Effects of spotted knapweed invasion and restoration treatments on ground beetle diversity abundance and distribution in Rocky Mountain savannas in Montana

Allison K. Hansen

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EFFECTS OF SPOTTED Knapweed Invasion and Restoration Treatments on Ground Beetle Diversity, Abundance, and Distribution in Rocky Mountain Savannas in Montana

by

Allison K. Hansen

B.S. University of Montana, Missoula, 2003

presented in partial fulfillment of the requirements for the degree of Master of Science

The University of Montana

May 2005

Approved by:

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Date

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Forestry and Conservation

Effects of Spotted Knapweed Invasion and Restoration Treatments on Ground Beetle Diversity, Abundance, and Distribution in Rocky Mountain Savannas in Montana

Director: Dr. Diana Six

I investigated the effects of spotted knapweed (knapweed) invasion and restoration treatments on ground beetle (carabid) diversity, abundance, and distribution in Rocky Mountain savannas. To determine how knapweed invasion affected carabids I analyzed carabid species and functional group (FG) diversity, community composition and structure, and related carabid species assemblages in savannas to important abiotic and biotic variables. Carabid species richness was similar between invaded and native sites; however, evenness was significantly different for both carabid species and FG between invaded and native sites. Higher beta diversity resulted in native sites relative to invaded sites. Polyphagous phytophages (PP) and specialist predators (SP) were more abundant in invaded sites while generalist predators (GP) were more abundant in native sites. PP and SP indicated invaded site conditions while GP indicated native site conditions.

Knapweed simplified carabid FG evenness. In addition, carabid species assemblages were more homogenous among invaded sites relative to native sites, and species distribution was mainly affected by cover of knapweed, soil moisture, and ground structural components.

To determine if and how herbicide treatments in knapweed-invaded habitats affected carabid communities, I analyzed species and FG composition and structure after herbicide restoration treatments. GP were significantly more abundant and good indicators of native sites compared to invaded sites, regardless of whether the sites were herbicide-treated or controls. PP and SP were significantly more abundant and good indicators of control sites relative to herbicide-treated sites regardless of whether the sites were native or invaded. PP feed primarily on forbs. The application of picloram herbicide, greatly reduced forb cover in this study, and thus may have indirectly affected carabid populations through its effects on forbs. The reduction of SP at herbicide-treated sites may be linked to concurrent decreases in Lepidoptera prey dependant on forbs. Moreover, a reduction of GP in invaded sites may indicate that the availability of their soil biota prey may be altered in invaded sites as a result of knapweed-induced changes. Herbicide treatments alone did not appear to restore invaded sites to the desired “pre-invasion” condition, at least in terms of carabid communities, in the time frame of this study.
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Chapter 1: Introduction

The goal of this study was to investigate the effects of spotted knapweed invasion and restoration treatments on ground beetle diversity, abundance, and distribution. Spotted knapweed, an exotic forb from Eurasia, is well established in many semi-arid grassland and open canopy forest habitats in North America. Ground beetles (Carabidae) have a cosmopolitan distribution and are widely recognized as useful indicators of environmental change and condition. Carabids exhibit strong habitat specificity and sensitivity to environmental gradients and may prove to be good indicators of ecological change resulting from exotic plant invasions and restoration treatments. In this introductory chapter, I present an overview of the known effects of spotted knapweed on biological communities, the life history characteristics of ground beetles, deterministic factors that regulate carabid populations, and the potential use of ground beetles as indicators of environmental change. I then present a list of long-term, overall, and specific project objectives.

Biological invasions

Biological invasions are one of the greatest threats to natural communities and are considered second in importance only to habitat destruction in causing losses of biodiversity (Keane and Crawley, 2002). Introduced exotic organisms are the primary cause of listing for approximately 400 of the 958 species currently considered under the U.S. Endangered Species Act. Additionally, exotic organisms pose the primary risk to 80% of endangered species in other regions of the world (Pimentel et al., 2000). Moreover, biological invasions pose significant threats to ecosystem integrity,
agriculture, rangelands, fisheries, and public health. Economic costs of exotics in the U.S. alone are estimated at $37 billion. These estimates do not include important, but less tangible, effects on native ecosystems (Pimentel et al., 2000).

The incidence of biological invasions has risen dramatically in recent decades (Hanfling and Kollmann, 2002). However, our knowledge of how such invasions impact native communities remains poor. Consequently, investigations on the effects of invasive exotics are imperative for understanding their impacts on native community structure and function, and for the conservation of native species and biodiversity (Williamson, 1996).

Approximately one out of every ten accidental or intentional exotic introductions is considered a serious ecological problem. The vast majority of introduced organisms, however, remain rare or do not establish in natural communities as a result of low propagule pressure or poor adaptation to conditions in the new environment (Williamson, 1996). For those few exotic species that do establish and flourish, their success is thought to be facilitated by a number of factors including a lack of natural enemies in their new environment, strong competitive interactions with native species, and an increased competitive ability through the reallocation of resources from defense to reproduction and growth (Hanfling and Kollmann, 2002; Keane and Crawley, 2002).

**Spotted knapweed**

Spotted knapweed (*Centaurea maculosa* Lam.), an aggressive plant from Eurasia, has invaded over seven million acres in the U.S. and Canada and continues to spread (French and Lacey, 1983). Economically speaking, spotted knapweed can decrease forage for livestock up to 96 percent (French and Lacey, 1983). Ecologically, indirect and direct effects of invasive weeds on ecosystem processes and functions
include a reduction in native plant diversity, alterations in soil chemistry, changes in fire and hydrological regimes, and an increase in soil erosion and water run-off (Jacobs and Sheley, 1998; Randall, 1996). Furthermore, North American plants and spotted knapweed lack a coevolutionary history. Consequently, *C. maculosa* may grow more successfully in its new North American habitat by suppressing native plants with allelopathic root exudates that in the native range of *C. maculosa* exert relatively little effect on plants that have evolved with it (Callaway and Aschehoug, 2000; Bais et al., 2002).

In the northern Rocky Mountains, spotted knapweed primarily threatens mixed bunchgrass/forb communities of prairies and savannas (Tyser, 1992). Once established, spotted knapweed forms dense, near monoculture stands, severely reducing native plant diversity and abundance (Tyser and Key, 1988; Tyser, 1992; Ortega and Pearson, in press). These extreme effects on plant communities may, in turn, precipitate negative effects on dependent fauna. Currently, the ecological effects of invasive plants on ecosystem processes and functions and potential subsequent bottom up effects of invasion on animal communities are not well known (Parker, 1999).

The diversity of organisms and the complexity of ecosystems make the identification of the many direct and indirect effects of biological invasions difficult. However, by studying organisms that display narrow ecological amplitudes, and therefore, those which are very sensitive to environmental gradients, we can begin to characterize many cause and effect relationships in invaded systems. Ideally, organisms used to study impacts should have well-known biologies so that changes in their diversity and abundance can be related to changes in the environment. The species used should
also be easy to monitor (Caro and O'Doherty 1999; Patton, 1987). Insects, particularly ground beetles, fit these criteria well. Ground beetles display descriptive species and community patterns due to each species unique adaptations, short generation times, and high fecundity.

*Ground beetles*

Ground beetles (Coleoptera: Carabidae) have been shown to be good indicators of environmental change (Lovei and Sunderland, 1996, Niemela et al. 2000). Carabids are the third largest family of beetles in North America with over 2,200 described species (Borror, 1989). Carabids are diverse in their ecological roles and are well represented in all major habitats except deserts (Thiele, 1977).

Several characteristics make carabids excellent organisms to monitor environmental change. Many species display strong habitat specificity and have low dispersal rates (Thiele, 1977; Grum, 1986; Maelfait and Desender, 1990; Michaels and McQuillan, 1995; Lovei and Sunderland, 1996; Lindroth, 1961-1969). They also have short generation times and high fecundity, therefore, changes in environmental favorability should rapidly translate to changes in distribution and population size. The distribution and abundance of these ground-dwelling arthropods is largely determined by their extreme sensitivity to temperature, humidity, soil characteristics, amount of litter, food availability, plant architecture, and season (Brose, 2003; Lovei and Sunderland, 1996; Holliday, 1991; Maelfait and Desender, 1990; Rushton et al., 1990; Butterfield et al., 1995). Carabids can be easily sampled using pitfall traps, and their taxonomy and ecological requirements are well studied (Thiele, 1977; Grum, 1986; Lovei and Sunderland, 1996; Lindroth, 1961-1969). Because of their ubiquity, sensitivity to
environmental gradients, and ease of sampling, carabids have been widely and successfully used as ecological indicators of ecosystem characteristics and change.

Life history

When using carabids as indicators of environmental condition or change, knowledge of each species' taxonomy, life history, and biology is important so that each species' characteristics, habitat preferences, and requirements can be related to the environmental variables being studied (Eyre, 1994; Rushton et al., 1990; Maelfait and Desender, 1990). Life cycle strategies, rate of development, dispersal dynamics, and food preferences are all important factors to consider when using carabids as indicators, as each of these characteristics indirectly provide information about environmental condition.

Life cycle strategies. Carabids undergo complete metamorphosis and the larval form is usually campodeiform (Thiele, 1977; Lovei and Sunderland, 1996). Usually larvae develop through three instars before pupation, although Harpalus and Amara species possess only two instars (Lovei and Sunderland, 1996).

Annual rhythm types of carabids. An annual rhythm is the seasonal period of reproduction for a species and is marked by a peak of locomotory activity during which mates are actively sought (den Boer and den Boer-Daanje, 1990; Thiele, 1977). The type of annual rhythm a carabid species displays is dependent upon each species' life history. Five different annual rhythms have been described for carabids (Lovei and Sunderland, 1996). The first type contains species that are spring breeders. These carabids reproduce in the spring and their larvae develop in late spring and summer and exhibit no larval dormancy. Adults (adults in many carabid species have been known to live more than.
one year) enter diapause prior to winter (den Boer and den Boer-Daanje, 1990). Adults require a change in photoperiod from short day (SD) to long day (LD) to become sexually mature (Paarmann, 1990).

The second type of annual rhythm is exhibited by species that over-winter as larvae and do not enter diapause as young adults. These species reproduce in summer and/or autumn. The third type of annual rhythm is exhibited by species with over-wintering larvae and young adults that enter diapause in spring prior to reproduction in late summer and/or autumn. It is important to note that for the second and third types of annual rhythms, over-wintering larvae require specific low temperature conditions for a set period of time to complete development (Paarmann, 1990).

The fourth type of annual rhythm is exhibited by species that display developmental plasticity and can facultatively breed in spring and/or autumn (Lovei and Sunderland, 1996; den Boer and den Boer-Daanje, 1990; Paarmann, 1990). This type of annual rhythm is exemplified by Poecilus lepidus, a species with a broad geographic distribution (central Italy to Norway and from the Atlantic coast to Siberia). Poecilus lepidus held under constant SD or LD conditions at a constant temperature can achieve sexual maturity under both photoperiod conditions, although sexual maturity takes significantly longer to achieve under SD conditions (4.4 months versus 2.5 months under LD conditions) (Paarmann, 1990).

The fifth type of annual rhythm is exhibited by species that require more than one year to complete a generation (den Boer and den Boer-Daanje, 1990). These species are more common in the subarctic zone than in temperate or tropical regions (Sota, 1986; den Boer and den Boer-Daanje, 1990).
The type of annual rhythm (seasonal reproductive peak) is species-specific (Thiele, 1977) and affects the time of year that dispersal of adults occurs. Furthermore, seasonal peak abundance of reproductive adults can be unimodal or bimodal depending on the species and habitat (den Boer and den Boer-Daanje, 1990). It is important to know which type of annual rhythm each carabid species at a site exhibits in order to sample at the appropriate times (Thiele, 1977; Lovei and Sunderland, 1996).

**Dispersal dynamics.** Dispersal dynamics greatly affect the distribution of carabid species. Furthermore, species with high dispersal abilities display different population dynamics and successional patterns than species with low dispersal (Lovei and Sunderland, 1996). Carabid morphology is often indicative of dispersal ability. Monomorphic macropterous (long-winged) species usually exhibit flight, while monomorphic brachypterous (short-winged) species are flightless. Some species are dimorphic, with different individuals of the same species displaying either macropterous and brachypterous traits (Lovei and Sunderland, 1996). These morphological traits affect dispersal dynamics and influence the proportions of brachypterous, macropterous, and dimorphic species in environments at different stages of succession as well as in ephemeral habitats (den Boer, 1970).

Monomorphic macropterous and dimorphic species have a greater capacity for dispersal than monomorphic brachypterous species since short-winged species are flightless (den Boer, 1970). Therefore, pioneer species are typically monomorphic macropterous and dimorphic species that thrive in early seral stages of succession and in ephemeral environments (den Boer, 1970). As succession proceeds, the proportion of macropterous and dimorphic species decrease as the proportion of brachypterous species
begin to increase due to colonization from the surrounding areas (Mader, 1986).

Because brachypterous species cannot colonize or recolonize an area through flight, when habitat change occurs (such as through disturbance) concomitant with fragmentation species with slow dispersal rates (brachypterous individuals) may at least temporarily become locally extinct (den Boer, 1970; Lovei and Sunderland, 1996).

The proportion of brachypterous and macropterous individuals in a dimorphic population tends to shift in favor of brachypterous individuals as time since colonization increases. Furthermore, the proportion of brachypterous individuals in a dimorphic population tends to increase over time in stable habitats (Lovei and Sunderland, 1996; Turin and den Boer, 1988; den Boer, 1970). The macropterous state in dimorphic species is typically determined in simple Mendelian fashion by recessive homozygous alleles. It has been hypothesized that after disturbance that the dominant alleles for brachyptery are introduced by colonizing or re-colonizing macropterous females, which are carrying eggs fertilized by brachypterous males (den Boer, 1970). Up to 80% of dispersing females carry fertilized eggs (Lovei and Sunderland, 1996).

**Food preferences.** Food availability is one of the most important factors determining the persistence of a carabid species in a habitat (Lovei and Sunderland, 1996). Effects of food availability are particularly critical to the larval stages which have poor dispersal abilities and therefore cannot disperse to locate food (Lovei and Sunderland, 1996). Therefore, adult female choice of oviposition sites is especially important in determining the success of larvae and the ability of a species to recolonize disturbed areas.
The majority of larvae and adult carabids are polyphagous feeders that eat both animal and plant materials. However, some are strictly phytophagous or carnivorous, and may be either generalist or specialist feeders within these broad categories. The number of predacious species in this family has been largely overestimated, with many new phytophagous and carrion-feeding species being discovered as feeding habits become more extensively studied. At present, little is known on the relative proportion of species in various trophic groups in most habitats (Lovei and Sunderland, 1996).

Population regulation - deterministic factors

Deterministic factors that regulate carabid populations should be thoroughly investigated before sampling and analysis is conducted. Factors regulating populations must be understood if relationships between species diversity and abundance and ecological change are to be detected and understood. Biotic factors (host abundance, host quality, natural enemies, and competitors), abiotic factors (i.e. soil characteristics, landscape, and climate), and disturbance are all importance mechanisms that may regulate insect populations (Berryman, 1986).

Biotic causes of mortality in carabid life stages. The biotic factors that contribute to mortality of carabids vary in type and importance by developmental stage. Mortality of carabid eggs may be caused by soil microfauna such as fungi and nematodes. Heessen (1981) estimated egg mortality in untreated litter at 83.3%, whereas egg mortality in heat-treated litter was estimated at 17.8% suggesting that microfauna in litter attribute to substantial egg mortality.

The larval stage of carabids is believed to be the most vulnerable stage to most biotic mortality factors, yet their cryptic nature precludes investigations into the relative
importance of larval mortality compared with other life stages. Nevertheless, Brusting et al. (1986) and Heessen and Brusting (1981) concluded that events, such as cannibalism, during the larval stage are the most important in regulating populations. Their conclusions were based on the results of laboratory and field experiments that found that larval population size was density dependent and that reductions in available food increased the rate of cannibalism. Evidence of mortality factors other than cannibalism affecting larval population size is scarce. However, laboratory and field experiments using larvae of *Nebria brevicollis* found that 25-97% mortality resulted when food quantity was decreased while 25% mortality was attributed to parasitism (Nelemans, 1987); however, parasitism generally is not believed to play a significant role in the regulation of carabid populations (Thiele, 1977).

Inter-specific predation is considered an important factor affecting mortality of adult carabids (Lovei and Sunderland, 1996), yet a general lack of studies on predation in these systems means that the relative significance of predators in carabid population regulation remains unknown. Insectivorous mammals, birds, and arthropods are known to prey on carabids (Thiele and sources within, 1977) but the degree to which such predation regulates carabid populations is unknown. Results of a study conducted in a shrub-steppe ecosystem in Southwest Wyoming suggest that the exclusion of rodents can result in an increase in the species richness and abundance of carabids (Parmeter and MacMahon, 1988) indicating an impact of predation. However, results from this study may be invalid. The authors assumed that a concurrent study in several of their plots (i.e. poisoning of harvester ants with Diazinone) would not affect carabid distribution and species richness. However, applications of insecticide can result in biased results due to
direct or indirect poisoning of carabids, or the presence of interspecific competition with ants where insecticides were not applied and ants are present. In addition, six of eight carabid species sampled in the study were present in very low numbers and as a result their absence in a plot may be attributed to sampling error and not necessarily predation.

**Competition.** Presently there is no strong evidence that intra- and inter-specific competition among carabids regulate population levels (Lovei and Sunderland, 1996). However, spiders and ants, which share a generalist surface-active predator guild with carabids, may compete or competitively displace carabid species (Wilson, 1990; Lovei and Sunderland, 1996). In a Finnish study, the abundance of four out of five carabid species was negatively correlated with abundance of *Formica* ants (Neimela, 1990). Kolbe (1968) also observed a dramatic decrease in carabid abundance around the vicinity of *Formica* nests. Moreover, Wilson (1990) postulated that high carabid species richness and abundance in Hawaii resulted from an adaptive radiation that was facilitated by a lack of competitors (ants never colonized the island of Hawaii, the eastern most island of the Pacific archipelagoes). Nevertheless, the lack of propinquity between carabids and ants and high species richness and abundance of carabids on ant depauperate islands is not in and of itself direct evidence of interspecific competition.

**Bottom-up effects.** Top-down factors that affect carabid populations including predation and parasitism were discussed in the previous section. Despite the fact that top-down forces may have significant effects on invertebrate populations, bottom-up forces may also be important in determining abundance of some species (Hunter and Price, 1992; Hunter et al., 1997). Bottom up forces such as host plant quality (Hunter et al. 1997), resource limitation (Root, 1973; Siemann, 1998), plant species diversity
(Murdoch, 1972; Southwood et al., 1979; Symstad et al., 2000; Siemann et al., 1998; Tilman et al. 1997), and plant structure (Dennis, et al., 1997; Brose, 2003; Denno et al., 2002; reviewed in Lawton, 1983) can all influence insect abundance and community composition.

Unfortunately, only a limited number of studies analyze direct bottom-up effects on carabid abundance and diversity. Nevertheless, Brose (2003) found that plant structure had a higher relative impact on carabid diversity than plant species diversity in early successional habitats (in contrast to Southwood et al. 1979 who suggested that plant diversity is more important in determining arthropod diversity in early successional habitats, whereas structural diversity becomes more important in determining arthropod diversity in later stages of succession). Brose (2003) attributed the impact of plant structure on carabid richness to the “enemy-free space hypothesis”, since larger carabid species may be more likely to escape predation in denser vegetation.

**Effects of exotic plants on carabids.** With the collapse of biogeographic barriers due to the global movement of organisms by humans, biological invasions of novel habitats by exotic species have lead to new associations between insects and plants, greatly altering native communities (McEvoy, 2002). Particular carabid species are commonly associated with particular vegetative types (Lovei and Sunderland, 1996; Thiele, 1977), thus the loss of suitable plant habitat and microclimate after invasion by exotic organisms, especially plants, may result in alterations in carabid community structure. For example, Herrera and Dudley (2003) found that carabids were more abundant in native riparian areas of California compared to riparian areas that were highly invaded by an exotic perennial grass (*Arundo donax*). The authors hypothesized
that a reduction in habitat heterogeneity (e.g. a more complex and thicker litter layer occurs at native sites) could be a major factor contributing to the observed reductions in ground arthropods among *Arundo* patches. Alternatively, Ellis et al (2000) concluded that the invasion of salt cedar (*Tamarix*) in riparian systems of New Mexico either did not affect abundance or increased abundance of carabids overall.

**Effects of herbicides on carabids.** Brust (1990) conducted a comprehensive laboratory, greenhouse, and field experiment examining the effects of four herbicides (atrazine, paraquat, simazine, and glyphosate) on five common carabid genera (*Amara* sp., *Agonum* sp., *Pterostichus* sp., *Anisodactylus* sp., and *Harpalus* sp.). Laboratory results found that none of the herbicides (all applied at recommended rates) produced acute (first two weeks) or chronic (from fifteen days up to a year) effects on carabid survival, longevity, or food consumption (all carabid species and sexes). Nonetheless, Brust (1990) warned that these results should not be generalized to all carabid species. In contrast to Brust’s findings and in line with his warning against generalizations of results, Muller (1971) found that nine different herbicides (applied in concentrations above current recommended field rates) had toxic effects on small carabid species, mainly those within the genus *Bembidion*.

In greenhouse choice experiments, Brust (1990) found that the herbicides atrazine and simazine had a repellant effect on carabids for up to three days. Likewise, Muller (1971) reported a repellant effect of 2.4D and Chlorpropham on *B. femoratum*. Repellant effects in greenhouse trials may translate into increased migration of carabids in the field, which in turn may alter species composition at a site after applications (Thiele, 1977).
Indirect effects of herbicides on carabids have been reported in agricultural fields (Brust, 1990; Prasse, 1985; and Thiele, 1977 and sources cited within). In these habitats it was a reduction in vegetation due to herbicide application and not direct toxic effects that affected the abundance of carabids (primarily large predators) (Brust, 1990). Elimination of plant biomass after application of herbicides is postulated to result in unfavorable microhabitat for larger carabids due to a reduction of prey, canopy cover, and an increase in soil surface temperatures (Brust, 1990; Prasse, 1985; and Thiele, 1977). Smaller carabids, which are typically phytophagous and which generally prefer open habitats, either remained unchanged in abundance (Brust, 1990) or increased in number (Thiele, 1977) after herbicide application.

**Carabids as indicator species**

Carabids have been widely used as indicators of environmental change, especially for assessing the effects of pollutants, degree of habitat destruction (Lovei and Sunderland, 1996; Casale, 1990; Mossakowski et al., 1990; Rushton et al., 1990), successional gradients after harvest treatments, and effects of prescribed burns (Richardson and Holliday, 1982; Grum, 1986; Mader, 1986; Szyszko, 1986; Holliday, 1991; Michaels and McQuillan, 1995; Niemela et al., 1996; Beaudry et al., 1997).

The vast majority of studies on carabids as environmental indicators have focused on carabid body size, species diversity, abundance, and dispersal dynamics to assess environmental change and/or impact, disregarding the interdependence among response variables (abundance of species) to explanatory variables (abiotic and biotic variables). However, with increased computational power and the availability of non-parametric multivariate statistical programs such analyses are now possible.
Fire. Carabids have been widely used as indicators of habitat change following the event of fire (Beaudry et al., 1997; Michaels and McQuillan, 1995; Holliday, 1992; Holliday, 1991; Richardson and Holliday, 1982). Compositional patterns of carabid assemblages after fire and during regeneration are a result of each species' unique dispersal mode, competitive ability, preference for physical components of the environment, and availability of prey (Holliday, 1991). Carabid species found in burned sites shortly after the event of fire are typically macropterous and smaller in size compared with species found later during regeneration (Holliday, 1991). With increasing time after fire, the proportion of brachypterous species at a site increases (Beaudry et al., 1997; Michaels and McQuillan, 1995; Holliday, 1991). It is thought that the increase in proportion of brachypterous species after fire is less affected by rates of immigration and more affected by habitat stability, since brachypterous species occur more often in relatively long-term and stable habitats (Niemela and Spence, 1999). Large brachypterous species may occur more often in stable habitats (i.e. later in succession after fire or in habitats of low fire frequency) compared to ephemeral or recently burned habitats as a consequence of their lower reproductive rates and limited mobility. They also may require certain habitat components only present later in succession after fire (Holliday, 1991).

Forest harvest practices. Carabids have also been used as indicators of habitat change after clearcutting and other forest harvest practices. The major determining factors on composition of carabid assemblages after clearcutting or similar forest harvest practices are dictated by age of forest stand (time since cutting) (Niemela et al., 1996). In recent clearcuts carabid species diversity tends to be high (Butterfield et al., 1995;
Niemela et al., 1996; Michaels and McQuillan, 1995). Conversely, carabid species richness and abundance in intermediate aged stands is often low (Niemela et al., 1996; Michaels and McQuillan, 1995). Low species richness and abundance during the stem-exclusion phase (intermediate age) may be attributed to the advancing simplification of the vegetation and stand structure. However, once forest succession progresses past the stem exclusion phase, carabid diversity increases due to an increased incidence of patch disturbances that create a diversity of successional stages and niches (Niemela et al., 1996; Michaels and McQuillan, 1995).

**Habitat destruction.** Carabids have also been used as indicators of the impacts of habitat destruction. Mossakowski et al. (1990) investigated the effects of habitat destruction (caused by military tanks) by analyzing carabid species richness. The number of species increased with increasing gradients of destruction (though sites experiencing the highest degree of destruction contained no carabids). It has been hypothesized that this positive correlation between species number and disturbance level is a result of increasing heterogeneity within the environment (e.g. the tank destruction created a matrix containing open and sandy patches). However, only species associated with one type of functional trophic group (macropterous polyphagous phytophages) responded positively to increased disturbance gradients whereas species in other trophic functional groups decreased in species number. Macropterous polyphagous phytophages are adapted to open, dry, low seral, and weedy type habitats as a result of their high dispersal ability (quickly recolonizes sites) in addition to their aptitude to consume a wide variety of vegetative materials. Accordingly, the mechanism responsible for an increase in species richness may be attributed more to niche partitioning as a result of this particular
trophic functional group's specializations to disturbed environments rather than heterogeneity of the environment.

**Habitat change from agricultural management.** Rushton et al. (1990) demonstrated the usefulness of carabids as indicators of various intensities of agricultural management in grasslands. Carabid assemblages at sites receiving different agricultural and pastoral management treatments were compared. Different carabid assemblages resulted depending on the intensity of management. Some species showed a negative correlation with increasing level of site management intensity. These species were mainly dominated by large, brachypterous species (such as those in the genus *Carabus*). One large brachypterous species (*Carabus violaceus*), however, did occur in intermediate management sites, but its presence there could be associated to its annual rhythm type. *Carabus violaceus* is an autumn breeder, whereas the other large, brachypterous species (e.g. *Carabus* species) breed in the spring. This difference in biology allows autumn breeding species to tolerate intermediate disturbance since autumn is a time of reduced disturbance in mid-intensity agricultural and pastoral landscapes. Some species that were primarily macropterous showed a positive correlation with increasing levels of management intensity (though all carabids avoided sites of extreme management intensity).

Ease of sampling, sensitivity to environmental gradients, short generation times and high fecundity, and well-known taxonomy and ecological requirements support the use of carabids as biologically meaningful indicators of environmental condition.
OBJECTIVES

Long-term objective: To understand the impacts biological invasions have on native communities.

Project objective: To characterize and describe the effects of spotted knapweed invasion and restoration treatments on ground beetle diversity and abundance in Rocky Mountain savannas.

Sub objectives:

(1) **Determine if and how spotted knapweed invasion affects carabid abundance and diversity.** In this part of my research, I placed carabid species into functional groups to compare their diversity and abundance between invaded and native sites. By delineating species into functional groups (based on species' life history, trophic group, and whether exotic or native) potential bottom-up effects of spotted knapweed on carabid populations can more easily be detected. Changes in functional group abundance can indicate direct or indirect bottom-up effects of spotted knapweed. Such effects can include changes in food availability due to a reduction in plant species diversity (thereby directly impacting phytophagous carabids or indirectly impacting predators by limiting their phytophagous prey). Bottom-up effects of spotted knapweed may also occur through changes in plant structure (simplification of vegetation), thereby increasing predation of particular carabid species (“enemy-free space hypothesis”), increasing hunting efficiency of predators (“hunting efficiency hypothesis”), or decreasing specialized niche spaces of particular species (“micro-habitat specialization hypothesis”).

(2) **Describe the relative value of different carabid assemblages found in Rocky Mountain savannas for indicating particular environmental conditions including the presence and absence of spotted knapweed.** For this part of my research, changes in carabid species distributions and abundances were related to important abiotic and biotic variables, including relative abundance of spotted knapweed, to determine which abiotic and biotic variables (explanatory variables) are the most
important for the composite change of abundance and distribution of all species (species composition and structure) (multivariate dependent variables). Therefore, particular species assemblages may indicate differences in environmental conditions between spotted knapweed-invaded and native sites.

(3) Determine if and how restoration treatments of spotted knapweed invaded savannas affect carabid abundance and diversity. One potential evaluation technique for the assessment of restoration success is the use of indicator species. Indicator species have been successfully used in site comparison studies to identify degrees of ecosystem change and condition, and to evaluate restoration efficacy. Indicator species and assemblages can be used to provide a gauge of restoration efficacy by using them to track changes in habitats after restoration treatments, and to identify whether or not an ecosystem is developing along a pre-identified desired trajectory (often a historical reference or a native site). In this part of my research, I used carabid diversity and abundance in native and knapweed-invaded sites to detect differences between reference sites (the desired reference condition, i.e. native sites) and restored sites. Differences in abundances of particular indicator species can indirectly indicate differences in particular abiotic and biotic factors between reference and restored sites. Changes in carabid species distributions and abundances were also related to important abiotic and biotic variables.
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CHAPTER TWO: Effects of spotted knapweed invasion on ground beetle (Coleoptera: Carabidae) assemblages in Rocky Mountain savannas

ABSTRACT

Biological invasions are known to alter native communities, yet evidence on effects of spotted knapweed invasion (a highly invasive exotic forb in western U.S. and Canada) on heterotroph communities is lacking even though bottom-up or indirect effects are likely to result. Here, I examine how spotted knapweed invasion affects carabid species and functional group diversity, community composition and structure (abundance), and relate carabid species assemblages in Rocky Mountain savannas to important abiotic and biotic variables, including the presence of spotted knapweed. Six study sites, three with high levels of spotted knapweed (invaded) and three with trace amounts of spotted knapweed (native), were established in Rocky Mountain savannas in MT. Carabid species abundance and environmental measurements were collected in 1999 and 2000 at 52 pitfall traps per site. Carabid species richness was similar between invaded and native sites; however evenness was significantly different for both carabid species and functional groups between invaded and native sites. Beta diversity was higher among native sites relative to invaded sites for both indices. Carabid species and functional group composition and structure differed significantly between invaded and native sample units. Carabid species composition and structure was more homogenous among invaded sample units relative to native sample units. Carabid functional group shifts between invaded and native sites were largely responsible for alterations in carabid species assemblages. Polyphagous phytophages and specialist predators were more abundant and indicated invaded sites, and generalist predators were more abundant and indicated native sites. Spotted knapweed invasion simplified carabid functional group evenness and influenced trophic groups differentially. In addition, carabid assemblages were more homogenous among invaded sites relative to native sites, and species distribution was mainly associated with cover of spotted knapweed, soil moisture, and ground structural components. As a result increased spotted knapweed invasion in Rocky Mountain savannas may lead to homogenous carabid assemblages on a landscape level.

INTRODUCTION

Biological invasions are becoming increasingly common worldwide. The collapse of biogeographic barriers due to increased global movement of organisms by humans has allowed invasions by nonindigenous organisms into novel habitats leading to new
associations between native and exotic biota, and in the process has often resulted in the alteration of native communities (McEvoy, 2002). Interactions among exotic organisms and their new environment can result in ecological and evolutionary shifts that may create new biotic community structures and compositions as well as direct and indirect alterations of the physical environment. Exotic species may influence indigenous species richness and abundance either directly through competition (Smith, 2005), predation (Grosholz et al, 2000), parasitism (Prenter et al, 2004), and effects on food availability (Schreiber et al., 2002), and/or indirectly through effects on trophic cascades and habitat modification (Crooks, 2002).

Spotted knapweed (*Centaurea maculosa* Lam.), an Eurasian perennial forb, is considered to be one of the most ecologically damaging invasive plants in western North America due to its extensive distribution (currently over seven million acres in the U.S. and Canada are invaded) (Duncan, 2001) and extreme negative effects on native communities (Rice et al., 1997). In the northern Rocky Mountains, spotted knapweed primarily threatens mixed bunchgrass and forb communities of prairies and savannas (Tyser, 1992). Once established, spotted knapweed forms dense, near monoculture stands. Direct and indirect effects of spotted knapweed invasion on ecosystem processes and functions include alterations in soil chemistry (LeJeune and Seastedt, 2001), changes in fire and hydrological regimes (Jacobs and Sheley, 1998; Randall, 1996), and increased soil erosion, sedimentation, and water run-off (Lacey et al. 1989). Effects of spotted knapweed invasion on autotroph community structure consist of a reduction in native plant diversity (Tyser and Key, 1988; Tyser, 1992; Ortega and Pearson, 2005), and a decrease in native forb, graminoid, and cryptogam cover (Tyser, 1992). Evidence on
effects of spotted knapweed invasion on heterotroph communities is lacking although bottom-up or indirect effects are likely to result. One group of heterotrophs that may be affected directly or indirectly by exotic plant invasions is insects (McEvoy, 2002). Insects play critical roles in determining ecosystem structure and function (Wilson, 1990; Wilson, 1992). Therefore, cascading effects resulting from altered insect communities due to invasive plants may influence entire systems.

The diversity of affected organisms and the complexity of native ecosystems make the characterization of the many direct and indirect effects of biological invasions difficult. However, by studying particular groups of organisms in affected communities that encompass diverse trophic groups (Bisevac and Majer, 1999; Williams, 2000), exhibit broad to narrow environmental amplitudes, possess high to low dispersal abilities, and are present in relatively high abundances (Caro and O'Doherty 1999) we can begin to characterize many cause and effect relationships in invaded systems. Ideally, organisms used to study impacts should have well-known biologies so that changes in their diversity and abundance can be related to changes in the environment. The species should also be easy to monitor (Caro and O'Doherty 1999). Many insects, including ground beetles (Carabidae), fit these criteria well. Carabids exhibit distinctive species-specific habitat requirements, short generation times, and high fecundity relative to many other organisms (Niemela, et al 2000) making them excellent organisms to investigate indirect and direct effects of spotted knapweed invasion.

Carabids are speciose, abundant, well-studied, easy to sample, and ubiquitous in most terrestrial habitats (Lindroth, 1961-1969; Thiele, 1977; Lovei and Sunderland, 1996). Carabids can be easily sampled using pitfall traps, and their taxonomy and
ecological requirements are well known (Thiele, 1977; Grum, 1986; Lovei and Sunderland, 1996; Lindroth, 1961-1969). Because of their ubiquity, sensitivity to environmental gradients, and ease of sampling, carabids are ideal insect candidates to examine for community effects of spotted knapweed invasion. Because carabids include more than one trophic group (Lovei and Sunderland, 1996), they can be used to assess indirect and direct effects of spotted knapweed invasion at several levels. Additionally, environmental changes caused by spotted knapweed may uniquely influence the distribution of carabids since many species are sensitive to environmental gradients. For example, the distribution and abundance of these ground-dwelling arthropods is largely determined by their extreme sensitivity to temperature, humidity, soil characteristics, amount of litter, food availability, plant architecture, and season (Brose, 2003; Lovei and Sunderland, 1996; Holliday, 1991; Maelfait and Desender, 1990; Rushton et al., 1990; Butterfield et al., 1995). Therefore, carabids may serve as sensitive gauges of ecological change caused by the invasion of spotted knapweed.

The primary objectives of my research were to determine how spotted knapweed invasion affects carabid species and functional group diversity, how carabid community composition and structure varies between invaded and native sites, and to relate carabid community composition and structure in Rocky Mountain savannas to abiotic and biotic variables, including the presence of spotted knapweed.

METHODS

Study sites

Six study sites, each ranging from 5-6 ha in size, were established on the Lolo National Forest in Missoula and Mineral Counties, MT. Three sites were moderately...
invaded with *C. maculosa* (the main exotic forb on sites) and three sites were invaded by only trace amounts of *C. maculosa* (hereafter referred to as native sites). Each study site consisted of sparsely forested grassland (ponderosa pine and Douglas-fir savanna) located within a matrix of denser Douglas-fir dominated forest. Common bunchgrasses occurring within these grasslands were bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg’s bluegrass (*Poa sandbergii* Vasey), and June grass (*Koeleria cristata* Pers.). Dominant native forbs occurring at the sites were arrowleaf balsamroot (*Balsamorhiza sagittata* Pursh (Nutt.)), lupine (*Lupinus spp.*), yarrow (*Achillea millefolium* L.), and blue-eyed Mary (*Collinsia parviflora* Lindl.). Sites were chosen that possessed similar physiographic characteristics including elevation (between 1300 and 1700m), soils, slope (30% average), and aspect (southwest). Soil types, classified to family, were determined using the Lolo National Forest Land Systems Inventory (1989). Soils at all sites were Inceptisols weathered from metasedimentary bedrock parent material. Twelve families of soil types were found to occur in total across sites.

*Collection and identification of carabids*

Pitfall traps were deployed at each of the six sites in 1999 and 2000 to sample the relative abundance of carabids. Traps were placed at equidistant spacing (20m) along four 250 m transects with a total of 13 traps per transect (52 per site). Transects ran perpendicular to the slope and were located 50 m apart. Four collection periods, each lasting for two-weeks, were chosen for sampling from mid-May until late September to ensure that peak dispersal periods of all carabid species would be sampled. Pitfall traps were made from 2L colorless plastic soda bottles, cut in half with the upper portion
inverted into the lower to act as a funnel. Traps were placed even with the soil surface. A 1% formalin solution was added to each trap to retard rotting of trapped insects during each two week trapping period.

Carabids were sorted from samples, counted, and identified to species based on Lindroth (1961-1969). Species identifications were verified by Dr. George E. Ball of the University of Alberta. All species were placed into functional groups based on life history, trophic level, and whether they were endemic or exotic. These traits were chosen to categorize carabids into functional groups since they have been shown to be important response variables to ecosystem change and disturbance (Richardson and Holliday, 1982; Grum, 1986; Mader, 1986; Szyszko, 1986; Casale, 1990; Mossakowski et al., 1990; Rushton et al., 1990; Holliday, 1991; Michaels and McQuillan, 1995; Niemela et al., 1996; Beaudry et al., 1997). Four functional groups were created: specialist predators, generalist predators, polyphagous phytophages (generalist herbivores), and exotic species (with 2, 6, 12, and 1 species falling within each group, respectively).

Vegetation measurements

Understory vegetation was measured in 5 m radius fixed plots established around each pitfall trap at each site. Ocular estimates were made of percent cover for the following plant functional groups: shrubs, native forbs, bunchgrasses, spotted knapweed, and cheatgrass (Bromus tectorum L.). Overstory vegetation was measured in trees per plot.

Physical environmental measurements

Soil moisture retention curves were estimated for all sites in June of 2004. A soil moisture retention curve relates soil moisture content to the soil’s matrix potential (the
amount of energy required to remove water from soil pores). The soil moisture retention relationship is important to quantify soil moisture availability in soils. Available soil moisture (amount of water released between -0.3 bar and -15 bar) is largely dependent on soil properties such as texture, structure, and organic matter within the soil (Klute, 1986). A soil moisture retention relationship was determined for each site to allow comparisons of soil moisture availability among sites. To do this, a soil probe was used to extract 3 cm diameter soil cores from the mineral soil line to a depth of 15.24 cm at each site. Two cores were randomly extracted along each of the four transects per site for a total of eight cores per site. Soil cores were oven dried at 80°C and individually sieved through a 2.0 mm screen. Each individual core was divided into five sub-samples for measuring soil moisture retention at five potential values (-0.3, -1, -5, -10, and -15 bar). A cellulose membrane pressure cell was used to measure water retention from -1 bar to -15 bar and a ceramic plate pressure cell was used to measure water retention at the potential value of -0.3 bar. The five potential values found per core were averaged by transect resulting in four sample units per site each consisting of five potential values. Each sample unit consisted of five continuous variables (potential values) for use in nonparametric multivariate analyses.

Soil types were determined for each site using the Lolo National Forest Land Systems Inventory (1989). Presence or absence of the various soil types found among all sites were determined for each site to form a total of twelve binary variables per site for use in nonparametric multivariate analysis.

Site variables such as bare ground, rock, woody debris, litter, and slope were measured in 1999 and 2000 at each site within a 5 m radius circular plot around each
pitfall trap. Percent bare ground (un-vegetated open ground), rock (surface rocks of fist size or larger), and woody debris (≥15 cm diameter (coarse) versus <15 cm diameter (fine)), were ocularly estimated to the nearest 1%, and litter was measured (depth to nearest 0.5 cm). Topography was classified as concave, convex, or flat, by describing the 5-m plot as compared to the area immediately surrounding it.

DATA ANALYSIS*

Carabid Diversity

Total abundance for each carabid species and functional group was calculated by pooling trap captures for each individual pitfall trap over all four sampling periods per year. Diversity measurements were calculated at each site for each carabid species and functional group using two metrics of species diversity (richness and evenness) independently to aid in elucidating community patterns. Because patterns of species richness and evenness are likely to be influenced by different mechanisms (Stirling and Wilsey, 2001), assessing them separately allows better discrimination of the processes that lead to alterations in community composition and structure (relative abundance). To determine whether species richness had been adequately sampled at each of the study sites, species accumulation curves were developed from the pitfall trap capture data (Magurran, 1988; Magurran, 2004). Species accumulation curves indicated that sampling was sufficient to capture species richness at five of the six sites. The first order jackknife estimate (Heltshe and Forrester, 1983) was used to assess estimated species richness for each site. The first order jackknife estimate is a non-parametric re-sampling method for

* See Appendix A for the extended data analysis

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estimating species richness and is resistant to bias caused by contagious distributions (Magurran, 1988). Moreover, the first order jackknife is the most precise and least biased method for predicting species richness when sample size is large (Palmer, 1990). The first order jackknife estimate is given as:

\[ S = S(\text{obs}) + L((n-1)/n) \]

Where \( L \) is the number of species only captured in one sample, \( S(\text{obs}) \) is the observed species number and \( n \) is the number of samples.

Evenness of carabid species and functional groups at each site was estimated using Simpson’s measure of evenness \( (E_{1/D}) \), which is simply the reciprocal form of Simpson’s dominance index \( (D) \) (Simpson, 1949) divided by the number of species in the sample (Smith and Wilson, 1996; Magurran, 2004). \( E_{1/D} \) ranges from 0-1 (zero represents minimum evenness) and is one of the best evenness measures available that is truly independent of species richness and weights rare and dominant species equally (Smith and Wilson, 1996; Magurran, 2004).

All diversity indices and confidence intervals were calculated using Species Diversity and Richness version 2.65 (Pisces Conservation, Ltd, UK). Bootstrapping was used to generate standard errors and 95% confidence limits. A two-tailed paired-sample t-test was used to define the mean population difference between observed and estimated species richness within sites. Two-sample t-tests were used to test mean differences of carabid species richness and species and functional group evenness between knapweed invaded and native sites (SPSS Inc., 2001).

Beta diversity, the amount of variation in species composition and structure among sites (Whittaker, 1972), was obtained using two estimators. First, I used average
within group distance (D), as a descriptor of compositional and structural change in n-dimensional hyperspace. D is a dissimilarity proportional coefficient based on Sorensen (Bray & Curtis) distance and was calculated by Multi-Response Permutation Procedures (MRPP) (described below). The second calculation of beta diversity, average half-changes $\beta_D$, uses D by linearizing its relationship with Beta diversity half changes, thereby improving the scale of dissimilarity (McCune and Grace, 2002). One half change is the amount of compositional and structural change resulting in 50% dissimilarity among habitats. Where $\beta_D$ is:

$$\beta_D = \frac{\log(1 - D)}{\log(0.5)}$$

Community analysis

For univariate analyses comparing abundance of carabid functional groups between invaded and native sites, Kruskal-Wallis test (Kruskal and Wallis, 1952) was used because data were not normal and could not be normalized through transformation, and did not display homoscedasticity (SPSS Inc., 2001). For multivariate analyses, PC-ORD, version 4.25 (McCune and Mefford, 1999) was used. For univariate and multivariate analyses carabid abundance for pitfall traps were pooled by transect, and environmental measurements around pitfall traps were averaged by transect resulting in four sample units per study site. Rare species (occurred in less than 5% of pitfall traps) were not included in multivariate analyses to reduce noise and enhance detection of community patterns (McCune and Grace, 2002). Only non-parametric multivariate analyses were used to analyze effects of spotted knapweed on species abundance as species distributions were positively skewed and data were discontinuous.
MRPP (Mielke, 1984), a non-parametric permutation procedure, was used to test for differences among a priori groups of knapweed-invaded and native sites by soil type, carabid functional group, and carabid species composition. Sorensen’s dissimilarity measure was chosen for MRPP to calculate the average distance within each group since this measure is robust for community data (McCune and Grace, 2002). The weighting used for MRPP to calculate Delta (weighted mean within group distance) was n/sum(n) (Mielke, 1984).

Indicator species analysis (ISA) (Dufrene and Legendre, 1997) was used to identify the species that best described differences between invaded and native sites based on two independent measurements of species distribution, specificity and fidelity (i.e. a species was specific to a particular group (specificity) and sampled abundantly and widespread in all samples of that group (fidelity)). The typology used for this analysis was a priori based on invaded and native sites. Potential indicator values (Inval) that can result from ISA can range from 0-100 where values > 25 signify a good indicator (Dufrene and Legendre, 1997). Significance of indicator values was estimated using Monte Carlo randomization set at 1000 permutations.

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1978) was used to relate carabid species assemblages among sample units in invaded and native sites. NMS was also used to relate soil-water response curves among all sample units in invaded and native sites for use in correlation analyses with carabid NMS axes. NMS iteratively searches for the best solution in a reduced dimensional space by minimizing departure from monotonicity from the dissimilarity distance in original dimensional space and the distance measure in reduced dimensional space (i.e. reducing stress) (McCune
and Grace, 2002). Kruskal's least squares monotonic transformation (Kruskal, 1964; Mather, 1976) was used to minimize stress. Sorensen's dissimilarity measure was used to calculate distances between sample units. A random number generator was used to calculate the starting coordinates for all sample units for each run. I conducted forty runs with real data stepping down in dimension from six axes to one axis for each run. A maximum of 400 iterations per run was used. Stress versus iteration number was plotted to assess the stability of the solution with 0.00001 as the stability criterion. To assess the dimensionality of each data set, the final stress versus the number of dimensions was plotted, and 50 randomized Monte Carlo permutations were implemented. Monte Carlo permutations were used to assess the probability that a similar final stress could be expected by chance for a particular dimension. Pearson's $r^2$ was used to correlate sample unit distances in a reduced dimensional space with distances in the original dimensional space to describe the percent of variation explained by the ordination.

To determine how carabid community structure related to environmental variables, Pearson product correlation analyses were performed using the carabid NMS axes. Prior to analysis, the constant 1 was added to nonnormal environmental values to accommodate zeros in the data set. Values were then log transformed. All statistical analyses were set at a significance level of alpha= 0.05. Only specialist predator dispersal peaks were captured in 2000 due to missing samples confining analysis only to specialist predator univariate tests in 2000.
Results

Carabid diversity

Observed and estimated carabid species richness differed significantly within sites (paired sample t-test: t=-3.141; df=5; P=0.026), however both observed and estimated richness did not differ significantly between invaded and native sites (two sample t-test: t=-.802 and -.763; df= 4 and 4; P=0.468 and 0.513, respectively) (Fig. 1, Table 1). Nevertheless, evenness was significantly different between invaded and native sites for both carabid species and functional groups (Fig. 2 and 3, Table 1). Species evenness was significantly higher in invaded sites than in native sites (two sample t-test: t=-2.743; df= 4; P=0.05) (Fig. 2). This higher evenness was related to a higher abundance of most carabid species which belonged to specialist predator and polyphagous phytophage functional groups in invaded sites relative to native sites. Conversely, most generalist predator species were lower in abundance in invaded sites compared to native sites.

Functional group evenness was significantly higher in invaded sites compared to native sites (two sample t-test: t= 8.391; df=4; P=0.001) (Fig. 3). This was because polyphagous phytophage and specialist predator functional groups were highly abundant (i.e. more dominant) whereas the generalist predator functional group was lower in abundance in invaded sites relative to native sites.

Univariate analyses and ISA results revealed differences in functional group abundances and species distributions between invaded and native sites. The generalist predator functional group was less abundant (Kruskal Wallis; P=0.007) in invaded sites, whereas specialist predator and phytophagous phytophage functional groups were more abundant (Kruskal Wallis; P=0.034 and P=0.166, respectively) in invaded sites (Fig. 4.

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There was no significant difference in exotic functional group abundance between invaded and native sites (Kruskal Wallis; \( P=0.93 \)) (Fig. 4, Table 2). In ISA two generalist predator species were good indicators of native sites (ISA: Indval= 66.7 and 74.0; \( P= 0.0030 \) and 0.0190 respectively) (Fig. 5). Conversely, one specialist predator and four phytophagous phytophage species were good indicators of spotted knapweed invaded sites (ISA: Inval= 74.4, 64.6, 69.9, 71.2, 73.6, and 74.4; \( P=0.0080, 0.0070, 0.0590, 0.0040, \) and 0.0080 respectively) (Fig. 5).

Beta diversity was higher in native sites than invaded sites for both \( D \) (0.49 and 0.41, respectively) and \( \beta_D \) (about 1 half change versus a 0.76 half change, respectively) (Table 1).

**Community structure and composition**

Multivariate analysis

Carabid community composition and structure analyzed by species was significantly different between invaded and native sites (MRPP: \( T= -3.87, A=0.06, P=0.0042 \)). Carabid functional group composition and structure was also significantly different between invaded and native sites (MRPP: \( T= -3.04, A=0.07, P= 0.0161 \)).

A NMS ordination of carabid species composition and structure yielded a 2-dimensional solution that explained 86% of the variation in the raw data with a final stress of 13.6, and a final instability of 0.00172 (\( P=0.0196 \)). Invaded sample units separated from most of the native sample units in species space except for some sample units in one of the native sites (N1) (Fig. 6). Separation of carabid species composition and structure between invaded and native sites was significant (MRPP, \( T= -3.87, A=0.06, P=0.0042 \)).
P=0.0042). In addition, invaded sample units clustered more tightly together in ordination space than native sample units, suggesting that species composition and structure is more homogenous in invaded sites compared to native sites (Fig. 6). These ordination results are corroborated by MRPP results; native sample units had a higher within group dissimilarity distance (D) than invaded sites (Table 1).

**Abiotic and biotic variables**

Soil type was not significantly different between invaded and native sites (MRPP: T= -1.32, A=0.189, P=0.10). A NMS ordination of soil-water response curves yielded a 2-dimensional solution that explained 97.4% of the variation in the raw data with a final stress of 8.158, and a final instability of 0.0000 (P=0.0196). Based on carabid NMS axis scores, carabid community composition and structure among sample units in invaded and native sites had a strong relationship to spotted knapweed cover, trees per acre, rock, litter, woody debris, and soil-moisture NMS axes (Table 3).

**DISCUSSION**

*Effects of spotted knapweed invasion on carabid diversity and abundance*

Although carabid species richness was similar between invaded and native sites, evenness was significantly different, suggesting that different mechanisms may be responsible for explaining the two metrics of carabid diversity in spotted knapweed invaded and native savannas. Consequently, richness and evenness should be examined independently in future studies to provide meaningful results when characterizing community patterns (Whittaker, 1965; Hurlbert, 1971; Legendre and Legendre, 1998;
Weiher and Keddy, 1999). Furthermore, patterns of species and functional group evenness were not similar for invaded and native sites (Figs. 2, 3).

The lack of correspondence between functional and species diversity is not surprising. Pletchey and Gaston (2002) found, using simulations, that species and functional diversity measures are not always in agreement because compositional differences may occur in communities that have equal numbers of species. For example, a community composed of 20 species that contains few functional groups has lower functional group diversity than a community with the same number of species but with a higher number of functional groups. As a result, functional diversity does not directly depend on the number of species but instead redundancy of species within functional groups (e.g. for a given number of species high species redundancy within functional groups results in lower functional group diversity) (Pletchey and Gaston, 2002).

Functional group diversity may be a more useful measure of ecological impacts than species diversity because in functional groups functional roles and traits of included species are based on life history and ecological tolerances not on phylogenetic classification. Consequently, when analyzing effects on communities by invasive organisms such as spotted knapweed, functional groups act as sensitive response variables and may serve as better gauges of compositional change compared with species (Olden, 2004).

In this study, patterns of carabid functional group diversity and species abundance between invaded and native sites are very similar to patterns found in previous studies analyzing the effects of disturbance and succession on carabid assemblages (Richardson and Holliday, 1982; Grum, 1986; Mader, 1986; Szyszko, 1986; Casale, 1990;
Mossakowski et al., 1990; Rushton et al., 1990; Holliday, 1991; Michaels and McQuillan, 1995; Niemela et al., 1996; Beaudry et al., 1997). Carabid species composition and structure is largely determined by each species’ life history attributes, preference for physical components of the environment, and availability of food. For example, in my study as well as in previous studies, it was found that long-winged polyphagous phytophages respond positively to increasing disturbance whereas species in other functional groups such as short-winged predators typically decrease in species richness and abundance as disturbance increases (Rushton et al., 1990; Holliday, 1991; Michaels and McQuillan, 1995; Niemela et al., 1996). Long-winged polyphagous phytophages are adapted to open, dry, low seral, and weedy habitats. They are adapted to lower soil moisture conditions, have the ability to consume a wide variety of vegetative materials including seeds of weedy vegetation, and they display high dispersal capabilities which allow them to quickly recolonize low seral habitats (Lindroth, 1961-1969; Thiele, 1977).

Predators often occur in habitats of later successional stages or in habitats that experience low frequency or low intensity disturbances (Niemela and Spence, 1999). This may be a consequence of their lower reproductive rates and more limited mobility in comparison with polyphagous phytophages, and because many require specific habitat components only present in late succession habitats (Holliday, 1991). Consequently, patterns of carabid functional group diversity and abundance between invaded and native sites detected in this study are very similar to patterns found in previous studies looking at effects of disturbance and successional gradients on carabids. In this study phytophagous phytophages were found to favor invaded habitats while generalist predators favored native habitats.
In contrast to generalist predators, specialist predators favored invaded sites relative to native sites in my study. Species within the specialist predator functional group (*Calosoma* spp.) specialize on Lepidoptera. Therefore, increases in these species may indicate that spotted knapweed supports an increase in the availability of their prey (Lepidoptera). An increased presence of native Noctuidae larvae was observed around spotted knapweed root balls and rosettes, and in turn, may supplement specialist predator food availability (especially since both specialist predators and Noctuidae larvae are nocturnal).

**Homogenization of carabid assemblages**

In this study, carabid assemblages were more diverse and heterogeneous in native sites than in invaded sites based on beta diversity and ordination results (Table 1, Figs. 3, 5,6). Low beta diversity, as found among invaded sites, results not only from low species compositional change but also when the same species consistently dominate sites (Magurran 2004). In this study, this was apparent in the invaded sites where polyphagous phytophage and specialist predator species were consistently more abundant in invaded sites relative to native sites. The carabid NMS ordination results in this study visually illustrate this concept of homogenization of carabid assemblages among invaded sites relative to native sites: invaded sample units clustered closer together in species space than did native sample units. Magurran (2004) hypothesizes that homogenous assemblages may result when a site is disturbed since only a particular subset of species that can tolerate rapidly changing environmental and ecological conditions can prevail.

*Relationships of abiotic and biotic variables to carabid assemblages*
Although soil types were not statistically different between invaded and native sites, soil-moisture response curves, which are a function of soil texture, structure, and organic matter, were unique for each site.* NMS axes derived from soil-moisture response curves showed a strong relationship to carabid community structure (Table 1). In addition, spotted knapweed cover, litter, rock, woody debris, and trees per acre also showed strong relationships to carabid community structure (Table 3). Interestingly, cover of spotted knapweed and one of the NMS soil-moisture response curve axes were highly correlated. Whether soil characteristics determine spotted knapweed distribution or spotted knapweed influences soil characteristics cannot be determined from my data. However, spotted knapweed is known to alter the organic matter and structure of soil (a function of soil moisture potential) (Lacey et al. 1989), which may in turn influence carabid distribution and community structure. Most likely environmental variables have synergistic direct and indirect effects with one another in determining carabid community structure.

Simplification of community composition as a result of biological invasions (i.e. biotic homogenization) has been reported in various systems for an array of taxonomic groups (Olden, et al. 2004). Even though biotic homogenization has been a trend over geologic time (Vermeij, 1991) global trade has accelerated current rates of the homogenization relative to historic rates by increasing the introduction of exotic species (Elton, 1958; Williamson, 1996; Vitousek et al., 1997; Mack et al., 2000). Consequently, homogenization of communities due to invasive species has fundamental implications for conservation and theory of invasion biology.

* See Appendix B for soil moisture response curves among all sites
Increased spotted knapweed invasion in Rocky Mountain savannas may lead to homogenous carabid assemblages on a landscape level. Potentially, native communities contain a mosaic of functional assemblages on a landscape level, which is maintained by natural variability due in part to fine-scale and coarse scale disturbances (e.g. rodent burrows and frost heaving of soils) and spatial variability in microscale environmental factors (e.g. soil characteristics, ground structural components, and vegetative types). In contrast to disturbance events, biological invasions are likely to permanently affect a community and may irreversibly reduce functional group variability of carabid assemblages. As spotted knapweed invades savannas, increased homogenization may occur within carabid assemblages by creating a favorable environment for some functional groups at the expense of others, thus lowering functional group diversity. Future research examining the effects of biological invasions on communities should consider the use of functional groups as response variables since functional groups serve as better gauges of ecological change compared to species diversity.

Spotted knapweed not only influences disturbance regimes and autotroph community structure, but it also affects heterotroph community structure. Alterations in heterotroph functional diversity may have subsequent effects on other biota by influencing the flow of energy, thereby altering food webs. If spotted knapweed homogenizes species composition on a community level, only a subset of opportunistic species will prevail while vulnerable species populations will decrease in abundance.
ACKNOWLEDGEMENTS

Yvette Ortega (Forest Service) was a major collaborator on this overall project and provided essential logistical assistance in addition to organizing field crews and conducting field sampling and field measurements. Dr. Diana L. Six provided crucial guidance and encouragement on this manuscript. George E. Ball provided valuable assistance on carabid species identifications. Dr. Tom DeLuca, Dr. Paul Alaback, Dr. Scott Mills, Doug Emlen, and Kerry Metlen offered helpful advice. This research was funded by Wildlife Ecology Research Unit of the Rocky Mountain Research Station, and the Bitterroot Ecosystem Management Research Project.
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Fig. 2.1 Mean observed and estimated species richness between invaded and native sites. Richness estimator used was the first order Jackknife. Error bar is +/- 1 standard deviation of the mean. n=3
Table 2.1 Carabid Diversity in spotted knapweed-invaded vs. native savanna sites in western Montana.

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional Group</th>
<th>Beta diversity^4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed richness</td>
<td>Estimated richness (sd)^2</td>
</tr>
<tr>
<td>Native:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N1</td>
<td>52</td>
<td>19</td>
</tr>
<tr>
<td>N2</td>
<td>52</td>
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<td>N3</td>
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<td>20</td>
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<td>Mean</td>
<td>52</td>
<td>19</td>
</tr>
<tr>
<td>Overall</td>
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</tr>
<tr>
<td>Invaded:</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>52</td>
<td>18</td>
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<td>Inv3</td>
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<td>20</td>
</tr>
<tr>
<td>Mean</td>
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<td>20</td>
</tr>
<tr>
<td>Overall</td>
<td>156</td>
<td></td>
</tr>
</tbody>
</table>

^1 N= number of pitfall traps/plots  
^2 Estimated richness was calculated using the first order Jackknife estimator,  
^3 Average half-changes= log (1-Average w/in group distance) /log (0.5)  
^4 E_{(1/D)} is the Simpson’s evenness measure.
Table 2.2  Kruskal Wallis’s test for differences in carabid functional groups between spotted knapweed-invaded versus native savanna sites in western Montana. n=24 sample units

<table>
<thead>
<tr>
<th>Year</th>
<th>Specialist Predator</th>
<th>Generalist Predator</th>
<th>Exotic Phytophage</th>
<th>Polyphagous Phytophage</th>
</tr>
</thead>
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<tr>
<td>1999</td>
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<td>4.888</td>
<td>7.214</td>
<td>0.008</td>
</tr>
<tr>
<td>2000</td>
<td>4.888</td>
<td>7.214</td>
<td>0.008</td>
<td>1.921</td>
</tr>
<tr>
<td>df</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Asymp. Sig.</td>
<td>0.034</td>
<td>0.027</td>
<td>0.007</td>
<td>0.930</td>
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</table>
Fig. 2.2 Simpson's Evenness index for carabids at each site with 95% confidence intervals (Bootstrapping). Inv1, Inv2, and Inv3 are the invaded sites and N1, N2, and N3 are native sites. n=52 pitfall traps
Fig. 2.3 Simpson's Evenness index for carabid functional groups at each site with 95% confidence Intervals (Bootstrapping). Inv1, Inv2, and Inv3 are the invaded sites and N1, N2, and N3 are the native sites. n=52 pitfalls.
Fig. 2.4 Mean carabid abundance in spotted knapweed-invaded and native savanna sites in western Montana. Kruskal-Wallis test for functional group differences between invaded and native sites. * indicates P<0.05. Error bar is +/- one standard error of mean.
Fig. 2.5 Indicator values of species characterizing native and spotted knapweed-invaded sites.

GP = generalist predator, PP = polyphagous phytophage,
and SP = specialist predator. * indicates P = 0.05, ** indicates P < 0.01.
Fig. 2.6 NMS Ordination of carabid assemblages in spotted knapweed-invaded and native savanna sites in western Montana and how they relate to one another among sample units. Two-dimensional solution of carabid assemblages among invaded (Iv) and native (N) sample units. n=24.
Table 2.3  Pearson correlation coefficients among environmental and axis variables. Numbers underlined represent significant correlations at P=0.05, two-tailed test, n=24. Variables are spotted knapweed cover (Knap), Trees per acre (TPA), percent rock (Rk), percent litter (Lit), percent woody debris (WD), soil-moisture retention ordination axes scores (Soil 1, Soil 2), and carabid ordination axes scores (Carabid 1, Carabid 2).

<table>
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<tr>
<th></th>
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<th>TPA</th>
<th>Rk</th>
<th>Lit</th>
<th>WD</th>
<th>Soil 1</th>
<th>Soil 2</th>
<th>Carabid 1</th>
<th>Carabid 2</th>
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<td>Knap</td>
<td>1</td>
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<td></td>
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<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Rk</td>
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<td>.148</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>.372</td>
<td>.513</td>
<td>1</td>
<td></td>
<td></td>
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</tr>
<tr>
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<td>.527</td>
<td>-.156</td>
<td>.308</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<td>Soil 1</td>
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<td>-.152</td>
<td>.435</td>
<td>-.021</td>
<td>-.243</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil 2</td>
<td>.724</td>
<td>-.216</td>
<td>.041</td>
<td>.135</td>
<td>-.179</td>
<td>-.171</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Carabid 1  .489  -.405  .327  .027  -.256  .639  .611  1
Carabid 2  -.135  .393  .457  .471  .424  -.044  -.166  .116  1

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CHAPTER THREE: Effects of herbicide restoration treatments on carabid functional group abundance in spotted knapweed-invaded Rocky Mountain savannas

ABSTRACT

While effects of herbicide treatments on autotroph communities in spotted knapweed-invaded grasslands are well recognized, cascading indirect effects of broadleaf herbicides on heterotroph communities are frequently overlooked. Here, I determine if and how herbicide treatments in spotted knapweed-invaded habitats affect ground beetle (Carabidae) species and functional group composition and structure (abundance). Sixteen study sites, eight invaded with spotted knapweed and eight native, were established in Rocky Mountain savannas in MT. Picloram herbicide was aerially applied in September 2002 to half of the eight spotted knapweed-invaded and half of the eight native sites. The remainder of invaded and native sites were not treated and served as controls. Carabid species abundance data was collected in 2003 at 26 pitfall trapping stations per site. Two-factor ANOVA, Multi-Response Permutation Procedures, and Indicator Species Analysis were used to compare carabid indicator species and functional groups among four experimental treatments: native, no herbicide; native, herbicide; weed, no herbicide; and weed, herbicide. Carabid species and functional group composition and structure differed significantly among all treatments. Generalist predators were significantly more abundant and good indicators of native sites compared to invaded sites, regardless of whether the sites were herbicide-treated or controls. Polyphagous phytophages and specialist predators were significantly more abundant and good indicators of control sites relative to herbicide-treated sites regardless of whether the sites were native or invaded. In the first year after treatment, herbicide treatments alone did not restore invaded habitats back to the same ecological trajectory as native sites in terms of carabid functional group and species composition and structure. A reduction of polyphagous phytophages and specialist predators in treated sites may indicate that the elimination of non-target forbs in herbicide-treated sites can negatively impact dependent organisms. Polyphagous phytophages feed primarily on forbs and the application of picloram, which greatly reduced forb cover in this study, may negatively affect them. A reduction of specialist predators may be linked to concurrent decreases in Lepidoptera prey, which depend on forbs. Moreover, a reduction of generalist predators in invaded sites may indicate that soil biota (the major prey of these predators) may be altered in invaded sites as a result of spotted knapweed-induced changes in ecosystem processes and functions. Herbicide treatments alone did not appear to restore invaded sites to the desired “pre-invasion” condition, at least in terms of carabid communities, in the time frame of this study. Longer term monitoring of herbicide-treated sites will be necessary to determine if such treatments eventually return spotted knapweed-affected sites to pre-invasion conditions, including those of carabid community composition and structure.
INTRODUCTION

Spotted knapweed, an introduced invasive forb from Eurasia, is one of the most ecologically and economically damaging plants in the northwest United States and Canada (Rice et al., 1997). In the northern Rocky Mountains, spotted knapweed alters ecosystem processes and functions (LeJeune and Seastedt, 2001; Jacobs and Sheley, 1998; Randall, 1996; Lacey et al. 1989), in addition to autotroph (Tyser and Key, 1988; Tyser, 1992; Ortega and Pearson, 2005) and heterotroph (Ortega et al. 2004; Hansen, et al. in prep.) community structure and composition. Furthermore, spotted knapweed invasion can reduce forage for livestock and native ungulates up to 60-96% in rangelands (French and Lacey, 1983; Bucher, 1984). Accordingly, management is necessary to limit the spread of spotted knapweed and to restore areas already impacted.

Currently, treatments for the restoration of spotted knapweed-invaded ecosystems rely primarily on ground or aerial spraying of broadleaf herbicides (Lolo NF, 2001, 2002; Bitterroot NF 2003). Over the short-term, herbicide treatments effectively decrease spotted knapweed biomass and increase grass cover (Tyser et al., 1998). However, whether such treatments actually “restore” affected ecosystems to a pre-invasion state or merely increase the cover of grasses is unknown. A large decrease in non-target forb cover and plant species richness has been documented after application with Picloram (Tordon©), the primary herbicide used in restoration efforts. This reduction occurs even after late summer applications, which are timed specifically to lower impacts on native forbs (Tyser et al., 1998; Kedzie-Webb, et al., 2002). Additionally, Picloram is known to leach into the soil profile and remain within the soil for over one year (Tyser et al., 1998), consequently affecting the viability of non-target forb seeds in the soil profile. Another
important consequence of broadleaf herbicide application in grasslands that may hamper restoration efforts is the facilitation of *Bromus tectorum* (an exotic grass) invasion (Y. Ortega, in prep). *Bromus tectorum* alters nutrient cycling (Evans et al. 2001), hydrology (Cline et al. 1977), fire regimes, and microbial communities (Belnap and Phillips, 2001) further exacerbating restoration efforts.

While effects of herbicide treatments on autotroph communities are well recognized, non-target effects of broadleaf herbicides on consumer assemblages are frequently overlooked. Since herbicides are the primary management tools for spotted knapweed (Sheley et al. 2000) and are now being extensively applied over public and private lands (Lolo NF, 2001, 2002; Bitterroot NF 2003), it is essential to understand how not only plants but also consumers are being affected by their use. Success of restoration efforts can potentially be evaluated by comparing particular higher level assemblages between “restored” habitats and reference pre-invasion habitats. Changes in presence and relative abundance of particular organisms may elucidate how closely restoration treatments come to returning ecosystems to pre-invasion conditions. Such knowledge will help researchers and managers understand if restoration treatments are achieving their goals, and are appropriate to implement or if treatments merely shift the ecosystem onto another undesired trajectory.

A useful way of assessing the efficacy of restoration treatments is to look at changes in populations of a taxonomically related group of organisms that are ubiquitous in a variety of habitats, sensitive to environmental changes, easy to sample, have well known biologies, possess short generation time and high fecundity, and which can be categorized into several trophic groups (Bisevac and Majer, 1999; Williams, 2000). One
such taxonomically-related group of organisms is the ground beetles (Carabidae). Ground beetles are a diverse group of predacious and herbivorous ground-dwelling insects that are widespread in invaded and un-invaded Rocky Mountain grassland savannas. The distribution and abundance of these beetles is largely determined by their extreme sensitivity to temperature, humidity, soil characteristics, amount of litter, food availability, and the time of season (Lovei and Sunderland, 1996; Holliday, 1991; Maelfait and Desender, 1990; Rushton et al., 1990; Butterfield et al., 1995). Changes in any of these ecological characteristics due to alterations to the environment, such as those occurring in response to exotic plant invasion, are often rapidly reflected in carabid populations.

Carabids can be easily sampled using pitfall traps, and their taxonomy and ecological requirements have been studied exhaustively (Thiele, 1977; Grum, 1986; Lovei and Sunderland, 1996; Lindroth, 1961-1969). Because of their ubiquity, sensitivity to environmental gradients, and relative ease of sampling, carabids have been widely and successfully used as ecological indicators of ecosystem characteristics and change (Niemela, et al 2000). These previous characteristics make them excellent candidate organisms for investigating indirect and direct effects of herbicide application on spotted knapweed-invaded habitats.

The primary objective of my research was to determine if and how herbicide treatment aimed at restoration of spotted knapweed-invaded savannas affect carabid communities in the year after application.

METHODS

Study design

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Sixteen sites (average 11.0 ha, SE = 1.49 ha) were established in Lolo National Forest in Missoula County, MT. Eight of the sites were heavily invaded with *C. maculosa* (hereafter referred to as invaded sites) and the other eight sites were either un-invaded or invaded by only trace amounts of *C. maculosa* (hereafter referred to as native sites). Each study site consisted of lightly forested grassland (ponderosa pine and Douglas-fir savanna), and was located within a matrix of dense Douglas-fir-dominated forest. Sites were chosen with similar physiographic characteristics including elevation (between 1300 and 1700m), soils, slope (30% average), and aspect (southwest) to control as much as possible for environmental variation.

The USDA Forest Service (Lolo National Forest) aerially applied picloram herbicide (at 1 pint/acre) randomly in September 2002 to half of the eight invaded sites and half of the eight native sites. The remainder of invaded and native sites were not treated and remained as controls. This resulted in the following four experimental treatments: native, no herbicide; native, herbicide; weed, no herbicide; and weed, herbicide. This study was a continuation of a previous study (in 1999 and 2000) looking at effects of spotted-knapweed invasion on carabids (hereafter referred to as the pretreatment study). Six of the study sites used in this study were also used in the pretreatment study allowing a comparison of results among the two studies. The entire study design is shown in Fig. 1. Post-treatment data was collected during 2003 and 2004, since treatment effects on arthropods should be measurable during this time frame (Samways, 1996).

*Collection and identification of carabids*
Pitfall traps, which have been shown to be an effective sampling method for carabids (Dufrene and Legendre, 1997), were deployed at each of the sixteen sites in 2003 to sample carabid relative abundances. Traps were located at equidistant spacing (20m) along four 250 m transects with a total of 6-7 traps per transect resulting in n=26 per site/ n=416 over all sites. Transects ran perpendicular to the slope and were located 50 m apart. Four collection dates, each lasting for a two-week period, were chosen for sampling from early June until late September to appropriately capture adult dispersal peaks of all carabid species. Pitfall traps were made from 2L colorless plastic soda bottles, cut in half with the upper portion inverted into the lower to act as a funnel. Traps were placed flush with the soil surface. A 1% formalin solution was added to each trap to retard rotting of trapped insects.

Carabids were sorted from samples, counted, and identified to species based on Lindroth (1961-1969). Species identifications were verified by Dr. George E. Ball of the University of Alberta. All species were placed into functional groups based on life history, trophic level, and whether they were endemic or exotic. These traits were chosen to categorize carabids into functional groups since they have been shown to be important response variables to ecosystem change and disturbance (Richardson and Holliday, 1982; Grum, 1986; Mader, 1986; Szyszko, 1986; Casale, 1990; Mossakowski et al., 1990; Rushton et al., 1990; Holliday, 1991; Michaels and McQuillan, 1995; Niemela et al., 1996; Beaudry et al., 1997). Four functional groups were created: specialist predators, generalist predators, polyphagous phytophages, and exotic species (with 2, 5, 14, and 1 species falling within each group, respectively) (Table 1).
Total abundance for each carabid species and functional group was calculated by pooling trap captures from individual pitfall traps for all four sampling periods by year. For all statistical analyses, carabid species and functional group abundance for pitfall traps were pooled by transect resulting in four sample units per study site.

Data Analyses

Multi-Response Permutation Procedures (MRPP) (Mielke, 1984), a non-parametric permutation procedure, was used to test for differences in carabid species and functional group composition and structure (abundance) among four a priori treatment groups of sites: native, no herbicide; native, herbicide; weed, no herbicide; and weed, herbicide. Sorensen's dissimilarity measure was chosen for MRPP to calculate the average distance within each group since this measure is robust for community data (McCune and Grace, 2002). The weighting used for MRPP to calculate Delta (weighted mean within group distance) was n/sum(n) (Mielke, 1984).

Carabid functional groups were compared among the four treatments using general linear models (SPSS Inc., 2001). Herbicide versus control sites (herbicide), invaded versus native sites (weed condition), and the interaction of herbicide and weed condition were included in models as fixed effects.

Indicator species analysis (ISA) (Dufrène and Legendre, 1997) was used to identify species within functional groups that best described differences between weed condition and herbicide treatments. ISA is based on two independent measurements of species distribution, specificity and fidelity (i.e. a species was specific to a particular group (specificity) and sampled abundantly and widespread in all samples of that group (fidelity)). The typology used for this analysis was a priori based on weed condition and
herbicide treatments. Potential indicator values (Inval) that can result from ISA can range from 0-100 where values > 25 signify a good indicator (Dufrene and Legendre, 1997). Significance of indicator values was estimated using Monte Carlo randomization set at 1000 permutations. For ISA, type I error rates were controlled at 10% since detecting potential population declines of individual species were favored over risking a high rate of non-detection (i.e. high rate of Type II error). All other statistical analyses were set at a significance level of alpha = 0.05. For MRPP and ISA, PC-ORD version 4.25 (McCune and Mefford, 1999) was used.

RESULTS

Community composition and structure

Carabid species captured in pitfall traps and their relative abundances are presented in Table 1. These species were categorized into the following functional groups: specialist predators, generalist predators, polyphagous phytophages, and an exotic species (Table 1). Functional groups were used since they were a more useful measure of ecological impacts of spotted knapweed invasion than individual species in the pretreatment study. In functional groups, functional roles and traits of included species are based on life history and ecological tolerances, and as a result, functional groups act as sensitive response variables and may serve as better gauges of compositional change compared to individual species (Olden, 2004).

Carabid community composition and structure, analyzed by species, was significantly different among a priori groups of native, no herbicide; native, herbicide; weed, no herbicide; and weed, herbicide sites (MRPP: T=-7.9429, A=0.0773, P=0.0000).
Carabid functional group composition and structure was also significantly different among the same *a priori* groups of sites (MRPP: \( T = -6.9077, A = 0.0855, P = 0.0000 \)).

*Weed condition and herbicide treatment effects on carabid functional groups*

Generalist predators were significantly more abundant in native sites compared to invaded sites (\( F = 22.6; \text{d.f.} = 1; P = 0.000 \)) (Fig. 2, Table 2), regardless of whether the sites were treated with herbicide or controls (\( F = 0.249; \text{d.f.} = 1; P = 0.620 \)) (Fig. 2, Table 2). There was no interaction between weed condition and herbicide treatments for generalist predators (\( F = 0.244; \text{d.f.} = 1; P = 0.623 \)) (Table 2).

Abundance of specialist predators was similar among invaded and native sites regardless of whether they were treated with herbicide or not (\( F = 2.137; \text{d.f.} = 1; P = 0.149 \)) (Fig. 3, Table 3). However, specialist predators were significantly more abundant in control sites than herbicide-treated sites regardless of whether they were native or invaded (\( F = 5.445; \text{d.f.} = 1; P = 0.023 \)) (Fig. 3, Table 3). There was no significant effect of interaction between weed condition and herbicide treatment for specialist predators (\( F = 0.328; \text{d.f.} = 1; P = 0.569 \)) (Table 3).

Abundance of polyphagous phytophages was similar among invaded and native sites (\( F = 0.030; \text{d.f.} = 1; P = 0.862 \)) (Fig. 4, Table 4). However, polyphagous phytophages were significantly more abundant in control sites than herbicide-treated sites for both weed conditions (\( F = 7.988; \text{d.f.} = 1; P = 0.006 \)) (Fig. 4, Table 4). There was no significant interaction between weed condition and herbicide treatment (\( F = 0.074, \text{d.f.} = 1, P = 0.786 \)) (Table 4).

Abundance of carabids in the exotic functional group was similar among invaded and native sites (\( F = 2.096, \text{d.f.} = 1; P = 0.153 \)), and among herbicide-treated and control
sites (F = 2.263; d.f. = 1; P = 0.138) (Table 5). There was no significant interaction between weed condition and herbicide treatment (F = 2.395, d.f = 1, P = 0.127) (Table 5).

*Weed condition and herbicide treatment effects on carabid species*

In ISA, four generalist predator species including one exotic species were moderate to good indicators of native sites (herbicide treated and control) (Fig. 5). Conversely, a specialist predator and polyphagous phytophage species were good indicators of spotted knapweed-invaded sites (herbicide treated and control) (Fig. 5).

For herbicide treatments, a specialist predator species and five polyphagous phytophage species were good indicators of control sites versus herbicide-treated sites (Fig. 6). Only one species, a polyphagous phytophage, was a good indicator of herbicide-treated sites (Fig. 6).

**DISCUSSION**

*Weed condition and herbicide effects on carabid functional groups and species*

Only the generalist predator functional group was significantly more abundant in native sites than in invaded sites. This higher abundance in native sites occurred regardless of whether sites were controls or treated with herbicides (Fig. 2, and Table 2). In addition, four generalist predator species were good indicators of native sites relative to invaded sites (herbicide-treated and control) (Fig. 5). These results indicate that indirect effects of spotted knapweed invasion on generalist predator populations (e.g. such as a change in prey availability) may be more important than direct physical effects of spotted knapweed invasion (e.g. a change in vegetative structure affecting capture
efficiency). Prey availability may continue to be limiting in spotted knapweed invaded habitats compared to native habitats even one year after herbicide treatment.

Both specialist predator and polyphagous phytophage functional groups were negatively affected by herbicide treatments (Fig. 3, Fig. 4, Table 3, and Table 4). Also, five species of polyphagous phytophages and a specialist predator species were found to be good indicators of control sites compared to herbicide-treated sites (invaded or native) (Fig. 6). Specialist predator and polyphagous phytophage abundance may have decreased in herbicide-treated sites compared to control sites regardless of whether they were invaded or native since both target and non-target forbs were killed by broadleaf herbicide application (Y. Ortega, unpublished data). A reduction in forbs may indirectly affect specialist predators by reducing their lepidopteron prey which are dependant upon forbs. For polyphagous phytophages, herbicide treatments may have directly reduced their food availability since they depend primarily on living, succulent plant material, such as ripening seeds, rosettes, blossoms, and pollen (Thiele, 1977). Furthermore, most polyphagous phytophages are likely to feed on forbs and not on grasses. Another potential explanation for a reduction in specialist predator and polyphagous phytophage species among herbicide-treated sites is direct toxicity of herbicide to carabids (Muller, 1971). However, given the results of previous studies looking at toxic effects of herbicides on carabids, direct toxicity of herbicide to carabids at the rate of application used in this study is highly unlikely (Brust, 1990).

Comparison of post-treatment results with pretreatment results

The same pattern of generalist predators favoring native sites relative to invaded sites found in this study was also found in the 1999 pretreatment study. The
agreement of results of these two studies indicates that one year after restoration herbicide treatments does not return the treated sites to pre-invasion conditions, and that critical habitat components and/or prey availability is still lacking for generalist predators in herbicide-treated invaded sites. For the polyphagous phytophage functional group the same pattern of equal distribution among native or invaded sites was found in the both the current study and the pretreatment study (Fig. 4, Table 4). However, the resolution of good indicator species differed in the two studies. In the pretreatment study, four polyphagous phytophage species were good indicators of invaded sites while in the current study only one species was a good indicator (Fig. 5). For specialist predators a different pattern was found in this study compared to the pre-treatment study. In the current study, specialist predators were not significantly more abundant in invaded sites compared to native sites as was found in the pretreatment study. However, a specialist predator species, *Calosoma luxatum* (Say), was found to be a good indicator of invaded sites compared to native sites in both studies (Fig. 5).

Results of pre-treatment and post-treatment studies for the specialist predator functional group may have differed due to factors other than experimental treatment effects. The abundance of members of this functional group may have decreased in invaded sites compared to native sites as a result of a large drought-induced reduction of spotted knapweed in the invaded sites. Spotted knapweed biomass decreased significantly in invaded sites with the onset of a severe drought in 2001 (Y. Ortega, unpublished data). This reduction of spotted knapweed may have indirectly affected the specialist predator’s prey (Lepidoptera), which depends on forbs. Similarly, the drought-induced reduction of spotted knapweed may have contributed to a decline in polyphagous
phytophage indicator species in invaded sites in this study compared to invaded sites in the pretreatment study. Through similar reasoning, specialist predator and polyphagous phytophage abundance may have decreased in the current study in both the native and invaded herbicide-treated sites compared to the native and invaded control sites since both target and non-target forbs were killed by broadleaf herbicide application (Y. Ortega, unpublished data), therefore indirectly and directly reducing their food availability.

Evaluation of restoration success

Restoration of knapweed-invaded sites back to “native” conditions by the use of herbicide does not appear to result one year after herbicide treatment. For example, specialist predators and polyphagous phytophages were negatively influenced by herbicide treatments potentially because of a reduction in non-target forbs. If non-target forbs are eliminated in herbicide-treated sites many dependent organisms may be negatively impacted. In addition, generalist predators were still significantly less abundant in herbicide-treated invaded sites compared to native sites. A reduction of generalist predators among invaded sites relative to native sites may indicate bottom-up effects of spotted knapweed invasion on their food availability. Potentially, generalist predator prey availability is lower in spotted knapweed invaded habitats as a result of altered soil biota food webs. The composition and relative abundance of soil biota may shift as a result of spotted knapweed-induced change in ecosystem processes and functions (LeJeune and Seastedt, 2001) (e.g. nutrient cycling and decomposition rates), which herbicide treatments alone cannot ameliorate. Conversely, the one-year time period after herbicide treatment that I assessed may be too short of a time frame to allow sites to recover to conditions supporting carabid communities indicative of native conditions.
Previous studies on herbicide effects of carabids

Currently, the only field studies analyzing the effects of herbicides on carabids have all been implemented in agricultural environments (Brust, 1990; Prasse, 1985; and Pollard, 1968). The results of this study conflict with those of Brust (1990), Prasse (1985), and Pollard (1968) who found that herbicide application to agricultural fields negatively affected the abundance of predator carabids one year after application. Elimination of plant biomass after application of herbicides was postulated to result in an unfavorable microhabitat for predators due to a reduction of prey, canopy cover, and an increase in soil surface temperatures (Brust, 1990; Prasse, 1985; and Thiele, 1977). Moreover, Brust (1990) found that herbicide application in agricultural fields did not affect the abundance of small carabids, which are typically phytophagous, one year after herbicide treatment. It was hypothesized that these small polyphagous phytophages either remain unchanged in abundance (Brust, 1990) or increase in number (Thiele, 1977) after herbicide treatment because they generally prefer open habitats (an open habitat results from plant biomass reductions due to herbicide application). Herbicide treatments after one year in spotted knapweed-invaded or native Rocky Mountain savannas do not appear to have the same effects on generalist predator or polyphagous phytophage abundance as herbicide treatments after one year in agricultural systems.

Future direction and research

Herbicide treatments alone do not restore invaded habitats back to the same ecological trajectory as native sites in terms of carabid functional group responses to herbicide treatments at least in the one year after treatment. Future assessments are necessary to effectively monitor restoration success since it takes time for organisms
associated with native habitats to recolonize, reproduce, and interact with other species. Assessments through time will indicate if restoration success is achieved and the time frame necessary for indicator organisms to effectively capture restoration success.

Carabids are important predators and herbivores in many terrestrial habitats, and in turn may indirectly indicate alterations in heterotroph and autotroph functional diversity on a fine scale. Future research on restoration success should be assessed with other organisms as well as carabids, such as meso- and micro- soil biota (to elucidate changes in nutrient cycling and decomposition), soil macro-biota (such as ants and grasshoppers), and small mammals, thereby covering functional diversity at a variety of scales and trophic levels.

ACKNOWLEDGEMENTS

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Table 3.1 Totals (Sum) and standard errors (SE) of carabid species abundance captured in pitfall traps by treatment (n= 16 sample units per treatment). Treatments are spotted knapweed-invaded herbicide-treated (InvHerb), spotted knapweed-invaded control (InvCon), native herbicide-treated (NativeHerb), and native control (NativeCon) sites located in Rocky Mountain savannas. Functional groups consist of GP= generalist predator, PP= polyphagous phytophage, SP= specialist predator, and Exotic= exotic species.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Functional Group</th>
<th>InvHerb Sum</th>
<th>InvHerb SE</th>
<th>InvCon Sum</th>
<th>InvCon SE</th>
<th>NativeHerb Sum</th>
<th>NativeHerb SE</th>
<th>NativeCon Sum</th>
<th>NativeCon SE</th>
</tr>
</thead>
<tbody>
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<td>Calosoma luxatum Say</td>
<td>SP</td>
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<td>1.65</td>
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<td>4.12</td>
<td>146</td>
<td>0.93</td>
<td>422</td>
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</tr>
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<td>1</td>
<td>0.02</td>
<td>34</td>
<td>0.48</td>
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<td>285</td>
<td>0.48</td>
<td>293</td>
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<td>1</td>
<td>0.02</td>
<td>1</td>
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<td>0.04</td>
<td>11</td>
<td>0.06</td>
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<td>0</td>
<td>0.00</td>
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<td>0.15</td>
<td>15</td>
<td>0.09</td>
<td>16</td>
<td>0.16</td>
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<tr>
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<td>0.66</td>
<td>473</td>
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<td>1.25</td>
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<td>Spp A. Amara spp.</td>
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<td>0.03</td>
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<td>Spp D. Amara spp.</td>
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<td>91</td>
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Fig. 3.1 Experimental study design of 8 native and 8 spotted knapweed-invaded sites in Rocky Mountain savannas. Four native and four spotted knapweed-invaded sites were treated with herbicide in 2002. An X represents six pretreatment study sites from 1999 and 2000. Actual locations and distances of sites from one another is not truly represented in this conceptual figure.
Fig. 3.2 Mean abundance of generalist predators captured in pitfall traps in spotted knapweed-invaded herbicide-treated (InvHerb), spotted knapweed-invaded control (InvCon), native herbicide-treated (NativeHerb), and native control (NativeCon) sites located in Rocky Mountain savannas. n= 4 sites per treatment. (bars equal +/- 1 SE of the mean). Asterisk denotes significance at P ≤ 0.05.
Fig. 3.3 Mean abundance of specialist predators captured in pitfall traps in spotted knapweed-invaded herbicide-treated (InvHerb), spotted knapweed-invaded control (InvCon), native herbicide-treated (NativeHerb), and native control (NativeCon) sites located in Rocky Mountain savannas. n = 4 sites per treatment. (bars equal +/- 1 SE of the mean). Asterisks denotes significance at P ≤ 0.05.
Fig. 3.4 Mean abundance of polyphagous phytophages captured in pitfall traps in spotted knapweed-invaded herbicide-treated (InvHerb), spotted knapweed-invaded control (InvCon), native herbicide-treated (NativeHerb), and native control (NativeCon) sites located in Rocky Mountain savannas. n= 4 sites per treatment. (bars equal +/- 1 SE of the mean). Asterisks denotes significance at P ≤ 0.05.
Table 3.2  Two factor and level ANOVA of generalist predator abundance (dependent variable) in spotted knapweed-invaded herbicide-treated, spotted knapweed-invaded control, native herbicide-treated, and native control sites located in Rocky Mountain savannas. Herbicide treatment (herbicide or control) and weed condition (native or invaded) were included as fixed factors.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
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<tr>
<td>Weed condition</td>
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<td>1683.523</td>
<td>22.636</td>
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<tr>
<td>H x W</td>
<td>18.142</td>
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<td>18.142</td>
<td>0.244</td>
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<tr>
<td>Error</td>
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<td></td>
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<td>Total</td>
<td>20554.000</td>
<td>65</td>
<td></td>
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Table 3.3 Two factor and level ANOVA of specialist predator abundance (dependent variable) in spotted knapweed-invaded herbicide-treated, spotted knapweed-invaded control, native herbicide-treated, and native control sites located in Rocky Mountain savannas. Herbicide treatment (herbicide or control) and weed condition (native or invaded) were included as fixed factors.

<table>
<thead>
<tr>
<th>Source</th>
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<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
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<tr>
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<tr>
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<td>H x W</td>
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<td>Error</td>
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<tr>
<td>Total</td>
<td>183222.538</td>
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Table 3.4  Two factor and level ANOVA of polyphagous phytophage abundance (dependent variable) in spotted knapweed-invaded herbicide-treated, spotted knapweed-invaded control, native herbicide-treated, and native control sites located in Rocky Mountain savannas. Herbicide treatment (herbicide or control) and weed condition (native or invaded) were included as fixed factors.

<table>
<thead>
<tr>
<th>Source</th>
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<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
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<td>1</td>
<td>31.279</td>
<td>0.030</td>
<td>0.862</td>
</tr>
<tr>
<td>H x W</td>
<td>76.794</td>
<td>1</td>
<td>76.794</td>
<td>0.074</td>
<td>0.786</td>
</tr>
<tr>
<td>Error</td>
<td>63056.305</td>
<td>61</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>160048.000</td>
<td>65</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Table 3.5  Two factor and level ANOVA exotic species abundance (dependent variable) in spotted knapweed-invaded herbicide-treated, spotted knapweed-invaded control, native herbicide-treated, and native control sites located in Rocky Mountain savannas. Herbicide treatment (herbicide or control) and weed condition (native or invaded) were included as fixed factors.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>132.754</td>
<td>3</td>
<td>44.251</td>
<td>2.229</td>
<td>0.094</td>
</tr>
<tr>
<td>Herbicide</td>
<td>41.629</td>
<td>1</td>
<td>41.629</td>
<td>0.249</td>
<td>0.620</td>
</tr>
<tr>
<td>Weed condition</td>
<td>44.942</td>
<td>1</td>
<td>44.942</td>
<td>22.636</td>
<td>0.000</td>
</tr>
<tr>
<td>H x W</td>
<td>47.562</td>
<td>1</td>
<td>47.562</td>
<td>0.244</td>
<td>0.623</td>
</tr>
<tr>
<td>Error</td>
<td>1211.246</td>
<td>61</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1409.000</td>
<td>65</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3.5 Indicator values of species characterizing weed condition (native or invaded sites).

GP= generalist predator, PP= polyphagous phytophage, Exotic= Exotic species, and SP= specialist predator. *indicates \( P \leq 0.10 \), **indicates \( P \leq 0.05 \), *** indicates \( P \leq 0.01 \).
Control treatment

100
80
60
40
20
0

Harpa helvis cinctus (PP) ***

Calosoma hexatum (SP) **

Amara latior (PP) ***

Spp. E (PP) **

Spp. D (PP) *

Spp. A (PP) *

Amara ellipsis (PP) ***

Herbicide treatment

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Chapter 4: Conclusions

Carabids have been proposed as good indicators of ecological change because of their ubiquity, sensitivity to environmental gradients, and ease of sampling. In this study, carabids were good response variables to ecological change between invaded and native, and herbicide treated and control sites when they were categorized into functional groups. Functional groups in this study were based on species life history, trophic level, and whether they were endemic or exotic. Consequently, four functional groups were created: specialist predators, generalist predators, polyphagous phytophages, and exotic species.

Functional groups may perform as better response variables for environmental change compared to species since species specific factors that influence individual populations, in addition to noise (environmental and statistical) are reduced when multiple members of the same functional group are merged together. Furthermore, all species within a functional group share a common trait or tolerance, and as a result, changes in functional group relative abundance may elucidate which components within the ecosystem are changing.

In this study, generalist predators were more abundant and good indicators of native sites relative to spotted knapweed-invaded sites. A reduction of generalist predators among invaded sites relative to native sites, even the year after herbicide treatment, may indicate bottom-up effects of spotted knapweed invasion on their food availability. Potentially, generalist predator prey availability is lower in spotted knapweed-invaded habitats as a result of altered soil biota food webs.

Specialist predators were more abundant and good indicators of invaded sites relative to native sites, yet decreased in invaded sites compared to native sites after a
large drought-induced reduction of spotted knapweed in the invaded sites. For the polyphagous phytophage functional group a pattern of equal distribution among native or invaded sites was found. However, the resolution of polyphagous phytophages being good indicator species of invaded sites diminished after the drought-induced reduction of spotted knapweed in the invaded sites. A reduction of polyphagous phytophages and specialist predators after the drought and herbicide-induced reduction of spotted knapweed among invaded sites and native forbs among native sites may indicate that the elimination of non-target (herbicide induced) and target forbs (herbicide and drought induced) may indirectly and directly reduce their food availability. Polyphagous phytophages feed primarily on forbs and the application of picloram, which greatly reduced forb cover in this study, may negatively affect them. A reduction of specialist predators may be linked to concurrent decreases in Lepidoptera prey, which depend on forbs.

In summary, carabid functional groups indicate that spotted knapweed may create a more favorable environment for some species (e.g. augmenting their food supply) at the expense of others (e.g. generalist predators and their prey). Alterations in heterotroph functional diversity may have subsequent effects on other biota by influencing the flow of energy, thereby altering food webs. In consideration to restoration of spotted knapweed invaded savannas, herbicide treatments alone did not appear to restore invaded sites to the desired "pre-invasion" condition, at least in terms of carabid communities, in the time frame of this study. Longer term monitoring of herbicide-treated sites, along with a greater diversity of indicators of multiple trophic levels and scales will be
necessary to determine if such treatments eventually return spotted knapweed-affected sites to pre-invasion conditions.
APPENDIX A: Chapter 2: Extended Data Analysis

Carabid Diversity

Evenness: Simpson's Measure of Evenness

Evenness of carabid species and functional groups was measured with Simpson's measure of evenness \((E_{1/D})\), which is simply the reciprocal form of Simpson's dominance index \((D)\) (Simpson, 1949) divided by the number of species in the sample (Smith and Wilson, 1996; Magurran, 2004). \(E_{1/D}\) ranges from 0-1 (zero represents minimum evenness) and is one of best evenness measures available that is truly independent of species richness, and weights rare and dominant species equally (Smith and Wilson, 1996; Magurran, 2004).

The statistic \(D\) (Simpson, 1949), which describes the probability that a second individual drawn from a population should be of the same species as the first, is given by:

\[
D = \sum_{i=1}^{S_{\text{obs}}} \frac{n_i^2}{N(N-1)}
\]

Where \(P_i^2\) is the proportion of individuals of ith species and \(S_{\text{obs}}\) is total species observed. In order to calculate the index the form appropriate to a finite community is used:

\[
P_i^2 = \frac{n_i(n_i-1)}{N(N-1)}
\]

Where \(n_i\) is the number of individuals in the ith species and \(N\) is the total individuals in the sample.

Simpson's measure of evenness then is:

\[
E_{1/D} = \left(\frac{1}{D}\right) \frac{S_{\text{obs}}}{S_{\text{obs}}}
\]
Community analysis

Multi-Response Permutation Procedures (MRPP)

MRPP (Mielke, 1984), a non-parametric permutation procedure, was used to test for differences among *a priori* groups of knapweed-invaded and native sites by soil type, carabid functional group, and carabid species composition. Sorensen's dissimilarity measure was chosen for MRPP to calculate the average distance within each group since this measure is robust for community data (McCune and Grace, 2002). The weighting \((C_i)\) used for MRPP to calculate Delta (weighted mean within group distance) was \(n/\text{sum}(n)\) (Mielke, 1984). Delta is used to calculate the T-statistic and the chance corrected within group agreement statistic (A). Delta is computed as:

\[
\delta = \sum_{i=1}^{g} C_i \times x_i
\]

Where \(g\) is the total number of groups, \(x_i\) is the average distance within each group, and \(C_i\) is the chosen weighting as stated above.

The T-statistic is analogous to the student's T test statistic except the distribution which is approximated is from Pearson type III distribution which is a continuous distribution that acknowledges three parameters under the null hypothesis (mean, standard deviation, and gamma) (McCune and Mefford, 1999). The larger the T statistic the greater the separation between groups. The P-value calculated from the T statistic is determined by numerical integration of the Pearson type III distribution.

The T statistic is given as:
\[ T = \frac{\text{observed } \delta - \text{expected } \delta}{\text{s.dev. of expected } \delta} \]

Where observed \( \delta \) is the observed distribution, expected \( \delta \) is the mean under the null hypothesis, and the standard deviation of expected \( \delta \) is the standard deviation under the null hypothesis.

The A statistic describes within group heterogeneity and is a description of effect size that is independent of sample size (whereas the T statistic is dependent on sample size). An A statistic of 1 indicates maximum within group homogeneity, 0 is what is expected by chance, and < 0 indicates less agreement within-groups. For community data the A statistic is usually below 0.1 (McCune and Grace, 2002). The A statistic is calculated as:

\[ A = 1 - \frac{\text{observed } \delta}{\text{expected } \delta} \]

Indicator Species Analysis

Indicator species analysis (ISA) (Dufrene and Legendre, 1997) was used to identify the species that best described differences between invaded and native sites based on two independent measurements of species distribution, specificity and fidelity (i.e. a species was specific to a particular group (specificity) and sampled abundantly and widespread in all samples of that group (fidelity)). The typology used for this analysis was \textit{a priori} based on invaded and native sites. Potential indicator values (Inval) that can result from ISA can range from 0-100 where values > 25 signify a good indicator (Dufrene and Legendre, 1997). Significance of indicator values was estimated using Monte Carlo randomization set at 1000 permutations.
The specificity measure is:

\[ A_{ij} = \frac{N_{\text{individuals}_{ij}}}{N_{\text{individuals}_j}} \]
Max when: species \( i \) is only present in cluster \( j \)
Where \( N_{\text{individuals}_{ij}} \) is the mean number of species \( i \) across sites of group \( j \), and
\( N_{\text{individuals}_j} \) is the sum of the mean number of individuals of species \( i \) over all groups.

The fidelity measure is:

\[ B_{ij} = \frac{N_{\text{sites}_{ij}}}{N_{\text{sites}_j}} \]
Max when: species \( i \) is present in all objects of cluster \( j \)
Where \( N_{\text{sites}_{ij}} \) is the number of sites in cluster \( j \) where species is present, and \( N_{\text{sites}_j} \) is the total number of sites in that cluster.

The indicator value (IndVal) is:

\[ A_{ij} \times B_{ij} \times 100 = \text{IndVal}_{ij} \]
\[ \max[\text{IndVal}_{ij}] = \text{IndVal} \]

The IndVal equation combines species relative abundance to its relative frequency of occurrence in various groups of samples. As a consequence there is a clear distinction between vagrant species (or individuals from sink populations) and indicator species, and in turn rare species will not indicate particular habitats or sample units. Moreover, the indicator index for a given species is independent of the other species' relative abundances and therefore scaled.

**Nonmetric multidimensional scaling**

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1978) was used to relate carabid species assemblages among all sample units in invaded and native sites. NMS was also used to relate soil-water potential among all sample units in invaded and native sites for incorporation in bivariate correlations with carabid NMS axes. The purpose of this ordination is to summarize a complex set of interrelationships in as few dimensions as possible. NMS is a very effective ordination method for
community data since it does not assume linear relationships among variables or multivariate normality, and eliminates the zero-truncation problem (Clark, 1993; McCune and Grace, 2002). NMS iteratively searches for the best solution in reduced dimensional space by minimizing departure from monotonicity from the dissimilarity distance in original dimensional space and the distance measure in reduced dimensional space (i.e. reducing stress) (McCune and Grace, 2002). Kruskal’s least squares monotonic transformation (Kruskal, 1964; Mather, 1976) was used to minimize stress. Sorensen’s dissimilarity measure was chosen to calculate the distances between sample units. A random number generator was used to calculate the starting coordinates for all sample units for each run. We conducted forty runs with real data stepping down in dimension from six axes to one axes for each run. A maximum of 400 iterations per run was chosen since the relationship between the number of iterations and the magnitude of stress rarely improves with a higher iteration number (McCune and Grace, 2002). Stress versus iteration was plotted to assess the stability of the solution with 0.00001 as the stability criterion. To assess the dimensionality of data sets the final stress versus the number of dimensions was plotted, and Monte Carlo permutations with 50 randomized runs were conducted. Monte Carlo permutations were used to assess the probability that a similar final stress could be expected by chance for a particular dimension. Clarke’s (1993) rule of thumb was used to evaluate the final stress level in order to assess the ordination’s quality of representation. Pearson’s $r^2$ was used to describe the percent of variation described by the ordination by correlating sample unit distances in reduced dimensional space with distances in the original dimensional space.
REFERENCES


APPENDICES B: Soil Moisture Response Curves for invaded and native sites
(Inv1, Inv2, Inv3 are the spotted knapweed invaded sites and N1, N2, and N3 are the native sites)