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Interactions between the invasive plant, *Centaurea maculosa*, and ant communities in
savannas in western Montana

by

Joseph M. Jensen

B.Sc. Principia College, Elsah, IL, 1994

presented in partial fulfillment of requirements

for the degree of

Masters of Science

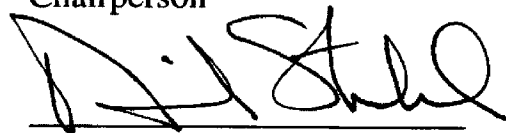
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
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Interactions between the invasive plant, *Centaurea maculosa*, and ant communities in savannas in western Montana

Chairperson: Diana Six 

In addition to reducing the biological diversity of native plant communities, the invasion of exotic plants can also affect the diversity of native fauna. I examined ant communities in western Montana to determine what effect the invasive plant *Centaurea maculosa* (spotted knapweed) may have on their diversity. I then investigated whether elaiosomes of the seeds of *C. maculosa* elicit seed-dispersing by ants, potentially providing a mechanism enhancing invasion of the exotic plant into undisturbed native communities. In the first part of my research, I found total species richness was greater in savannas invaded by *C. maculosa*. In addition, ant genera, *Formica* species groups, functional groups, and reproductive ants were more abundant at invaded sites. These findings suggest that the majority of ant communities were more robust in areas invaded by *C. maculosa*. In the second part of my research, I found that ants dispersed the seeds of *C. maculosa* and ignored the seeds of two native plants, *Balsamorhiza sagittata* (a forb) and *Psuedoroegneria spicata* (a bunchgrass). In addition, I found that ant dispersal of *C. maculosa* seeds was not affected by the presence of native seeds indicating that the response is not diminished in native communities. Combined, these findings demonstrate that *C. maculosa*'s invasion facilitates portions of ant communities and that some ants disperse *C. maculosa* seeds. If the ant species facilitated by the invasion of *C. maculosa* are also the ants dispersing the plant's seeds then a new mutualistic relationship has formed that now contributes to the invasiveness of *C. maculosa*.

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Chapter 1

Literature Review

“In the beginning there were no weeds.”

A. S. Crafts

Invasive plants pose a major threat to native flora and fauna altering native ecosystems and typically reducing the diversity and abundance of native species. In order to understand these interactions better I studied the effects of the invasive weed *C. maculosa* on ant communities in western Montana savannas. In addition, I also investigated the dispersal of *C. maculosa* seeds by native ants to determine if this may be a mechanism enhancing *C. maculosa*'s invasiveness.

Introduction

Since people began traveling among biomes there have been anthropogenic introductions of plants and animals. As Neolithic farmers moved their crops into Europe, they carried invasive Middle Eastern plants with them, and Polynesians introduced rats across the Pacific as they colonized new islands (Crosby 1986). As global traffic has increased, so has the rate of introductions, with humans now surpassing natural vectors as the principal dispersers of vascular plants (Radosевич et al. 1997, Mack et al. 2000, Mack and Lonsdale 2001).

While many plants and animals are unintentionally introduced, often in bilge water and soil ballast on ships, in foreign crop seed, or in various types of imported plant matter, the majority of introduced plants and vertebrates have been intentionally introduced as livestock and agricultural or horticultural plants (Pimentel et al. 2000). Of

the 600 known established exotic plants in New England alone, sixty percent were intentionally introduced, and across the United States, about 5000 horticultural plants have “escaped” into native ecosystems (Pimentel et al. 2000, Mack and Lonsdale 2001).

While exotic plant introductions occur constantly, very few of these plants are able to establish. Many of the exotic plants that establish require disturbance to persist and have little impact on their new habitat. However, the relatively few exotic plants that can invade and dominate intact native systems cause significant economic and ecological damage. These plants are termed invasive (Mack et al. 2000, Pimentel et al. 2000).

Invasive plants incur direct and indirect costs. Direct costs include losses in output due to diminished harvest and the reduction of livestock due to lost forage or habitat (Mack et al. 2000, Pimentel et al. 2000). Invasive plants cause a 12% reduction in agricultural yields in the United States, costing the agricultural industry about \$27 billion dollars annually. Indirect costs, including costs of controlling invasives in both agricultural and natural ecosystems, add an additional cost of approximately \$137 billion dollars annually in the United States (Pimentel et al. 2000).

In addition to their economic costs, invasive species are extremely destructive to the ecosystems they invade. Globally, as many as 80% of endangered species are threatened by non-natives (Pimentel et al. 2000). While invaders often displace natives due to competitive superiority, their most insidious ecological threat is the alteration of fundamental ecological processes (Mack et al. 2000).

Purple loosestrife (*Lythrum salicaria* Linnaeus) exemplifies the extreme impact an exotic plant may have on a native ecosystem. Since its introduction from Europe in the early 1800’s as an ornamental plant, it has invaded 48 states and continues to spread

through wetlands at a rate of 115,000 hectares per year (Edwards et al. 1995). In affected wetlands it clogs waterways, altering natural cycles and reducing water and light availability and has reduced the abundance and biomass of at least 44 plants and animals, including the endangered Bog turtle (*Clemmys muhlenbergii* Schoepff). Purple loosestrife's direct and indirect costs total 44 million dollars annually (Pimentel et al. 2000).

Another invasive plant, European cheatgrass (*Bromus tectorum* Linnaeus), has invaded five million hectares of rangeland in Idaho and Utah alone. In addition to changing native plant community composition, cheatgrass also alters natural fire regimes in invaded areas. Prior to its introduction, prairies burned every 60-100 years, but since the introduction of cheat-grass the prairies now burn every 3-5 years (Pimentel et al. 2000).

Finally, in Florida, the Australian paperbark tree (*Melaleuca quinquenervia* Blake) has replaced cypress, sawgrass, and other community-defining species across large expanses of southern Florida. In addition to displacing native plants, the paper bark tree provides poor habitat for native animals, depletes water tables, and, as with cheatgrass, alters the fire regime in invaded communities (Mack et al. 2000, Pimentel et al. 2000). These fundamental changes in the ecosystem result in dramatically altered post-invasion ecosystems, which exclude native species and tenaciously resist restoration efforts.

Each of these invasive plants outcompetes natives for resources, threatening rare plants and animals and altering natural plant communities. However, in addition, they also alter basic biotic and abiotic processes fundamentally altering the systems they

invade (Pimentel et al. 2000). Such deep changes not only alter floral and faunal communities, but also can change the processes that define an ecosystem.

Centaurea maculosa

One such invader, *Centaurea maculosa* Lamark (spotted knapweed) is a highly invasive deeply tap-rooted short-lived perennial (Jacobs and Sheley 1998). Its seeds germinate in the fall or spring, depending on temperature and moisture availability (Sheley et al. 1998). In the first year of growth, plants develop a simple rosette and maximize root growth, but do not flower (Watson and Renney 1974). In the spring of the second year, the root crown replenishes the rosette and by May flower stalks usually bolt, producing up to six stems and forming 25-30 flower heads per plant (Watson and Renney 1974). Buds form in early June and flowers develop from July to September. Seeds drop from dried flower heads upon maturity in mid to late August (Sheley et al. 1998).

The first introduction of *C. maculosa* was believed to have been in the late 1800's in Victoria, British Columbia (Strong et al. 1979). However, it is likely to have been introduced multiple times since then in contaminated alfalfa seed and ballast (Sheley et al. 1998). Since its introduction, *C. maculosa* has invaded 15 states including every county in Montana, Idaho, Wyoming, and Washington (Jacobs and Sheley 1998). The weed currently infests 2.9 million ha of woodland and grasslands in nine western states, parts of Alaska, and Canada (DiTomasco 2000).

Impacts of *C. maculosa*

Centaurea maculosa aggressively invades native communities, reducing the richness and diversity of native flora and fauna (Watson and Renney 1974, Tyser et al. 1998, DiTomasco 2000, Kedzie-Webb et al. 2001, Yeates and Williams). For example, in

a *Festuca scabrella* (Torrey) and *F. idahoensis* (Elmer)-dominated grassland in Glacier National Park, species richness of native plants was inversely related to *C. maculosa* density (Tyser et al. 1998). Where *C. maculosa* was densest, native species richness was lowest and native plant species richness increased as knapweed stem density decreased towards the perimeter of the *C. maculosa* stands (Tyser et al. 1998). In addition, over a three-year period, density of *C. maculosa* almost doubled while the frequency of seven of the original 38 native plants declined, and none increased. Additionally, five locally rare species were lost, and only one new rare species was found (Tyser et al. 1998).

Invasion by *C. maculosa* has also been linked to substantial reductions in diversity to native flora and fauna (Tyser et al. 1998, DiTomasco 2000, Kedzie-Webb et al. 2001). *C. maculosa* reduces native plant diversity (Ortega and Pearson, in prep) and native grasshopper and myriapod diversity (Six and Ortega, in prep; Six, et al. in prep). In addition, several early studies report that while wild ungulates will eat *C. maculosa* rosettes, mature plants are not grazed (Strong et al. 1979) and in areas which are heavily invaded by knapweed, ungulate community diversity decreased (Jacobs and Sheley 1998, Sheley et al. 1998). Elk use, as estimated by pellet groups per hectare, was 98% lower on range dominated by *C. maculosa* compared to bunchgrass dominated grasslands (Sheley et al. 1998).

In contrast, another study found that on grasslands in Idaho, elk and both whitetail and mule deer readily browsed on *C. maculosa* and that *C. maculosa* provided substantial nutritional value to the cervids (Wright and Kelsey 1997). However, *C. maculosa* invasion may favor whitetail deer over elk and mule deer, because whitetail deer consumed *C. maculosa* more readily than they did the native grasses and sedges (Wright

and Kelsey 1997). If their greater willingness to consume *C. maculosa* translates to greater fitness when the weed is prevalent, then *C. maculosa* invasion may contribute to the encroachment of whitetail deer on what has been historically mule deer habitat.

In addition to its effects on biotic factors, *C. maculosa* also alters fundamental abiotic factors. *C. maculosa*-invaded areas have been linked to a 56% increase in erosion and 192% increase in sediment yield compared to ecosystems dominated by native grasses (Kedzie-Webb et al. 2001). It has also been suggested, although not demonstrated, that *C. maculosa* may alter water tables (Zimdahl 1999). Such systematic changes disrupt native flora and fauna and alter communities so fundamentally that restoration to pre-invasion conditions becomes unlikely.

Effects of Disturbance on Invertebrate Communities

Invertebrate communities are fundamental components of ecosystems. They are extremely sensitive to changes in their habitat, often rapidly responding to ecological changes (Majer and Delabie 1999, Panzer and Schwartz 2000, Haddad et al. 2001, Kruess and Tschardtke 2002). Many studies document alterations in invertebrate communities due to perturbations in plant communities. Often, insect communities become more complex and abundant in response to increased plant richness and abundance or plant biomass (Perfecto and Vandermeer 1996, Haddad et al. 2001). Similarly, reductions in plant diversity typically result in reductions in invertebrate richness and abundance (Kruess and Tschardtke 2002). Reductions in native invertebrate communities often coincide with the replacement of native plant communities with invasive plants. Given invertebrate's integral nature in most ecosystems, such sensitivity to bottom up effects is

not surprising. However, invertebrate communities do not always respond to changes in plant communities.

One study assaying the effects of fire management on insect communities found that leaf hopper and butterfly assemblages did not differ significantly between managed areas and forests where fire was entirely excluded (Panzer and Schwartz 2000). These results are initially surprising, because it seems that when a major abiotic variable such as fire frequency is altered, insect communities would reflect the change as well. However, some insects are well adapted to disturbance or more mobile and therefore do not respond to all perturbations.

While changes in ecosystems may not be reflected in entire insect communities, the changes can sometimes be detected when looking at particular taxonomic and functional groups within the community. Occasionally the entire community will not respond to an environmental change, but subgroups, may be affected, leading to changes in the abundance and diversity of particular functional groups or genera (Simila et al. 2002).

Ants: Formicidae

Ants are an invertebrate group likely to be highly sensitive to changes in native plant communities caused by invasion of *C. maculosa*. While many ant species are generalists with respect to behavior and feeding, others are highly specialized. Globally, behavioral specialists include, but are not limited to, social parasites, slave makers, plant symbionts, and army ants, while feeding specialists include granivores, fungus growers, carnivores, and sap feeders, to name a few. Such functional variety coupled with their

high degree of interaction with their environment make ant communities very sensitive to many environmental changes (Folgarait 1998, Agosti et al. 2000).

Ant communities are highly sensitive to both abiotic (Majer 1984, Andersen 1993, Bisevac and Majer 1999) and biotic (Perfecto and Vandermeer 1996, Suarez et al. 1998, Majer and Delabie 1999, Agosti et al. 2000, Andersen 2000) environmental changes. Ant communities have demonstrated sensitivity to industrial by-products (Andersen 1993), perturbations in litter and sunlight (Perfecto and Vandermeer 1996), anthropomorphic habitat fragmentation (Suarez et al. 1998), deforestation (Majer and Delabie 1999), and mining (Majer 1984, Bisevac and Majer 1999). The breadth of environmental changes affecting ant communities is not surprising given how integral they are in most ecosystems which they inhabit (Holldobler and Wilson 1990, Andersen 2000). While no work has been done assaying the effects of invasive plants on ant communities, their sensitivity to environmental changes makes it highly likely that the changes to native communities caused by *C. maculosa* will also alter ant community diversity (Tyser et al. 1998, DiTomasco 2000, Kedzie-Webb et al. 2001).

Proposed Mechanisms for *C. maculosa*'s Invasiveness

The mechanisms by which *C. maculosa* enters and dominates native communities are not well understood. Its invasiveness is likely linked to a number of factors. These may include the inundation of native seed banks with long-lived seeds (Davis et al. 1993), the production of allelopathic chemicals (Bais et al. 2003b), escape from biotic constraints such as predators (Mack et al. 2000), and the exploitation of underutilized niches in invaded areas (Jacobs and Sheley 1999, Mack et al. 2000).

Centaurea maculosa plants produce thousands of seeds, inundating native seed banks (Sheley et al. 1998). In addition, *C. maculosa* seeds are long lived. In a lab experiment, 50% of seeds tested were viable after five years and 25% were viable after eight years. In a field experiment in a moderately invaded area, only five percent of seeds were viable after seven years; however, this still equated to approximately 400,000 viable seeds per hectare (Davis et al. 1993). The inundation of the native seed bank with long-lived seeds increases the ability of the plant to exploit new sites, as they become available.

Allelopathy has been suggested as a mechanism contributing to *C. maculosa*'s invasiveness (Locken and Kelsey 1987, Callaway and Aschehaug 2000, Ridenour and Callaway 2001, Bais et al. 2003a, Bais et al. 2003b). Controlled greenhouse experiments indicated that *Centaurea* species release organic compounds that reduce the growth of native plants, increasing *Centaurea*'s competitiveness. When *C. maculosa* and its close relative *C. diffusa* (Lamarck) were grown in pots with plants native to Palouse prairies, the native plants grew smaller than when they were grown alone or with other natives. But when activated carbon was included in the soil (to absorb organic compounds such as potentially allelopathic compounds), the deleterious effects of both *Centaurea* species were largely ameliorated (Callaway and Aschehaug 2000, Ridenour and Callaway 2001).

Early research in this area focused on the potential allelopathic effects of the compound cnicin which has been isolated from *C. maculosa* roots, leaves, and shoots. However, cnicin, while toxic in high doses, was not found near *C. maculosa* at levels harmful to native plants (Locken and Kelsey 1987). Recently the search for allelopathic chemicals has shifted to the compound (-)-catechin (Bais et al. 2003a, Bais et al. 2003b,

Hierro and Callaway 2003). Current studies have isolated (\pm)-catechin from root exudates of *C. maculosa*. While (+)-catechin has been identified as an anti-microbial agent, (-)-catechin has been demonstrated to be toxic to other plants both in lab and field experiments, making it a likely allelopathic compound (Bais et al. 2003a, Hierro and Callaway 2003).

Another widely hypothesized explanation for invasive dominance of natives is the loss of historic predators, parasites, and/or pathogens upon transportation of the invader (Rejmanek 1995, Mack et al. 2000). It has been widely suggested that many invasive plants are able to thrive because organisms that have evolved mechanisms for thwarting the plant's defenses are not present in the newly invaded ecosystems. It is this hypothesis which suggests that importing the invaders' natural predators, typically insects, can reduce the fitness of invasive plants, but such controls have produced only limited success (Mack et al. 2000).

While many hypotheses have been proposed explaining the invasiveness of *C. maculosa*, one possible advantage which has not been investigated is myrmecochory, the dispersal of seeds by ants responding to elaiosomes.

Myrmecochory and Elaiosomes

Centaurea maculosa seeds develop elaiosomes, nodes that contain proteins, lipids, carbohydrates, and/or other nutrients (Beattie 1985, Brew et al. 1989). These elaiosomes promote myrmecochory, the dispersal of seeds by ants specifically in response to the elaiosomes (Pemberton and Delilah 1990). Some ants collect and disperse diaspores (seeds with elaiosomes), removing the elaiosome for consumption before discarding the seed (Turnbull and Culver 1983, Brew et al. 1989, Pemberton and Delilah

1990, Hughes et al. 1994). Ants select for and disperse diaspores at a much greater rate than they do seeds alone. When presented with a choice of diaspores, elaiosomes, or seeds, ants removed the diaspores and elaiosomes within eight hours, while 80-89% of the elaiosome-free seeds remained even after seven days (Brew et al. 1989).

Plants producing elaiosomes vary considerably, as do the components of the elaiosomes themselves. In one study, thirteen plant families in groups as phylogenetically distant as monocots and dicots were found to produce elaiosome-bearing seeds (Pemberton and Delilah 1990). The nutritional composition of elaiosomes is also highly variable. Of 41 plants producing elaiosome-bearing seeds, 38 contained lipids, and 31 sugars, and 16 included protein. Many of the elaiosomes also contained the vitamins B₁ and C (Beattie 1985).

Several studies have found two fatty acids, ricinoleic acid and oleic acid in elaiosomes (Marshall et al. 1979, Beattie 1985, Brew et al. 1989). Ricinoleic acid is an important nutrient for ant larval development and this initially led researchers to believe this acid was the main ant attractant. However, another study demonstrated that some ants are more attracted to oleic acid, which acts as a necrophoric pheromone in the nest, eliciting a corpse-carrying response (Wilson et al. 1958, Brew et al. 1989, Gordon 1999). When some ants encounter objects covered in oleic acid they remove the object to their midden (refuse pile) located outside the nest. The behavioral response of ants to this compound is so strong that in one study, living ants treated with oleic acid were carried "live and kicking" by their nest mates to the midden (Wilson et al. 1958).

The diglyceride 1:2-diolein is also found in some elaiosomes and when 1:2-diolein was placed on bits of paper an ant in the genus *Aphaenogaster* removed 1:2-

diolein more often than the other lipid components, including ricinoleic and oleic acid (Marshall et al. 1979). As diglycerides are important components in the hemolymph of some insects, ants responding to diglyceride 1:2-diolein likely are simply reacting to the diglyceride as they would to insect prey (Beattie 1985).

Benefits of Myrmecochory to Plants

Plants with elaiosome-bearing seeds have evolved a variety of mechanisms for eliciting myrmecochory, depending on the behavior of local ants. While it is clear that ants removing elaiosome-bearing seeds receive a nutritional reward, the benefits of myrmecochory to plants are not as clear. Four benefits have been widely suggested.

First, seeds removed by ants may be less likely to be preyed upon by rodents and other granivorous predators (Rice 1986, Andersen 1988, Pemberton and Delilah 1990). Seeds represent a substantial nutritional resource exploited by many animals, and many plants lose a large percentage of their seeds to granivores. One study found that seeds removed by ants were less frequently consumed by rodents (Andersen 1988). However, another experiment demonstrated that some rodents target the nutritional elaiosome, while incidentally or opportunistically eating the seeds. Therefore, ant dispersal of seeds alone did not reduce rodent predation, but removal of the elaiosome did (Boyd 2001). In addition, timing of seed release in combination with myrmecochory may increase benefit to the plant. For example, plants that have evolved under nocturnal rodent predation typically release their seeds early in the day, making them available to diurnal ants that then disperse the seeds and remove the elaiosomes before the nocturnal rodents begin to forage (Turnbull and Culver 1983).

Not all ants are myrmecochorous, and in some habitats where myrmecochory occurs the most frequently, ants are the chief granivores (Andersen 1988). In one such habitat in Western Australia, insectivorous ants removed diaspores before granivorous ants and generalists consumed the seeds (Hughes et al. 1994). In the examples of both the rodents and the granivorous ants, myrmecochory reduces seed consumption.

In Arizona, the harvester ant *Pogonomyrmex barbatus* (F. Smith) is a granivore, and local plants may have evolved elaiosomes in response to predation by the ant . Foragers encountering oleic acid covered paper removed them to the nest just as they would a seed or scavenged food item. However, *P. barbatus* responsible for cleaning the nest removed the paper pieces to the nests midden (refuse pile), suggesting that collected seeds are not consumed, but rather dispersed to middens (Gordon 1999).

The second proposed benefit is that elaiosome-bearing seeds are removed to nutrient rich sites. Many ants, whether responding to oleic acid or disposing of seeds after consuming elaiosomes, remove elaiosome-bearing seeds to the midden. (Davidson and Morton 1981, Beattie and Culver 1983, Andersen 1988, Pemberton and Delilah 1990). Middens contain frass, ant corpses, and other nest refuse and are often rich in nutrients which may enhance seed germination. While, investigations into *Formica canadensis* (Santschi) nest sites demonstrated no significant differences in the soil near middens and outlying soils, middens of *Myrmica discontinua* (Weber) had soils that were richer in oxygen, nitrogen, phosphorous, and had reduced levels of cadmium (a toxin) (Beattie and Culver 1983). In addition, other studies have demonstrated that seeds dispersed by ants produce seedlings which emerged from the soil earlier (Rice 1986). They also had greater initial survival, survived longer, and grew larger when growing from seeds dispersed to

ant middens versus non-midden sites (Davidson and Morton 1981, Beattie and Culver 1983).

The third proposed benefit of myrmecochory is the avoidance of parental competition (Rice 1986, Andersen 1988, Pemberton and Delilah 1990). Many plants, *C. maculosa* among them, have limited dispersal ranges. Short range dispersal not only leaves new plants vulnerable to parasites and predators associated with their parent plants, but the young plants are forced to compete with the parent plant for resources. As free sites near the parent plant are often limited, dispersing away from the parent plant may be beneficial to the seedling (Green 1983).

Finally, the fourth proposed benefit is that myrmecochory may increase the dispersal distances of some plants. Myrmecochory was demonstrated in Australia to provide a mean dispersal of 2.1 meters (Andersen 1988). In addition, myrmecochory occasionally results in long distance seed dispersal (one ant was observed dispersing a seed 77 m) (Andersen 1988). Myrmecochory likely benefits plants like *C. maculosa*, which have relatively short dispersal distances (about 1m) by increasing distance of seed dispersal.

My Research

The goal of this research was to investigate how invasion by *C. maculosa* affects ant communities, and whether ants may play a role in dispersing *C. maculosa* seeds thus enhancing its invasiveness. Ant communities in ponderosa pine savannas in western Montana that have been invaded by *C. maculosa* were compared to those which have experienced only minor, or no, invasion. Ant communities were compared at a coarse

scale (among sites) and a fine scale (within sites) to determine how ant communities respond invasion by *C. maculosa*.

Hypothesis One:

The invasion of *C. maculosa* alters native fauna by altering both native plant communities and local abiotic factors. I predict that ant diversity will be altered by the invasion of *C. maculosa*.

Objective One: Investigate effects of invasion by *C. maculosa* on ant communities.

H₀: Ant community diversity is unaffected by invasion by *C. maculosa*.

H₁: Ant community diversity is reduced by invasion by *C. maculosa*.

H₂: Ant community diversity is increased by invasion by *C. maculosa*.

Hypothesis Two:

Elaiosomes elicit myrmecochory. Because *C. maculosa* seeds possess elaiosomes, I predict that ants will disperse *C. maculosa* seeds. Furthermore, given that most plants native to Palouse prairies do not possess elaiosomes, I predict that ants will preferentially select and disperse *C. maculosa* seeds and largely ignore the seeds of natives.

Objective Two: Determine if ants preferentially disperse *C. maculosa* seeds over seeds of dominant natives.

H₀: Ants will ignore *C. maculosa* and the seeds of native plants.

H₁: Ants will remove equal amounts of *C. maculosa* and native plant seeds.

H₂: Ants will remove more native plant seeds than *C. maculosa* seeds.

H₃: Ants will remove more *C. maculosa* seeds than native plant seeds.

Objective Three: Determine if ants remove different amounts of *C. maculosa* and native seeds when seeds are presented together, verses when seeds are presented independently.

H₀: Seed removal will not vary between choice and no choice offerings.

H₁: Ants will remove more *C. maculosa* when seeds are presented together.

H₂: Ants will remove more native plant seeds when seeds are presented together.

H₃: Ants will remove more *C. maculosa* when seeds are presented alone.

H₂: Ants will remove more native plant seeds when seeds are presented alone.

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Chapter 2

Response of ant communities to *Centaurea maculosa* (spotted knapweed) invasion in Rocky Mountain savannas in western Montana

Abstract

In addition to reducing the biological diversity of native plant communities, the invasion of exotic plants can affect the diversity of native fauna. I examined ant communities at eight sites in Rocky Mountain savannas in western Montana to determine how the invasive plant *Centaurea maculosa*, spotted knapweed, affects ant communities. Four sites in the study were dominated by *C. maculosa* (invaded) while four sites were uninvaded or contained only trace amounts of *C. maculosa* (native). Ant communities were sampled with pitfall traps set for a two-week period in May and in September in 1999 and 2000. Estimates of percent cover were made at each pitfall trap for *C. maculosa*, other forbs, grasses, exposed rock, woody debris, and litter. Aspect and slope were also measured. Species richness and the occurrence of ant species, *Formica* species groups, genera, functional groups, and reproductive ants were compared between native and invaded sites. The ant communities in native and invaded sites were also compared using non-metric multidimensional scaling (NMS). Each ordinal axis from NMS was then tested for correlation with percent cover estimates, slope, and aspect to determine if these variables influenced the composition of ant communities. I found that species richness was higher in savannas invaded by *C. maculosa* than in native sites. In addition, reproductive ants and most ant genera, *Formica* species groups, and functional groups were more prevalent at invaded sites. Native and invaded sites segregated in the NMS ordination where *C. maculosa* was highly correlated with all three axes produced. These results demonstrate that ant community diversity and prevalence increases in areas invaded by *C. maculosa* and that *C. maculosa* influences the composition of ant communities.

Introduction

Invasive plants alter native community composition and often reduce the abundance and diversity of native flora and fauna. Typically, invasive plants reduce native plant species diversity, in part by eliminating rare species. In addition, as many as 80% of endangered species globally are threatened by invasive plants (Mack et al. 2000, Pimentel et al. 2000). While many exotic plants have been intentionally released, more often they are accidentally introduced in bilge water or in imported plant matter

(Pimentel et al. 2000, Mack and Lonsdale 2001). Once established, invasive plants spread rapidly through native systems, tenaciously resisting restoration efforts.

Since its initial introduction from Eurasia in the late 1800s, most likely in contaminated alfalfa seed, the invasive plant *Centaurea maculosa* Lamark (spotted knapweed), has infested over 2.9 million ha in the western United States and Canada (Sheley et al. 1998, DiTomasco 2000). Once established, *C. maculosa* dominates native ecosystems, reducing the diversity and abundance of native plants (Watson and Renney 1974, Jacobs and Sheley 1998, Schultz and Crone 1998, Tyser et al. 1998). These reductions in native plant communities often cause reductions of native animal diversity as well (Strong et al. 1979, Wright and Kelsey 1997, Sheley et al. 1998).

Invertebrate communities are particularly sensitive to changes in plant communities (Majer and Delabie 1999, Panzer and Schwartz 2000, Haddad et al. 2001, Kruess and Tscharntke 2002). Typically, insect communities become more diverse in response to increases in plant richness and abundance or plant biomass (Perfecto and Vandermeer 1996, Haddad et al. 2001). Conversely, reductions in plant community diversity, such as often occurs after invasion by exotic plants, usually reduce invertebrate richness and abundance (Kruess and Tscharntke 2002).

Ant communities have been shown to respond to environmental changes (Majer 1984, Perfecto and Vandermeer 1996, Suarez et al. 1998, Bisevac and Majer 1999, Majer and Delabie 1999, Agosti et al. 2000, Andersen 2000). Ant communities are sensitive to many types of environmental perturbations including changes in litter and sunlight (Perfecto and Vandermeer 1996), habitat fragmentation (Suarez et al. 1998), deforestation (Majer and Delabie 1999), and mining (Majer 1984, Bisevac and Majer

1999). However, to my knowledge no work has been done investigating the effects of invasive plants on ant communities. The sensitivity of ants to a broad array of environmental change suggests that invasion by *C. maculosa* will also alter native ant communities.

This study had two objectives. First, little is known about ants occurring in savannas in western Montana. Therefore, I characterized ant communities to provide baseline information for future research. Second, I determined how ant communities in these savannas respond to the invasion by *C. maculosa*.

Materials and Methods

Eight study sites were established in Rocky Mountain savannas in the Lolo National Forest in western Montana. Sites were located on southwest facing slopes and ranged in elevation between 1300 to 1700 m. Four sites were extensively invaded by *C. maculosa* (hereafter referred to as invaded sites). The remaining four sites were uninvaded or had only trace amounts of *C. maculosa* (hereafter referred to as native sites).

Each site was located in savannas surrounded by a denser matrix of Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forest. Study sites were dominated by native bunchgrasses, primarily bluebunch wheatgrass (*Psuedoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*). The dominant native forb at the sites was arrowleaf balsamroot (*Balsamorhiza sagittata*) (See Ortega and Pearson (2005) for a detailed account of plant communities at the sites).

Four transects were established at each site perpendicular to the slope and 50 m apart. Ants were collected in pitfall traps set for a two-week period in May and in

September in 1999 and 2000. Traps were placed systematically every 20 m along each transect for a total of 13 pitfall traps per transect and 52 traps per site. Pitfall traps were fashioned from plastic two-liter bottle with the neck removed and inverted to serve as a funnel. A cup containing a 1% formalin solution was placed below the funnel to collect samples. In addition, ocular estimates of percent cover in a 5 m radius plot around each pitfall trap were made for *C. maculosa*, *B. sagittata*, shrubs, bunchgrasses, *Bromus* spp. (an exotic), 'non-*C. maculosa* or *B. sagittata* forb species', exposed rock, and litter. Slope and aspect were also measured at each pitfall trap.

Ants were identified to species using Creighton (1950) and Wheeler (1986). In addition, because *Formica* is a highly speciose and abundant genus in temperate regions (Wheeler and Wheeler 1986), it was further divided into species groups (analogous to subgenera).

Ant species were also categorized into functional groups according to Andersen (1997). Functional groups combine species based on ecological criteria rather than phylogenetic similarity. The use of functional groups in community analyses allowed me to determine how ecological changes associated with the invasion of *C. maculosa* altered the ant communities and their use of savannas.

In addition, the number of winged queens and males (hereafter referred to as reproductives) captured was recorded. The presence of reproductives in a trap indicates that a nearby ant colony has entered a reproductive cycle. Reproductive cycles are only initiated when resources support an increased outlay of energy and are indicative of a healthy, vigorous colony.

Data analyses

I constructed species accumulation curves by trapping period for native and invaded sites to determine if the complete ant community was sampled. Curves were produced using Species Diversity and Richness version 2.65 (Henderson and Seaby 2001).

Richness and occurrence analyses

I used a mixed linear model (PROC MIXED, SAS 1999) to compare total species richness between pitfall traps at invaded and native sites. In addition, I used a mixed logistic regression model (GLIM MIXED, SAS 1999) to determine if occurrence (presence/absence) in pitfall traps varied between invaded and native sites for species, *Formica* species groups, genera, functional group, and reproductive ants (hereafter collectively referred to as groups of interest). Only those groups of interest captured at more than five percent of all pitfall traps were included in mixed logistic regression analysis. Species collected in less than five percent of pitfalls were combined and tested as a single group, Rare Species. For this analysis, the May and September sampling periods were combined by year, and for both models, year was treated as a repeated measure, and site, and year by site, were treated as fixed effects.

Community analyses

I also analyzed ant species occurrence using NMS (non-metric multidimensional scaling, Mc Cune and Mefford 1999). All species collected were included in NMS analysis. To reduce the noise associated by large numbers of zeros, occurrence data were transformed using the Beals Smoothing method (Beals 1984). Ordinal axes were tested for correlation with percent cover estimates, slope, and aspect using Spearman Rank Order Correlation using SigmaStat version 2.03 (SigmaStat 1995).

In NMS analysis, I used Sørensen distance with a random starting number and 40 runs with real data. I juxtaposed real data with random data sets in 20 runs using the Monte Carlo test, and I chose the highest dimensionality with less than five percent of randomized runs having lower or equal stress to actual data and a final stress of less than 20. I deemed the solution stable when it reached an instability of < 0.0005 or 50 iterations.

Results

A total of 33 species of ants were captured across all sites (Table 1). Figure 1 presents species accumulation curves for ants captured in native and invaded sites by year. For each site type (native and invaded) there were 208 pitfall traps per trapping period per year (52 pitfall traps x 4 sites). The curves indicated that the trapping intensity was sufficient to sample ant species richness at the sites.

Richness and occurrence analyses

Species: Total species richness was significantly greater at invaded sites (DF = 1, 408; $F = 9.63$; $P < 0.01$) [Least Square Means (SE): Native sites = 3.81(0.09); Invaded sites = 4.19 (0.09)]. There was a site and year effect but no effect of *C. maculosa* by year. Of the 33 ant species sampled, 11 were collected in five percent or more of all pitfall traps. Two species, *F. haemorrhoidalis* and *My. emeryana* were omitted from species level analysis due to model instability that resulted from their extremely low occurrence or absence from some sites. Therefore, only nine species were included in the final analyses. The 23 species that occurred in less than five percent of pitfall traps were included in the analysis as the group 'Rare Species' (Table 1).

Two species were less prevalent in invaded sites than in native sites (Table 2). *Camponotus vicinus* occurred 32% less often and *F. neogagates* 22% less often in pitfall traps at sites invaded by *C. maculosa*. In contrast, *F. argentea* was found 10% more often and *La. neoniger* 50% more often in invaded sites (Table 2). Ants in the Rare Species group also occurred 50% more often in invaded sites. The remaining six species did not differ in occurrence between invaded and native sites (Table 2).

Formica species groups: Three of the four *Formica* species groups sampled were found in more than five percent of pitfall traps and included in the mixed logistic regression model. Both the *Formica fusca* and *rufa* species groups were more prevalent at invaded sites (Table 2). Ants in the *fusca* group occurred 10% more often and ants in the *rufa* group 200% more often in pitfall traps at sites invaded by *C. maculosa* than at native sites. Alternately, ants in the *neogagates* group occurred 20% less often in pitfall traps at invaded sites (Table 2).

Genera: Six genera were collected in five percent or more of pitfall traps and included in analyses. However, the genus *Aphaenogaster* was only represented by one species, *A. uinta* (Table 2).

Lasius occurred 88% more often and *Myrmica* 275% more often in pitfall traps at sites invaded by *C. maculosa* than in native sites (Table 2). However, *Camponotus* were 31% less common in pitfall traps at invaded sites. Finally, occurrence of *Aphaenogaster*, *Formica* and *Leptothorax* did not differ between native and invaded sites (Table 2).

Functional Groups: Pitfall traps captured ants in the functional groups Subordinate Camponotini, Cold Climate Specialists, Cryptic Species, Generalized Myrmicinae, Opportunists, and Specialist Predators (Andersen 1997). Subordinate

Camponotini are large behaviorally submissive ants in *Camponotus*. Cold Climate Specialists are typically found in cooler, temperate zones or at higher elevations where they are typically behaviorally dominant to other ants. Cryptic Species predominantly live and forage underground and have few interactions with other ants. Generalized Myrmicinae are very common and found in most habitats, though typically they are less common in forests. Opportunists are unspecialized ants often found in disturbed areas or in areas with little ant diversity such as temperate regions. Finally, Specialist Predators have highly specialized diets and several enslave other ants.

Members of the functional groups Subordinate Camponotini, Cold Climate Specialists, and Opportunists, were collected in five percent or more of the pitfall traps. Cold Climate Specialists were 43% more prevalent in pitfall traps at sites invaded by *C. maculosa*. Opportunists, however, were only 3% more prevalent in pitfall traps at invaded sites. Conversely, Subordinate Camponotini occurred 31% less often in pitfall traps at invaded (Table 2).

Reproductives: Both winged queens and males were found in more than five percent of pitfall traps. Winged queens were 38% more prevalent and males 167% more prevalent in pitfall traps at sites invaded by *C. maculosa* than in native sites (Table 2).

Community Analysis

NMS ordination yielded three axes with a stress of 19.22 and instability of 0.008 ($p = 0.045$) demonstrating that the ordination accurately describes the ant community. However, the relatively high stress indicates that inferences made from this ordination should be conservative. Native sites separated from invaded sites on each axis (Figure 2), indicating that occurrence of ant species differed between invaded and native sites. All

three axes were highly correlated ($p < 0.01$) with percent cover estimates for *C. maculosa* to a 5 m radius (Table 3), demonstrating that in addition to large scale site differences between invaded and native sites, fine scale changes in *C. maculosa* cover also affect ant communities.

Percent cover estimates for the dominant forb, *B. sagittata*, did not correlate with any axis. However, the percent cover estimate for ‘non-*C. maculosa* or *B. sagittata* forbs’ was highly correlated with all three axes ($p < 0.01$). Percent cover estimates for exposed rock and woody debris were also highly correlated with all three axes ($p < 0.01$). In addition, the percent cover estimate of shrubs and aspect correlated with axis one and three, and axis two and three, respectively, while slope correlated only with axis two. Finally, percent cover estimates for litter and *Bromus* spp. did not correlate with any of the axes (Table 3).

Discussion

Invasive plants typically reduce the species diversity of native communities (DiTomasco 2000, Kedzie-Webb et al. 2001). Therefore, I expected that ant communities at sites invaded by *C. maculosa* would exhibit lower diversity than ant communities at native sites. However, ant species richness was higher at invaded sites, and most ant genera, *Formica* species groups, and functional groups were more prevalent at invaded sites. In addition, rare species and reproductives were captured more often in savannas invaded by *C. maculosa* (Table 2). These findings demonstrate that the ant communities found at invaded sites were more diverse, abundant, and productive than those found at sites dominated by native plants.

While the invasion of *C. maculosa* increased the prevalence of most groups within ant communities, not all groups were more prevalent at invaded sites. Ants in the functional group Subordinate Camponotini and ants in the *Formica* species group *neogagates* were both less prevalent at sites dominated *C. maculosa*. The ant species in both Subordinate Camponotini and *neogagates* are behaviorally submissive. Therefore, it is possible that the increased occurrence of behaviorally dominant ants at invaded sites may be responsible for the reduced prevalence of Subordinate Camponotini and *neogagates* at these sites.

Behavioral dominance is a common phenomenon in ant communities. Behaviorally dominant ant species subordinate other ant species by guarding food resources, preying on or enslaving other species, and preventing other ants from leaving their nest to forage. Such behaviors can alter foraging patterns and limit the foraging success of submissive ants, potentially reducing the colony size and productivity of the behaviorally submissive species.

Subordinate Camponotini are typically behaviorally submissive to ant species in the Dominant Dolchoderinae functional group. However, while no Dominant Dolchoderinae were captured in this study, in the absence of Dominant Dolchoderinae, Cold Climate Specialists are often behaviorally dominant (Andersen 1997). Cold Climate Specialists were more prevalent at sites invaded by *C. maculosa*, which may have led to decreases in Subordinate Camponotini.

The *neogagates* species group also occurred more frequently at native sites. Ants in the *neogagates* species group may aggressively defend their nests, but typically they are timid ants, and often they are preyed upon or enslaved by other *Formica* species

(specifically from the *sanguinea* group) and ants in the genus *Polyergus* (Creighton 1950, Wheeler and Wheeler 1986). However, *F. curiosa* was the only *sanguinea* species found in this study and neither it nor *P. breviceps*, the only member of *Polyergus* sampled, were common. However, in the absence of high numbers of their usual predators, other ant species common in temperate regions, such as Cold Climate Specialists, may prey upon *neogagates*. If these predators are more common in invaded savannas, then the prevalence of the *neogagates* species group would likely decline in savannas invaded by *C. maculosa*.

Of particular note is the 200% increase in the prevalence of ants in the *rufa* species group in savannas invaded by *C. maculosa*. Ants in the *rufa* species group are Cold Climate Specialists. Species in the *rufa* group typically are extremely aggressive and, like other Cold Climate Specialists, they are behaviorally dominant in temperate regions (Andersen 1997). The greatly increased prevalence of species in the *rufa* group at invaded sites may have a major impact on behaviorally submissive ants.

However, regardless of the cause, the prevalence of Subordinate Camponotini and the *neogagates* group declined at invaded sites, while species richness and the occurrence of all other groups of interest increased. This shift in ant communities at invaded sites suggests that ant communities were fundamentally altered by the invasion of *C. maculosa*. Overall, ant communities in invaded savannas were more abundant, more diverse, and more productive than those found in savannas dominated by native plants.

These differences in ant communities between invaded and native savannas were strongly linked to invasion by *C. maculosa*. In NMS plots, native and invaded sites segregated from each other (Figure 2) and percent cover of *C. maculosa* strongly

influenced all three of the ordinal axes (Table 3). These results indicate that changes associated with the invasion of *C. maculosa* played a key role influencing ant communities. However, 'non-*C. maculosa* or *B. sagittata* forbs', exposed rock, and woody debris also influenced the ordinal axes indicating that they also may affect ant communities.

Environmental changes caused by the invasion of *C. maculosa* appear to be facilitating some ant groups in these savanna communities. The mechanism underlying this facilitation is unknown, but may include alterations to the environment making invaded sites more favorable to ants. The response of ant communities to 'non-*C. maculosa* or *B. sagittata* forbs', exposed rock, and woody debris demonstrates their sensitivity to environmental change. If the invasion of *C. maculosa* into Rocky Mountain savannas has altered abiotic or biotic factors, making savannas more favorable to ant communities, then these changes are likely to facilitate ant communities.

Another possible explanation for the increased abundance, diversity, and productivity of ant communities at invaded sites is the presence of elaiosomes on seeds of *C. maculosa*. Elaiosomes are nutrient rich nodes that elicit myrmecochory, the dispersal of seeds by ants responding specifically to the nutritional reward. Myrmecochorous ants collect elaiosome-bearing seeds, later removing elaiosomes and discarding the seed.

Myrmecochory is a mutualistic relationship between ants and plants. Ants gain a nutritional compensation, and in return myrmecochorous seeds may be dispersed further, be more likely to germinate, suffer less predation, and avoid competition with parent plants (Brew et al. 1989, Hughes et al. 1994). Because few plants native to Rocky Mountain savannas have been found to produce elaiosome-bearing seeds, the elaiosomes

on *C. maculosa* seeds may provide an important new food subsidy to ant communities in savannas invaded by *C. maculosa*. Such a subsidy could enable colonies to grow larger and reproduce more often and with increased fecundity.

Myrmecochory is a widespread phenomenon, common in many ecosystems. Studies conducted in other ecosystems have demonstrated myrmecochory by many of the ant functional groups found in western Montana including Cold Climate Specialists (Pemberton 1988, Hughes and Westoby 1990), Opportunists (Andersen 1988, Hughes and Westoby 1990, Hughes and Westoby 1992), and Subordinate Camponotini (Andersen 1988). These studies suggest that ants in many functional groups found in savannas in western Montana may also be myrmecochorous. In addition, my study testing for myrmecochory of *C. maculosa* seeds in western Montana savannas found that three native ant species *La. alienus*, *My. emeryana*, and *F. lasioides* all disperse *C. maculosa* seeds.

The elaiosomes of *C. maculosa* may subsidize myrmecochorous ant species in invaded savannas, supporting larger populations among ant species that consume the nutritious reward. For example, *La. alienus* and species in *Myrmica* both disperse seeds of *C. maculosa* (chapter 3, this thesis) and both were more prevalent in this study at invaded sites (*My. emeryana* was also found in this study but as previously stated, was not tested due to its instability in the model).

Findings for *F. lasioides*, the third ant species observed dispersing *C. maculosa* seeds, were not conclusive so it is difficult to speculate whether the elaiosomes produced by *C. maculosa* subsidize *F. lasioides*. However, the two other native ant species found dispersing *C. maculosa* seeds were considerably more prevalent in invaded savannas than

in those dominated by native plants. This suggests that elaiosomes may subsidize some myrmecochorous species, supporting greater population levels at sites where the nutritional reward is available.

The interaction between the invasive plant, *C. maculosa*, and native myrmecochorous ants may form a new mutualism that facilitates the invasion of *C. maculosa* into undisturbed habitats. Myrmecochory may increase the dispersal distance of *C. maculosa* seeds, augmenting the rate of invasion into undisturbed habitats, while diminishing seed predation, and increasing germination rates. At the same time, nutritional subsidies to ants may support higher populations of myrmecochorous ants, further facilitating the dispersal of *C. maculosa* seeds.

In this study, I found that ant communities in areas invaded by *C. maculosa* were more abundant, more diverse, and produced more reproductives than ant communities in savannas dominated by native plants. These findings strongly suggest that the invasion of *C. maculosa* facilitates ant communities. Furthermore, myrmecochory may bolster the invasibility of *C. maculosa*, augmenting the rate of *C. maculosa*'s invasion into native communities by increasing the dispersal distance of *C. maculosa* seeds and potentially enhancing seed survival and germination rates. The facilitation of ant communities by the invasion of *C. maculosa* coupled with the myrmecochory of *C. maculosa* seeds suggests that a new mutualism has formed between *C. maculosa* and native ants. The effects on native ecosystems of such mutualism are likely considerable and warrant further research.

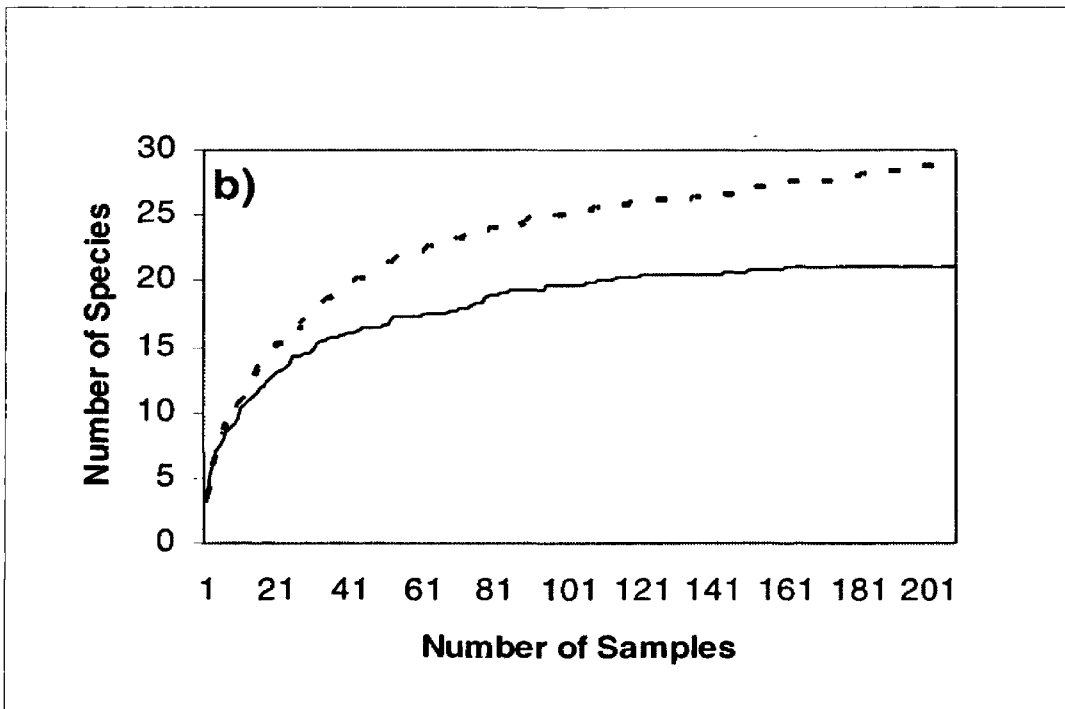
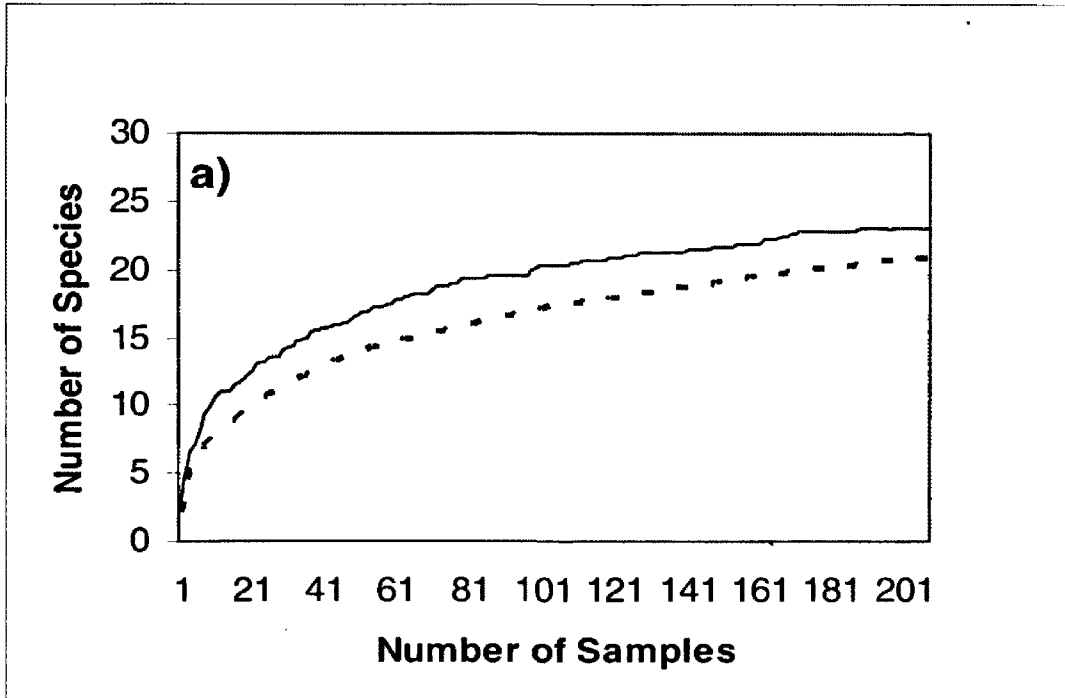
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Figure 1: Species accumulation curves for ants collected at eight sites on Rocky Mountain savannas in western Montana in 1999 and 2000. Native plant communities dominated four sites and four sites were invaded by *C. maculosa*. Samples were collected from pitfall traps set for two weeks in May and two weeks in September of 1999 and 2000. Dashed lines represent native sites and solid lines represent sites invaded by *C. maculosa*. (a) May 1999, b) May 2000, c) September 1999, and d) September 2000)



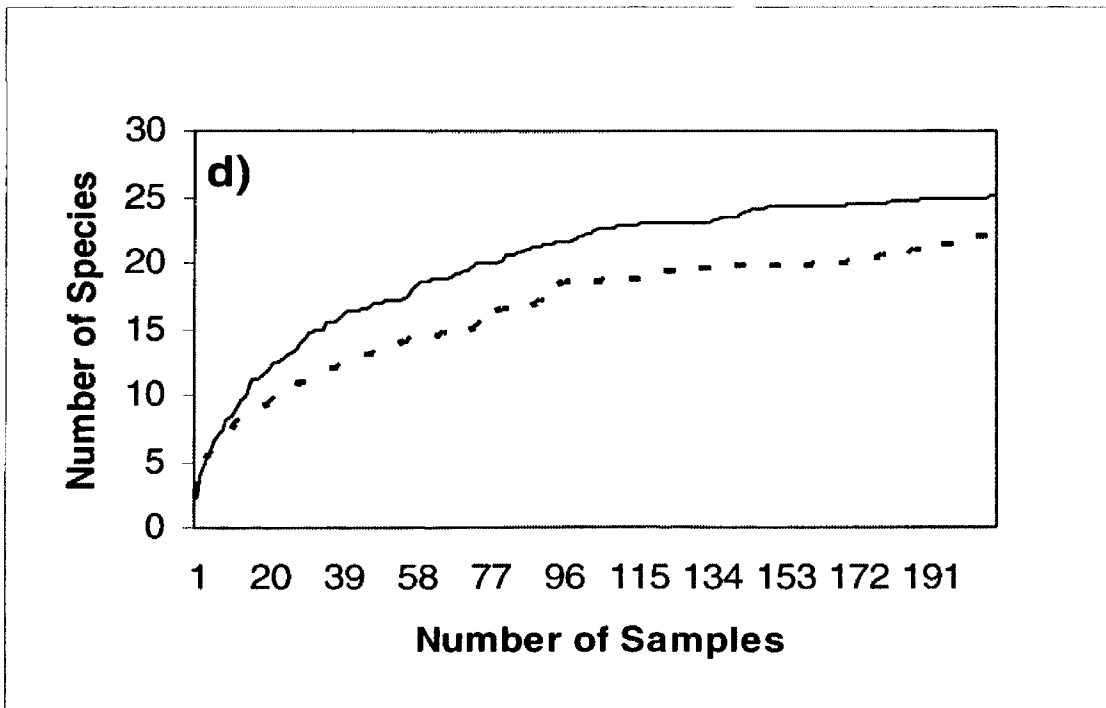
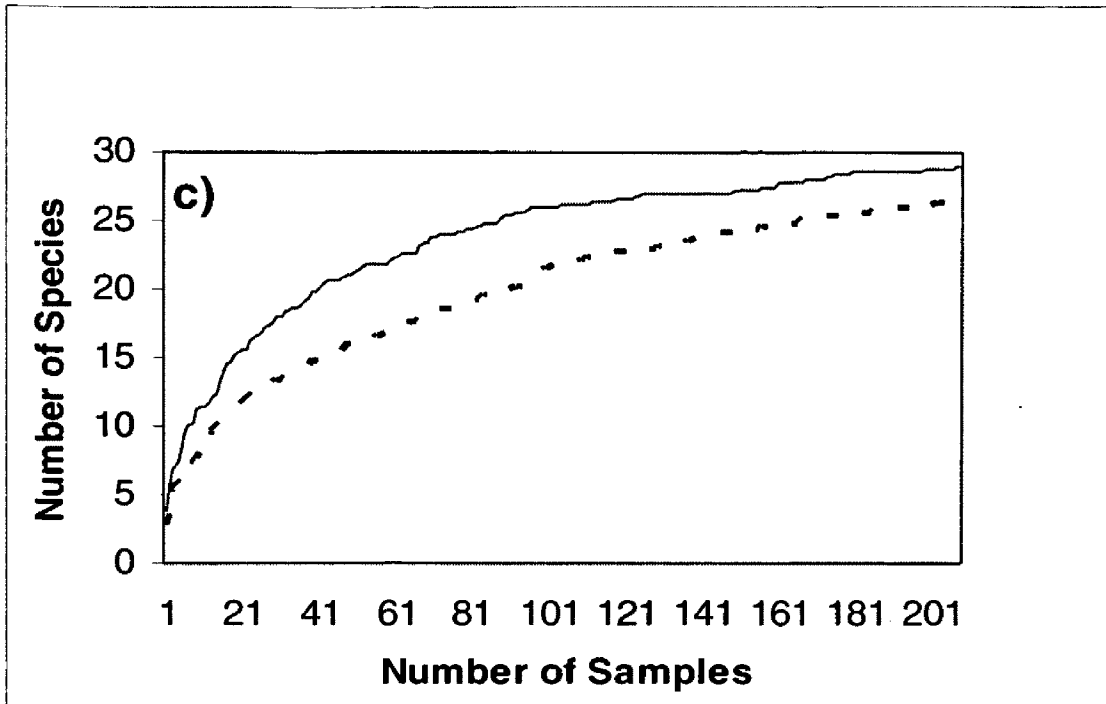


Figure 2: NMS ordination comparing eight sites on Rocky Mountain savannas in western Montana in 1999 and 2000. Four sites were heavily invaded by *C. maculosa* while native plants dominated the four other sites. Native sites 1999 (■), native sites 2000 (◆), invaded sites 1999 (+), and invaded sites 2000 (*) are compared on three ordinal axes. Native sites segregated from invaded sites on all three axes (Mann-Whitney rank sum test: $n = 408, 410$; axis 1 : $T = 186127.0, p < 0.01$; axis 2: $T = 159689.0; p = 0.03$; axis 3; $T = 190832.0; p < 0.01$). The final result required 50 iterations to achieve a final stress of 19.21 and final instability of 0.008 ($p = 0.045$).

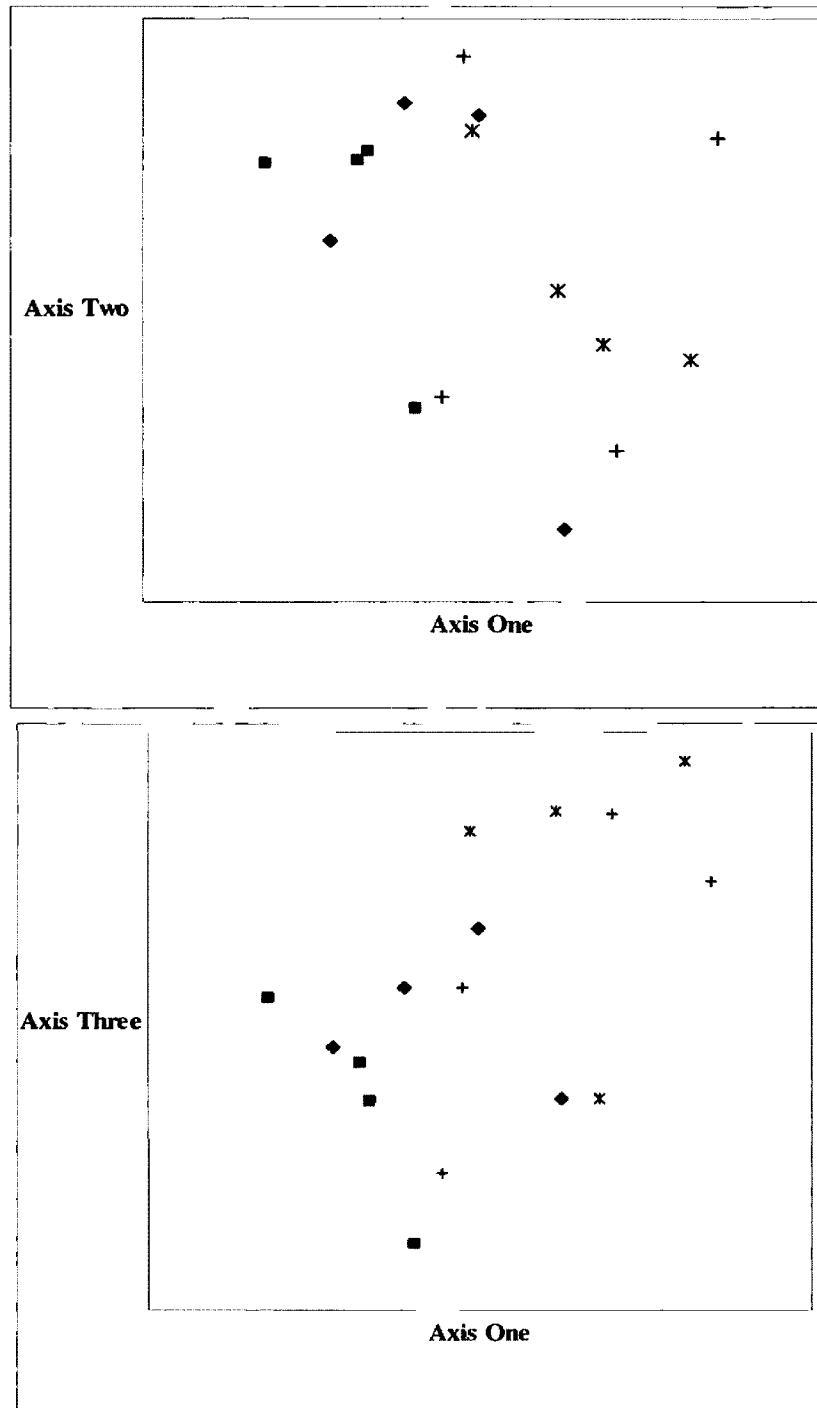


Table 1: Total occurrence of ant species, *Formica* species groups, functional groups, and reproductive ants for all pitfall trap captures combined for eight sites in Rocky Mountain savannas in western Montana in 1999 and 2000. Four sites were dominated by native plant species and four were invaded by *C. maculosa*. * Indicates those found at greater than 5% of pitfall traps. Functional Groups: C: Cold Climate Specialist, Cr: Cryptic Species, G: Generalized Myrmicinae, O: Opportunist, Sp: Specialist Predators, S: Subordinate Camponotini.

	<i>Formica</i> Species Group	Functional Groups	<u>Native Sites</u>							
			<u>BT</u>		<u>GN</u>		<u>PP</u>		<u>SW</u>	
			1999	2000	1999	2000	1999	2000	1999	2000
<i>Aphaenogaster uinta</i> *		O	72	70	73	77	82	88	71	82
<i>Camponotus pennsylvanicus</i>		S	1	1	0	0	1	0	3	2
<i>Ca. vicinus</i> *		S	45	49	55	50	48	49	21	21
<i>Cremogaster spp</i>		G	1	0	0	0	0	0	0	0
<i>Formica lasioides</i> *	<i>neogagates</i>	O	3	1	3	19	4	6	2	2
<i>F. neogagates</i> *	<i>neogagates</i>	O	41	22	49	56	37	26	75	77
<i>F. argentea</i> *	<i>fusca</i>	O	62	54	56	45	64	66	40	25
<i>F. hewitt</i>	<i>fusca</i>	O	1	0	0	0	0	0	0	0
<i>F. occulta</i>	<i>fusca</i>	O	2	3	2	0	5	4	5	3
<i>F. pilicornis</i>	<i>fusca</i>	C	1	0	12	0	4	0	0	1
<i>F. querquetulana</i>	<i>fusca</i>	C	0	0	1	0	1	1	2	2
<i>F. coloradensis</i>	<i>rufa</i>	C	0	0	1	0	0	0	3	3
<i>F. dakotensis</i>	<i>rufa</i>	C	0	0	0	0	0	0	0	0
<i>F. haemorrhoidalis</i> *	<i>rufa</i>	C	0	0	4	1	4	2	11	3
<i>F. obscuripes</i>	<i>rufa</i>	C	0	2	0	0	0	0	0	0
<i>F. orea</i>	<i>rufa</i>	C	0	0	0	0	0	0	1	3
<i>F. planipilis</i>	<i>rufa</i>	C	0	0	0	0	0	0	4	2
<i>F. subnitens</i>	<i>rufa</i>	C	0	0	0	0	0	0	1	0
<i>F. curiosa</i>	<i>sanguinea</i>	O	1	0	0	0	4	6	0	0
<i>Lasius alienus</i> *		C	1	1	10	3	5	6	6	14
<i>La. fallax</i>		C	0	2	0	2	0	2	0	3
<i>La. neoniger</i> *		C	18	6	8	17	4	10	4	3
<i>La. sitiens</i>		C	0	0	0	0	0	0	1	0
<i>Leptothorax crassipilis</i>		C	0	0	0	0	1	0	1	2
<i>Le. nevadensis</i> *		C	11	7	8	16	12	7	8	20
<i>Le. provancheri</i>		C	0	0	1	0	0	0	0	0
<i>Le. rugatulus</i>		C	1	1	0	3	0	4	0	2
<i>Manica hunteri</i>		C	0	0	0	0	0	0	0	1
<i>Myrmica emeryana</i> *		O	0	0	2	0	0	0	7	6
<i>My. fractifornis</i>		O	1	0	0	1	1	0	1	4
<i>My. lobifrons</i>		O	0	0	2	0	0	1	2	2
<i>Polyergus breviceps</i>		Sp	0	0	0	0	0	0	0	1
<i>Solenopsis molesta</i>		Cr	1	0	2	4	2	0	1	1
Queens*		N/A	18	26	15	12	21	31	15	18
Males *		N/A	3	10	3	3	4	17	2	6

Invaded Sites

	<u>ED</u>		<u>KY</u>		<u>LM</u>		<u>UM</u>	
	1999	2000	1999	2000	1999	2000	1999	2000
<i>Aphaenogaster uinta*</i>	80	96	65	75	70	85	83	84
<i>Camponotus pennsylvanicus</i>	1	0	0	1	1	0	3	3
<i>Ca. vicinus*</i>	53	48	21	21	11	13	22	22
<i>Crezogaster spp</i>	0	0	0	0	0	0	0	0
<i>Formica lasioides*</i>	5	2	1	0	6	5	14	12
<i>F. neogagates*</i>	18	14	10	22	44	54	66	54
<i>F. argentea*</i>	78	62	60	49	35	25	78	60
<i>F. hewitt</i>	0	0	0	5	1	0	0	0
<i>F. occulta</i>	3	0	5	0	4	1	9	3
<i>F. pilicornis</i>	4	0	0	0	6	4	1	1
<i>F. querquetulana</i>	2	5	1	0	2	4	0	4
<i>F. coloradensis</i>	0	0	0	0	5	0	2	0
<i>F. dakotensis</i>	0	0	0	0	0	1	0	1
<i>F. haemorrhoidalis*</i>	17	10	5	3	12	9	11	7
<i>F. obscuripes</i>	0	0	0	0	15	0	0	1
<i>F. orea</i>	0	0	0	0	1	0	1	0
<i>F. planipilis</i>	0	0	0	0	2	6	0	0
<i>F. subnitens</i>	0	0	0	0	0	0	0	0
<i>F. curiosa</i>	1	1	4	1	0	0	1	2
<i>Lasius alienus*</i>	4	8	3	4	6	3	25	14
<i>La. fallux</i>	1	5	0	1	2	0	2	3
<i>La. neoniger*</i>	17	23	16	33	13	11	37	15
<i>La. sitiens</i>	0	0	0	0	0	0	1	3
<i>Leptothorax crassipilis</i>	0	0	0	0	0	0	1	2
<i>Le. nevadensis*</i>	9	13	4	18	12	12	13	10
<i>Le. provancheri</i>	0	0	0	0	0	0	0	0
<i>Le. rugatulus</i>	0	1	0	0	4	2	0	0
<i>Manica hunteri</i>	1	1	0	0	1	0	2	0
<i>Myrmica. emeryana*</i>	0	1	10	7	4	3	10	6
<i>My. fractiformis</i>	1	1	5	11	2	0	9	7
<i>My. lobifrons</i>	0	0	1	3	5	16	4	4
<i>Polyergus breviceps</i>	2	0	0	0	0	0	2	0
<i>Solenopsis molesta</i>	0	6	2	1	0	0	4	2
Queens*	19	31	18	35	15	27	31	41
Males *	7	17	5	14	6	18	13	32

Table 2: The probability of ant species, genera, *Formica* groups, functional groups, and reproductive ants occurring in pitfall traps in eight sites located in Rocky Mountain savannas in western Montana in 1999 and 2000. Native plants dominated four of the sites and four sites were invaded by *C. maculosa*. Groups were tested using a mixed logistic regression model with pitfall traps treated as a repeated measure and year, season, and site as fixed effects. * Indicates groups demonstrating a site effect. † Indicates groups demonstrating a year effect. Only *F. occulta* demonstrated a *C. maculosa* by year effect. Degrees of Freedom = 1, 408-529.

	<i>F</i>	<i>P</i>	Frequency of occurrence in pitfall traps – native sites	Frequency of occurrence in pitfall traps – invaded sites
<i>A. uinta</i>	2.18	0.14	0.91	0.94
<i>C. vicinus</i> *	21.73	<0.01	0.63	0.43
<i>F. lasiodies</i> *	0.00	0.99	0.06	0.06
<i>F. occulta</i> * †	0.42	0.52	0.05	0.04
<i>F. neogates</i> *	10.78	<0.01	0.65	0.51
<i>F. argentea</i> * †	4.49	0.03	0.72	0.79
<i>La. alienus</i> *	2.12	0.15	0.08	0.12
<i>La. neoniger</i> *	33.80	<0.01	0.14	0.34
<i>Le. nevadensis</i>	0.31	0.58	0.18	0.20
Rare Species *	14.70	<0.01	0.26	0.39
<i>Formica</i> †	0.01	0.94	0.92	0.92
<i>fusca</i> group * †	4.68	0.03	0.73	0.80
<i>neogates</i> group *	10.75	<0.01	0.69	0.55
<i>rufa</i> group * †	16.81	<0.01	0.07	0.21
<i>Lasius</i> *	30.04	<0.01	0.24	0.45
<i>Leptothorax</i> †	0.06	0.80	0.21	0.22
<i>Myrmica</i> *	11.79	<0.01	0.04	0.15
Subordinate Camponotini/ <i>Camponotus</i> *	19.97	<0.01	0.64	0.44
Cold Climate Specialists *	26.50	<0.01	0.46	0.66
Opportunists	4.25	0.04	0.95	0.98
Queens * †	12.49	<0.01	0.34	0.47
Males * †	24.38	<0.01	0.09	0.24

Table 3: Results of Spearman Rank Order Correlation analysis between NMS ordinal axes and percent cover estimates of environmental factors and measurements of aspect and slope at eight sites in Rocky Mountain savannas in western Montana in 1999 and 2000. Percent cover estimates were made for a 5 m radius circular plots located at each pitfall sampling point.

	<u>Axis 1</u>		<u>Axis 2</u>		<u>Axis 3</u>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>C. maculosa</i>	0.15	<0.01	-0.15	<0.01	0.12	<0.01
<i>B. sagittata</i>	-0.05	0.18	-0.01	0.902	-0.08	0.02
Non <i>C. maculosa</i> or <i>B. sagittata</i> forbs	0.09	<0.01	-0.09	<0.01	0.12	<0.01
Shrub species	0.08	0.02	-0.05	0.162	0.15	<0.01
Bunch grass species	-0.09	<0.01	0.07	0.04	-0.05	0.18
<i>Bromus spp</i>	-0.04	0.23	-0.04	0.218	0.07	0.05
Exposed Rock	-0.16	<0.01	0.18	<0.01	-0.15	<0.01
Woody Debris	0.07	<0.01	-0.08	<0.01	-0.09	<0.01
Litter	<0.01	0.88	-0.02	0.515	0.06	0.09
Aspect	0.04	0.28	0.11	<0.01	0.13	<0.01
Slope	-0.06	0.08	0.22	<0.01	0.11	<0.01

Chapter 3

Myrmecochory of the exotic plant, *Centaurea maculosa* (spotted knapweed): a mechanism potentially enhancing invasiveness

Abstract

I hypothesized that the elaiosomes of seeds of *Centaurea maculosa* (spotted knapweed) elicit seed-dispersing behavior by ants (myrmecochory) potentially providing a mechanism enhancing invasion of the plant into undisturbed native communities. Seeds that elicit myrmecochory produce elaiosomes, small nutrient rich nodes. Ants collect and disperse elaiosome-bearing seeds, later consuming the elaiosome, but usually discarding the seed intact at a distance from the parent plant. The seeds of *C. maculosa* possess elaiosomes suggesting that dispersal of the plant's seeds and its ability to rapidly spread into undisturbed habitats may be enhanced by myrmecochory. I tested for myrmecochory at two Palouse prairie sites in Montana by presenting seeds of *C. maculosa* and two native dominants, *Balsamorhiza sagittata* (a forb) and *Psuedoroegneria spicata* (a bunchgrass). Seeds were presented in choice (seeds of all three plants) and no choice (seeds of only one plant) treatments. At both study sites, ants readily dispersed the seeds of the invasive plant, *C. maculosa*, while virtually ignoring seeds of the native plants, *B. sagittata* and *P. spicata*. In addition, ant preference was not influenced when all three seeds were presented together. Different ant species were observed removing seeds from stations at each site indicating that myrmecochory of *C. maculosa* seeds is not restricted to one ant species but rather may be a generalized response by many ants across communities. Our results indicate that myrmecochory may be a mechanism of seed dispersal, and invasion, by *C. maculosa* into native plant communities.

Introduction

Myrmecochory, the dispersal of seeds by ants in response to elaiosomes, is an important mechanism of dispersal for many plants in many ecosystems (Brew et al. 1989). Elaiosomes are nutrient rich nodes produced on seeds of plants occurring in at least 67 families (Pemberton and Delilah 1990). Some elaiosomes attract ants by chemically mimicking insect prey, others contain chemicals similar to those emitted by dead ants and subsequently stimulate corpse removal behaviors by nest mates, and some

simply provide an opportune quality food source (Brew et al. 1989, Hughes et al. 1994, Gordon 1999).

Regardless of how elaiosomes elicit myrmecochory, the interaction between ants and myrmecochorous plants appears, in many cases, to be mutualistic. While the benefit to the ant is primarily nutritional, myrmecochory can benefit the plant in a number of ways. Myrmecochorous ants can disperse seeds to nutrient rich sites (Davidson and Morton 1981, Pemberton and Delilah 1990), reduce granivory (Rice 1986, Andersen 1988), diminish competition between plants and their offspring (Rice 1986, Pemberton and Delilah 1990), and increase seed dispersal distances (Andersen 1988). Ants collect elaiosome-bearing seeds, consume the elaiosome, and then discard the seed, usually after moving the seed a distance away from the parent plant (Beattie and Culver 1983, Pemberton and Delilah 1990). Most myrmecochorous ants consume elaiosomes without consuming or damaging the seed. However, some myrmecochorous ants consume a portion of seeds along with the elaiosomes, dispersing only a subset of the total seeds collected intact. In addition to myrmecochory, in some ecosystems, dyszoochory, the incidental dispersal of seeds by granivorous ant species, can also be an important mechanism for seed dispersal (Milesi and Casenave 2004). Dyszoochorous plants do not produce elaiosomes. Instead, ants preying upon seeds inadvertently lose or discard seeds while carrying them back to the nest for consumption.

Forty-seven exotic plant species in 13 families have been found to produce elaiosomes on their seeds, suggesting that myrmecochory of seeds of exotic plants may not be uncommon (Pemberton and Delilah 1990) and may be a major factor enhancing their invasiveness. One such exotic, *Centaurea maculosa* (Lamarck), is a short-lived

perennial that has invaded much of the western continental United States, including every county in Montana, Idaho, Wyoming, Washington, and portions of western and central Canada and Alaska (Jacobs and Sheley 1998, DiTomasco 2000). Currently, the plant infests over 2.9 million hectares of woodlands and grasslands in nine western states and Canada (DiTomasco 2000).

Unlike many exotic plants, *C. maculosa* is capable of invading pristine native sites without prior anthropogenic disturbance (DiTomasco 2000). Myrmecochory may provide a mechanism for *C. maculosa* to rapidly spread into such undisturbed native systems. Furthermore, the invasion of *C. maculosa* may alter the behavior of native ants, thereby altering existing interactions among ants and native plants. While few plants native to the Palouse prairies of western Montana produce elaiosomes, the invasion of a plant that produces diaspores (elaiosomes plus seeds) may disturb the natural dyszoochory of native plants. Invasion by an exotic myrmecochorous plant into a native ecosystem where ants disperse seeds of native plants (either through myrmecochory or dyszoochory) may alter dispersal of native seeds by altering ant behavior in favor of dispersal of seeds of the exotic.

To determine if ants disperse the seeds of *C. maculosa* and what effect this may have on the dispersal of native seeds, I tested for myrmecochory of seeds of *C. maculosa* and two native plant species at two Palouse prairie sites in western Montana.

The study addressed the following questions: (1) Do ants disperse seeds of *C. maculosa*? (2) Do ants disperse seeds of dominant native plants? (3) Does seed dispersal differ when native and *C. maculosa* seeds are presented together versus when they are presented independently?

Materials and Methods

The study was conducted at two Palouse prairie sites (Nye: 46° 55.57'N, 114° 0.4'W, Benson: 46° 55.40'N, 114° 1.48'W) located near Missoula, MT, USA. Both sites were located on northwesterly aspects at 1500-1700 m elevation. Native perennial bunchgrasses dominated both sites, primarily *Psuedoroegneria spicata* (Pursh) and *Festuca idahoensis* (Elmer). The dominant forb at both sites, also a perennial, was *Balsamorhiza sagittata* (Prush.).

At the Nye site, two parallel transects were established 25 m apart. On each transect, 20 stations were established, each separated by 20 m. At the Benson site, two transects 25 m apart were also established, but due to spatial constraints one transect included 23 stations and the remaining 17 stations were included in the second transect.

Seeds were presented in treatment and control enclosure stations to test for myrmecochory. Treatment enclosures consisted of double-walled structures 5 cm high with outer wall dimensions of 14 cm x 24 cm, inner wall dimensions of 11 cm x 21 cm, and constructed of 7.5 mm mesh hardware cloth. The double wall reduced disruption of seeds by grasshoppers (which regularly forced their way inside single-walled enclosures in a preliminary trial).

Control stations were single-walled cages 11 cm long x 21 cm wide x 5 cm high made of aluminum window screening with a 2 mm mesh. The smallest ants at the sites could not pass through this mesh. Furthermore, no seeds used in the study were small enough to fit through the mesh, and therefore, could not be removed even if ants gained entry. The control stations were located approximately 4 m from the first, tenth, and

twentieth treatment stations on the first transect and the first and tenth treatment stations on the second transect.

Centaurea maculosa, *P. spicata*, and *B. sagittata* seeds were used to test for myrmecochory. *Psuedoroegneria spicata* and *B. sagittata* were chosen to represent native grasses and forbs, respectively. While neither *P. spicata* nor *B. sagittata* seeds possess elaiosomes, this is typical for most plants native to Palouse prairies.

Psuedoroegneria spicata and *B. sagittata* seeds were purchased from Sunmark Seeds (Troutdale, OR). *Centaurea maculosa* seeds were collected locally in Missoula County, MT, approximately seven days prior to use and frozen at -22°C in sealed plastic bags until the day they were placed into the field (to avoid degradation of the elaiosomes). Native seeds were also frozen prior to placement in the field.

In all enclosure stations, seeds were presented inside the enclosures in cups. In each enclosure three shallow cups were recessed into a cardboard tray fitted snugly inside the cage and placed level with the ground. In no-choice treatments a single seed type was presented in the middle cup of the tray, while in choice treatments and in control stations, seeds of all three species were ordered randomly among the three cups. Four grams of each seed type were placed in individual cups each day in treatment and control stations. (Four grams equates to approximately 400 *B. sagittata* seeds, 2000 *C. maculosa* seeds, and 800 *P. spicata* seeds). Preliminary trials demonstrated that four grams exceeded the amount of seeds removed by ants from a single station during a single day.

The experiment was conducted over four days at each site in early September 2003. All three focal plants were present at the site and were producing seeds during this time. Over the course of the four days, each treatment (choice, no choice *C. maculosa*, no

choice *P. spicata*, no choice *B. sagittata*) was systematically offered at each station on the transects. At the Nye site, the experiment was conducted over four consecutive days. However, due to a period of unseasonably cold and wet weather, the experiment at the Benson site was interrupted for four days between the first and second days of the experiment.

Most ant species native to temperate latitudes are diurnal foragers (Andersen 1997). Therefore, seeds were presented in the exclosures only during daylight hours to avoid disruption of exclosures by nocturnal seed feeders such as mice. Seeds were placed in stations by 0800 and retrieved by 1900 each day and were retrieved in the same order in which they were distributed.

Finally, as seeds were retrieved from stations on the last day of the experiment at each site, we collected all ants observed removing seeds from stations. Ant specimens were stored in 95 percent ethyl alcohol and later identified to species.

Data analyses

A two-way ANOVA test was used to determine the effect of 'Seed Type' and 'Presentation' (choice vs. no choice) on removal of seeds by ants. While data were not normally distributed, ANOVA tests are valid with large sample sizes such as those used in this study (Tabachnick and Fidell 1989). Both 'Seed Type' and 'Presentation' were treated as repeated measures, and the Benson and Nye sites were tested separately. Effects of day and station position were not significant and removed from the model.

We compared control and treatment weights to determine if ants removed seeds from each station. Because 'Presentation' and day were found to have no effect, we pooled 'Presentation' at each site over all four days of the trial. We then compared these

pooled treatment weights to pooled weights for controls using the Mann-Whitney Ranked Sum test. A nonparametric test was used because the data were non-normal and could not be normalized using appropriate transformations

The weight of seeds removed from treatment stations by ants was determined by subtracting the post-exposure weight of seeds from each treatment station from the mean post-exposure weight of the corresponding seed type from control stations exposed during the same day.

All analyses were conducted using SigmaStat version 2.03 (SPSS, Chicago, IL).

Results

At both sites, ants removed seeds of *C. maculosa* from treatment stations, but not seeds of *B. sagittata* or *P. spicata* (Table 1). Furthermore, 'Presentation' (choice or no choice) did not affect removal rates of seeds by ants (Table 2).

At the Benson site, over all four days, ants removed a mean of 0.103 ± 0.016 g (mean \pm 1 SE) of *C. maculosa* seeds (approx. 52 seeds) from each treatment station. While, over the four days of the experiment at the Nye site, ants removed a mean of 0.39 ± 0.044 g of *C. maculosa* (approx. 195 seeds) from each treatment station. At the Benson site, ants did not remove native seeds from treatment stations (-0.005 ± 0.005 g for *B. sagittata*, -0.008 ± 0.002 g for *P. spicata*). Similarly, no seeds of the natives were removed at the Nye site (-0.003 ± 0.004 g for *B. sagittata*, -0.006 ± 0.004 g for *P. spicata*) (Fig. 1).

The finer mesh of the control stations provided more surface area than the course mesh of treatment stations, likely absorbing more solar heat and potentially resulting in a greater loss of moisture from seeds in control stations than in treatment stations.

Consequently, weights of seeds from control stations were slightly less than those at treatment stations, resulting in negative values for removal weights for seeds of *B. sagittata* and *P. spicata*. Regardless, at both sites, weights of seeds of *B. sagittata* and *P. spicata* in treatment stations were not significantly different than weights of *B. sagittata* and *P. spicata* seeds in control stations (Table 1).

At the Nye site, seeds were observed being removed from stations by *Formica lasiodes* (Emery) and *Lasius alienus* (Mayr), while at the Benson site *Myrmica fracticornis* (Emery) was observed removing seeds. At each site, ants were only observed removing *C. maculosa* seeds from stations, never seeds of the native plants.

Discussion

At both study sites, ants readily dispersed the seeds of the invasive plant, *C. maculosa*, while virtually ignoring seeds of the native plants, *B. sagittata* and *P. spicata*. In addition, ant preference was not influenced when all three seeds were presented together.

While these results suggest that ants are responding to the elaiosome on *C. maculosa* seeds and that ants disperse the plant, seed size and collection methods may also have affected seed removal from the stations. The seeds of *C. maculosa* were the smallest of the three seeds. While all three of the ant species collected removing *C. maculosa* seeds were large enough to remove *P. spicata* seeds; they may have been unable to remove the relatively large seeds of *B. sagittata*. In addition, seeds of the two native plants were purchased and not collected locally. It is possible that a difference in collection methods or seed age may have affected the attractiveness of the native seeds to ants. However, ant response to elaiosomes is well documented (Turnbull and Culver

1983, Brew et al. 1989, Pemberton and Delilah 1990, Hughes et al. 1994). Previous findings demonstrating ant dispersal in response to elaiosomes coupled with the results of this study strongly suggest that ants are responding to and dispersing *C. maculosa* seeds in response to elaiosomes.

While native ants likely respond to elaiosomes and disperse the seeds of *C. maculosa*, they are probably not dispersing native plant seeds which lack elaiosomes. Ant communities in temperate regions of North America are dominated by generalists, and lack many of the specialists feeder groups found in arid and tropical climates (Creighton 1950, Holldobler and Wilson 1990). Most ant species in Palouse prairies in western Montana are generalist feeders consuming dead animals and easily available plant matter (Andersen 1997). The lack of specialist granivores in Palouse prairies suggests native ant species are not dyszoochorous and that the seeds of plants native to these prairies (and lacking elaiosomes) are not dispersed by ants in these ecosystems.

Several highly invasive plants including *Cirsium arvense* L. (Canada thistle), *C. diffusa* Lamarck (diffuse knapweed), *Euphorbia escula* L. (leafy spurge), and *Potentilla recta* L. (sulfur cinquefoil) produce elaiosome-bearing seeds, suggesting that myrmecochory of seeds of invasive exotic plants by native ants may be common (Pemberton and Delilah 1990). In addition, *F. lasiodies*, an ant observed dispersing *C. maculosa* seeds in this study, has also been observed dispersing the elaiosome-bearing seeds of the invasive shrub, *Cytisus scoparius* (L.) (Bossard 1991). In that study, *F. lasiodies* were observed carrying some seeds to their nest, dispersing some seeds before discarding them, and consuming some elaiosomes without dispersing the seeds. In another study, two *Formica* spp. and one *Lasius* spp. were observed dispersing the

elaiosome-bearing seeds of another invasive plant, leafy spurge, *E. escula* (Selleck et al. 1962, Pemberton 1988). This suggests that myrmecochory of seeds of exotic invasive weeds may occur broadly, even by unspecialized native ants found in temperate climates.

Myrmecochory occurring as a generalized response by a wide range of ant species could potentially facilitate the invasiveness of exotic plants in their new environments. Furthermore, different behaviors by different ant species are likely to affect the degree to which myrmecochory facilitates invasiveness. For example, in a study of the invasive shrub, *C. scoparius*, different ants at different sites dispersed the seeds of the plant in different ways that could potentially affect the distribution and survival of the seeds. At one site, only a single ant species, *Aphaenogaster occidentalis* (Emery), dispersed the shrub's seeds. The ant consistently returned to the nest before removing the elaiosome and discarding the seeds, resulting in a strong reduction in predation of seeds by grouse and quail, and a concentration of seeds and seedlings around the nests of the ants (Bossard 1991). In contrast, at another site where seven species of ants, including *A. occidentalis*, dispersed seeds of the plant, each ant species had a different foraging behavior which likely affected how the seeds were dispersed and ultimately their survival. Two species carried seeds to their nest, two species carried seeds a short distance prior to discarding them, one species removed the elaiosome without dispersing the seed, and two species had variable behaviors.

If different species of ants vary in their seed-handling behaviors and distances of seed dispersal of the seeds of *C. maculosa*, such variability may have a profound impact on the rate of spread, distribution of seeds, and survival of seedlings and mature seed-bearing plants at a given site. Further work identifying which ant species are

myrmecochorous in invaded areas and in areas at risk of invasion, and studies of their seed-handling behaviors and seed survival rates after myrmecochory, may help us understand how *C. maculosa* and other myrmecochorous invasive plants spread and establish in their new environments. Such studies should consider not only effects of myrmecochory on dispersal, but also include the effects of myrmecochory on other aspects of plant establishment and success.

The presence of seeds of *C. maculosa* had no effect on ant behavior toward native plant seeds, which were largely ignored by the ants. Seed of the native plants that we tested did not possess elaiosomes and local ants did not appear to disperse their seeds. However, in ecosystems where native plants possess elaiosomes or incidental dispersal by seed predators does occur, fewer seeds of native plants may be dispersed if ants are focusing a portion or all of their foraging efforts on invasive plants seeds. Furthermore, if exotic elaiosome-bearing seeds are preferred over native seeds normally dispersed by ants, this would act to decrease native plants at a site while increasing the exotic. In either case, the effect would exacerbate any negative effects of exotic plant invasion on native plant communities by reducing dispersal of natives in favor of dispersal of the exotic.

In addition, the direct positive effects of myrmecochory to invasive plants could in turn, facilitate ant populations, resulting in positive feedback. Jensen (2005) found that several species of ants are more likely to occur in *C. maculosa*-invaded northern Rocky Mountain savannas than in native-dominated savannas. The reason for increased occurrence of ants in *C. maculosa*-dominated savannas is not known, but may relate to an increase in nutrients from elaiosomes or environmental changes due to invasion that make invaded savannas more favorable to these ants.

In this study, native ants clearly responded to, and dispersed seeds of, *C. maculosa*. Myrmecochory of *C. maculosa* seeds may be an important mechanism facilitating the invasiveness of this plant. Ants in our study dispersed relatively large numbers of seeds from the treatment stations indicating that dispersal of *C. maculosa* seeds by ants on both site and landscape levels could be considerable. However, research into distance of dispersal by ants and how different ant species may differentially affect the dispersal, seedling success and rate of spread of the weed are needed to fully understand how myrmecochory may affect the invasiveness of this plant.

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Figure 1. Mean *B. sagittata*, *C. maculosa*, and *P. spicata* seeds removed (g) by ants at two Palouse prairie sites (a Benson, b Nye) in western Montana. Error bars indicate the standard error of the mean.

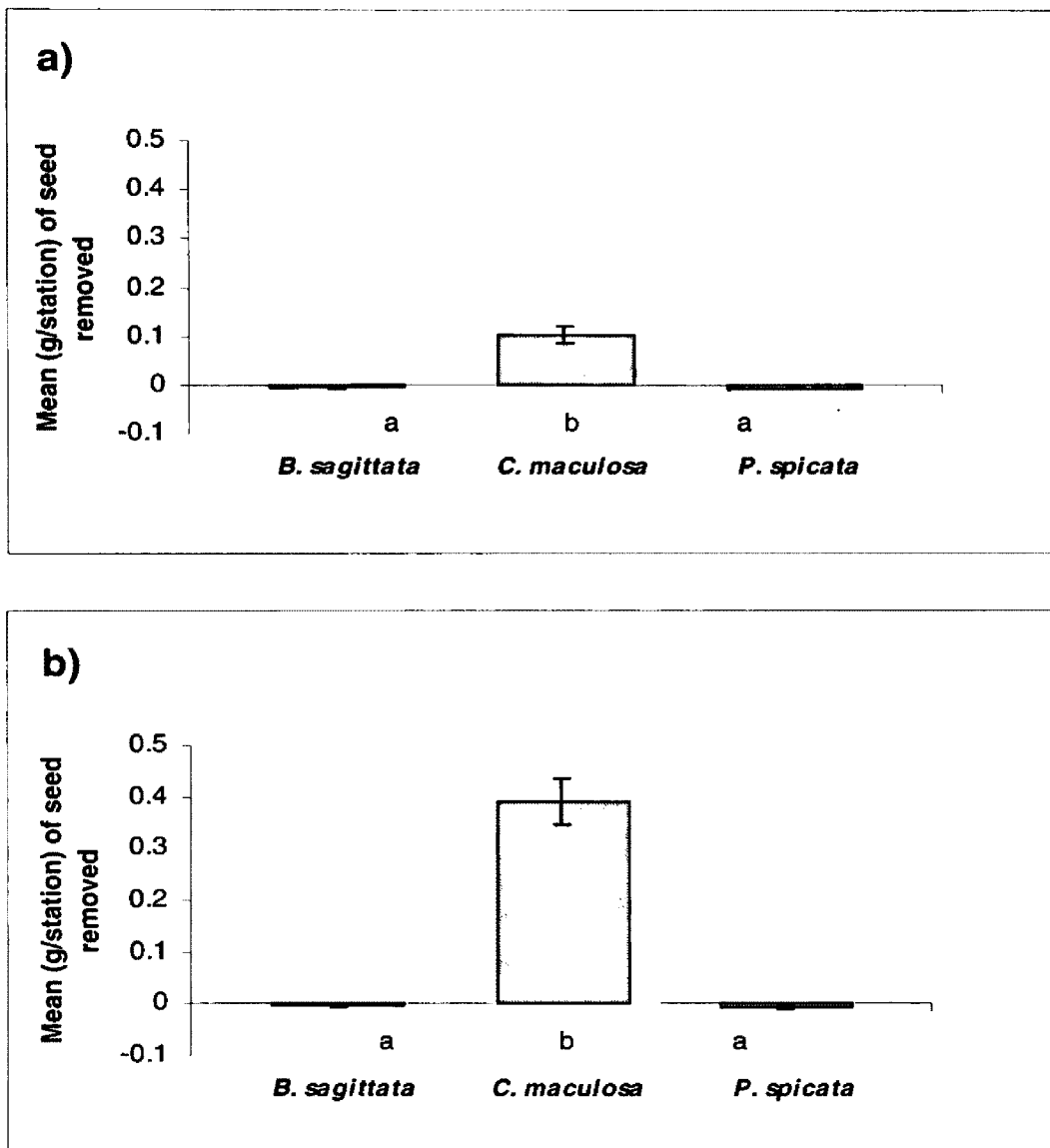


Table 1. Man-Whitney Rank Sum test results comparing the removal of *B. sagittata*, *C. maculosa*, and *P. spicata* seeds from stations exposed to ants vs. control stations where ants were excluded. Tests were conducted on two sites on Palouse prairies in western Montana.

Benson Site:

	T	n (control)	n (stations)	P
<i>B. sagittata</i>	828.00	20	80	0.12
<i>C. maculosa</i>	1338.50	20	80	<0.01
<i>P. spicata</i>	821.50	20	80	0.11

Nye Site:

	T	n (control)	n (stations)	P
<i>B. sagittata</i>	940.00	20	78	0.66
<i>C. maculosa</i>	1593.00	20	79	<0.01
<i>P. spicata</i>	900.50	20	79	0.39

Table 2. Results of ANOVA on removal of *B. sagittata*, *C. maculosa*, and *P. spicata* seeds by ants from treatment stations placed at two Palouse prairie study sites in western Montana. Presentation indicates choice and no choice treatments. Seed Type indicates the three types of seeds presented to ants at the sites. Both 'Seed Type' and 'Presentation' were treated as repeated measures.

Benson Site:

	DF	MS	F	P
Presentation	1	0.00009	0.0213	0.885
Seed Type	2	0.322	32.787	<0.001
Presentation x Seed Species	2	0.0007	0.166	0.847
Residual	235			

Nye Site:

	DF	MS	F	P
Presentation	1	0.0131	0.697	0.409
Seed Type	2	4.138	48.425	<0.001
Presentation x Seed Species	2	0.0142	0.794	0.456
Residual	235			