

Can Disruption of an Ant–Plant Mutualism Explain a Lack of Recovery of Forest Herbs in Post-agricultural Forests of New York?

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Abstract - A substantial proportion New York’s forests regenerated following agricultural abandonment around the turn of the 20th century. Many myrmecochorous (ant-dispersed) plant species are lacking in these forests decades after land abandonment despite being present in residual stands. To determine if disruption to this ant–plant mutualism can partially explain the current distribution patterns of myrmecochorous plants, we quantified the proportion of seeds removed by ants while accounting for predation by rodents in residual and post-agricultural forests. We experimentally manipulated ant access and controlled for rodent access to seeds of 3 myrmecochorous understory herbs in 3 paired residual and post-agricultural forests in central New York. We identified *Aphaenogaster rudis* as the primary seed disperser. We found no difference in mean (± 1 SE) proportion of seeds removed by ants between residual stands ($73.7\% \pm 7.7\%$) and post-agricultural stands ($75.8\% \pm 7.9\%$). Rodents removed few to no seeds ($5.3\% \pm 1.5\%$), but an invasive slug, *Arion subfuscus* (Dusky Arion), was observed removing elaiosomes from seeds in both stand types. Our data indicated neither a lack of ant-dispersal activity nor excessive rodent predation would be limiting to dispersal of myrmecochorous seeds in post-agricultural forests during the period of our study. Given the presence of *A. rudis* in post-agricultural stands, programs to assist plant migration will likely be sufficient to reestablish this ant–plant mutualism in degraded sites.

Introduction

Mutualisms provide a framework on which the complexity of a community unfolds. Animal pollinators ensure plant reproductive success and animal seed-dispersers enhance plant germination success (Bond 1994). Mutualistic systems provide necessary ecosystem services, though the resiliency of these interactions in the face of change requires continued investigation (Kearns et al. 1998). For example, large-scale habitat fragmentation and land-use legacies can disrupt plant–animal mutualisms, e.g., pollination in dry subtropical forests (Aizen and Feinsinger 1994) and distribution patterns of native understory forbs in temperate mesic deciduous forests (Mitchell et al. 2002) appear to be consistent with dispersal limitations by biological agents. These disruptions may result in regional extirpation of species (Harris and Johnson 2004). In northeastern North America, disruption of a key seed-dispersal mutualism, myrmecochory (the dispersal of plant diaspores by ants), may be limiting reestablishment of understory flowering plants (Beattie et al. 1979).

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Understory flowering plants account for a majority of vascular plant diversity in temperate forests (Flinn and Vellend 2005), and an estimated 30% of understory herbs in northeastern deciduous forests produce elaiosome-bearing seeds (Beattie and Culver 1981). Elaiosomes are lipid-rich seed appendages that are used as a food source by ants (Edwards et al. 2006). *Aphaenogaster rudis* Enzmann, a species in the *A. fulva–rudis–texana* group (MacGown 2003), is the primary native ant species dispersing seeds in North American temperate forests, and often acts as a “keystone mutualist” (Ness et al. 2009) by removing as many as 88% of the seeds it encounters (Pudlo et al. 1980). If a seed is brought back to an *A. rudis* nest, the elaiosome is removed and the seed discarded (Boulay et al. 2009) culminating in increased seedling survival rates with dispersal (Ohkawara et al. 1996). The elaiosome also provides benefits to the ant colonies that consume them. One study found colonies of *A. rudis* that were fed elaiosomes of intact diaspores of *Sanguinaria canadensis* L. (Bloodroot) produced gynes (the primary reproductive females of social insects) at higher rates than control colonies (Morales and Heithaus 1998). However, Warren et al. (2019) recently reported conflicting short- and long-term effects of elaiosome supplementation and removal on ant colonies, suggesting myrmecochory may instead be a commensal or parasitic relationship in some circumstances. Nevertheless, given the considerable extent of myrmecochory in the northeastern United States, severing this interaction through land-use change or altered forest microhabitat structure, which may locally extirpate ants capable of dispersal, could have long-lasting effects on these species as well as the overall community associated with these organisms.

A substantial proportion of central New York’s forest cover is post-agricultural regeneration from the turn of the 20th century. For example, 80% of the forest cover in Onondaga County, NY, is comprised of even-aged stands less than a century old (Nyland et al. 1986). These post-agricultural forests possess understory communities that are altered relative to residual forest communities (Griffiths and McGee 2018), and these land-use legacies may persist for centuries (Honnay et al. 2002, Vellend et al. 2007). Many myrmecochores are not present in these forests nearly a century after land abandonment (Flinn and Vellend 2005) and thus their presence can be used as indicators of residual, uncleared forests (Bellemare et al. 2002, Griffiths and McGee 2018, Harrelson and Matlack 2006, Matlack 1994, McLachlan and Bazely 2001). This trend may in part be explained by dispersal limitations from source populations in residual stands to relatively depauperate post-agricultural stands.

A meta-analysis performed by Gómez and Espadaler (2013) found that >40% of myrmecochorous seeds globally were dispersed <1 m from the parent plant. This may help explain trends observed in central New York by Griffiths and McGee (2018) where, across 103 herbaceous plant taxa and 4 modes of diaspore dispersal (myrmecochory, anemochory, zoochory, and barochory), myrmecochores had the lowest migration rate into post-agricultural forests across a contiguous boundary with adjacent residual forests. Furthermore, a study performed in the southern Appalachian Highlands (Mitchell et al. 2002) found low species richness of myrmecochores in small forest patches with high intensities of past land-use. In these

instances where there is an unsuitable matrix habitat, such as human development, between residual and post-agricultural forests, migration rates between the forests may drop to nearly zero.

Migration rates and reestablishment of native forest understory herbs may also be hindered by other factors within post-agricultural stands. For example, lower seed densities, altered microhabitat, and disturbed plant-community composition in post-agricultural forests may alter foraging patterns of seed predators, increasing risk of predation (Stuhler and Orrock 2016). Rodents and gastropods have been observed disrupting ant–plant mutualisms (Dunphy et al. 2016, Heithaus 1981, Ness and Bressmer 2005, Ruhren and Dudash 1996), with some observing increased rodent predation in post-agricultural forests (Stuhler and Orrock 2016). How the above factors may contribute to trends in myrmecochore distribution across New York's forests is not well understood, and is the focus of this study.

We quantified proportion of seeds removed in residual and post-agricultural forests in central New York to discern if lack of myrmecochores in post-agricultural forests relates to seed removal by ants and/or predation by rodents. If the proportion of seeds removed by ants were lower in post-agricultural forests, we expect localized ant extirpation may explain the lack of myrmecochores. If the proportion of seeds removed by rodents were higher than by ants in either residual or post-agricultural forests, we expect seed predation may explain the lack of myrmecochores. If the proportion of seeds removed by ants was the same in each forest type, we expect some other mechanism, such as establishment limitations, may explain the lack of myrmecochores. To test these hypotheses, we asked the following questions: (1) Are ants capable of myrmecochory (notably *A. rudis*) present in both residual and post-agricultural forests? (2) Does the proportion of seeds removed by ants differ from that predated on by rodents in either residual or post-agricultural forests? (3) Does the proportion of seeds removed by either rodents or ants differ between residual and post-agricultural forests?

Field-Site Description

Our study was carried out at 3 sites in Onondaga and Cortland counties, NY: SUNY ESF Heiberg Memorial Forest, Tully (HEIB); the Baltimore Woods Nature Center, Marcellus (BW); and the Town of Skaneateles Conservation Area, Skaneateles (SCA). We chose residual and post-agricultural forest stands at these sites using 1936 and 1938 aerial photographs accessed from the Cornell Institute for Resource Information Systems Aerial Photograph Collection (Cornell University Library Digital Collection 2015). Our site inspection further revealed remnant stone walls and lack of microtopography indicating past cultivation (Griffiths and McGee 2018). Given the presence of brush and small trees at the post-agricultural sites in the 1936/1938 photographs, we concluded these sites were abandoned between 1920 and the time the photos were taken (Fig. 1). Furthermore, increment core data from our post-agricultural stand at SCA indicate this site was abandoned by 1935. Paired stands were 0.7 km apart at BW, 1.2 km at HEIB, and 0.3 km at SCA.

While the post-agricultural stands are secondary successional, and the residual stands have received periodic, selective harvests, all sites were fully stocked, had complete canopy closure, and each of the pairs of stands carried roughly the same basal area, with the exception of HEIB (Table 1). At HEIB, the post-agricultural stand had a slightly lower basal area, reflecting the removal of plantation *Pinus strobus* L. (Eastern White Pine) overstory ~20 years ago. Residual stands were dominated by *Acer saccharum* Marshall (Sugar Maple), *Fagus grandifolia* Ehrh.

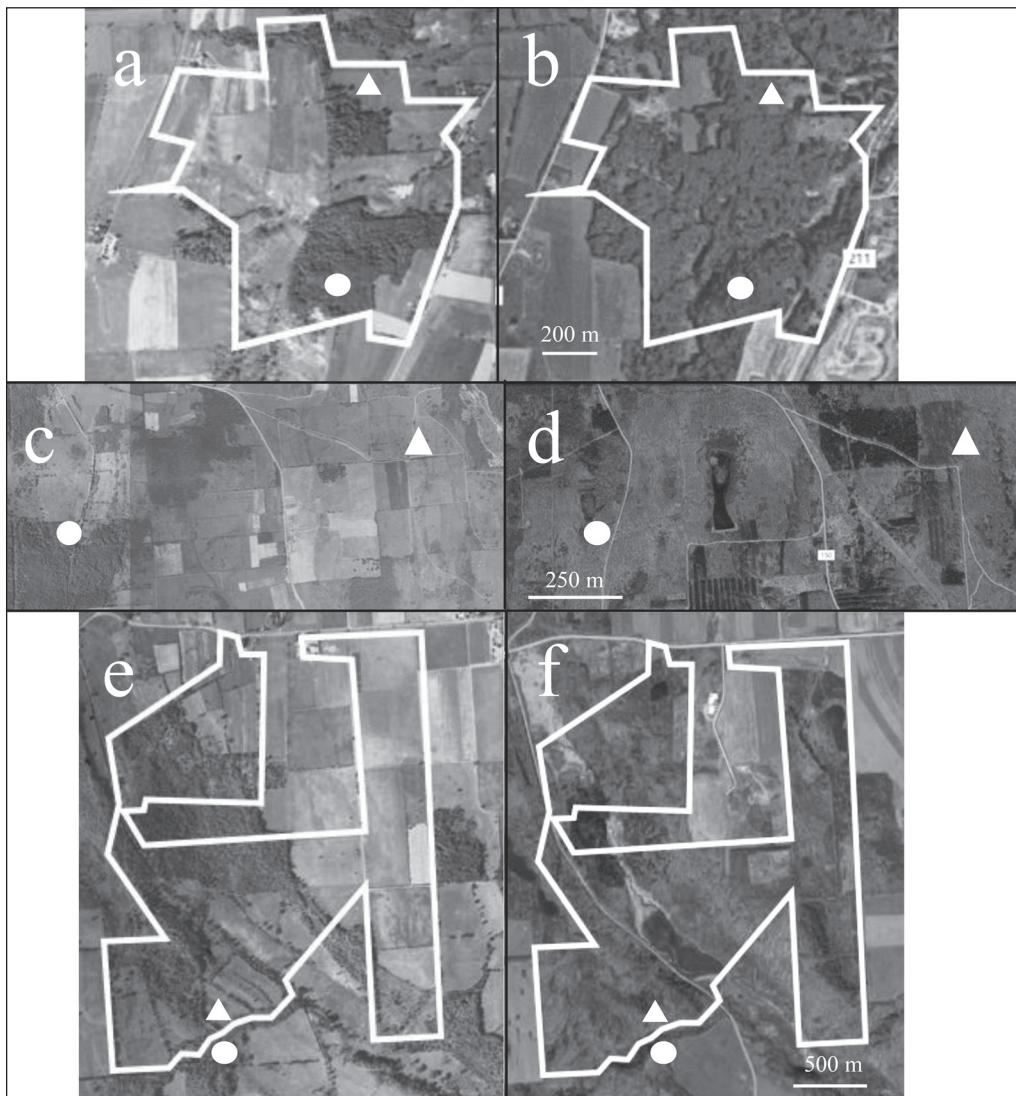


Figure 1. Aerial photographs from (e) 1936 and (a, c) 1938 on the left (Cornell University Library Digital Collections 2015) and current satellite images (Google Maps 2018a–c) (right) of residual (circles) and post-agricultural (triangles) stands at (a, b) Baltimore Woods Nature Center, (c, d) Heiberg Memorial Forest, and (e, f) Skaneateles Conservation Area. The Baltimore Woods Nature Center is outlined in white in (a) and (b), and the Skaneateles Conservation Area is outlined in white in (e) and (f).

(American Beech), *Tilia americana* L. (Basswood), *Prunus serotina* Ehrh. (Black Cherry), and *Fraxinus americana* L. (White Ash). Post-agricultural stands were dominated by Sugar Maple, Black Cherry, White Ash, *Acer rubrum* L. (Red Maple), and *Carya cordiformis* (Wangenh.) K. Koch (Bitternut Hickory). Uneven-aged residual stands all possessed better developed seedling and sapling layers than their respective, paired post-agricultural stands (Table 1). Further, the residual stands possessed a greater richness of myrmecochores. *Asarum canadense* L. (Wild Ginger), *Claytonia caroliniana* Michx. (Carolina Spring Beauty), *Dicentra* spp. (bleeding heart), *Erythronium americanum* Ker Gawler (Trout-Lily), Bloodroot, *Trillium* spp. (trillium), *Uvularia grandiflora* J.E. Smith (Large-flowered Bellwort), and *Viola* spp. (violet) were all present at the BW residual stand, with none occurring in the paired post-agricultural stand. Likewise, all the above species except Wild Ginger were present at SCA residual, with only violets in the paired post-agricultural stand. Carolina Spring Beauty, trilliums, Trout-Lily, and violets were all present at HEIB residual, while only Trout-Lily was found in the paired post-agricultural stand.

Methods

Our study included 3 spring ephemerals: Carolina Spring Beauty, Bloodroot, and *Trillium erectum* L. (Red Trillium). These myrmecochores (Beattie and Culver 1981, Handel et al. 1981) were chosen based upon their local abundance of seed during the study period. Carolina Spring Beauty produces fruit in late May to early June, Bloodroot in late June, and Red Trillium in mid-July (N.G. Kiel, pers. observ.).

Our field experiment was set up in paired residual and post-agricultural forest stands at each of the 3 sites. We established 4 treatments to test for both rodent predation and seed removal by ants in both stand types: (1) all access (control with no exclusion), (2) rodent access (ants excluded), (3) ant access (rodents excluded), and (4) no access (negative control with both ants and rodents excluded). We set out 7 seeds of either Carolina Spring Beauty, Bloodroot, or Red Trillium in seed “depots”

Table 1. 2016 forest stand characteristics of residual (R) and post-agricultural (PA) stands at Baltimore Woods Nature Center (BW), Skaneateles Conservation Area (SCA), and Heiberg Memorial Forest (HEIB). Seedling = live tree <1.4 m tall, sapling = live tree ≥1.4 m tall and <10 cm DBH, and tree = live tree ≥1.4 m tall and ≥10 cm DBH. Forest edge is defined as a road or field.

Site	Stand type	Seedling density (no. ha ⁻¹)	Sapling density (no. ha ⁻¹)	Tree density (no. ha ⁻¹)	Tree basal area (m ² ha ⁻¹)	Soil bulk density (g cm ⁻³)	Distance to forest edge (m)
BW	R	17,500	1444	369	49.1	0.68	110
BW	PA	11,389	369	550	49.8	0.79	80
SCA	R	62,778	1025	419	34.7	0.60	100
SCA	PA	31,111	475	521	38.3	0.67	200
HEIB	R	56,315	1638	525	36.1	0.57	50
HEIB	PA	22,778	934	675	25.3	0.51	60

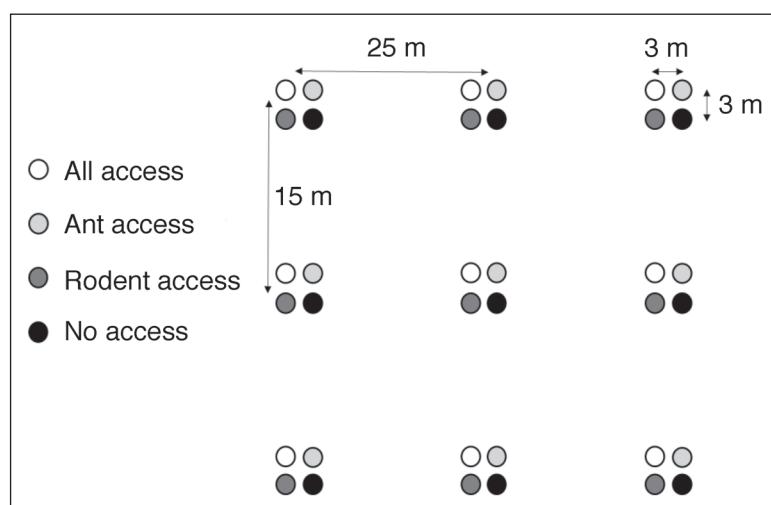
for each replicate of each treatment. Depots consisted of a plastic petri dish 10-cm in diameter. To exclude rodents, we used cages made of 19-gauge, 1.25-cm mesh, metal hardware fencing, measuring 60 cm in circumference and 15 cm tall with a closed top and dug 3 cm into the ground. To exclude ants and other arthropods, we applied a 1-cm-wide band of Tanglefoot®, a resinous substance that prevents crawling insects from accessing certain areas (e.g., keeping tree pests off of trees), to the outer edge of petri dishes. The no access depots had both the cage and Tanglefoot; The all access depots had neither.

We set out 9 depot clusters, consisting of 1 depot of each of the 4 treatments, in 3 transects of 3 clusters in each stand. Within each cluster, treatments were assorted randomly in a 3 m x 3 m square. We spaced clusters in the same transect 15 m apart and placed transects 25 m apart and parallel to one another (Fig. 2). Seeds were set out in the morning and checked every 24 hrs for 48 hrs. At each interval, we recorded the number of seeds remaining in each depot. We conducted this procedure for Carolina Spring Beauty in late May, Bloodroot in early June, and Red Trillium in late July 2017. These experimental periods corresponded to the availability of the respective species' seed (N.G. Kiel, pers. observ.). A total of 54 depots of each treatment were set out across all stands and sites for each species.

We collected ants from sites over 1 week in mid-July. We set out 5 petri dishes baited with tuna at 25-m intervals through each stand to attract ants, near to where seed depots had been installed. For 45 min, we collected ants from baits if they carried away pieces of tuna and/or interacted with tuna. We later identified ants to species where possible using online resources and keys (MacGown 2003, Wild 2002).

We analyzed data using a split-plot experimental design where site was the whole plot (BW, SCA, and HEIB), land-use history was the split-plot (residual and post-agricultural stands), and depot type the split split-plot (all access, ant access, rodent access, and no access). We used analysis of variance (ANOVA) to test for differences in the proportion of seeds removed among the independent variables (sites, stands, treatments, and species), followed by a Fisher's least significant

Figure 2. Layout of depots within each stand. Individual circles represent depots (petri dishes with seeds and treatment type), which are arranged in clusters of 4 depots, 1 each of the 4 treatment types.



difference test. We performed another ANOVA followed by a Fisher's least significant difference test for each treatment by stand type within each species. Statistical analyses were performed using SAS version 9.4 (SAS Institute, Cary, NC).

Results

Individuals of the *A. fulva–rudis–texana* group (hereafter *A. rudis*, given the complexity of this species group; MacGown 2003) were collected from both residual and post-agricultural stands at all 3 sites using tuna baits. Other species found included *Myrmica rubra* (L.), with individuals collected from both stands at SCA and the residual stand at BW, and *Camponotus* spp, with individuals collected from the residual stand at BW.

Seed-removal rates differed among sites and depot types, but not between the different stand types (Table 2). Overall proportion of seeds removed (all species across all depot types; ± 1 SE) at HEIB ($30.2 \pm 10.2\%$) was $\sim 2/3$ that of SCA ($44.6 \pm 16.2\%$) and $\sim 3/4$ that of BW ($41.9 \pm 15.0\%$) (ANOVA: $F_{2,5} = 4.39$, $P = 0.037$; Fisher's LSD: $P < 0.05$). We found no difference in the proportion of seeds removed between stand types, with $73.7 \pm 7.7\%$ of seeds removed from ant access depots in residual stands and $75.8 \pm 7.9\%$ seeds removed from ant access depots in post-agricultural stands (ANOVA: $F_{1,4} = 0.12$, $P = 0.74$; Fig. 3).

Rodent predation on seeds was practically non-existent at our sites, with only $5.3 \pm 1.5\%$ of seeds removed from rodent access depots across all 3 sites and all 3 species. Accordingly, the proportion of seeds removed from rodent access depots did not differ from no access depots (0%). Both rodent access and no access depots differed from the other 2 depot types (ANOVA: $F_{3,5} = 99.52$, $P < 0.0001$; Fisher's LSD: $P < 0.01$), as all access ($75.5 \pm 6.7\%$) and ant access ($74.8 \pm 5.7\%$) depots had upwards of 14 times more seed removal than rodent access depots across all species. This consistent pattern of removal is distinguished by species in Figure 4.

Finally, the proportion of seeds removed from all access depots differed between the 3 species tested, as both Red Trillium ($58 \pm 6\%$) and Carolina Spring Beauty ($71 \pm 10\%$) were between $\sim 2/3$ and $\sim 4/5$ that of Bloodroot ($95 \pm 3\%$) (ANOVA: $F_{2,5} = 11.93$, $P < 0.01$; Fig. 5).

Table 2. *F*-table summarizing results of split-plot ANOVA of seed removal from ant depots. In this analysis, site was the whole plot (BW, SCA, and HEIB), land-use history (stand type) was the split-plot (residual and post-agricultural stands), and depot type the split split-plot (all access, ant access, rodent access, and no access).

	df	Type III SS	<i>F</i> -value	<i>P</i>
Site	2	0.093	4.39	0.037
Land-use	1	<<0.001	0.01	0.930
Site*Land-use	2	0.015	0.70	0.520
Depot type	3	3.160	99.52	<0.0001
Land-use*depot type	3	0.002	0.05	0.980
Error	12	0.130		
Total	23	3.400		

Figure 3. Mean (\pm SE) proportion of seeds removed from ant access depots after 48 hours between residual and post-agricultural stands with combined site and species data.

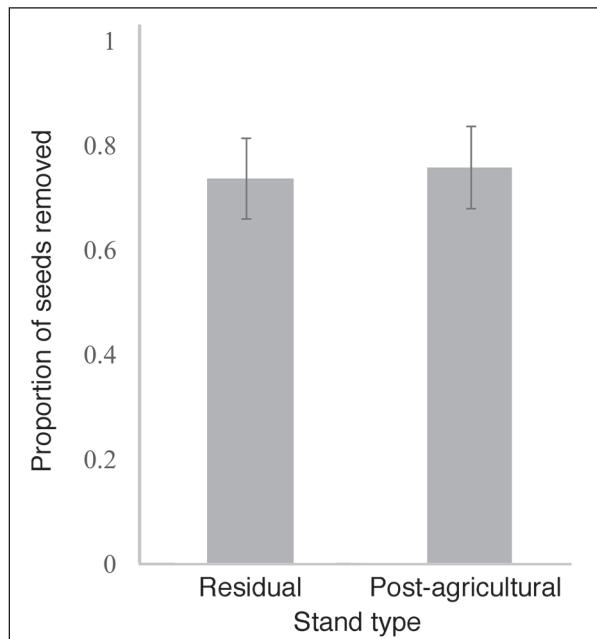
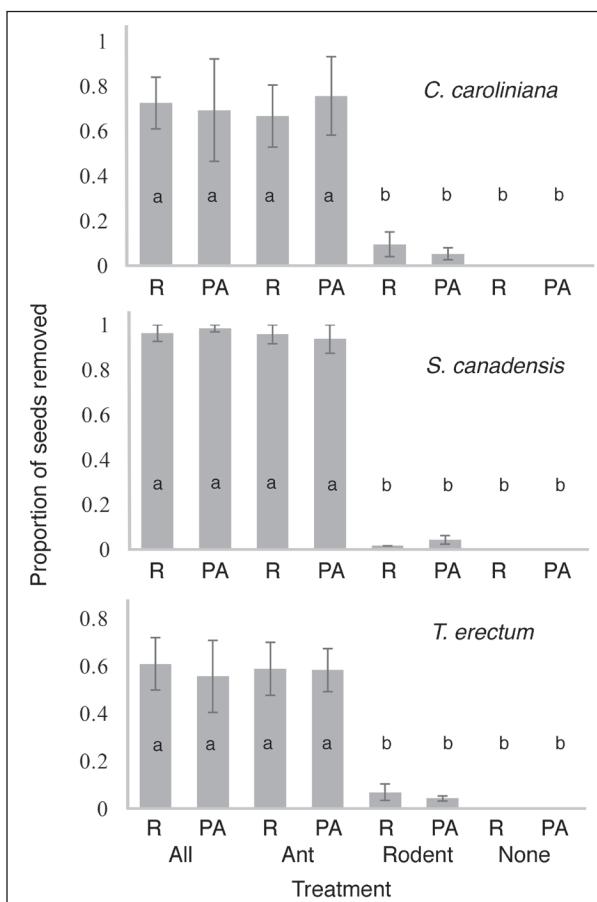


Figure 4. Mean (\pm SE) proportion of seeds removed of each species after 48 hours by treatment type and stand type. R = residual stands; PA = post-agricultural stands; All = all access; Ant = ant access; Rodent = rodent access; None = no access. Treatments with the same letter within species are not significantly different from one another (Fisher's LSD $\alpha = 0.05$).



Discussion

It appears neither ant extirpation nor seed predation can fully explain the lack of myrmecochorous plant species in post-agricultural forest stands we studied. With regards to ant extirpation, *A. rudis* was present in all residual and post-agricultural stands tested, which is consistent with trends reported in other studies in eastern North America (Mitchell et al. 2002, Ness et al. 2009). Both *M. rubra* (Prior et al. 2014) and *Camponotus* sp. (Mitchell et al. 2002) are known to disperse seeds, but seemingly not to the extent of *A. rudis*. There is some discrepancy among studies as to the relationship between ant and myrmecochore abundance, richness, and diversity in forest stands. For example, Mitchell et al. (2002) found individuals of *A. rudis* more frequently in small patches with a more intense land-use history, along with low ant abundance and richness at sites with high myrmecochore abundance and richness. Conversely, a meta-analysis performed by Ness et al. (2009) found *A. rudis* densities were positively correlated with myrmecochore densities at 3 nested spatial scales in eastern North American forests. Measuring *A. rudis* nest densities within our forest stands and relating these to myrmecochore stem density and patch size would add to the growing body of knowledge on this mutualism in eastern mesic deciduous forests.

Rodents did not function as seed predators in our study system as evidenced by the low proportion of seeds removed from rodent access depots. Furthermore, the

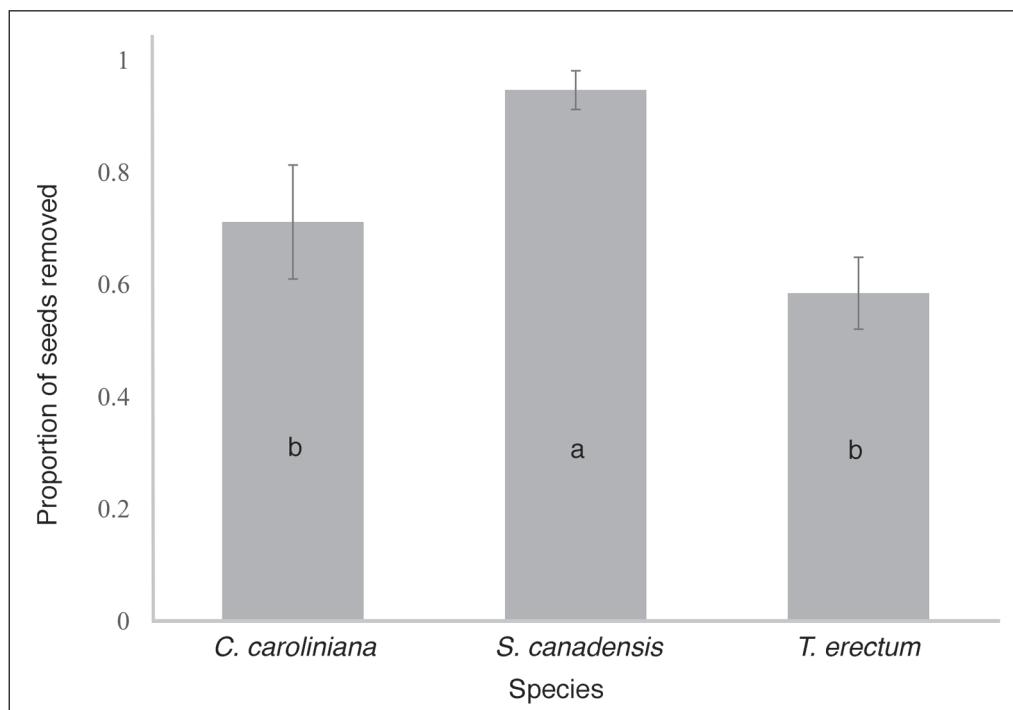


Figure 5. Mean (\pm SE) proportion of seeds removed of each species from the ant access depots after 48 hours with combined site and stand data. Species with the same letter are not significantly different from one another (Fisher's LSD $\alpha = 0.05$).

comparable removal of seeds from all access and ant access depots for each species suggests organisms capable of taking seeds from ant access depots (i.e., ants) are the primary removers of seeds from all access depots rather than rodents. We cannot say for certain whether lack of rodent predation was a result of low rodent density or a lack of interest in myrmecochorous seeds as a food source in our forest stands; however, rodent populations in the nearby central Adirondacks were low during the period of our study (S. McNulty, Adirondack Ecological Center, Newcomb, NY, pers. comm.). Similar studies have also found no significant effect of rodents on seed dispersal/removal in deciduous forests (Dunphy et al. 2016, Smith et al. 1989b), but Heithaus (1981) found rodents to cause significant seed mortality, particularly when ants were excluded. These conflicting results indicate a need for more studies over greater temporal and spatial scales to elucidate the impact of seed predation by rodents on dispersal in the myrmecochorous plant guild.

While rodents did not impact seed dispersal in our study, non-native gastropods of the species complex *Arion subfuscus/fuscus* (Mollusca, Pulmonata, Arionidae) were observed indirectly inhibiting dispersal through “elaiosome robbery” (Fig. 6), the process of elaiosome removal without seed dispersal (Dunphy et al. 2016). Many *Arion* species have been introduced around the world and have become pests, including *Arion subfuscus* (Draparnaud) (Dusky Arion) in central New York (Beyer and Saari 1978). Because of both its documented presence in New York and the phylogenetic complexity of the *Arion* genus (Pinceel et al. 2004), we refer to the slug species in our study as Dusky Arion. Dusky Arion was observed in both residual and post-agricultural stands. While elaiosome robbery does not necessarily explain the lack of myrmecochores in post-agricultural stands, the phenomenon does lower seed dispersal (Dunphy et al. 2016). Red Trillium appeared to be more

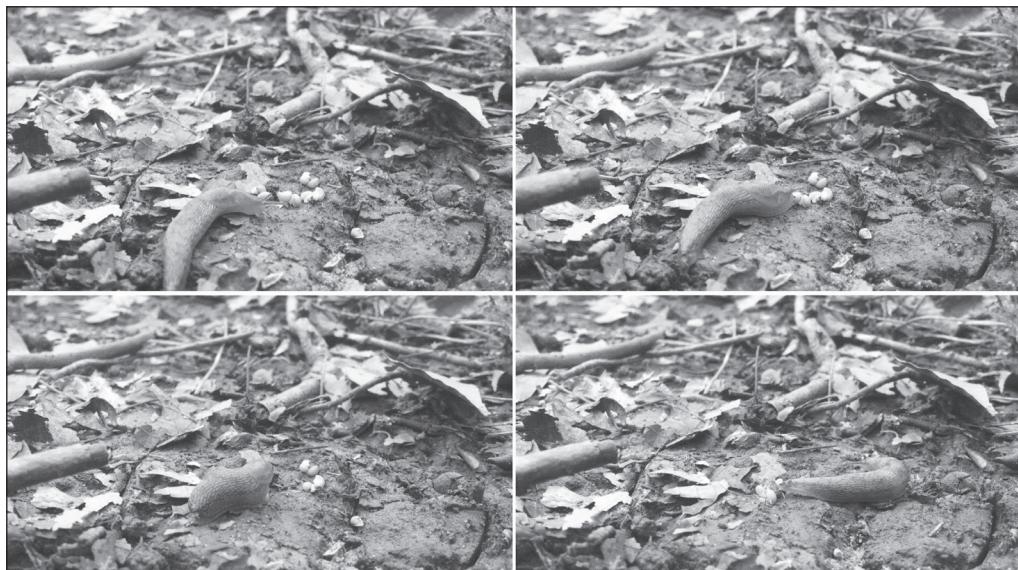


Figure 6. A gastropod (likely the invasive *Arion subfuscus*) removing elaiosomes of (*Trillium grandiflorum* Mich. (White Trillium) seeds without dispersing the seeds.

affected by elaiosome robbery than the other plant species in our study (N. Kiel, pers. observ.). This result may be a function of the elaiosome size or the timing of seed drop (mid- to late July). Future studies are needed to quantify the impacts of elaiosome robbery on Red Trillium and other myrmecochore species.

With *A. rufa* present and capable of dispersal in post-agricultural forests, lack of reestablishment by myrmecochores may be alternatively explained by ant satiation in residual stands, slow migration rates as a function of dispersal distance, establishment limitations, or a combination of these factors. As myrmecochores were completely extirpated from early successional forests by past land-use, natural reestablishment must be derived from nearby residual forests containing source populations of these species. Ants may become satiated in large myrmecochore populations common in residual stands (Smith et al. 1989a), thereby lowering dispersal rates. Though we did not quantify myrmecochore density at our sites and thus cannot test the satiation hypothesis, all residual stands possessed greater myrmecochore richness than their corresponding post-agricultural stands. Additionally, the mean dispersal distance of myrmecochorous seeds in the northern hemisphere is 1.16 m, with a median of 0.53 m (Gómez and Espadaler 2013). Reliance on short-distance dispersal, interspersed with infrequent long-distance dispersal events, could result in slow recolonization of myrmecochores, as shown by the failure of myrmecochore establishment in post-agricultural forests from adjacent residual forests (Bossuyt et al. 1999, Dzwonko and Loster 1992, Griffiths and McGee 2018, Matlack 1994). Given that some post-agricultural stands in central New York are separated from residual stands by an often complex and extensive matrix habitat, dispersal across these fragmented systems into isolated patches drops precipitously (Grashof-Bokdam and Geertsema 1998, Matlack 1994). These land-use barriers could further reduce the proportion of seeds dispersing and may even make long-distance dispersal functionally impossible. However, if myrmecochores can become established in post-agricultural forests through transplantation of either seeds, rhizomes, or individuals, this mutualism may be reestablished and foster the recovery of plant communities in these forests.

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