifolia* and *A. canadense* by 22.5% compared to the calculated spread rate without redispersal (Table 1). The spread rate was higher for *A. canadense* than for *H. arifolia* because *A. canadense* has higher reproduction and growth rates (Appendix B). Invasion speed increased as removal rate increased under both dispersal scenarios (Fig. 3). As Zelikova et al. (2008) showed that removal rate varies linearly with *A. rudis* abundance, we can then infer that an increase in *A. rudis* abundance increases population spread rate.

3.4. Cumulative dispersal distance

Redispersal also affects the shape of the composite dispersal kernel. In our population dynamics model, we assumed a nonparametric dispersal kernel for both initial ant dispersal and redispersal. In order to compare the shapes of the composite dispersal kernels for primary dispersal and secondary dispersal, we assumed a Gamma-distributed kernel (as in Giladi, 2004) for both initial ant dispersal and redispersal. We simulated dispersal in two dimensions, with the direction of dispersal drawn from a uniform distribution on $(0, 2\pi)$ at each dispersal step, with probability of
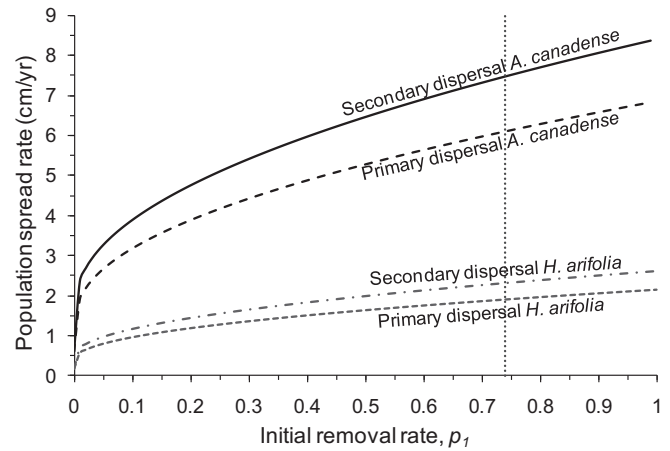
Table 1
Comparison each dispersal scenario on the spatial dynamics of *H. arifolia* and *A. canadense*, including the population spread rate and the mean and standard deviation of cumulative dispersal distance.

Movement	*H. arifolia* spread rate (cm/yr)	*A. canadense* spread rate (cm/yr)	Mean cumulative distance (cm)	Standard deviation (cm)
Autochorous Dispersal	0.17	0.60	0.50	0.81
Primary Dispersal	1.89	6.10	54.75	48.77
Secondary Dispersal	2.32	7.47	67.85	59.87

Fig. 3. The invasion speed versus initial removal rate of seeds. The vertical line represents the reported results for population spread with an initial removal rate of 74%. Note that primary dispersal is the convolution of autochorous dispersal and initial ant dispersal and secondary dispersal in the convolution of primary dispersal and redispersal by ants.

initial ant dispersal, $p_1 = 0.74$ (Ness et al., 2009) and probability of redispersal, $p_2 = 0.93$ (data herein). The addition of redispersal to the composite dispersal kernel increased the mean distance of dispersal of the seed away from the parent by 24% and increased the variance (Table 1). The effect of redispersal on the location and spread of the dispersal kernel shows that the cumulative dispersal distance from the parent plant is greater and more variable than previously thought.

4. Discussion

Here, we have shown ants redisperse the seeds of the understory herb, *A. canadense*, out of their nests and into the surrounding leaf litter. Redispersal from the nest has been noted before (Heithaus, 1986) for *Sanguinaria canadensis* seeds by *A. rudis*, but we provide the first documentation of the extent of redispersal and its consequences for spatial population dynamics in eastern North American forests (though there are many examples in European forests; see Gorb and Gorb, 2003). Overall, the data indicate *A. rudis* redisperses a majority of seeds, ∼93%, from the nest at distances comparable to measures of primary dispersal (see Culver and Beattie, 1978; Giladi, 2004; Gómez and Espadaler, 1998; Kalisz et al., 1999; Zelikova et al., 2008). Redispersal increases the mean dispersal distance of seeds by *A. rudis* by 24%. Integrating the redispersal data with a demographic model suggests redispersal may increase the speed of population spread for *H. arifolia* and *A. canadense* by 22.5%. The sensitivity of population spread rate to changes in removal rate and *A. rudis* abundance serves to highlight the importance of *A. rudis* to the spread of local understory herbs. In addition, the keystone disperser is sensitive to climate change (Warren et al., 2011) and invasive species (Rodriguez-Cabal et al., 2011), which may decrease *A. rudis* abundance, which will diminish the overall spread rate of myrmecochores, marginalize the effect of redispersal on spread rates, and may lead to the decline of the myrmecochore population (Rodriguez-Cabal et al., 2011).

There are now direct observations of the redispersal of three common wildflowers in eastern North American forests by *A. rudis*, the keystone disperser: *A. canadense*, *H. arifolia* (evidence herein) and *S. canadensis* (Heithaus, 1986). Though two of the myrmecochores in our study present a "handle" even after

elaiosome removal that may aid in redispersal (personal observation), *S. canadensis* is a larger seed that is round and smooth after elaiosome removal. It appears that *A. rudis* has the ability to redisperse seeds of a variety of structures. However, further observation is necessary to confirm whether this observation generalizes to all myrmecochores dispersed by *A. rudis*. In European temperate forests, the seed structure after elaiosome removal and the redispersing ant mandible size both affect the redispersal frequency and distance of seeds from the nest (Gómez et al., 2005). In eastern North American forests, the primary seed disperser *A. rudis* is nearly omnipresent in deciduous forests, with the exception of some marginal habitats (Ness et al., 2009). *A. rudis* is also able to redisperse a range of seed types. Therefore, we suspect that redispersal is a widespread phenomenon for myrmecochores in eastern North American temperate deciduous forests.

4.1. Ant dispersal and migration rates

Although redispersal is common in myrmecochorous relationships, our study is the first to model redispersal and its effects on population spread rate explicitly. The spread rate we estimate for primary dispersal is much smaller than previously calculated spread rates for *H. arifolia* (see Giladi, 2004). The difference is most likely due to our focus on dispersal by only *A. rudis*, and the previous study's overestimation of fecundity, which was guided by the need to satisfy model assumptions (Giladi, 2004). In addition, we consider movement in two dimensions, which provides a more conservative estimate of population spread rate than models that consider movement only in one dimension (Lewis et al., 2006). With our addition of redispersal to the model, the population spread rate that we estimate is still small and falls short of the post-glaciation migration rates necessary to account for current myrmecochore ranges in eastern North America (Cain et al., 1998; Vellend et al., 2003). The discrepancy may occur due to the omission from our model of rare, long-distance dispersal events by other ant species or vertebrates that may account for dispersal at a continental scale (Myers et al., 2004; Vellend et al., 2003). If non-standard dispersal events are common, omission of long-distance dispersal may inflate the perceived increase in population spread rate due to the addition of redispersal in our model. Even if redispersal does not account for population spread at a continental scale, it does affect the local dispersal distance of seeds, which may affect the local plant population fitness and the benefits plants receive from myrmecochory more generally.

4.2. Plant benefits from dispersal

Redispersal changes our understanding of potential explanations for the evolution of myrmecochory based on the benefits offered to plants, at least in eastern North American temperate forests. There are three prominent hypotheses for plant benefits from myrmecochory: the predator avoidance hypothesis, the directed dispersal hypothesis, and the distance dispersal hypothesis (reviewed in Giladi, 2006). In some systems, the avoidance of fire is a potential benefit to burial within a nest, though this is not relevant to our temperate deciduous forest system. We consider each potential benefit in turn.

4.2.1. Directed dispersal

The directed dispersal hypothesis argues the chief advantage of myrmecochory is ants disperse seeds to locations where plant fitness is higher than it would be if seeds were dispersed randomly, a so-called "site effect." For example, dispersal into ant nests may provide a nutrient-rich environment that increases plant fitness and survivorship (Beattie and Culver, 1983; Culver and Beattie, 1978; Hanzawa et al., 1988; Giladi, 2006), an effect often cited as a primary benefit to plants in European temperate forests (Culver and Beattie, 1980; Gorb et al., 2000; Gorb and Gorb, 2003) and for the few myrmecochore species in the western North American meadows (Beattie and Culver, 1983; Hanzawa et al., 1988). The seed-dispersing ant species in the European temperate forest habitats (generally *Formica* spp.) have nutrient-rich, long-term (often many-year) nest sites (Culver and Beattie, 1980; Gorb et al., 2000; Gorb and Gorb, 2003; Smallwood, 1982a). In addition, redispersal in some European forests places the seeds in middens at territory borders, which are often nutrient-rich and beneficial to germination (Gorb et al., 2000).

In direct contrast to the European temperate forest system, the benefits from directed dispersal do not necessarily apply to eastern North American temperate forests if the majority of seeds do not end up inside nests or even in middens outside the nest. The keystone disperser in eastern North American forests, *A. rudis*, has temporary (mean 20 days) nest locations (Culver and Beattie, 1978; Smallwood, 1982a, b) and redisperses a majority of seeds outside the nest into the surrounding leaf litter (data herein). Therefore, any benefit that nutrient enrichment or burial within the nest provides may not apply to the majority of dispersed seeds in the eastern North American system. Instead, the possible benefits due to directed dispersal would only arise if the placement of seeds outside of nests is non-random and in favorable locations. Perhaps seeds tend to be redispersed to sunnier areas on the forest floor near the nest (Smallwood, 1982b) or scattered throughout the litter layer (Gonzalez, 1972). Either location may be favorable for germinating understory herbs, but such tendencies are, for now, speculation. Evidence to support such speculation would require a reevaluation of the assumption of isotropic redispersal in our model. In practice, however, the final locations of the seed appear to be similar to the initial location of the seed at dehiscence (within the leaf litter), with the important exception that the seed is no longer near the parent or siblings.

4.2.2. Predator avoidance

In the predator-avoidance hypothesis, both initial dispersal and subsequent burial of seeds by ants reduce the ability of predators to locate and obtain seeds (Culver and Beattie, 1978; Heithaus, 1981; Giladi, 2006). In our study, however, the high rate of redispersal indicates seeds may not experience safety from predators (or potential safety) through burial in *A. rudis* nests. In the context of predation, the only potential selective advantage of myrmecochory when ants redisperse seeds is the reduction of the seed density in the area around the nest which in turn leads to lower predation rates by density-dependent granivores, such as rodents (Heithaus, 1981).

4.2.3. Distance dispersal

The distance dispersal hypothesis proposes that seed dispersal reduces competition between parents and offspring, as well as among siblings (Andersen, 1988; Giladi, 2006). Support for the hypothesis is common in studies of primary dispersal in temperate forests (reviewed in Giladi, 2006). In these studies, understory herbs experience reduced competition and density-dependent effects at relatively short distances from the parent (and each other) due to ant dispersal (Heithaus, 1986; Higashi et al., 1989; Kalisz et al., 1999; Giladi, 2006; Gorb and Gorb, 2003). The redispersal of seeds outside the nest increases the

mean, variance and maximum possible dispersal distance of the seed from the parent plant. Consequently, redispersal, like primary dispersal, decreases the density of seeds around the parent. It also decreases the density of seeds within and around ant nests, and thus seedling density. Increased distances from the parent and reduced seedling density are also effects of redispersal in European temperate forests (Gorb et al., 2000). Several studies have shown that an increase in local seed density decreases the survival and growth of seedlings and adults of *H. arifolia* (Giladi, 2004; Gonzalez, 1972) as well as for other temperate forest myrmecochores (Culver and Beattie, 1980; Heithaus, 1986; Higashi et al., 1989; Kalisz et al., 1999). Therefore, the increase in dispersal distance and potential decrease in seedling density due to redispersal ought to augment myrmecochore population fitness, though this is difficult to assess given the length of time to reproduction in some myrmecochores (Zelikova et al., 2011). As we previously stated, some studies suggest both predator-avoidance and directed dispersal as drivers of the origin of myrmecochory in eastern North American. If redispersal is common, though, those benefits are contingent on dispersal away from the parent in the first place (dispersal distance). Therefore, the documentation of redispersal supports the proposal that dispersal for distance is a driver of the evolution and origin of myrmecochory in the eastern temperate forests of North America. All other possible benefits of myrmecochory for temperate forest understory in eastern North America may be secondary to the simple need for dispersal away from the parent and siblings.

4.3. Other consequences of redispersal

We must address two additional questions in light of redispersal by *A. rudis*. The first question is how redispersal affects the germination rates of myrmecochores and ultimately their population fitness. Several studies show that simply the handling of the seeds by ants has a positive effect on germination rates (Culver and Beattie, 1978, 1980) and redispersal is beneficial in European systems (Gorb et al., 2000). Concrete evidence, though, for the benefits of redispersal to germination for the eastern North American system does not yet exist. The second question that remains is why *A. rudis* expends the energy to remove the seeds from the nest. In lab colonies, seeds fed to the colonies and remain in the nest often grow a fungus (personal observation). Smallwood (1982a) noted that ants, such as *A. rudis*, might frequently relocate nests to avoid the accumulation of waste and fungus in the nest. Redispersal may simply be the result of the ants cleaning out their nests to avoid such accumulation, which in lab colony nests proved fatal to the ants (personal observation). The possible effects of such a fungus on germination and survival of seedlings are still unknown. Despite more than a century of study of myrmecochory (Sernander, 1906), there is still much to learn.

Acknowledgments

Appendix A

The model

The model uses an integrodifference equation to combine the population projection matrix $\mathbf{B}$ for the myrmecochore and the movement matrix $\mathbf{K}(x,y)$ for seed dispersal to find the population density for each stage at location x at time $t + 1$:

$$\mathbf{n}(x, t + 1) = \int_{-\infty}^{\infty} [\mathbf{K}(x, y) \circ \mathbf{B}]\mathbf{n}(y, t)\mathrm{d}y, \tag{A.1}$$

where $\circ$ stands for the Hadamard product (element by element multiplication) (Neubert and Caswell, 2000). The population projection matrix consists of the transition rates, survival rates and fecundity, of all defined life stages in the population from one year to the next year.

Population spread rate

To calculate the speed of invasion, we must first make some assumptions. First, in addition to the requirement for the population projection matrix $\mathbf{B}$ to be positive and primitive, we must assume the dominant eigen value of $\mathbf{B}$ is greater than one (which is true for our data) to ensure the population will still grow when small. Second, we assumed that all dispersal kernels have a moment-generating function (mgf), $m(s)$, with shape parameter s, to ensure an upper bound exists for the rate of spread (i.e., spread rate cannot be infinite). Finally, we assume that if the population reaches a steady state, i.e., the stable-stage distribution, then the population has a traveling wave front of a fixed shape that moves at a constant rate, c. Based on these assumptions, Neubert and Caswell (2000), (Appendix A) show that the upper bound on the invasion wave speed, c^*, is

$$c^* = \min_{s>0}\left[\frac{1}{s}\ln\rho(s)\right], \tag{A.2}$$

where $\rho(s)$ is the dominant eigenvalue of the matrix $\mathbf{B} \circ \mathbf{M}(s)$.

Dispersal kernels

The dispersal kernels for the three dispersal scenarios are as follows.

Autochorous dispersal
The autochorous dispersal kernel for movement from the plant to a new location x_0 follows a half-normal distribution. We generated 1000 distances from a half-normal distribution based on the observation the plants do not have the ability to disperse seeds further than 2 cm from the base. The mean is 0.53 cm and the standard deviation is 0.40 for the half-normal. Since an explicit formula for the half-normal does not exist, we fit an empirical moment generating function (see below) to the generated data to determine $M_0(S)$, the moment-generating function for autochorous dispersal.

Primary dispersal
The composite moment-generating function for primary dispersal, from location x_0 to location x_1 is

$$M_1(s) = [1 - p_1 + p_1 M_1'(s)]M_0(s). \tag{A.3}$$

where $M_1'(s)$ is the mgf for the measured dispersal kernel for ant dispersal from the plant to the nest and each seed has

a probability p_1 of being dispersed by an ant. We assume the two processes, plant dispersal and initial ant dispersal, are independent.

Secondary dispersal

The composite mgf for secondary dispersal is

$$M_2(s) = (1 - p_1)M_0(s) + (1 - p_2)p_1 M_1'(s)M_0(s)$$
$$+ p_2 p_1 M_2'(s)M_1'(s)M_0(s). \tag{A.4}$$

Where $M_2'(s)$ is the mgf for the measured (re)dispersal kernel for redispersal from the nest and p_2 is the probability of redispersal from the nest.

Empirical moment generating function

In order to avoid assumptions about the distribution of the dispersal kernels $k_1'(x_1 - x_0)$ and $k_2'(x_2 - x_1)$, we will use a nonparametric estimator of the moment generating function for $M_1'(s)$ and $M_2'(s)$ (Clark et al., 2001). Our data are radial distances ($r = |x - y|$) from either a seed depot (or "plant") or an *A. rudis* nest. Given N radial distances $r_1, \ldots, r_N$, we assume the distances are independent, identically distributed random variables. Then we can estimate the moment generating function with the directional empirical moment generating function,

$$M_N^E(s) = \frac{1}{N} \sum_{i=1}^{N} I_0(sr_i), \quad 0 \leq s < \infty \tag{A.5}$$

where I_0 is the modified Bessel function of the first kind and zeroth order (Neubert and Parker, 2004; Lewis et al., 2006). We chose the directional moment generating function because it provides an unbiased estimate of wave speed (Lewis et al., 2006). We assume that dispersal is identical in all directions and thus the rate of movement is the same in all directions.

Appendix B

Demographic projection matrices for H. arifolia and A. canadense

Table B.1
Asarum canadense average population projection matrix with population growth rate $\lambda = 1.062$ (Cain and Damman, 1997).

	Year t			
	Stage	Seedling	Yearling	Lateral shoot	Mature
Year $t + 1$	Seedling	0.000	0.000	0.0875	0.390
	Yearling	0.500	0.000	0.000	0.000
	Lateral Shoot	0.000	0.000	0.015	0.155
	Mature	0.000	0.730	0.703	0.828

Appendix C

Individual nest information

Table C.1
Information for the mean, standard deviation, median redispersal distances (measured in cm), the number of workers, and the type of nest. Also included are the proportion of seeds redispersed and the proportion of seeds recovered from the field observations of the redispersal of *Asarum canadense* by *Aphaenogaster rudis*.

Nest	Mean	SD	Median	Workers	Type	Redispersal	Recovery
1	28.34	25.09	11.75	140	3	0.98	0.63
2	29.66	20.16	22.50	NA	2	1.00	0.53
3	41.25	35.41	25.00	90	1	1.00	0.53
4	42.02	37.92	28.50	145	1	0.98	0.47
5	41.78	29.35	36.00	88	1	1.00	0.69
6[a]	45.58	29.46	36.25	122	1	1.00	0.83
7	37.82	20.31	37.00	186	3	0.92	0.98
8	54.80	27.99	40.00	143	1	1.00	0.58
9	37.83	29.96	43.25	104	2	0.88	0.52
10[a]	47.56	25.06	44.25	285	2	1.00	0.84
11	49.80	26.76	45.00	37	1	0.98	0.54
12	57.58	30.60	49.00	NA	1	1.00	0.66
13	49.58	38.22	51.75	126	2	0.86	0.64
14	50.06	16.22	58.00	45	2	1.00	0.38
15	51.40	36.47	59.50	14	2	0.86	0.90
16[a]	68.33	44.73	61.50	100	1	0.97	0.26
17	66.19	22.96	66.75	84	2	0.97	0.83
18	72.92	30.35	83.00	NA	1	1.00	0.74
19	99.95	22.51	97.50	NA	1	1.00	0.42
20	106.13	23.83	111.75	81	1	1.00	0.29

1 = Leaf.
2 = Log.
3 = Mixed.
[a] Colony moved − closest colony with seeds present counted.

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Table B.2
Hexastylis arifolia average population projection matrix with population growth rate $\lambda = 1.017$ (Giladi, 2004).

	Year t						
	Stage	Seedling	Sub-adult	Non-reproductive	Small	Medium	Large	Dormant
Year $t + 1$	Seedling	0.000	0.000	0.000	0.000	0.003	0.215	0.000
	Sub-adult	0.631	0.468	0.023	0.006	0.006	0.000	0.103
	Non-reproductive	0.124	0.345	0.541	0.087	0.017	0.020	0.289
	Small	0.000	0.026	0.243	0.503	0.113	0.025	0.402
	Medium	0.000	0.000	0.032	0.207	0.318	0.152	0.081
	Large	0.000	0.000	0.013	0.106	0.410	0.677	0.125
	Dormant	0.030	0.079	0.108	0.078	0.110	0.100	0.000

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