

# Myrmecochory and *Corema conradii* at the Cape Cod National Seashore: Exploring the benefits of ant seed dispersal in a coastal environment

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## BACKGROUND

The dispersal of seeds by ants, called myrmecochory, is a primary mode of seed dispersal for many plants, and although geographically widespread, it is particularly prevalent in certain bio- regions around the world (Giladi 2006; Lengyel et al. 2010) . Globally, myrmecochory has been documented in 4.5% of all angiosperms and 17% of all plant families, and has evolved independently over 100 times, demonstrating that there are strong environmental pressures that select for the dispersal of seeds by ants. Most of these evolutionary lineages are of Australian, South African, or northern temperate origin (Lengyel et al. 2010). Myrmecochores of northern temperate origin are mostly herbaceous understory plants (Beattie & Culver 1981; Lengyel et al. 2009) adapted to mesic soils, cool winters, and mild to warm summers. In contrast to the myrmecochores of the temperate deciduous forest, South African and Australian myrmecochores are typically sclerophyllous trees or shrubs, which occur on impoverished soils in forest, savannah, and heathland communities (Rice & Westoby 1981; Milewski 1982; Bond & Slingsby 1983). The plant form, soil features, and environmental pressures that characterize myrmecochorous regions of the Southern Hemisphere (Beattie & Hughes 2002) also characterize the northeastern coastal plain of North America.

The plant adaptation eliciting a myrmecochorous relationship is the elaiosome (also called aril), which is a fleshy growth that develops on the outside of the seed or fruit when ripe (Fig 1). Elaiosomes attract ants because of the specialized fatty acids, sterols and other nutrients they contain (Gammans et al. 2005), with certain nutrients mimicking the insect prey of ants (Hughes et al. 1994). Foraging ants transport the fruit or seed, bearing an elaiosome, to their nest (Culver & Beattie 1978), where they eat the elaiosome or feed it to developing larvae. The remaining intact seed or fruit, minus the elaiosome, is 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 & Westoby 1992; Canner 2010; Aranda-Rickert & Fracchia 2011; Canner et al. 2012). Through this mutualism, ants benefit from having a supplemental food source, which adds to the fitness of their colony (Hanzawa et al. 1988; Gammans et al. 2005; Giladi 2006; Fokuhl et al. 2012), and plants benefit from having their seed dispersed in the landscape (Beattie 1985; Canner et al. 2012).



Fig 1. *Corema conradii* fruit with fruit, bearing elaiosomes. Photo: E. Hilley.

The benefits to plants of having their seeds dispersed by ants have been studied across ecosystem types and are most often explained by three general hypotheses: (1) The predator-avoidance theory, which assumes that predator pressures are the greatest at the parent plant and

that the rapid removal of seeds away from the parent plant will reduce levels of predation (Janzen 1970b; Heithaus 1981; Bond & Slingsby 1984; Beattie 1985; Ohkawara & Higashi 1994; Ness et al. 2009); (2) The distance dispersal theory, which assumes that there is reduced competition for resources between parent and offspring or among siblings away from the parent plant (Andersen & Morrison 1998; Giladi 2006); and (3) The directed dispersal theory, which assumes that seeds are dispersed to sites that favor germination or seedling survival because of improved soil conditions (usually referring to soils at the nest) (Beattie 1985; Hanzawa et al. 1988; Giladi 2006).

To our knowledge, there are no studies that focus on myrmecochory in the coastal region of the northeastern United States, in particular coastal heathlands, where it is likely that 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 that is threatened throughout its range (NHESP 2007), has a seed dispersal relationship with ants (Martine et al. 2005). *Corema conradii*'s life history is dependent on fire. Fire kills the adult *C. conradii* plant, burning it to the ground, and seeds germinate in the subsequent years. After a fire "burn footprints" mark the locations where mature *C. conradii* plants existed in the landscape; burn footprints are comprised of dead root material, charred organic matter, and dry mineral soil (Figure 2). *Corema conradii* seedlings appear to germinate more readily outside the burn footprint (personal observation).



Fig 2. The burn footprint of a *C. conradii* individual. Photo: E. Hilley.

## STUDY GOALS AND OBJECTIVES

This study was conducted in the coastal heathlands at Marconi Wireless Receiving Station (41°54'50N, 69°58'20W) at Cape Cod National Seashore (CCNS), Wellfleet, MA, USA. Our study aimed to explore the mutualistic relationship between ants and *C. conradii* at the Cape Cod National Seashore, Wellfleet, 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) Identify possible predators of *C. conradii* fruit, (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. We hypothesized that ants disperse fruit to locations outside of what would become *C. conradii* burn footprints and that seedling survival would be greater at these locations, thereby conferring benefits to *C. conradii* of having its seeds dispersed by ants. *Corema conradii* burn footprints may be a hostile nursery for *C. conradii* seedlings because the dark organic material of the burn footprint may create an area of lower albedo and greater heat absorption, as well as water diversion and interception that contribute to unsuccessful germination and/or seedling establishment. Further, volatile compounds in the leaves and stems of flammable plants such as *C. conradii* may increase the intensity of the burn at the parent plant, thereby reducing the

viability of seeds. Dispersal of *C. conradii* seeds outside of burn footprints may also relax the density of seedlings at or immediately surrounding burn footprints, thereby reducing sibling competition.

## RESULTS

**Objective 1.** Record the time period and duration that *C. conradii* provides elaiosomes to ants.

The mean duration of fruiting for *C. conradii* individuals ( $n = 28$ ) was 27 days ( $\pm 1.18$ ), ranging from 16 to 39 days per individual. Twenty-four *C. conradii* individuals (86%) began fruiting by June 3 and 25 plants (90%) finished fruiting by July 2.

**Objective 2.** Quantify the number of fruits that *C. conradii* produces.

The number of fruits produced by a single *C. conradii* individual ranged from 6,925 fruits for a 0.23 m<sup>2</sup>-sized plant to 96,177 fruits for a 2.5 m<sup>2</sup>-sized plant or 13 fruits per cm<sup>2</sup> (ranging from 6.4 to 23.4 fruits cm<sup>-2</sup>). The number of fruits produced by *C. conradii* individuals and the size of the individual were significantly positively correlated ( $R^2 = 0.887$ ,  $p < 0.0001$ ).

**Objective 3.** Identify the manner in which *C. conradii* fruits are displayed to foraging ants.

Fruit collected in dishes placed under *C. conradii* individuals accounted for an average of 62% of the fruit produced, ranging from 43 to 85% per plant. We detected a significant positive correlation between the number of fruits produced and the amount of fruit-fall ( $R^2 = 0.587$ ,  $p < 0.0001$ ). In other words, we observed that *C. conradii* fruit drops singly to the ground under the parent plant where they are available to foraging ants. In contrast, many myrmecochores of the temperate forest are displayed in clusters on or near the ground, while still attached to the arching stem of the plant.

**Objective 4.** Identify possible predators of *C. conradii* fruit.

Our predator enclosure experiment was designed to test the predator avoidance theory with respect to small mammals and birds, and did not take into account seed-eating (i.e., granivorous) ants and other seed-eating invertebrates. Fruit baiting stations were designed to include and exclude larger seed predators. Because the mean number of fruits that ants removed from baiting stations with wire mesh (mean  $7.8 \pm 0.34$ ) to exclude rodents and baiting stations without wire mesh (mean  $7.7 \pm 0.34$ ) was not statistically different (Wilcoxon Signed-rank test,  $S = -40.500$ ,  $p = 0.6155$ ) our results did not support the predator avoidance theory. Our results showed that larger predators such as rodents were not significant predators of *C. conradii* fruit.

**Objective 5.** Determine the species of ants that disperse *C. conradii* fruit.

We recorded 188 total ant-fruit interactions, of which 159 (85%) resulted in fruit being dispersed; 29 (15%) resulted in the elaiosomes being consumed *in situ*. Of the 159 dispersal interactions, 144 (91%) resulted in the fruit being dispersed to the nest. Eight ant species were observed dispersing *C. conradii* fruits to their nest (Table 1), and two ant species were observed consuming the elaiosomes *in situ* (*Crematogaster linaleolata* and a species in the genus *Temnothorax*) (Table 2). Appendix A includes a complete list of ant species observed while

conducting research during the 2011 and 2012. Ants were identified with the assistance of Aaron Ellison, Senior Research Fellow at Harvard Forest.

*Aphaenogaster treatae* and *F. dolosa* were responsible for nearly 60% of all dispersals to nests, with *A. treatae* representing over half of these dispersals. 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 greater number of dispersals despite their relative abundance.

Table 1. Ant species observed dispersing *Corema conradii* fruit to the nest (n = 144) at Marconi wireless receiving station, Wellfleet, MA, USA. Species with an asterisk were grouped into the category ‘Other’ for analysis.

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

Table 2. Interactions involving eating the fruit *in situ* and dispersal to the nest for *Crematogaster linaleolata* and *Temnothorax* sp. at Marconi wireless receiving station, Wellfleet, MA, USA.

Ant species	Number of dispersal events	Number of dispersal events to the nest	Mean $\pm$ SE distance (cm)	Max distance (cm)	Number of eat events
<i>Crematogaster linaleolata</i>	1	1	22 $\pm$ 0.0	22	10
<i>Temnothorax</i> sp.	7	0	15 $\pm$ 3.09	27	19

**Objective 6.** Calculate the distance that ants disperse fruit.

The average distance that ants dispersed fruit in our study was 1.36 m (Figure 3a), which is fairly consistent with a global average mean of 1.0 m (Lengyel et al. 2009); however, it is more similar to the mean at which ants disperse fruit in the Southern Hemisphere (1.52 m) than that of the Northern Hemisphere (0.79 m) (Gómez & Espadaler 1998). The longer dispersal distances in the Southern Hemisphere are likely due to the generally large size of ant dispersers (Gómez & Espadaler 1998; Ness et al. 2004) as well as the generally less vegetated foraging grounds as a result of regular, periodic fires (Parr et al. 2007). Longer dispersal distances in ecosystems such as the heathlands of northeastern North America, where shrub-form myrmecochores rather than smaller herbaceous plants dominate, may be necessary to maintain gene flow among populations and to perpetuate seedling recruitment (Lengyl 2009). Dispersal distance curves for the different ant species (*A. treatae*, *F. lasoides*, *F. dolosa*, and *F. subsericea*) showed variability in the distances these species dispersed fruit (Figure 4).

The distance dispersal theory claims that the dispersal of seeds away from the parent plant reduces competition between parent and offspring and between siblings. Our study supported the distance dispersal theory because ants dispersed fruit a greater distance than fruit is dispersed by primary dispersal (e.g., gravity, ballistic, water) and because our dispersal curve revealed a high peak and a long tail. Such dispersal curves reflect an environmental situation in which sites that are favorable for seedling establishment are limited (Green 1983; Andersen 1988). Ants dispersing shorter distances to more proximate nest locations represent the peak of the curve and the tail is generated by longer distance dispersers that transport seeds to sites more favorable for seedling establishment (Anderson & Morrison 1988; Gomez & Espadaler 1998). Our distance dispersal curve shows a high peak at the 0.5 m class, with a long tail to the curve extending to 6.4 m. Limited sites for seedling establishment at our study site could be due to the stochastic disturbance-dependent life history of *C. conradii* (i.e., the unknown duration of time between recruitment events) (Anderson 1988).

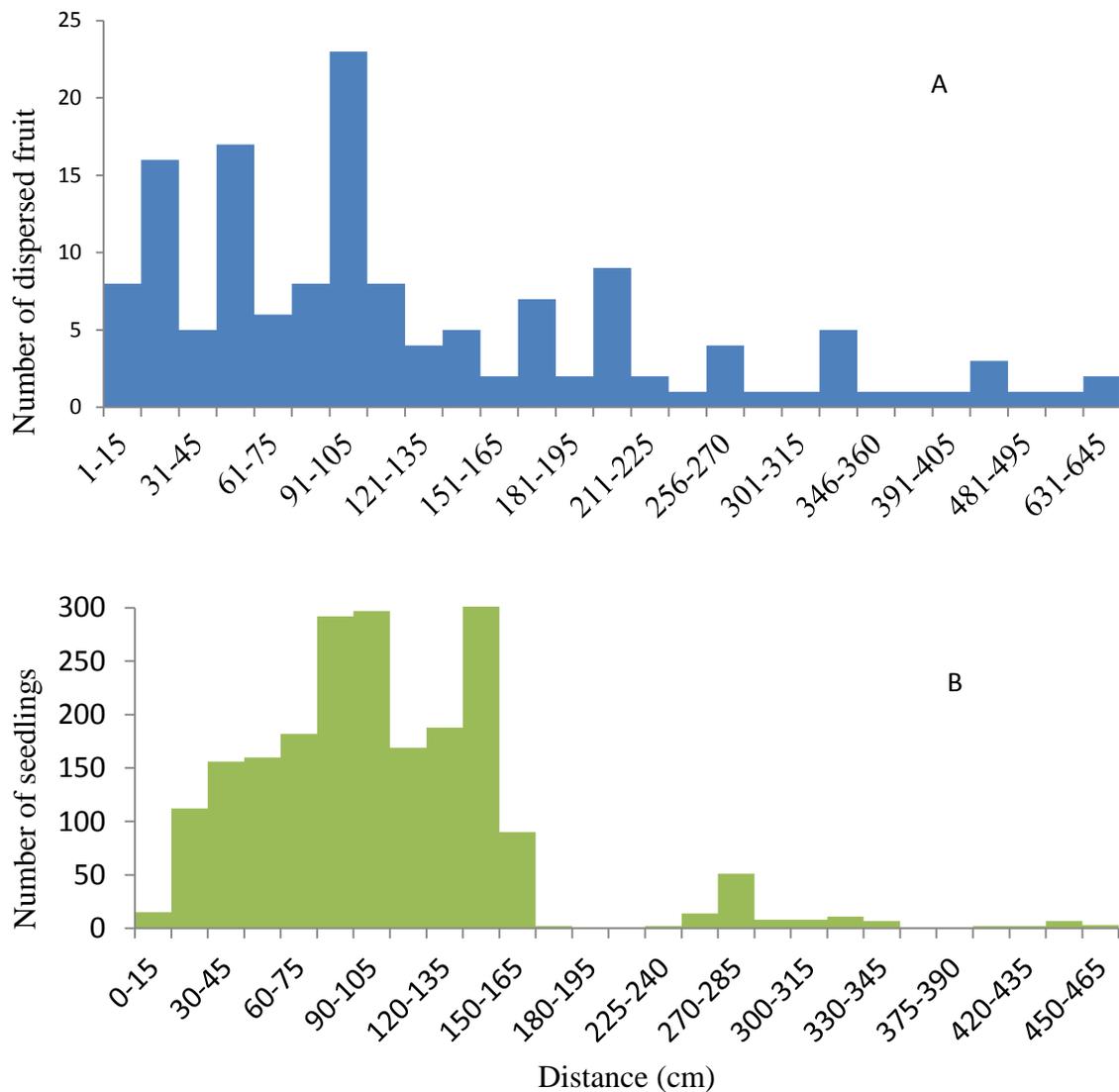


Figure 3. Frequency distribution curves for (a) distance ants dispersed fruit to the nest (n = 144) from the center of *Corema conradii* burn footprints and (b) the distance of seedlings (n = 2,087) from the center of *C. conradii* burn footprints at Marconi wireless receiving station, Wellfleet, MA, USA. Seedlings were not recorded past 152 cm when seedlings were found within this distance, which consisted of 80% of the 288 transects, therefore there is missing information past 152 cm

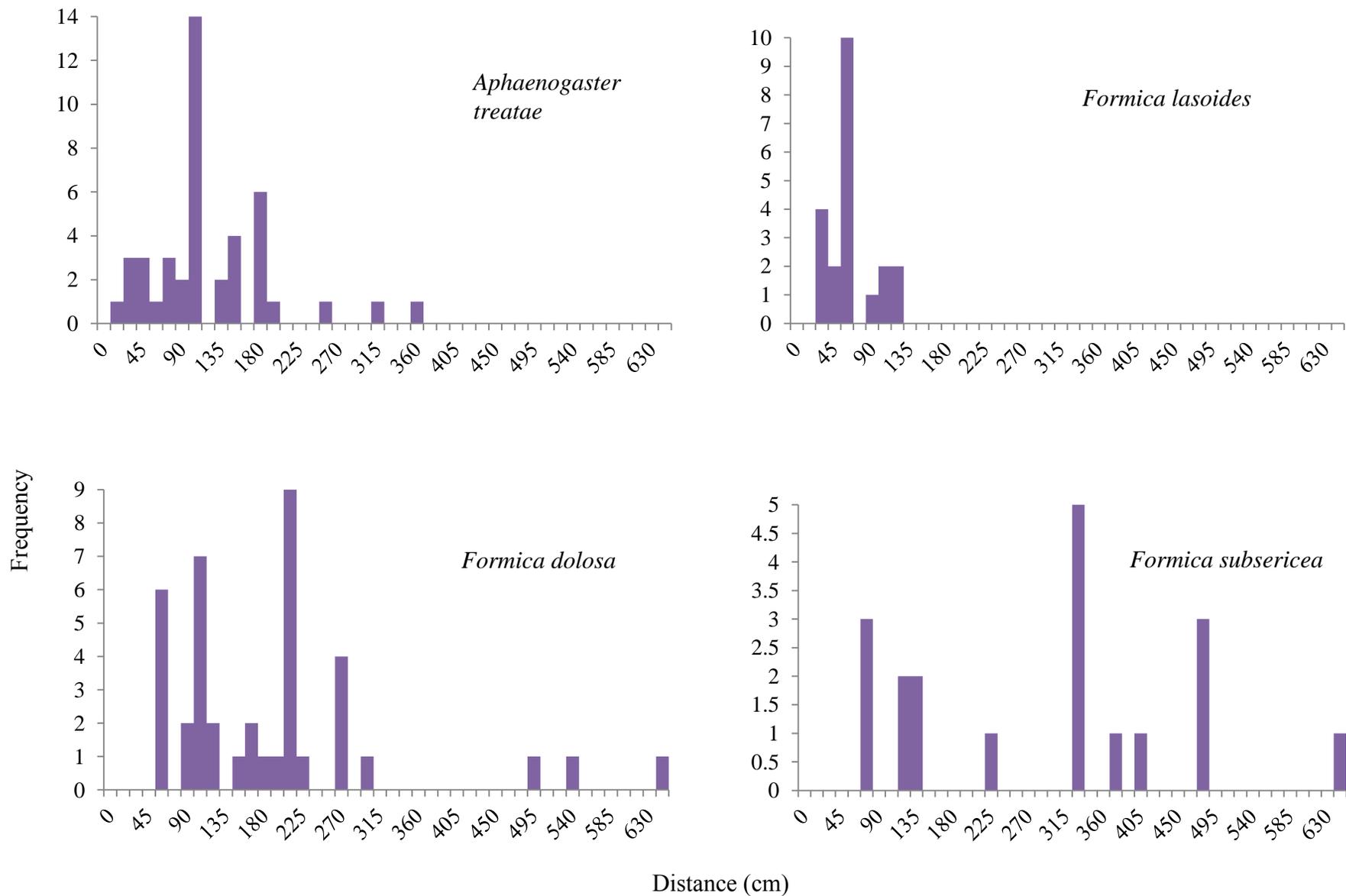


Figure 4. Frequency distribution curves for the distance (cm) ant species dispersed fruit from the center of *C. conradii* burn footprints at Marconi Wireless Receiving Station, Wellfleet, MA, USA. *Aphaenogaster treatae* (mean = 114 cm  $\pm$  10.87), *F. lasoides* (mean = 59 cm, SE = 6.28), *F. dolosa* (mean = 183 cm, SE = 20.26), *F. subsericea* (mean = 282 cm, SE = 38.72).

**Objective 7.** Investigate whether ants transport fruit to substrate types that favor seedling survival.

Our study found that ants brought fruit outside of burn footprints to substrate types where seedlings were found. The mean distance of seedlings recorded within 152 cm of *C. conradii* burn footprints (94% of seedlings) was 93 ( $\pm 0.88$ ) cm ( $n = 1961$ ). The overall mean distance of all seedlings from the center of burn footprints to 456 cm was 105 ( $\pm 1.39$ ) cm ( $n = 2087$ ), showing high frequencies between 75 to 105 cm and again between 135 to 150 cm (Figure 3b). Seedlings were recorded outside of the burn footprint 90% of the time and ants dispersed fruit outside the burn footprint 82% of the time (Figure 5). Ants dispersed fruits most often to organic and bare mineral substrates (47% and 36%, respectively) and seedlings were found growing most often in organic and bare mineral soil (32% and 58%, respectively) (Figure 6). In contrast, ants dispersed fruit to *C. conradii* burn footprints least often (17%) and seedlings were found in burn footprints least often (10%).

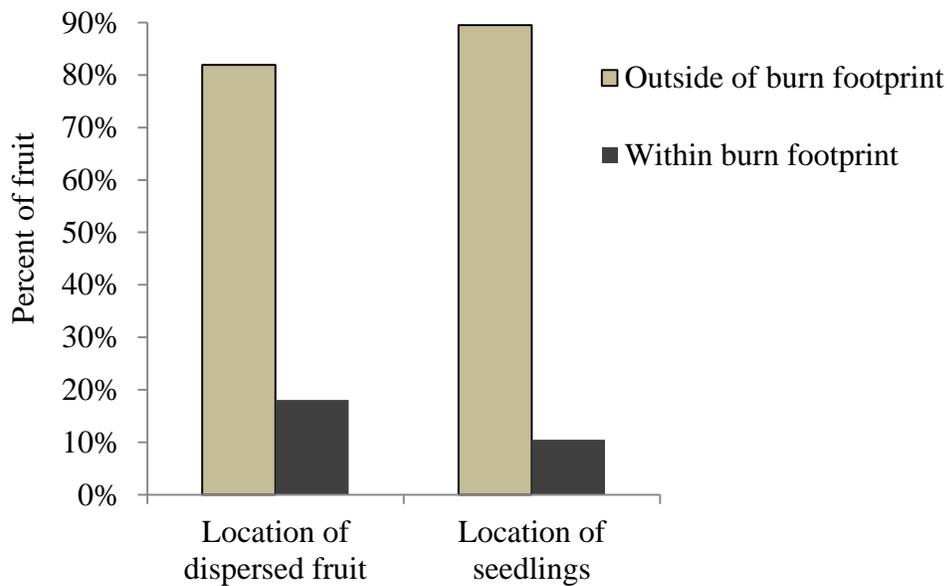


Figure 5. Total percent of *Corema conradii* fruit dispersed and seedlings located inside and outside of *C. conradii* burn footprints at Marconi wireless receiving station, Wellfleet, MA, USA.

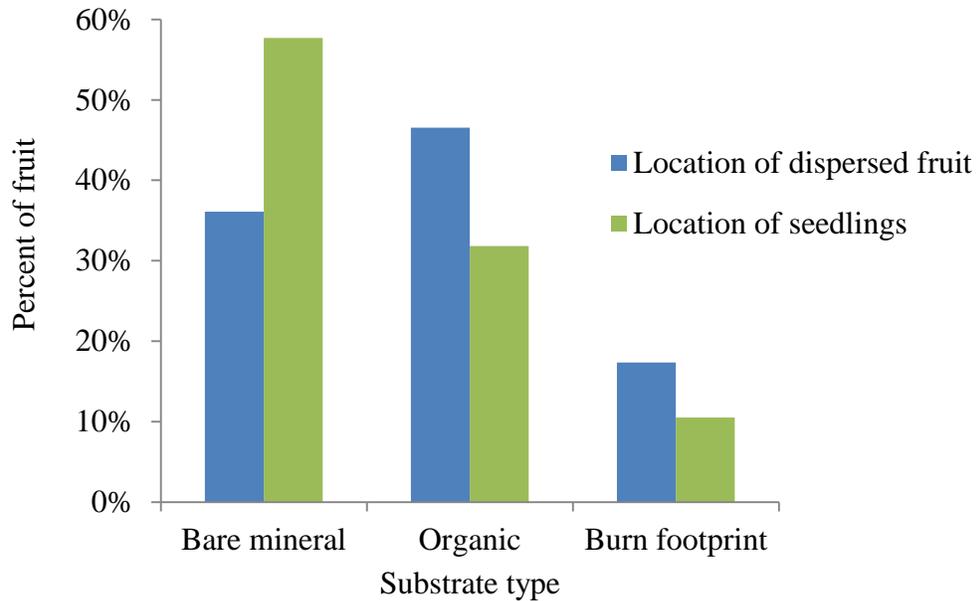


Figure 6. Total percent of *Corema conradii* fruit dispersed and seedlings recorded inside and outside of *C. conradii* burn footprints at Marconi wireless receiving station, Wellfleet, MA, USA.

**Hypothesis:** We hypothesized that ants disperse fruit to locations outside of what would become *C. conradii* burn footprints and that seedling survival would be greater at these locations, thereby conferring benefits to *C. conradii* of having its seeds dispersed by ants.

We hypothesized that *C. conradii* benefits by having its fruit dispersed to locations outside of what will become the burn footprint post fire because burn footprints pose an unsatisfactory nursery for seed germination and seedling establishment. Our findings suggest that *C. conradii* has co-evolved with ant seed dispersers to optimize its reproductive viability by having its fruits dispersed away from the parent plant. We observed that ants consistently brought fruit outside of burn footprints to substrate types where 90% of our recorded seedlings were found. Further, in many cases seedlings we observed in the burn footprints were dead or in poor condition due to what appeared to be desiccation. We speculate that depleted nutrients and unsatisfactory substrate conditions at the burn footprint preclude the germination and/or growth of seedlings for several reasons. Volatile compounds released from the leaves and stems of the parent *C. conradii* plant may persist for some time in the burn footprint and preclude seedling establishment (Bond et al. 1984; Bradshaw et al. 2011; Keeley et al. 2011), and high fire intensity may limit available nutrients, destroy beneficial soil microbes, and create a water repellent layer (DeBano 1990).

### **Additional Analysis and Results related to burn season treatments**

Although we did not quantify the abundance of seedlings or the distance of seedlings from burn footprints immediately following mass germination on burn plots, it was clear that following germination seedlings are widespread with a less apparent pattern to their dispersion on the landscape. As seedlings died off over time after mass germination and the length of time

since the 2009 burn increased, the pattern of dispersion appeared less random with fewer seedlings and an increased distance from burn footprints (Figure 7). Also, seedling distance from burn footprints on spring plots was significantly greater than the seedling distance from burn footprints on summer plots, which was significantly greater than the seedling distance on fall burn plots (Figure 7). The most likely explanation for our observation is that seedlings that emerge *en masse* in spring plots have more time to succumb to desiccation or other causes of mortality and there is a higher seedling mortality in proximity to burn footprints because suitable sites for seedling establishment are located a distance away from burn footprints (i.e., parent plant) (Janzen 1970a; Heithaus 1981; Bond & Slingsby 1984; Beattie 1985; Hanzawa et al. 1988; Ohkawara & Higashi 1994; Andersen & Morrison 1998; Giladi 2006; Ness et al. 2009).

Ant dispersal results in the location of *C. conradii* fruit distances away from the parent plant. This dispersion in the landscape increases the chances that seeds will be located to sites with improved conditions for germination and seedling establishment. Our study was not set up to determine seedling survivorship; however, an additional factor that may contribute to differences in the abundance of seedlings on the burn plots is the season of the burn. Bond et al. (1984) found that variability in seedling establishment post-fire was strongly correlated to the burn season, with fall burns resulting in the highest rates of seedling establishment and spring burns resulting in low rates of seedling establishment.

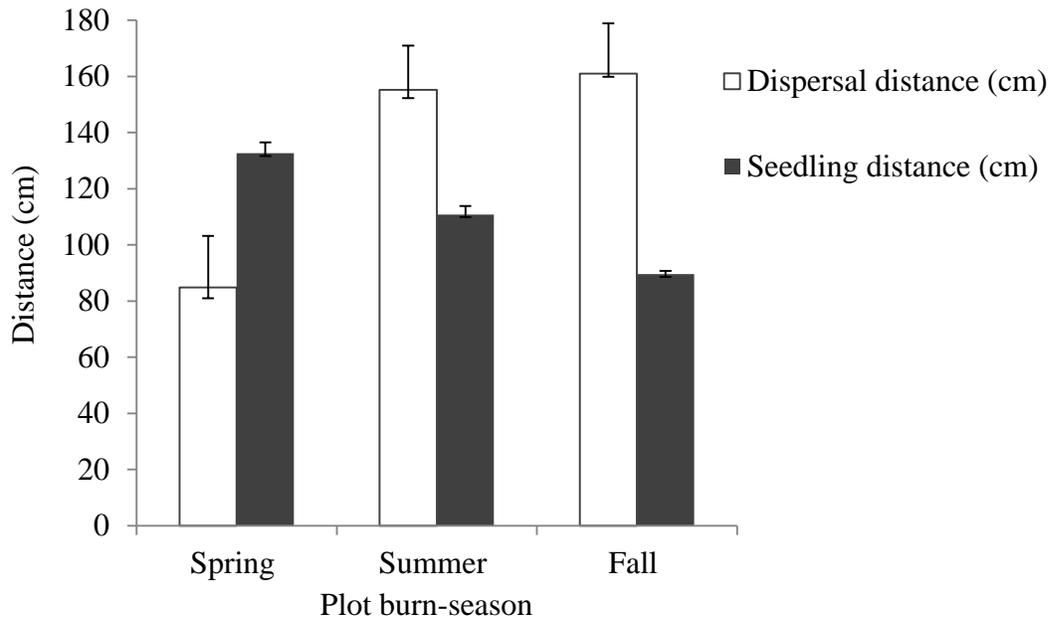


Figure 7. Ant dispersal distance (cm) and distance of seedlings from the center of *C. conradii* burn footprints for plots (n = 9) burned in the spring, summer and fall (3 plots each) at Marconi Wireless Receiving Station, Wellfleet, MA, USA. Bars show means, error bars show standard error, and different letters show statistically significant differences ( $p < 0.05$ ) between burn seasons among dispersal distance and seedling distance.

## APPENDIX A

Ant species observed while conducting field studies in 2011 and 2012 at Marconi Wireless Receiving Station, Wellfleet, MA, USA.

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Ant species	Dispersal to nest	Occurrence
<i>Aphaenogaster treatae</i>	Yes	Common
<i>Camponotus americana</i>	Not observed	Common
<i>Crematogaster linaleolata</i>	Yes	Common
<i>Dolichoderus mariae</i>	Not observed	Uncommon
<i>Dolichoderus plagiatus</i>	Uncertain	Uncommon
<i>Formica dulosa</i>	Yes	Common
<i>Formica exsectoides</i>	Not observed	Common
<i>Formica incerta</i>	Yes	Uncommon
<i>Formica lasiodes</i>	Yes	Common
<i>Formica subsericea</i>	Yes	Common
<i>Lasius neoniger</i>	Yes	Common
<i>Myrmica americana</i>	Yes	Common
<i>Polyergus lucidus</i>	Not observed	Uncommon
<i>Prenolepsis imparis</i>	Uncertain	Uncommon
<i>Tapinoma sessile</i>	Not observed	Uncommon
<i>Temnothorax sp.</i>	Not observed	Common
<i>Temnothorax texanus</i>	Yes (2001 only)	Common

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