

Vulnerable broom crowberry (*Corema conradii*) benefits from ant seed dispersal in coastal US heathlands

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Abstract Ant seed dispersal is a globally important mutualism that occurs in over 10,000 plant species. Relatively little research has been conducted on ant seed dispersal of *Corema conradii* (broom crowberry), a key constituent of globally threatened coastal heathland ecosystems where fire is part of the disturbance regime. We conducted field studies at Cape Cod National Seashore, MA, USA to better understand the fruiting biology of *C. conradii* and to explore the benefits of ant seed dispersal. We identified how *C. conradii* fruit is displayed to foraging ants, determined the ant species that disperse *C. conradii* fruit, and quantified the distance that ants disperse fruit. We hypothesized that ants would disperse fruit away from *C. conradii* parent plants that become burn footprints following fire, to ensure seed dispersal to suitable germination sites, where we expected to find higher seedling establishment. We recorded eight ant species dispersing the fruit of *C. conradii* an average distance of 136 cm (± 10.45) (range: 7–641 cm). Two ant species, *Aphaenogaster treatae* and *Formica dolosa*,

dispersed 60 % of fruit in fruit-baiting experiments, suggesting they may function as primary dispersers in this system. Ants dispersed fruit outside the burn footprints 82 % of the time, and seedlings occurred outside the burn footprints 90 % of the time. Our results suggest that ant seed dispersal confers important reproductive benefits to *C. conradii* by directing seed dispersal sufficient distances away from parent plants onto suitable substrates for germination after intense, episodic fires.

Keywords Elaiosomes · Endangered plants · Fire adaptation · Mutualism · Myrmecochory

Introduction

The dispersal of seeds by ants, or myrmecochory, is a primary mode of seed dispersal for many plants worldwide (Giladi 2006; Lengyel et al. 2010). Globally, myrmecochory occurs in 17 % of plant families and has evolved independently over 100 times, indicating strong selection for ant seed dispersal (Dunn et al. 2007). The plant adaptation eliciting myrmecochory is the elaiosome, a fleshy growth that develops on the outside of ripe seed or fruit. Elaiosomes contain specialized fatty acids, sterols, and other nutrients (Gammans et al. 2005). Foraging ants transport fruit or seeds bearing elaiosomes to their nests (Culver and Beattie 1978), where they eat the elaiosomes or feed them to developing larvae. The

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remaining intact fruit or seeds, minus elaiosomes, are either left in the nest or deposited outside the nest in middens or in scattered locations around the nest (Hanzawa et al. 1988; Dunwiddie 1990; Hughes and Westoby 1992; Canner 2010; Aranda-Rickert and Fracchia 2011; Canner et al. 2012). Ants benefit from myrmecochory by having a supplemental food source that improves colony fitness (Hanzawa et al. 1988; Gammans et al. 2005; Giladi 2006; Fokuhl et al. 2012), and plants benefit from improved seed dispersal (Beattie 1985; Canner et al. 2012). Globally, ant seed dispersal distances range from 0.01 to 77 m (average 1.0 m) (Gómez and Espadaler 1998; Lengyel et al. 2009).

The benefits to plants of ant seed dispersal are typically explained by three theories: (1) the predator-avoidance theory, which posits that predator pressures are greatest at the parent plant and rapid removal of seeds away from the parent plant reduces predation (Janzen 1970; Heithaus 1981; Bond and Slingsby 1984; Beattie 1985; Ohkawara and Higashi 1994; Ness et al. 2009); (2) the distance dispersal theory, which posits that competition for resources between parent and offspring or among siblings is lower some distance away from the parent plant (Andersen and Morrison 1998; Giladi 2006); and (3) The directed dispersal theory, which posits that seeds are dispersed to sites that favor germination or seedling survival because of improved soil conditions (usually at the ant nest) (Beattie 1985, Hanzawa et al. 1988; Giladi 2006).

To our knowledge, no studies on myrmecochory have been conducted in the coastal heathlands of the northeastern US, where ants play an important role in dispersing the seeds of many plants. Dunwiddie (1990) documented that *Corema conradii* (broom crowberry), an endemic subshrub of the northeastern coastal plain that inhabits coastal heathlands and is threatened throughout its range (NHESP 2007), has a seed dispersal relationship with ants (Martine et al. 2005). However, the role of ants in the natural history of *C. conradii* has scarcely been investigated, despite that *C. conradii* is a key constituent of coastal heathland ecosystems.

In addition to its myrmecochorous relationship with ants, *C. conradii*'s reproductive viability is dependent upon regular fire. Fire kills adult *C. conradii* plants, burning them to the ground, and seeds germinate in subsequent years. After a fire "burn footprints"

comprised of dead root material, charred organic matter, and dry mineral soil mark the locations where mature *C. conradii* plants existed (Online Resource 1). Although we occasionally observe haphazard germination of *C. conradii* seeds in burn footprints, *C. conradii* seeds appear to germinate and seedlings appear to survive more readily outside burn footprints. Dunwiddie (1990) and Martine et al. (2005) documented that *C. conradii* seeds germinate prolifically 15–20 months post-fire and then experience very high seedling mortality. *C. conradii* seeds at our study site germinate abundantly approximately 20- to 24-months post-fire (David Crary, Cape Cod National Seashore, personal communication). Unsatisfactory substrate conditions within burn footprints may select for delayed seed germination or may preclude seed germination and/or seedling establishment altogether. High fire intensity can adversely affect soil conditions (DeBano 1991), and volatile compounds released from burned *C. conradii* plants may persist in the burn footprint for some time (Bond et al. 1984; Bradshaw et al. 2011; Keeley et al. 2011).

In this study, we explored the mutualistic relationship between ants and *C. conradii* at Cape Cod National Seashore, MA, USA. Our goals were to better understand the fruiting biology of *C. conradii*, identify characteristics of the ant-plant mutualism, and explore the benefits to *C. conradii* of ant seed dispersal. Our specific objectives were to (1) record the time period and duration that *C. conradii* provide elaiosomes to ants; (2) quantify the number of fruits that *C. conradii* produces; (3) identify the manner in which *C. conradii* fruits are displayed to foraging ants; (4) assess whether fruits and seeds are consumed by other predators; (5) determine the species of ants that disperse *C. conradii* fruit; (6) calculate the distance that ants disperse fruit; and (7) investigate whether ants transport fruit to substrate types that favor seedling survival.

Methods

Study location

This study was conducted in the Marconi coastal heathlands (41°54'50N, 69°58'20W), Cape Cod National Seashore (CCNS), Wellfleet, MA, USA (Online Resource 2). Located on the western shore of the Atlantic Ocean, the Marconi heathlands are

subject to wind driven salt spray and underlain by sandy, glacial outwash deposits (Fletcher 1993). The site has an annual average high temperature of 13.2 °C and low of 6.5 °C, and the annual average precipitation is 119.5 cm (National Climatic Data Center 2013). The mean fire return interval at these coastal heathlands was historically 6–10 years (National Park Service 2014). The US Army cleared the site between 1943 and 1961, and it has since revegetated as early successional sandplain heathlands and grasslands, and scrub oak (*Quercus ilicifolia*)–pitch pine (*Pinus rigida*) communities. Given the globally rare status, ecological significance, and cultural esthetic of sandplain heathlands, CCNS mechanically removes and periodically burns canopy vegetation to maintain these communities.

Study species

Corema conradii is a twiggy subshrub in the family Ericaceae that has winter-persistent, needle-like leaves. The species is endemic to northeastern North America, where it occurs as widely separated populations primarily along the coast from Nova Scotia to NJ (Natural Heritage and Endangered Species Program 2007). *C. conradii* is listed as critically imperiled to vulnerable throughout its range except in Nova Scotia (NatureServe 2015) and was recently delisted as a plant of special concern in MA, partly because of its protection within CCNS. *C. conradii* fruits (1–1.5 mm diameter) ripen in late May–early June and are dry round drupes that typically enclose three seeds (Gleason and Cronquist 1991). White fleshy elaiosomes develop at the base of the fruit while fruits are still attached to the stem (Online Resource 3) (Dunwiddie 1990; Gleason and Cronquist 1991).

Experimental design

Fruiting biology and rodent exclusion experiments

To address our study objectives pertaining to *C. conradii*'s fruiting biology, we conducted experiments to determine (1) the duration of fruiting during which *C. conradii* provides elaiosomes to ants; (2) the number of fruits produced by *C. conradii*; and (3) the manner in which *C. conradii* fruits are displayed to foraging ants. To assess whether seed predation at the parent plant is a selective pressure that may drive

myrmecochory with benefits to *C. conradii*, we used predator exclusion experiments to determine (4) whether *C. conradii* has significant seed predators that prey on fruit or seed beneath the parent plant.

To evaluate these questions, we randomly selected 28 female *C. conradii* individuals in seven different areas at Marconi (four plants per area) (Online Resource 4). To obtain a widely distributed representation of the *C. conradii* population at Marconi, we selected study areas based on their scattered locations throughout the site and the presence of mature *C. conradii* individuals.

To determine the duration of fruiting, we monitored each *C. conradii* plant for the presence of fruit 2–3 times per week from May 7 to July 9, 2012. To avoid overlooking straggler fruit and to standardize the termination of fruiting, we determined a plant to be fruiting when $\geq 10\%$ of fruit bore elaiosomes and terminating fruiting when $\leq 10\%$ of remaining fruit bore elaiosomes.

Calculating the number of fruits produced per *C. conradii* individual was a three-step process. First, we determined the area (m²) occupied by each *C. conradii* individual by outlining the perimeter of each plant using a bendable wire. We then placed the wire outline of each plant over a poster board grid with 6.45-cm squares and counted the squares within the wire outline to obtain an estimated area occupied by each plant. Second, we calculated the average number of fruit-bearing stems for each *C. conradii* individual by counting fruit-bearing stems within a 4.3-cm diameter quadrat positioned at 12.7-cm intervals along two measuring tapes laid over each plant in north–south and east–west orientations. Third, we determined the average number of fruit per stem. Because *C. conradii* fruit are tiny and vary in abundance per stem, it was not possible to count them without stripping the fruit from plants. Thus, a proxy for the number of fruits per stem was obtained for each study area by laying two measuring tapes in the same orientation as above over four randomly selected *C. conradii* individuals within each area. We stripped and counted the fruit from one stem at each 12.7-cm interval along the measuring tapes and calculated an average number of fruit per stem. Fruit produced per *C. conradii* individual was calculated by multiplying the number of fruit per stem by the average number of fruit-bearing stems on the plant and extrapolating out to the area of the plant.

To determine how fruits are displayed to ants, we evaluated whether there was a correlation between the number of fruit produced and the fruit that fell to the ground beneath the parent plant (fruit-fall). To do this, we placed fruit collection dishes under each *C. conradii* individual to passively collect fruit-fall from May 25 to Aug 30, 2012. Fruit in the dishes were counted 2–3 times per week. The number and sizes of collection dishes placed under a plant depended on the size of the plant and the available space to position dishes among the dense twigs, resulting in one to four dishes under each plant. Collection dishes were round plastic saucers either 10.16 cm diameter (81.1 cm²) or 15.24 cm diameter (182.39 cm²) with 3.175 cm sides. We covered the dishes with ¼-inch wire mesh to prevent rodents and other larger predators from removing fruit. To prevent ants and other insects from climbing into containers and removing fruits, we painted the outside of each collection dish with Insect-a-Slip Insect Barrier Fluon Teflon® (DuPont™, Wilmington, Delaware).

To explore whether predation at the *C. conradii* parent plant acts as a selective pressure for myrmecochory we placed paired fruit-baiting stations side by side at the outer perimeter of each of the 28 *C. conradii* individuals to determine whether the plant has other significant seed predators (e.g., rodents). Stations consisted of 8.2 × 6.2 cm rectangular dishes with 5-mm sides. One station was covered with ¼-inch wire mesh to exclude rodents and other larger fruit predators, and one was left uncovered (Online Resource 5). Ten *C. conradii* fruits bearing elaiosomes were placed in each station and left for 24 rain-free hours, after which we recorded the number of fruits remaining in each station. We sampled all 28 *C. conradii* individuals for three 24-hour periods, and eight plants were sampled one additional time ($n = 92$) from June 8 to July 10, 2012.

Ant seed dispersal and seedling experiments

Our additional study objectives were to (5) identify the ant species dispersing seeds; (6) calculate the distance ants disperse seeds; and (7) investigate whether ants transport seeds to substrate types that favor seedling survival. To address these objectives, we carried out two separate experiments on nine 30 × 30 m plots at our study site. These plots were burned in 2009—three each in spring, summer, and fall. Results from studies

in similar systems document that ant communities recover from fire within 8–18 months (Jackson and Fox 1996; York 2000; Farji-Brener et al. 2002; Parr et al. 2004; Vasconcelos et al. 2008; Underwood and Christian 2009) where favorable habitat conditions are restored or maintained as at our study site. For our experiments, we divided each burn plot into a matrix of nine 10 × 10 m subplots (Online Resource 6). Sampling in burned plots ensured that we could visually observe ant activity (we could not visually track ants in unburned plots, which had dense bearberry [*Arctostaphylos uva-ursi*] and *C. conradii* groundcover) and that we had access to *C. conradii* seedlings that germinate post-fire (unburned plots contained no *C. conradii* seedlings). Further, burned plots represent the natural patchiness of fire-dependent coastal heathlands and represent the necessary conditions for *C. conradii* regeneration.

To evaluate ant species, dispersal distance, dispersal location, and substrate type onto which seeds were dispersed, we conducted fruit-baiting experiments on 27 randomly selected 10 × 10 m subplots (3 per burn plot) sampled once each from June 27 to July 12, 2012. To sample a subplot, one fruit-baiting station was placed at the center of each of nine *C. conradii* burn footprints that best fit a 3 × 3 m matrix (Online Resource 6). Each fruit-baiting station was a large, plastic yogurt container top (10.2 cm diameter with 3 mm sides). We baited each station with four *C. conradii* fruits and monitored ant-fruit interactions by moving among stations for 30 min, recording ant species and behavior towards the fruit. Within those 30 min, we added fruit to stations when ants removed fruits, maintaining four fruit per station, when we did not directly observe the dispersal interaction because we were monitoring another station. For these experiments, we collected ripe *C. conradii* fruit from plants other than our original 28 study plants, to avoid biasing the fruiting biology experiments detailed above.

For each ant-fruit interaction observed, we identified ants to genus or species and recorded their behavior towards the fruit (disperse versus consume the elaiosome in situ). When fruits were dispersed, we recorded the dispersal distance by visually tracking ants and measuring the distance with a measuring tape. We also recorded whether the fruit was dropped, lost by the observer, or transported to the nest, as well as the substrate type onto which the ant deposited each

fruit (burn footprint, bare mineral soil, and organic material [fine and coarse leaf litter, pine needles, and live vegetation]). Some ant species employ a recruitment foraging strategy where ants of the same colony are recruited to the discovered food source, resulting in rapid removal of fruit, especially if the station is in close proximity to the nest. Other ant species discover food sources individually and are less likely to remove fruit as quickly (Aranda-Rickert and Fracchia 2011). Thus, when we observed repeated dispersal events from one baiting station to the same nest, we recorded no more than four dispersal events to minimize bias in our dispersal distance calculations caused by differences in foraging strategy and/or proximity of a station to a nest. When we observed ants consuming fruits, we only recorded the consumption event once per station, per species regardless of the number of ants observed, because numerous individuals of each species congregate at the same fruit and/or move between various fruits at the station. Analysis of dispersal distances was performed using just dispersal events to the nest ($n = 144$), which accounted for 91 % of dispersal events. Ant species that conducted <10 dispersal events to the nest were grouped together in the category ‘Other’.

To further explore the benefits of having its fruit dispersed by ants, we measured the distance of *C. conradii* seedlings from the center of burn footprints, their location inside or outside a burn footprint, and the substrate type in which they were growing. We identified 36 *C. conradii* individual burn footprints (four burn footprints in each of the 9 burn plots) and established eight transects originating from the center of each burn footprint and radiating out 152 cm (Online Resource 6). We then measured the distance from the center of the burn footprint to each *C. conradii* seedling growing along each transect, recorded its presence within or outside the burn footprint, and recorded the substrate type in which it was growing (burn footprint, bare mineral soil, and organic material). We defined seedlings as plants ≥ 1.0 cm tall or plants <1.0 cm tall that had secondary branching. We only recorded seedlings that fell within 2.54 cm to either side of transects or within 2.54 cm of a recorded seedling. If seedlings were not encountered within 152 cm of the center of the burn footprint, then the transect was extended another 152 cm and then another 152 cm (maximum extension 456 cm).

Data analysis

We compared the number of days that *C. conradii* bore fruit among the seven study areas using one-way ANOVA, as our data met the assumptions for use of parametric statistics. When ANOVA detected significant differences in fruiting days among the study areas, we performed means comparisons among the areas using eight separate t-tests and determined differences to be significant at the Bonferonni-adjusted $\alpha = 0.0062$ ($\alpha = 0.05/8$) (McDonald 2009).

Fruit-fall data did not meet the assumptions for use of parametric statistics; thus, data for fruit-fall and the number of fruit produced were Log_{10} transformed to normalize their distribution. We performed linear regression analysis to evaluate relationships between the number of fruits produced by *C. conradii*, plant size, and the amount of fruit-fall, using individual *C. conradii* ($n = 28$) as replicates. The difference values for fruit taken from stations with wire mesh and fruit taken from stations without wire mesh were used to test for normality and were non-normally distributed even after log transformation. Thus, we used a non-parametric Wilcoxon Signed-Rank analysis to test for significant differences between the numbers of fruit removed from stations with and without wire mesh, with paired fruit-baiting stations as replicates ($n = 91$).

Ant dispersal distance data did not meet the assumptions necessary for use of parametric statistics before or after log transformation. Thus, non-parametric Kruskal–Wallis tests were used to compare ant dispersal distance among plots burned in the spring, summer, and fall ($n = 3$ each season) and to compare the dispersal distances among ant species (*Aphaenogaster treatae*, *Formica dolosa*, *Formica lasoides*, *Formica subsericea*, and ‘Other’), using dispersal events to the nest as replicates ($n = 144$). Data for seedling distances from the center of burn footprints did not meet normality assumptions before or after log transformations. Thus, we used a non-parametric Kruskal–Wallis test to compare seedling distances among plots burned in the spring, summer, and fall ($n = 3$ each season), using recorded seedlings as replicates ($n = 2087$). When Kruskal–Wallis tests detected significant differences in both the distances that ants dispersed seeds among the burn seasons, and the distances of seedlings from burn footprints among the burn seasons, three separate Wilcoxon Rank-sum

tests were performed for means comparisons using the Bonferonni-adjusted $\alpha = 0.0167$ ($\alpha = 0.05/3$). When the Kruskal–Wallis test detected significant differences in seed dispersal distances, 10 separate Wilcoxon Rank-sum tests were used for means comparisons using the Bonferonni-adjusted $\alpha = 0.005$ ($\alpha = 0.05/10$).

We used frequency distributions to analyze the dispersal distances for the four ant species that conducted >10 dispersals (*A. treatae*, *F. dolosa*, *F. subsericea*, and *F. lasoides*) and tested for normal distributions using the Shapiro–Wilks test.

All data were analyzed using JMP (v.10.0.0, 2012, SAS Institute Inc., Cary, NC). Statistical significance was determined at $\alpha \leq 0.05$ unless otherwise noted (e.g., when Bonferonni adjustment was applied).

Results

Fruiting biology and rodent exclusion

The mean duration of fruiting for *C. conradii* individuals ($n = 28$) was 27 (± 1.18) days (range: 16–39 days). Twenty-four *C. conradii* individuals (86 %) began fruiting by June 3 and 25 plants (90 %) finished fruiting by July 2.

The average area covered by *C. conradii* individuals was 0.55 (± 0.10) m^2 (range: 0.13 – 2.5 m^2), and the number of fruits produced by a single *C. conradii* individual ranged from 6925 (0.23 m^2 plant) to 96,177 (2.5 m^2 plant). The number of fruits produced by *C. conradii* individuals and plant size were significantly

positively correlated ($R^2 = 0.887$, $P < 0.0001$). The average number of fruits produced was 13 cm^{-2} (range: 6.4 – 23.4 cm^{-2}). Fruit collected in dishes placed under *C. conradii* individuals accounted for an average of 62 % of the fruit produced (range: 43–85 % per plant). We detected a significant positive correlation between the number of fruits produced and the amount of fruit-fall ($R^2 = 0.587$, $P < 0.0001$).

The mean number of fruits that ants removed from baiting stations with wire mesh (7.8 ± 0.34) that excluded rodents and baiting stations without wire mesh (7.7 ± 0.34) was not statistically different (Wilcoxon Signed-rank test, $S = -40.500$, $P = 0.6155$).

Ant seed dispersal and seedling dynamics

We recorded 188 ant-fruit interactions, of which 159 (85 %) resulted in seeds being dispersed and 29 (15 %) in elaiosomes being consumed in situ (Online Resource 7). Of the 159 dispersal interactions, 144 (91 %) resulted in fruit dispersal to the nest, seven (4 %) were dropped by the ant, and eight (5 %) were visually lost by the observer.

We observed eight ant species dispersing *C. conradii* seeds to their nests (Table 1), and two ant species consumed the elaiosomes in situ (*Crematogaster lineolata* and *Temnothorax* sp.) (Online Resource 8). Overall, ants dispersed seeds an average of 136 (± 10.45) cm from the center of burn footprints to their nests, with 70 % of dispersal distances falling within 152 cm of the center of the *C. conradii* burn footprint (Online Resource 9). *A. treatae* (43 dispersals) and *F. dolosa* (40 dispersals) were responsible for the majority

Table 1 Relative importance and dispersal distance patterns of ant species that dispersed *C. conradii* fruit to their nests ($n = 144$ dispersal events), Marconi heathlands, Cape Cod, MA, USA

Ant species	Number of events	Percent of total (%)	Mean \pm SE distance (cm)	Max distance (cm)
<i>Aphaenogaster treatae</i>	43	30	114 ± 10.87	352
<i>Formica dolosa</i>	40	28	183 ± 20.26	632
<i>Formica lasiodes</i>	21	15	59 ± 6.28	115
<i>Formica subsericea</i>	19	13	282 ± 38.72	641
<i>Myrmica americana</i> *	8	6	56 ± 12.26	107
<i>Formica incerta</i> *	6	4	37 ± 14.38	108
<i>Lasius neoniger</i> *	6	4	11 ± 1.58	15
<i>Crematogaster lineolata</i> *	1	1	22 ± 0.0	22
Other	21	15	36 ± 7.22	108

Asterisks denote species grouped into ‘Other’ for analysis

of dispersal events (nearly 60%). *F. subsericea* dispersed fruit the furthest distance (up to 641 cm) and *Lasius neoniger* dispersed fruits the shortest distance (up to 7 cm). Dispersal distance curves for *A. treatae*, *F. lasoides*, *F. dolosa*, and *F. subsericea* all come from non-normal distributions except *F. subsericea* (Shapiro–Wilks test, $W = 0.919$, $P = 0.108$), which demonstrates high variability in the distances these species dispersed seeds (Online Resource 10). The mean distance that *A. treatae*, *F. dolosa*, *F. subsericea*, *F. lasoides*, and ‘Other’ dispersed fruit to their nest differed significantly ($\chi^2 = 66.361$, $P < 0.0001$), but dispersal distances did not differ between *F. subsericea* and *F. dolosa* ($\chi^2 = 5.389$, $P = 0.02$, Familywise error rate = 0.005).

The mean distance of seedlings recorded ($n = 1961$) within 152 cm of the center of *C. conradii* burn footprints (94 % of seedlings) was 93 (± 0.88) cm. The overall mean distance of all seedlings recorded ($n = 2087$) from the center of burn footprints to 456 cm was 105 (± 1.39) cm, showing high frequencies between 75 and 105 cm and again between 135 and 150 cm (Online Resource 8). Seedlings were recorded outside the burn footprint 90 % of the time and ants dispersed fruit outside the burn footprint 82 % of the time (Fig. 1). Ants dispersed fruits most often to bare mineral soil and organic material substrates (36 and 47 % of dispersal events, respectively) and seedlings were found growing most often in bare mineral soil and organic material (58 and 32 % of observations, respectively). In contrast, ants dispersed seeds to *C. conradii* burn footprints least often (17 % of observations) and seedlings were found in burn footprints least often (10 % of observations) (Fig. 2).

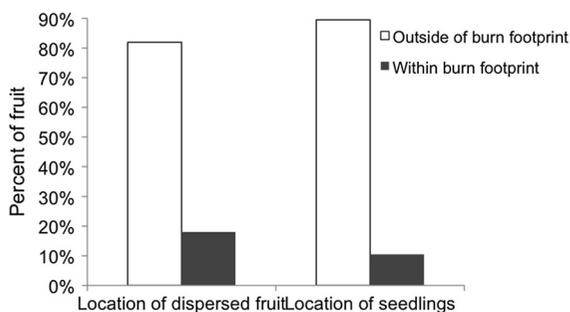


Fig. 1 Total percent of *C. conradii* fruit dispersed and seedlings located inside and outside the *C. conradii* burn footprints, Marconi heathlands, Cape Cod, MA, USA

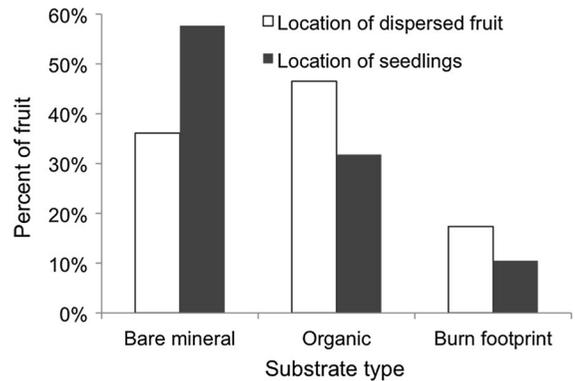


Fig. 2 Total percent of *C. conradii* fruit dispersed and seedlings documented on bare mineral soil, organic material, and burn footprint substrates, Marconi heathlands, Cape Cod, MA, USA

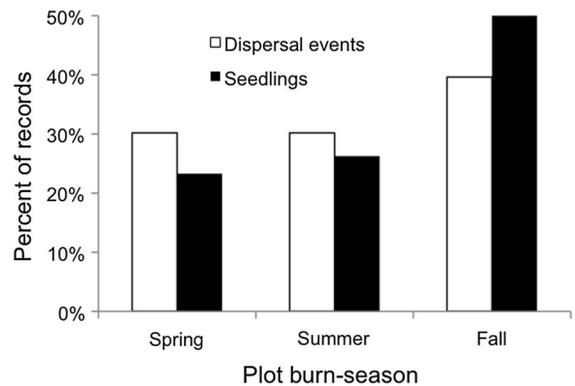


Fig. 3 Percentage of dispersal events from *C. conradii* burn footprints to the nest ($n = 144$) and of seedlings growing along transects through *C. conradii* burn footprints ($n = 2087$) in burn plots, Marconi heathlands, Cape Cod, MA, USA

We recorded twice the number of *C. conradii* seedlings in fall burn plots than spring and summer burn plots, and the greatest number of dispersal events to nests occurred in fall burn plots (Fig. 3). The distance ants dispersed fruit among the three burn seasons differed significantly (Kruskal–Wallis test, $\chi^2 = 24.53$, $P < 0.0001$), and dispersal distances were significantly different between spring and fall burn plots (Wilcoxon Rank-sum test, $\chi^2 = 19.36$, $P < 0.0001$, Familywise error rate = 0.0167) and between spring and summer burn plots ($\chi^2 = 17.74$, $P < 0.0001$, Familywise error rate = 0.0167) (Fig. 4). Specifically, dispersal distance was furthest in plots burned in fall and shortest in plots burned in spring. The distance of seedlings away from *C.*

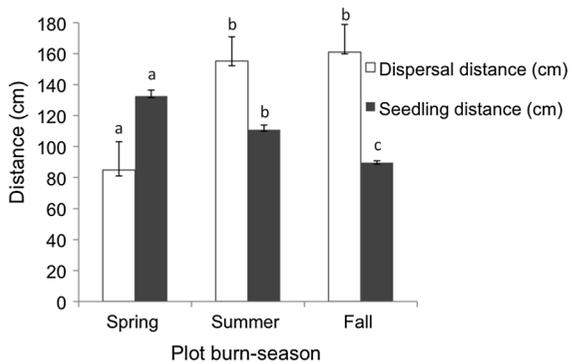


Fig. 4 Mean \pm SE of ant dispersal distance (cm) and distance of seedlings from the center of *C. conradii* burn footprints in burn plots ($n = 9$), Marconi heathlands, Cape Cod, MA, USA. Different letters represent statistically significant differences in pairwise comparisons (Wilcoxon Rank-sum test, Familywise error rate = 0.0167 for each comparison) among burn seasons within each response variable. Seedling distance pairwise comparisons: fall versus spring: $\chi^2 = 75.68$, $P < 0.0001$; fall versus summer: $\chi^2 = 25.05$, $P < 0.0001$; spring versus summer: $\chi^2 = 10.43$, $P < 0.001$. Ant dispersal distance pairwise comparisons: spring versus fall: $\chi^2 = 19.36$, $P < 0.0001$; spring versus summer: $\chi^2 = 17.74$, $P < 0.0001$; fall versus summer: $\chi^2 = 0.30$, $P < 0.58$

conradii burn footprints was significantly different among the three burn seasons (Kruskal–Wallis test, $\chi^2 = 80.20$, $P < 0.0001$), and all pairwise comparisons were significantly different (Fig. 4).

Discussion

We recorded eight ant species dispersing the seeds of *C. conradii*. Of these, *Aphaenogaster treatae* and *Formica dolosa* were responsible for nearly 60 % of all dispersals to nests, with *A. treatae* representing over half of these dispersals, suggesting that *A. treatae* and *F. dolosa* may be the primary dispersers at our study site. Thus, our findings support the more recent understanding that myrmecochory functions as an unevenly diffuse mutualism where one or more ant species are responsible for a disproportionately high number of dispersals despite their relative abundance. Historically, myrmecochory was thought to function as a diffuse mutualism in which many ant species contributed equally to seed dispersal (Garrido et al. 2002), but recent studies have documented unevenly diffuse mutualisms (Gove et al. 2007; Aranda-Rickert and Fracchia 2011).

We observed that *C. conradii* provides several ant species with abundant fruit, despite bearing elaiosomes on average only 27 days each spring. *C. conradii* passively drops fruit to the ground in a concentrated area under the parent plant where foraging ants can discover them. While some of these ants will become effective dispersers, this strategy also invites fruit or seed predators (Heithaus 1981; Beattie 1985; Andersen 1987; Ness et al. 2009). The predator-avoidance theory posits that predation of seeds or fruit is highest at the parent plant, and therefore predation pressure is reduced by rapid removal of seeds away from the parent plant. Although supported by various studies (Heithaus 1981; Bond and Slingsby 1984; Giladi 2006), our study does not support this theory because we observed no difference in the number of fruits removed from fruit-baiting stations that included versus excluded mammal and bird predators. While our baiting stations were not designed to exclude granivorous ants and invertebrates, we never observed granivorous ants preying upon *C. conradii* fruit. The only other invertebrates we observed consuming *C. conradii* fruits were caterpillars and only while fruit was still attached to the parent plant; thus, caterpillar predation would not drive ants to rapidly disperse fruits away from parent plants.

The average distance that ants dispersed fruit at our study site was 1.36 m, which is farther than the mean dispersal distance in other Northern Hemisphere systems (0.79 m) (Gómez and Espadaler 1998). Longer dispersal distances in northeastern North American heathlands, where shrub-form myrmecochores rather than smaller herbaceous plants dominate, may be necessary to maintain gene flow among populations and perpetuate seedling recruitment (Lengyel et al. 2009). At our site, fire may both facilitate longer seed dispersal distances and help maintain ant species diversity by creating open habitat conditions with the exposed soils preferred by many ant species, particularly dispersers in fire prone ecosystems (Ellison 2012; Toro et al. 2013). Longer dispersal distances and an increase in dispersal rate post-fire, particularly after fall burns, may be *C. conradii*'s best strategy for optimizing fitness. It is possible that conducting our study in burned plots resulted in observing longer dispersal distances than we might observe under living plants; thus, follow up studies in which ant seed dispersal is characterized in pre-burn or unburned plots would shed light on actual dispersal distances under living plants.

Despite the relatively short distances that ants disperse fruit compared to vertebrate dispersers, plants incur benefits if ant dispersal distances exceed primary dispersal distances (Culver and Beattie 1978). Given that *C. conradii* fruit drops to the ground directly beneath parent plants, the plant benefits from subsequent dispersal by ants away from parent plants. Further, our distance dispersal curve revealed a high peak at 0.5 m and long tail extending to 6.4 m, which reflects an environment in which sites favorable for seedling establishment are limited (Green 1983; Andersen 1987). Ants that disperse seeds shorter distances to more proximate nest locations represent the peak of the curve, while the tail reflects longer distance dispersers that transport seeds to sites more favorable for seedling establishment (Andersen and Morrison 1998; Gómez and Espadaler 1998). Distance dispersal reduces the density of seeds and seedlings at the parent plant, thereby reducing competition between the parent plant and offspring and among siblings (Whitney 2002; Parr et al. 2007; Canner et al. 2012). Because prolific germination of *C. conradii* only occurs after fire, which almost always kills the parent plant, parent-offspring competition is likely not relevant in our study species (Bond and Slingsby 1983). Ant seed dispersal may benefit *C. conradii* by reducing sibling competition; this could be tested by characterizing ant seed dispersal under and around living parent plants just before a prescribed burn.

Due to inhospitable post-fire substrate conditions, we hypothesized that *C. conradii* benefits from having its seeds dispersed away from parent plants that become burn footprints after fire. We observed that ants consistently carried fruit outside of burn footprints to substrate types where 90 % of our recorded seedlings were found, and most seedlings we observed within burn footprints were dead or dying from desiccation. This suggests that the relationship between ants and *C. conradii* helps to optimize its reproductive viability via fruit dispersal away from parent plants that provide unfavorable substrates after fire.

The directed dispersal theory posits that seeds are dispersed to microsites that benefit germination or seedling survival because of improved soil conditions at the nest site (Beattie and Culver 1981, 1983; Beattie 1985; Hanzawa et al. 1988; Giladi 2006). However, many common seed dispersers in temperate regions, especially *Aphaenogaster*, do not establish long-term

nest sites necessary to improve soil conditions (Culver and Beattie 1978). Thus, at our study site, advantages to *C. conradii* conferred by directed dispersal may not result from better soil conditions at the nest, both because *Aphaenogaster* is an important disperser here and because we frequently observed ants carrying seeds away from their nests after having consumed elaiosomes, i.e., seeds did not remain buried in nests. Thus, our study supports the directed dispersal theory not because ants carried seeds to nest sites with favorable soil conditions, but rather because ants carried fruit outside burn footprints to more favorable substrate types (where we also observed significantly higher *C. conradii* seedling density).

The fire avoidance theory posits that seed burial in the nest benefits seedling establishment in fire prone ecosystems (Beattie 1985; Giladi 2006). The fact that some ant species we observed in burned areas carried seeds away from nests after consuming elaiosomes suggests that the fire avoidance theory is not operating in our study system. The precise mechanism that triggers *C. conradii* to germinate post-fire is not understood, but *C. conradii* seeds may require contact with fire, heat, or smoke (Reyes and Traubaud 2009; Bradshaw et al. 2011; Keeley et al. 2011). If so, then seed burial in ant nests would not benefit seedling establishment. Conversely, if fire compromises seed viability, then some seed burial may be advantageous. At the Marconi heathlands, *C. conradii* seed burial by ants may or may not be important; rather, it may be more important that seeds are carried away from parent plants that become post-fire burn footprints with unsuitable substrate conditions for seed germination and seedling establishment.

Conservation strategies to preserve imperiled *C. conradii* populations and their exceptional heathland communities should prioritize the vital role of ant seed dispersers and the maintenance of intact ant assemblages (Parr et al. 2007). Maintaining ant species diversity requires conserving various habitat types or successional stages of vegetation (Toro et al. 2013) to support niche partitioning among ant species. Burning not only perpetuates *C. conradii* by removing vegetation and triggering seed germination but also helps maintain ant species diversity by creating open bare mineral habitat preferred by some species and by creating a simplified foraging landscape that enables detection of fruits and longer foraging distances (Gibb and Parr 2010). Mowing or mechanical removal of

woody vegetation may provide some of the same benefits as burning (Pierce and Moll 1994) but may not provide the variety of habitat niches for ants that fire creates. Further, to our knowledge, no research documents *C. conradii* seed germination *en masse* following mowing or cutting as with fire.

Because *C. conradii* populations survive fire as seed, fire intervals should be established that allow plants to reach reproductive stage (e.g., 5-year intervals: William Patterson, University of Massachusetts, personal communication). Managing *C. conradii* populations by burning small patches, ideally in fall (Bond et al. 1984; personal observation), will maintain diversity of age structure and thus population reproductive viability, and will also buffer against large scale losses should a fire result in poor recruitment (Dunwiddie 1990; Martine et al. 2005).

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