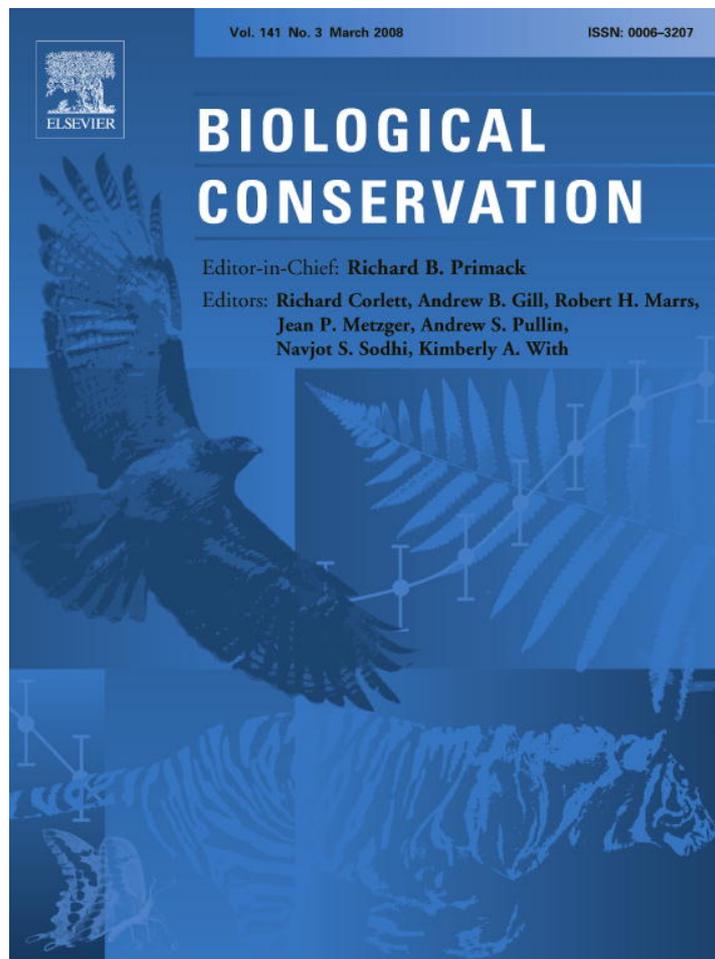


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Forest edges and landscape history shape interactions between plants, seed-dispersing ants and seed predators

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ABSTRACT

Ant-dispersed plants are often conspicuously rare in young forests and near forest edges. We monitored the distributions of five ant-dispersed plant taxa, the seed-collecting ant community, and variation in seed predation pressure by rodents in a 350-acre mesic forest in northern New York, USA to assess the incidence and effect of plant–animal interactions within the context of landscape history and proximity to forest edges. Sample plots were located in young and older forest stands (distinguished based on an 1880 map for forest cover) at varying distances from the forest edge. All five plant taxa were rarer in plots near forest edges, although diversity was more strongly influenced by landscape history. A sixth herbaceous species, one dispersed by vertebrates, was not influenced by forest edge proximity. The most effective seed-collecting ant, *Aphaenogaster rudis*, was less common in forest edge plots relative to interior plots, and predation pressure by small mammals was almost twice as great in plots near forest edges. Exclusion experiments demonstrated that ants (mutualists) and rodents (seed predators) compete for access to seeds, that ants can provide seeds some protection from mammal predation in most plots, and that the density of ant-dispersed plants is correlated with the proportion of rodent-accessible seeds that are collected by *Aphaenogaster*. Greater predation pressure and a paucity of ant mutualists may contribute to the rarity of ant-dispersed plants in edge habitats relative to forest interiors.

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1. Introduction

Most forests in the eastern United States are derived from abandoned agricultural or logging lands (Foster, 1992; Flinn and Marks, 2004) and are surrounded by edges that abut a matrix of dissimilar habitat. The plant communities in the interiors of older and/or historically undisturbed forests can differ greatly from those found in secondary forests (Peterken and Game, 1984; Meier et al., 1995; Pearson et al., 1998; Jules, 1998; Bellemare et al., 2002; Mitchell et al., 2002) or at forest edges (Murcia, 1995; Laurance et al., 2001; Honnay et al., 2004; Roy and Blois, 2006). Non-exclusive explanations for these differences include differences in soil (Vellend, 2005;

Tomimatsu and Ohara, 2004) and micro-environmental characteristics (Matlack, 1993; Laurance et al., 2001), disturbance-induced extirpations (Meier et al., 1995; Jules, 1998) and isolation from source populations (Flinn and Marks, 2004; Flinn and Vellend, 2005; Ries et al., 2004; Laurance et al., 2001; Pearson et al., 1998; Ruben et al., 1999). Some plant species may be present in secondary forests or edge habitats but nonetheless have lower seedling recruitment rates (Tomimatsu and Ohara, 2004; Jules, 1998; Jules and Rathcke, 1999). One explanation for these differences in plant recruitment is that interactions with animals, including pollinators (Jules and Rathcke, 1999), seed dispersers (Pudlo et al., 1980; Galetti et al., 2003; Ness, 2004; Lopes de Melo et al., 2006), seed

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predators (Jules and Rathcke, 1999; Tallmon et al., 2003; Meiner and LoGuidice, 2003) and grazers (Cote et al., 2004) can differ among the interiors of older forests, secondary forests and forest edges (reviewed in Murcia, 1995; Fagan et al., 1999; Ries et al., 2004).

Our work focused on myrmecochorous (ant-dispersed) plants, a guild that can comprise 40% of the herbaceous species and 60% of emergent stems in plots within eastern U.S. forests (Beattie and Culver, 1981; Handel et al., 1981). This guild, however, is conspicuously rare in young forests (Meier et al., 1995; Pearson et al., 1998; Mitchell et al., 2002; Flinn and Marks, 2004; Flinn and Vellend, 2005) and at forest edges (Jules and Rathcke, 1999; Tomimatsu and Ohara, 2004; Roy and Blois, 2006), relative to wind- or vertebrate-dispersed plant species. This loss contributes strongly to the differences in plant communities noted among these habitats and older forest interiors.

The conservation of myrmecochorous herbs requires more than overcoming dispersal limitation (Ruhlen and Handel, 2003; Vellend, 2005). Understanding the plants' interactions with mutualists and natural enemies, and how these interactions change from forest edge to interior and across a successional sequence, is also essential. Myrmecochorous seeds attract ants with an attached lipid-rich food body, called an elaiosome, that is fed to larvae in the colony's nest (Morales and Heithaus, 1998). The seed is typically unharmed and the transportation disperses and can protect seeds from predators (Ruhlen and Dudash, 1996; Heithaus, 1981; Ohkawara and Higashi, 1994). Ants can differ in quality as plant partners, and changes in ant community composition can influence myrmecochore density and community composition (Christian, 2001). The importance of suitable ant partners can be heightened in the presence of high densities of mammalian seed predators (Fedriani et al., 2004). Intriguingly, there is some evidence that landscape history and proximity to edges may also influence the distributions of seed-dispersing ants (Pudlo et al., 1980; Heithaus and Humes, 2003; Ness, 2004) and seed-eating rodents (Jules and Rathcke, 1999; Tallmon et al., 2003; Meiner and LoGuidice, 2003), guilds that could help or hinder the retention and restoration of myrmecochorous communities.

Here, we distinguish the effects of landscape history and proximity to forest edges on plant communities and their interactions with animals within a 150-acre forest in northern New York state. We test four hypotheses: (1) landscape history and the proximity to the forest edge predict variation in plant densities, although this pattern differs among ant- and vertebrate-dispersed plants, (2) particular ant taxa are well-suited to act as plant mutualists, (3) the quality and/or quantity of prospective ant mutualists available to plants are influenced by landscape history and proximity to forest edges, and (4) within-forest differences in partner quality predict seed-dispersal and seed mortality.

2. Methods

2.1. Study site

The study site is a 150-acre temperate deciduous forest adjacent to city of Saratoga Springs, New York (43.06N, 73.47W). In 1880, the property was part of >1000 acre estate that included

an accurately mapped private park and woodland (Fig. 1). That estate was abandoned in 1899, at which time secondary succession began in the former parkland areas and continued in the historically forested areas. Sporadic logging occurred in the winter of 1916. The land was purchased by Skidmore College in 1960, and the modern mixed-age forest includes numerous walking trails on the remnants of old carriage trails.

2.2. Grid cells

We divided the forest into 35 grid cells of 0.1 min (6 s) latitude by 0.1 min longitude (approximately 130 × 158 m), and described the land-use in 1880, distance to forest edge, and distance to historical edge of each cell. We described 1880 land-use by overlaying our coordinate grid on the 1880 map and categorizing each cell as (1) forested (>90% tree cover in 1880) (2) mostly forested (50–90% tree cover in 1880) or (3) partially forested (<50% tree cover in 1880). The distance to the nearest modern edge was measured with ESRI Arc Map from the coordinate center of each cell to the nearest edge judged to be ecologically significant. These edges included electrical power line right of ways, railroad tracks, and automobile roads (Fig. 1). If modern edge effects are strong, historical edges may also be influential. We estimated distance to historical edge for each cell using the same methodology as above, although we used the 1880 map and most edges were the intersections of forest and mansion lawns. Some cells were centered in 'lawn' in the 1880s; here the distance to the forest edge was treated as a negative number. As a result, historical edge distances could range from high and positive (i.e., cells deep in the 1880 forest) to zero (cells centered at the intersection of 1880 forest and lawn) to high and negative (cells far outside the 1880 forest).

2.3. Plant distribution

We determined the distribution of five myrmecochorous taxa (*Sanguinaria canadensis*, *Trillium* spp. (*T. grandiflorum* and *erectum*), *Hepatica nobilis*, *Asarum canadense*, and *Uvularia* spp. (*U. grandifolia*, *perfoliata* and *sessilifolia*) and one vertebrate-dispersed species (*Podophyllum peltatum*, by turtles; Braun and Brooks, 1987) in the 35 cells in June, 2006. The North Woods includes at least 14 myrmecochorous species; we chose these taxa because they are easily distinguished from other plants and recognizable at a distance. All our focal taxa except *Trillium* are clonal. Because we sought to avoid negatively affecting the forest during our sampling, we hiked all existing and remnant trails in each cell, and hiked off-trail in areas where trails were rare. Every 10 m, we recorded the presence or absence of each plant species within 5 m of each side of our path. We used a handheld Magellan Meridian Platinum GPS unit to record the coordinates of the center of each 10 m microsite. We described plant densities for each taxon as the proportion of microsites occupied in each grid cell (mean ± SD = 56 ± 24 microsites inspected per grid cell). Our focus on grid cells, rather than individual 10 m transects, diminishes the importance of within-forest heterogeneity in the accuracy of the GPS units (i.e., instances when accuracy is >10 m, as can occur

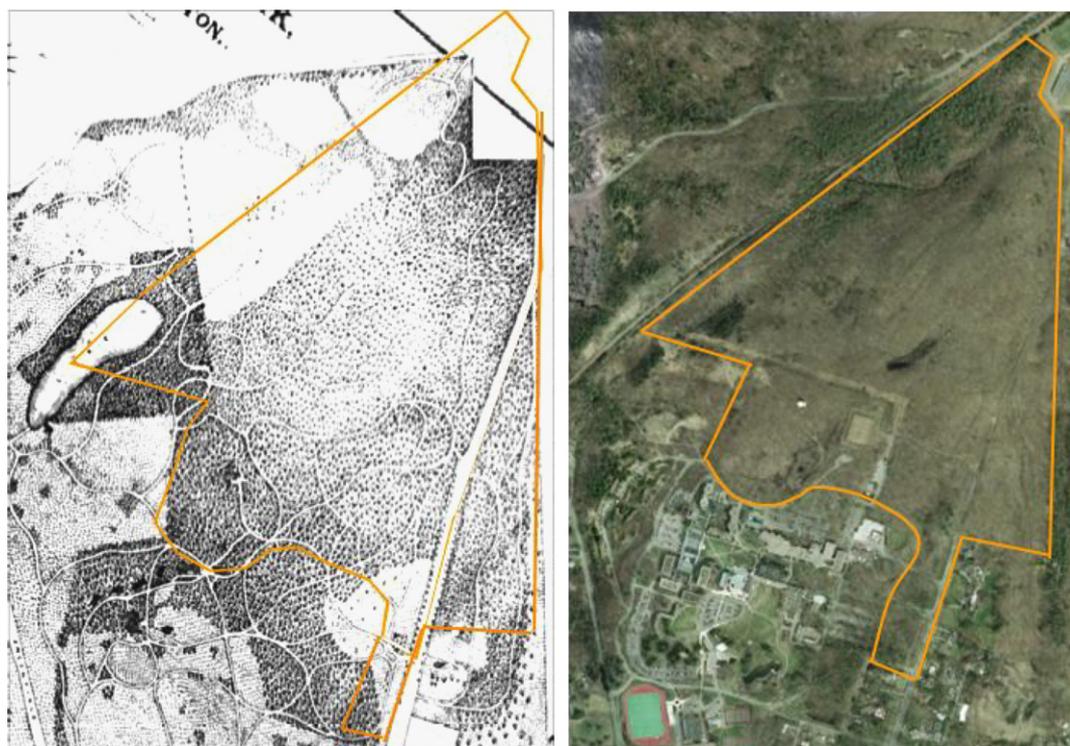


Fig. 1 – Map (1880) and aerial photograph (2004) of the North Woods forest in Saratoga Springs, New York, USA. Forested areas in the 1880 map are stippled. The modern forest is bounded by electrical power line right of ways (south-center in forest, railroad tracks (northeast), and automobile roads (southeast, south and northeast boundaries). Outline indicates the area surveyed for ant-dispersed plants and seed-collecting ants.

due to changing forest cover, topography, etc.). The proportion of sampled microsites that were off-trail was similar between grid cells in the three landscape history types (ANOVA, $F = 0.43$, $df = 2.31$, $p = 0.65$) and was similar among cells of varying distances from the forest edge (simple linear regression, $F = 0.37$, $df = 37$, $p = 0.55$).

Stepwise ANOVAs were used to measure how the plant densities were affected by proximity to the nearest edge of the modern forest, position in the landscape relative to the 1880 forest edge, landscape history and interactions between landscape history and the two forest edge measures. The least significant independent variables were removed until the model only included significant ($p < 0.05$) terms. Models were created to describe inter-cell variation in densities of the six plant taxa, variation in the taxa richness of the five myrmecochorous taxa (per cell) and variation in diversity of myrmecochorous species. Proportions were arcsine-transformed prior to statistical analysis. Diversity was estimated using Shannon's index, a measure that incorporates both taxonomic richness and relative abundance of our five myrmecochores. Cells that included no focal plants, or only one species, were omitted from this analysis (in both cases the diversity index is zero).

2.3.1. Ant-seed observations

Seed collection is a necessary precondition to a successful ant-seed mutualism, and can confer protection against seed predators (see below). We monitored ant behaviors to con-

trast the suitability of different ant species as prospective seed collectors and to identify the 'best' prospective plant mutualists. We observed single *Sanguinaria canadensis* seeds on 8×5 cm white cards for 40 min. We recorded the identity of each ant that walked on the cards and noted whether the worker removed the seed from the card (defined as seed 'discoveries' and 'collections', respectively). After a seed collection event or 40 min, we moved ≥ 10 m and repeated the trial with a new seed.

Seed-ant observations were performed in July 2006, using seeds collected from a local population. Seeds were stored in the freezer prior to use, a protocol with no apparent effect on ant behavior (Heithaus, 1981). Because our intent was to contrast the responses of different ant taxa to seeds (rather than the proportion of available seeds collected by any one taxa), we performed our observations in several grid cells with varying ant communities (see below). We did not test the hypothesis that ant responses to seeds varied with edge proximity or landscape history.

We used a chi-square analysis to test whether the likelihood of seed collection differs among ant species. We contrasted the responses of different ant species to seeds (frequency of inspecting versus ignoring) and the responses of inspectors (collect seeds versus abandon). Because it is difficult to distinguish ant individuals in the field, we treated each encounter as an independent event if that individual worker was lost from sight between encounters. Observations were not distinguished by grid cell.

2.3.2. Ant distribution

We used tuna baits to estimate the distribution of ants among the 35 cells in July 2006. Because tuna and elaiosomes both include diglycerides, a compound attractive to ants, tuna baits are often used to describe the seed-collecting ant communities (e.g., Mitchell et al., 2002; Heithaus and Humes, 2003). We created a 4 × 4 grid of notecards in a 20 m × 20 m square at the center of each grid cell. Although all our grid cells are squares, the forested (and hence, surveyed) portion of that cell may only include a fraction of that circumscribed space. We identified the cell's 'center' by calculating the average transect point from the plant census within each cell. We placed a piece of wet tuna on each card and recorded the ant species present at each card after 45–60 min. All ant surveys were performed between 6:00 and 12:00 am, and we avoided sampling during particularly wet or warm periods of the day.

We used stepwise ANOVAs to describe how the ant species richness (number of species per baiting grid) and the density of the two most common ant taxa, *Aphaenogaster rudis* and *Myrmica* spp., were affected by proximity to the edge of the modern forest, position in the landscape relative to the 1880 forest edge, landscape history and interactions between landscape history and the two forest edge measures.

We used three simple linear regressions to test the hypotheses that myrmecochore density at the cell scale increased with the frequency of *Aphaenogaster*, *Myrmica* spp., and ant species richness at the baiting grids. Myrmecochore density was estimated as the sum of the likelihoods of seeing each of the five focal plant taxa in a 10 m transect within that plot.

We estimated a cumulative collection index for each cell based on ant community composition and the likelihood of seed collection by each taxon (estimated from the tuna baiting and seed trials, respectively). The cumulative seed collection index (C_{plot}) was estimated as

$$C_{\text{plot}} = \sum B_i C_i$$

where B_i is the number of tuna baits occupied by ant taxon i , and C_i is the likelihood that that taxon i collects a seed (when coming within 4 cm on a note card).

2.3.3. Rodent predation pressure and seed collection by ants

We monitored seed removal by ants and rodents by excluding different groups from seed depots. We created a 3 × 2 grid of "stations" at the same sites used for the ant distribution sampling in 15 of our cells. Each of the six stations included three depots of six *S. canadensis* seeds. The three depots were separated by 30 cm, and included three types: (1) rodent exclusion (1.5 cm mesh cages with seeds in a Petri dish), (2) ant exclusion (on a 10 cm high inverted cup with flouon coating the sides), and (3) full access depot (seeds placed in a Petri dish). Ants can collect seeds surrounded by cages to which rodents cannot gain access to, and rodents can remove seeds placed on top of flouon-lined cups that ants cannot climb (Turnbull and Culver, 1983; Heithaus, 1981). Although the ant-inaccessible depots could be visited by a variety of animals including rodents, birds and wasps, we inferred that rodents were the primary seed collectors because of the chewed seed coats on and surrounding the ant-inaccessible depots (but not the rodent-inaccessible depots; see also Heithaus, 1981). Depots were exposed to foragers for 24 h.

We tested the hypothesis that ants and rodents compete for seeds by contrasting the number of seeds collected at the three depots types. We used a one-sided paired t-test to compare the sum of seeds collected at the ants- and rodents-only depots with the sum of those collected at the depots accessible to both groups, and treated each plot as a replicate ($n = 15$).

We used two simple linear regressions to test the hypothesis that seed collection rates by ants can be predicted from local-scale ant species composition. We estimated the proportion of seeds collected by ants when rodents and ants both have access to the seeds (as would occur in nature) as

$$P_{AR} = P_A - P_A P_R \frac{P_R}{P_A + P_R}$$

where P_A is the probability of a seed being collected by an ant when only ants have access, P_R is the probability of a seed being collected by a rodent when only rodents have access, and P_{AR} is the probability of a seed being collected by an ant when both ants and rodents have access (Turnbull and Culver, 1983). We used the proportion of seeds collected within a plot to which rodents were denied access, and the proportion of seeds collected by ants where rodents also had access to the seeds as dependent variables.

Based on differences in the distribution of the ant and plant taxa in the forest interior versus forest edge (see below), we tested the hypothesis that seed predation by rodents was greater along forest edges. We used a one-sided t-test to contrast the identities of seed collectors (rodents predators versus ant mutualists) in cells 0–50 m from the forest edge (mean distance ± SD = 34 ± 19) and >50 m from the edge (range = 75–190 m; mean ± SD = 123 ± 47), using individual seed baiting grids ($n = 15$) as replicates. We predicted the proportion of seeds collected by ants (P_A) would be greater in the interiors, the proportion collected by rodents (P_R) greater along the edges, and that the combined effect of these differences in collection would be to increase the likelihood of seed collection by ants in the presence of rodents (P_{AR}) in forest interiors. Proportions were arcsine-transformed prior to analysis.

We used simple linear regressions to test the hypotheses that myrmecochore density would increase with (1) the proportion of rodent-accessible seeds collected by ants (P_{AR}) in the 15 cells, and (2) the proportion of rodent-accessible seeds that were collected by *A. rudis*, an ant species known to be an effective mutualist. We estimated the latter proportion as the product of P_{AR} and the proportion of the cumulative collection index (see above) attributable to *Aphaenogaster*.

2.3.4. Edge effects, treating forest edges as replicates

The preceding analyses of plant and ant distributions treat individual cells as if they were independent replicates, ignoring that some cells share the same forest edges (and, as a result, are 'psuedoreplicates' of that particular edge). To address this complication, we estimated the mean densities of myrmecochorous plants (mean plant taxa per 100 m²) and *Aphaenogaster* ants (proportion of baits discovered) at the cells where the forest intersected each of the five 'matrix' habitats (an electrical powerline (south-center in forest), a railroad (northeast boundary), an automobile road (southeast), a

college campus (south), and an athletic field (northeast)), and at adjacent forest interior cells (Fig. 1). These estimates were calculated from 24 cells (means derived from an average of 2.8 edge and 1.8 interior cells in each edge-interior pair). We used two one-sided t-tests, paired by matrix, to test the hypotheses that the densities of myrmecochores and *Aphaenogaster* would be greater in the interior cells of the five edge-interior replicates. The average distances to the matrix habitats were 30 ± 9 m (\pm SD) for edge cells and 117 ± 50 m for interior cells. The analyses did not include cells that were equidistant from multiple edges, such as the innermost forest cells (mean \pm SD = 209 ± 61 m, $n = 5$) and several cells on the forest edge (45 ± 42 m, $n = 6$).

The locations and lower replication of our seed predation experiments ($n = 15$ grid cells) precluded a similar analysis to contrast seed predation pressure among these same paired sites.

3. Results

3.1. Plant distribution

As a guild, ant-dispersed plants were markedly rarer in young forest stands, relative to mixed or older forest stands (mean taxa per 10 m \pm SD = 0.43 ± 0.51 , $n = 4$; 1.06 ± 0.52 , $n = 5$, and 1.27 ± 0.83 , $n = 18$, respectively). Plant diversity was also least in young forest stands (mean \pm SD for $H = 0.54 \pm 0.34$ for four cells with multiple taxa and $H = 0$ for the remaining four cells) and indistinguishable in stands partially- or fully-forested in 1880 ($H = 1.09 \pm 0.22$ and 1.10 ± 0.35 , respectively, with 24 or 26 cells having multiple taxa). Grid cells (i.e., forest stands) centered closer than 100 m from an edge had 2.9 ± 2.0 taxa (mean \pm SD) of the five taxa possible, and cells centered >100 m from the edge had 4.7 ± 0.5 taxa ($n = 23$ and 11, respectively).

All the myrmecochores were rarer near the forest edge (Fig. 2), and most models did not include a significant

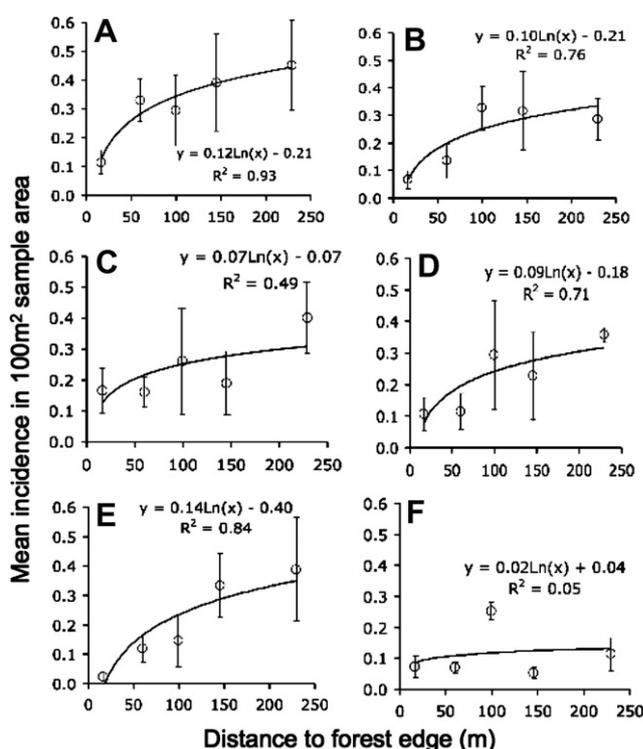


Fig. 2 – The proportion of 100 m² plots that included each plant taxa. (A) *Trillium* spp., (B) *Sanguinaria canadensis*, (C) *Uvularia* spp., (D) *Hepatica nobilis*, (E) *Asarum canadense*, (F) *Podophyllum peltatum*. Average responses for 130 × 160 m plots are shown in 40 m increments. Best-fit lines and SE bars are shown.

landscape history effect when proximity to the forest edge was included in the original model (Table 1). The models explained 22–54% of the intra-forest variation in plant distributions (*Asarum canadense*: $F = 31.42$, $df = 1.33$, $p > 0.0001$, $r^2 =$

Table 1 – The most parsimonious analysis of variance models to predict plant and ant distributions among thirty five 130 × 180 m grids

Taxa	Predictor	F	df	p
<i>Asarum canadense</i>	Modern edge	31.42	1	0.0001
<i>Hepatica nobilis</i>	Modern edge	9.78	1	0.004
	1880 edge proximity	11.08	1	0.0023
<i>Podophyllum peltatum</i>	1880 edge proximity	7.62	1	0.009
<i>Sanguinaria canadensis</i>	Modern edge	10.91	1	0.0023
<i>Trillium</i> spp.	Modern edge	9.44	1	0.004
<i>Uvularia</i> spp.	Landscape history	4.47	2	0.021
	Modern edge	0.005	1	0.945
	History × modern edge	5.88	2	0.007
<i>Myrmecochores</i> density	Modern edge	38.86	1	0.0001
<i>Myrmecochores</i> richness	Modern edge	16.08	1	0.0003
<i>Myrmecochores</i> diversity	Landscape history	4.69	2	0.0185
<i>Aphaenogaster rudis</i>	Modern edge	5.94	1	0.021
	1880 edge proximity	4.26	1	0.048
<i>Myrmica</i> spp.	ns			

The original models included proximity to the nearest edge of the modern forest, position in the landscape relative to the 1880 forest edge, landscape history and interactions between landscape history and the two forest edge measures. The least significant independent variables were removed until the model only included significant ($p < 0.05$) terms.

0.49; *Hepatica nobilis*: $F = 11.47$, $df = 2.31$, $p = 0.002$, $r^2 = 0.43$; *Sanguinaria canadensis*: $F = 10.91$, $df = 1.33$, $p = 0.0023$, $r^2 = 0.25$; *Trillium* spp.: $F = 9.43$, $df = 1.33$, $p > 0.004$, $r^2 = 0.22$; *Uvularia* spp.: $F = 6.59$, $df = 5.28$, $p = 0.004$, $r^2 = 0.54$; myrmecochores as a guild: $F = 38.85$, $df = 1.33$, $p > 0.0001$; $r^2 = 0.54$). The model for the vertebrate-dispersed plant, *Podophyllum peltatum*, was the least predictive ($F = 7.62$, $df = 1.32$, $p = 0.009$; $r^2 = 0.19$) and did not include a significant modern edge effect (Table 1, Fig. 2).

Plant densities were similar in 'on-trail' versus 'off trail' microsites, although *Trillium* was marginally more common in off-trail microsites (paired t-test, paired by grid cells with both microsite types; $t = 1.76$, $df = 15$, $p = 0.098$) and *Uvularia* was marginally more common in on-trail microsites (paired t-test, $t = 1.52$, $df = 15$, $p = 0.15$).

3.2. Ant-seed observations

We observed 155 ant-seed interactions involving seven ant taxa. The likelihood that ants walking on the card made contact with the seed differed among ant species ($X^2 = 13.32$, $v = 6$, $p < 0.05$), as did the likelihood that 'contacting' ants collected the seeds ($X^2 = 28.26$, $v = 5$, $p < 0.001$; Table 2). *A. rudis* and *Myrmica* spp. were the two taxa most likely to collect seeds, although *Aphaenogaster* collected a significantly greater percentage of discovered seeds than did *Myrmica* (85% and 47%, respectively, $X^2 = 14.61$, $v = 1$, $p < 0.001$). *Camponotus* and *Lasius* spp. collected approximately 25% of the seeds they encountered, and *Leptothorax*, *Stenamma* and *Crematogaster* spp. collected seeds in less than 8% of their encounters.

3.2.1. Ant distribution

A. rudis and *Myrmica* spp. were the ant taxa observed most frequently at the tuna baits (Table 2). Variation in ant species richness and total ant activity at baits were not predicted by 1880 land-use, proximity to the forest edge or interactions between those two variables (non-significant models in both cases). *A. rudis* was observed in all baiting grids, although density was greatest in cells farther from the modern forest edge and 1880 forest edge (simple linear regression, $F = 11.53$, $df = 1, 33$, $p = 0.018$; $r^2 = 0.26$; Table 1; Fig. 3). *Aphaenogaster* ants were almost twice as common at baits in cells >100 m from the modern forest edge than in grids closer to the edge (mean \pm SD = 6.6 ± 3.2 and 3.8 ± 2.1 baits per grid). The density of *Myrmica* spp., the second most common taxon, was not influenced by landscape history or proximity to the forest edge (Fig. 3).

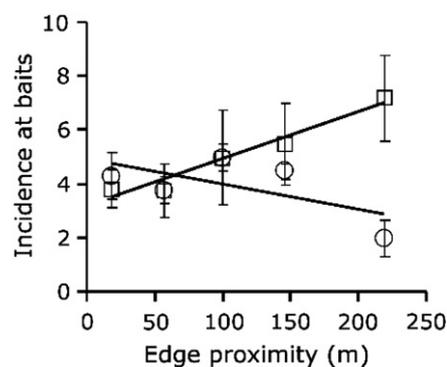


Fig. 3 – Number of baits discovered by *Aphaenogaster rudis* and *Myrmica* ants (open squares and circles, respectively) as a function of distance to the forest edge. Average responses among plots in 40 m increments are shown, and bars indicate standard errors. Best-fit lines are shown (*Aphaenogaster rudis*: $y = 0.018x + 3.19$; $r^2 = 0.95$; *Myrmica* spp.: $y = -0.0093x + 4.91$; $r^2 = 0.40$).

Myrmecochore density was correlated with the incidence of *Aphaenogaster* at baits (simple linear regression, $F = 14.5$, $df = 1.33$, $p = 0.0006$; $R^2 = 0.31$), but not the incidence of *Myrmica* spp. ($F = 0.40$, $df = 1.33$, $p = 0.53$) nor ant species richness ($F = 0.15$, $df = 1.33$, $p = 0.70$) at the baiting grids. Cumulative seed collection indices for the cells varied by almost an order of magnitude (range: 1.9–11.7); that variation was correlated with among-grid variation in the incidence of *Aphaenogaster* at baits (simple linear regression, $F = 140.4$, $df = 1, 33$, $p < 0.00001$; $R^2 = 0.81$).

3.2.2. Rodent predation pressure and seed collection by ants
Both ants and rodents collected a majority of the available seeds when the other group was denied access (mean proportion \pm SD = 0.62 ± 0.28 and 0.71 ± 0.27 , respectively). Among-plot variation in the collection of rodent-inaccessible seeds by ants was significantly correlated with the cumulative seed collection indices ($F = 9.5$, $df = 1, 13$, $p = 0.009$, $R^2 = 0.42$). The total number of seeds taken by ants and rodents foraging separately exceeded the number taken from depots accessible to both groups in 13 of the 15 sites (one-sided paired t test, $t = 4.94$, $df = 14$, $p = 0.00011$). This competition with rodents decreased the proportion of seeds collected by ants by more than a third (mean $P_{AR} \pm$ SD = 0.39 ± 0.24), although the proportion was still positively related to the cumulative seed collection index ($F = 8.8$, $df = 1.13$, $p = 0.011$, $R^2 = 0.41$).

Table 2 – Seed discoveries, seed collections, and mean number of tuna baits occupied (per baiting grid) by seven ant taxa

Ant genus	Observations	Discoveries	Collections	# Baits occupied (\pm SD)
<i>Aphaenogaster</i>	34	29	29	4.6 ± 2.8
<i>Myrmica</i>	87	54	41	4.0 ± 2.5
<i>Camponotus</i>	16	7	4	1.0 ± 1.5
<i>Lasius</i>	4	3	1	0.1 ± 0.5
<i>Laptothorax</i>	12	6	1	0.6 ± 0.9
<i>Crematogaster</i>	1	0	0	0.2 ± 0.8
<i>Stenamma</i>	1	1	0	0

Rodents collected a greater proportion of ant-inaccessible seeds in seed grids ≤ 50 m from the forest edge, relative to more interior seed grids (mean $P_R \pm SD = 0.80 \pm 0.24$ and 0.52 ± 0.26 , $n = 10$ and 5 , respectively; one-sided $t = 2.21$, $df = 13$, $p = 0.023$). Ants collected a smaller proportion of rodent-inaccessible seeds in seed grids ≤ 50 m from the forest edge, although that difference was not significant (mean $P_A \pm SD = 0.56 \pm 0.29$ and 0.72 ± 0.30 , respectively, one-sided $t = 1.34$, $df = 13$, $p = 0.101$). As a result of these two trends, the proportion of seeds exposed to both seed predators (rodents) and mutualists (ants) that were collected by mutualists was significantly greater in the forest interior than at the forest edge (mean $P_{AR} \pm SD = 0.54 \pm 0.21$ and 0.31 ± 0.21 , respectively, one-sided $t = 2.07$, $df = 13$, $p = 0.029$).

The density of myrmecochorous plants in the fifteen cells was not significantly correlated with the proportion of rodent-accessible seeds that were collected by ants as a group (P_{AR} ; $F = 1.79$, $df = 1.13$, $p = 0.20$) but it was correlated with the proportion of those seeds that were collected by *Aphaenogaster* ants ($F = 5.46$, $df = 1.13$, $p = 0.036$, $R^2 = 0.30$). This proportion was twice as great in cells > 50 m from the forest edge, relative to edge cells (mean $\pm SD = 0.36 \pm 0.14$ and 0.18 ± 0.13 , respectively).

3.2.3. Edge effects, treating forest edges as replicates

The mean densities of myrmecochorous plants was greater in the forest interior than near the forest edge (mean plant taxa per $100 \text{ m}^2 = 1.4$ and 0.7 , respectively; one-sided, paired $t = 3.09$, $df = 4$, $p = 0.02$). *Aphaenogaster* ants discovered a greater proportion of baits in the forest interior, relative to sites near the forest edges (mean proportion of baits = 0.38 and 0.22 , respectively; one-sided, paired $t = 2.56$, $df = 4$, $p = 0.03$).

4. Discussion

Our study demonstrated pronounced edge effects on all five ant-dispersed plant taxa, the most effective seed-collecting ant species, and seed predators. We found little effect of landscape history (here, 1880 land-use) on plant or ant density after accounting for the effects of proximity to the forest edge. We also demonstrated that seed predation pressure exerted by small mammals was greater at forest edges, a pattern that may be exacerbated by decreased seed collection by ants at forest edge sites relative to forest interiors. We believe the landscape variation in the incidence of the ant-seed mutualism (and, as a result, changes in predation rates by rodents) contribute to the constrained distribution of the ant-dispersed plants. Below, we discuss how these dynamics may be important to the retention and restoration of these communities in forests.

We found a > 10 -fold difference among ant taxa in the likelihood of collecting seeds adapted for dispersal by ants (see also Pudlo et al., 1980). We used seed collection to measure how the potential for successful ant-plant mutualisms changes with landscape history and proximity to the forest edge. The act of seed collection is the step most clearly related to protection from rodent predators (see also Heithaus, 1981; Smith et al., 1989; Ruhren and Dudash, 1996), although post-collection criteria, including the distance (Ness et al., 2004), direction (Ness, 2004) and destination seeds are dispersed, are also critical to plants. Seed collection might be

more accurately described as a necessary precondition to a successful ant-seed mutualism; our fieldwork distinguished ants that are unsuitable as mutualists from those that could be mutualists. We described the suitability of ants as seed collectors based on interactions with *Sanguinaria canadensis*, a plant species that produces relatively large seeds (Beattie et al., 1979). Although any one species is an imperfect surrogate for a community, experiments with relatively large seeds provide a conservative estimate of an ant community's collection abilities (Beattie et al., 1979; Christian, 2001). Perhaps as a result, studies focused on the retention, restoration, or threats to myrmecochorous plants often focus on species with large seeds (e.g., Pudlo et al., 1980; Christian, 2001; Ruhren and Handel, 2003; Ness, 2004).

If ant taxa differ in their quality as plant partners, among-taxa variation in response to forest landscapes may influence plants. The incidence of *Aphaenogaster* at baits, and, as a result, the likelihood of seed collection by *Aphaenogaster*, progressively increases towards the forest interior (Fig. 3). Edge effects have been demonstrated for many organisms (e.g., bird, frogs, plants and fungi in Drinnan, 2005); to our knowledge this is the first demonstration of edges affecting an important seed-dispersing ant. Intriguingly, the density of myrmecochorous herbs (taxa per 100 m^2) increases in a similar fashion along that edge to interior gradient (Fig. 2), and is correlated with the incidence of *A. rudis* at baits and the proportion of seeds collected by *A. rudis*. Because *A. rudis* workers disperse seeds sufficient distances to avoid competition with maternal plants (Giladi, 2006), bury seeds in shallow, nutrient-rich nests where germination is likely (Ruhren and Dudash, 1996), and produce more queens when provided access to elaiosomes (Morales and Heithaus, 1998), this ant may be a particularly effective mutualist. In contrast, other ant species may disperse seeds to sites unsuitable for germination and plant growth (e.g., *Camponotus* foragers occasionally carry seeds to arboreal nests). The ease of discovering *Aphaenogaster* (here, an inspection of tuna baits after 40 min), combined with its suitability as a myrmecochore mutualist, may make the density of this ant a useful surrogate measure of habitat suitability for myrmecochores. Restoration efforts may also be more effective if they are guided by a pre-restoration survey of the ant communities in prospective sites. We note, however, that if post-collection events such as directed dispersal, seed inhumation and alate production shape the distributions of the ant and/or plant participants, the rarity of both groups at the forest edges may be attributable to positive feedbacks between the plant guild and this ant. Intriguingly, the edge effects detected in our forest stands may be indirect ones (i.e., derived from the historical responses of the partner taxon).

Rodent predation pressure was almost twice as great in sites within 50 m of the forest edge, relative to more interior sites. As a result, seed emigration and the seed-to-seedling transition may be sufficiently challenging at forests edges to hamper dispersal within and between forests (e.g., from interiors to edges or between edges of disjunct forests; see also Aune et al., 2005). Because competition between ants and rodents 'rescues' a proportion of seeds from rodent predation in most sites (edge or otherwise), the retention and restoration of myrmecochorous plant communities should be most successful in sites where the seeds have access to ant mutualists.

Our estimate of cumulative seed collection services, one that combined measures of ant density and the predilection of individual species to collect seeds they encounter, accurately predicted the among-cell variation in seed collection by ants even after including the effects of rodent predation pressure. Although other studies have documented changes in vulnerability of seeds to predation at the edges of temperate deciduous forests (Ostfeld et al., 1997; Jules and Rathcke, 1999; Tallmon et al., 2003; Meiner and LoGuidice, 2003), our study distinguishes the contributions of two phenomena (predation pressure and availability of protective mutualists) that can modify vulnerability across the edge gradient. We have no evidence whether the ant-seed interaction continues to confer protection to plants after they escape predation as new seeds exposed on the soil surface. Attacks by subsequent natural enemies, such as *Odocoileus virginianus*, may also be greater near forest edges, however deer herbivory is similar among myrmecochorous and non-myrmecochorous herbs (Ruhen and Handel, 2003) and unlikely to disproportionately limit the ant-dispersed plant guild.

Our hypothesis that changing interactions with ants across an edge to interior gradient influence myrmecochorous plants was supported by the lack of a discernable edge effect on the vertebrate-dispersed species, *P. peltatum*. *Podophyllum peltatum* was unique among our six taxa for being equally common at forest edges and interiors. Although *P. peltatum* is only one species, this lack of detrimental edge or land-use history effects for vertebrate-dispersed species is consistent with that observed in other temperate deciduous forests (Flinn and Marks, 2004; Flinn and Vellend, 2005; Bellemare et al., 2002; Honnay et al., 2004).

A typical 'myrmecochore' has a combination of traits that may diminish the importance of the ant-seed-rodent interactions highlighted in this study. Many myrmecochores, including most taxa included in this study, are long-lived plants capable of vegetative reproduction. These plants can 'disperse' via growth as well as seed-dispersal, and populations can survive even when (or where) seed recruitment is negligible (Pudlo et al., 1980). Nonetheless, seeds may be critical to these plants for several reasons. These herbaceous clones often expand vegetatively only a few centimeters per year (Whigham, 2004), whereas ants transport collected seeds an average of 0.87 m (northern hemisphere mean; Gomez and Espadaler, 1998). Seeds also represent the products of sexual recombination; seed recruitment is essential if distinct (and perhaps monoclonal) populations are to be linked (Honnay and Bossuyt, 2005). Even long-lived myrmecochorous plants cannot survive the perpetual loss of seeds to predation (Jules, 1998; Christian, 2001; Tallmon et al., 2003). Last, myrmecochores typically produce few, large seeds. This strategy may exacerbate the negative consequences of seed predation (i.e., the consequences of the loss of an individual seed is greater), and is associated with greater vulnerability in the face of land-use change (Verheyen et al., 2003).

The effect of historical land-use on ant-dispersed plants detected in our study was less pronounced than in other studies (e.g., Meier et al., 1995; Mitchell et al., 2002). The correlation between landscape history and the incidence of edge habitat is one explanation for these different conclusions. Although our young forest patches included lower densities

of ant-dispersed plants, they were typically closer to the forest edge than were the older forest patches (mean \pm SD = 45 \pm 47 m ($n=8$) and 96 \pm 77 m ($n=21$) from forest edge, respectively). Younger forests often surround older forests (e.g., propagules from remnant woodlots colonize adjacent old fields). In this common scenario, the younger forests may be disproportionately exposed to the 'hard' edges of an inhospitable matrix habitat, whereas the older forest experiences the 'soft' edges of the surrounding regrowth forest. The apparent influence of historical land-use may mask the influence of modern edge distance if the variables are not parsed. Large forests also tend to include more myrmecochores (Meier et al., 1995; Pearson et al., 1998; Mitchell et al., 2002); this pattern could reflect the lower ratio of edge to interior habitats in those forests. A second explanation is that the variation in landscape history among our sites may be less influential than that in other studies. All the young forest patches included in our study are derived from lawns that were periodically grazed by sheep. Herbaceous populations may recover more quickly on landscapes used as lawns or subjected to limited logging, relative to those used intensively for agriculture or grazing (Peterken and Game, 1984; Pearson et al., 1998; Mitchell et al., 2002; Bellemare et al., 2002).

We may have reached different conclusions from earlier studies because we addressed our questions at larger (and perhaps as a result, coarser) spatial and demographic scales. We described plant density at a relatively large spatial scale (the proportion of 10 \times 10 m microsites occupied within a 130 \times 160 m plot), one we believed was appropriate for describing these plants. Myrmecochorous plants often occur in aggregations (Whigham, 2004); these patches may indicate the borders of interactions with suitable mutualists (e.g., an ant colony and/or mycorrhizae), the extent of clonal growth by a genet, or some combination of the two. Our focus on the occupation of 100 m² microsites by six taxa provides a robust description of the distribution of aggregations of each taxa in the forest, and avoids misidentifying forest stands (i.e., 130 \times 160 m cells) with sporadic clonal aggregations as densely occupied (as a stem count might suggest). Our measure of density was not meant to distinguish large aggregations from solitary plants or juveniles from reproductives, nor can it detect the finer scale demographic changes reported in studies that focus on populations of a single species (Pudlo et al., 1980; Ruhen and Handel, 2003; Tallmon et al., 2003; Tomimatsu and Ohara, 2004; Vellend, 2005).

Our fieldwork produced an unprecedented map of the distributions and interactions of plants, mutualists and natural enemies across the edges and interiors of a forest with a known land-use history. All five of our myrmecochorous plant taxa were rarest in edge habitats (see also Jules and Rathcke, 1999; Tomimatsu and Ohara, 2004), a pattern not exhibited by the vertebrate-dispersed *P. peltatum*. Within-forest variation in the incidence of seed collection by rodents versus ants is one explanation for the constrained distribution of the five ant-dispersed plant taxa (see also Tallmon et al., 2003 regarding *Trillium ovatum*). Mutualistic seed-dispersing ants, such as *A. rudis*, are progressively rarer near forest edges and along a continuum of relatively intact to disturbed forests (Pudlo et al., 1980), sites where seeds may be maximally vulnerable to rodent predation. Analogous 'severed mutualisms' have

been demonstrated for avian frugivores and an African endemic tree (Cordeiro and Howe, 2003). If a majority of the herbaceous stems in eastern US forests are adapted for mutualisms with ants (Beattie and Culver, 1981; Handel et al., 1981), the shortage of seed dispersers/protectors we document may be a common phenomenon, one that occurs in direct proportion to the 'edginess' and disturbance of modern forests.

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