

TOWARD ECOLOGICALLY-BASED MANAGEMENT:
BIODIVERSITY AND ECOSYSTEM FUNCTIONS IN
INTENSIVELY MANAGED AGROECOSYSTEMS

by

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ABSTRACT

Concerns about intensive, chemically-based agriculture have precipitated a call for ecologically-based practices. We investigated the ramifications of two such practices. First, we investigated targeted sheep grazing for cover-crop termination. Second, we compared the community dynamics of carabid beetles (Coleoptera:Carabidae), a group of beneficial insects in agroecosystems, among three vegetation systems in alfalfa (*Medicago sativa* L.) production.

Cover-crops are grown to improve soil quality and reduce erosion. While cover-crops do not provide a direct source of revenue, integrating livestock grazing to terminate them could provide alternative revenue. We conducted a two year study of the impacts terminating cover-crops with sheep grazing on soil quality, weed and carabid communities, and crop yield in a diversified vegetable market garden. In 2012 and 2013, we seeded a four species cover-crop that was terminated by either tractor mowing or sheep grazing following a completely randomized design. In 2013, we planted spinach, kohlrabi, and lettuce into previously grazed or mowed plots following a split-plot design. The cover-crop provided forage worth \$24.00 - \$44.00 ha⁻¹ as a grazing lease. There were no differences in soil chemistry, compaction, temperature or moisture between grazed and mowed plots. Despite temporal shifts in weed and carabid community structure, we found no differences in those communities between termination methods. Finally, cash crop yields did not differ between strategies. Our results suggest that this practice can provide an economic benefit for producers without detrimental agronomic or ecological consequences.

Alfalfa is the third biggest crop in Montana by gross revenue. As a perennial crop, it can allow for high populations of pest and beneficial insects. Practices that favor predatory insects could enhance biological control of pests. We conducted a two year study investigating carabid community dynamics and habitat preferences of common carabid species under three habitat management strategies: monoculture alfalfa, barely nurse-cropped alfalfa and uncultivated refugia. Our results indicate that carabid communities vary among the three systems. Barley nurse-crop systems had greater total carabid activity-density than either of the other two system, which suggests that nurse-cropping may be an effective habitat management strategy to enhance carabid populations.

CHAPTER ONE

BACKGROUND, LITERATURE REVIEW
AND RESEARCH OBJECTIVESIntroduction

Anthropocentric needs for fuel, fiber, food, and timber continue to grow as global population increases. Currently, croplands and pasture together comprise an estimated 4.91×10^9 ha, or approximately 38% of Earth's ice-free terrestrial surface (Foley et al. 2011). This represents an almost five-fold increase in the total amount of cultivated land occurring from the beginning of the 16th century to the latter half of the 20th century (Foley et al. 2005). Thanks to major technological advances from the Green Revolution such as nitrate fertilizers, pesticides, and mechanization, the expansion of cultivated land has quelled since the mid 20th century despite a monumental increase in production (Matson et al. 1997). However, both expanded land use and synthetic inputs have had major environmental consequences including conservation of biodiversity.

On the one hand, increased land use for cultivation results in habitat loss when humans convert natural ecosystems to intensively managed agricultural systems. Such habitat loss is a major factor driving species extinctions and population declines worldwide (Pimm et al. 1995). On the other hand, intensifying production on existing system through heavy use of off-farm inputs such as pesticides and synthetic fertilizers can lead to the evolution of resistant pest populations, morbidity and mortality to non-target organisms, eutrophication of adjacent watersheds and increase reliance on fossil

fuels (Foley et al. 2005). These imbalances have precipitated a call for the incorporation of an ecological approach to agriculture where landscapes are managed for multiple services including yield of marketable commodities, clean water and air, pollination, pest regulation, carbon storage and others (Altieri et al. 1983, Robertson and Alexander 1992, Matson et al. 1998, Robertson and Swinton 2005).

Literature Review

Biodiversity and Ecosystem Functions

Biodiversity plays a vital role in ecosystem functioning. The composition and abundance of species and genotypes that comprise an ecosystem determines which functions it will perform and the extent to which these function will be performed (Cardinale et al. 2006). Thus, to reduce the reliance of off-farm synthetic inputs effectively, the organisms that comprise a production ecosystem must perform the functions such as pollination, nutrient cycling, herbivore predation, and regulation of hydrological processes while maintaining acceptable levels of sustainable food, fuel, fiber, and timber production (Brussaard 1997, Altieri 1999, Shennan 2008). In intensively managed agroecosystems, producers rely primarily on a suite of mechanical and/or chemical practices to maintain crop yields in the face of variable environmental conditions. Yet, these practice could have unintended impacts on biodiversity. Hence, land managers interested in enhancing the environmental sustainability of their production settings must ask: how do management practices modify biodiversity and how

do these changes, in turn, alter the ecosystem functions that affect production and overall system stability?

To address these questions, we must understand which diversity metrics are most important for ecosystem functions. Does species richness, evenness, composition or abundance have the strongest effect ecosystem function? Vandermeer et al. (2002) posit three hypotheses for how biodiversity and ecosystem function interact. First, increased biodiversity may have a facilitative effect on ecosystem function. Under the “facilitative hypothesis,” species richness is important because a community with more species or genotypes will perform a more complete complement of ecological functions than would a species poor community. Second, increased biodiversity may be functionally redundant. This “redundancy hypothesis” suggests that a particular suite of species and genotypes will perform all of an ecosystem's functions and additional species or genotypes added to a community will simply perform the same function. Species composition is therefore the most important community parameter under this hypothesis. Third, the “insurance hypothesis,” postulates that increased biodiversity may buffer against perturbations to ecosystem functioning because of functional redundancy. In other words, while a smaller subset of species or genotypes may perform the full complement of ecological functions, more species or genotypes in a community may ensure that those functions continue through disturbance events. Under the “insurance hypothesis,” both richness and composition are important for ecosystem function. Identifying which of these hypotheses best describes the interaction of biodiversity and

ecosystem function will allow land managers to implement practices that facilitate biologically-mediated functions and reduce the need for off-farm synthetic inputs.

Certain community parameters may be more important drivers for some functions than they are for others and their relative importance may be determined by the constituent taxa and their trophic interactions. For example, Crowder et al. (2010) manipulated evenness of potato beetle (*Leptinotarsa decemlineata* Say) predators and parasitoids in a potato (*Solanum tuberosum* L.) field. Increasing predator and parasitoid evenness independently increased *S. tuberosum* productivity and *L. decemlineata* mortality. These results suggest that natural enemy suppression of *L. decemlineata* increased with predator and parasitoid community evenness. Species richness, however, had a synergistic effect on pea aphid (*Acyrtosiphon pisum* Harris) in an alfalfa crop (Cardinale et al. 2003). Finally, Straub and Snyder (2006) found that predator species composition was more important than richness or evenness for green peach aphid (*Myzus persicae* Sulzer) suppression in potato fields. Thus, land managers should understand both which species are present in an ecosystem and which community parameters are driving ecological services in order to implement management practices that facilitate those services.

The species that comprise managed ecosystems, including agroecosystems, constitute either the planned or the associated biodiversity. Planned biodiversity consists of the species that the land manager intentionally includes in the system. Associated biodiversity is the suite of the organisms, including pest, beneficial, and neutral species that while not intentionally introduced into the system by the land manager, live in or

colonize it from adjacent habitats (Vandermeer and Perfecto 1995, Altieri 1999, Vandermeer et al. 2002). Changes in the associated biodiversity therefore can have major consequences for pest pressures, as well as ecosystem services such as pest management and pollination. Planned biodiversity in intensively managed ecosystems such as cropping systems dictates associated biodiversity (Matson et al. 1997). In general, increasing spatial and temporal habitat heterogeneity results in an enhancement of the associated biodiversity (Benton et al. 2003). Land managers can achieve this goal with practices such as intercropping, planting shelterbelts, and designing diversified cropping systems. Rotating commodity crops, replacing fallow with cover crops and living mulches can also increase the associated biodiversity by enhancing temporal heterogeneity (Altieri 1999).

Carabid Beetles, Biodiversity, and Conservation Biocontrol

Ground beetles (Coleoptera:Carabidae) comprise one of the most abundant and diverse families in the Coleoptera order and are abundant in northern temperate agroecosystems (Lovei and Sunderland 1996). Carabid diets are diverse and include both zoophagy and phytophagy (Toft and Bilde 2002). Most carabid beetles are generalist predators and will consume a variety of prey taxa; however, some species of carabids show dietary preferences for certain taxa (Toft and Bilde 2002). For example, *Loricera pilicornis* (F.) specializes on springtails (Entognatha:Collembola) for prey (Kromp 1999), and most of the paussine subfamily (Carabidae:Paussinae) is myrmecophilous, invading ant (Hymenoptera:Formicidae) colonies and feeding on their broods (Geiselhardt et al.

2007). However, the Carabidae collectively preys on a multitude of organisms including arthropods (Lovei and Sunderland 1996), mollusks (Symondson 1994, Bohan et al. 2000), and annelids (Toft and Bilde 2002) many of which are considered pestiferous organisms in agroecosystems. Thus carabid beetles may provide a beneficial pest-suppression ecological function in agroecosystems.

Despite their recognition as generalist predators, many carabids exhibit phytophagy, consuming plant tissues such as leaves, fruits and seeds. Seed predation in particular has been well studied because of its agronomic importance for conservation biocontrol of weeds. While numerous taxa exhibit some degree of seed predation, the diets of the Harpalini, Amarini and Zabirini tribes are primarily seed predators (Tooley and Brust 2002). Numerous studies demonstrate that these seed predators taxa can be important sinks of seed of weed species (Brust 1994, Menalled et al. 2007, Gaines and Gratton 2010).

Because of their dispersal ability and habitat selectivity, ground beetle communities shift markedly at small spatial and temporal scales in response to changes in habitat structure and prey availability (Lovei and Sunderland 1996, Holland et al. 2002). For example, Gardner et al. (1997) found that carabid communities shifted in response to soil organic matter, as well as heather (*Calluna spp.* Salisb.) biomass and height in Scottish heather moorlands. Moreover, they found that while carabid taxa preferring open-canopy habitats occurred in heavily sheep-grazed sites, those preferring closed canopy and mesic conditions, did not invade heavily grazed habitats. These results suggest that sheep grazing alters habitat structure and thus directs carabid community

towards an assemblage of species that prefer dry open habitats. Therefore, changes in carabid beetle communities may serve as a sensitive proxy to measure the effect of management practices on the associated biodiversity of intensively managed ecosystems. Holland et al. (2002), however, caution that in pitfall trapping, the most common method for carabid community monitoring, density and activity are confounded. Using Carabidae as a bioindicator taxon may therefore obfuscate some trends in the macroarthropod community fluctuations.

Associated Plant Diversity and Ecosystem Services

Undesired plant species (i.e., weeds) are often blamed as major impediment to crop productivity because they compete with crop plants for resources (Aldrich 1987). However, weeds may also confer valuable ecological benefits for agroecosystems. Weeds may enhance pollinator diversity (Carvalho et al. 2011), natural pest arthropod suppression (Altieri and Letourneau 1982), and nutrient cycling (Shennan 2008). Weed populations often fluctuate in response to management practices such as grazing (Popay and Field 1996), nutrient addition (Davis et al. 2000), and management systems (Menalled et al. 2001). Understanding the ecological processes that direct plant community assemblage and weed populations will allow land managers to implement practices that maximize the benefits from non-crop plants while keeping weed species below deleterious abundances.

Associated plant diversity can provide a variety of ecological services that would otherwise require the use of synthetic inputs (Jordan and Vatovec 2004). For example, Altieri and Letourneau 1982) argue that increasing plant diversity within crops or

adjacent to agricultural fields increases predatory insect abundance. Carvalheiro et al. (2011) found that higher diversity of non-crop plants in agroecosystems and greater proximity to natural habitats increased pollinator species richness in a South African sunflower (*Helianthus annuus* L.) plantation. The increase in pollinator species richness secondarily increased the number of flowers that honeybees (*Apis mellifera* L.), the most abundant pollinator, visited. Increased pollinator richness also increased *H. annuus* yields between 47% and 74% compared with sites pollinated exclusive by *A. mellifera*. Finally, non-crop plants may serve as valuable hosts for arbuscular mycorrhizal fungi (AMF). Jordan and Vatovec (2004) suggested that because some weed species maintain mutualisms with multiple species of AMF, weeds help maintain a diverse AMF propagule pool that can infect crops. In agreement, Feldmann and Boyle (1999) found that weeding non-crop AMF host plants reduced corn (*Zea mays* L.) biomass by 28%. In summary, land managers seeking to reduce synthetic herbicide inputs should avoid a “zero-tolerance” weed management strategy, because this may limit the associated plant biodiversity from provisioning functions that can reduce crop damage or increase crop productivity. However, quantifying the degree to which weed abundance and diversity could be tolerated or even promoted remains a major research challenge.

Soil Quality in Intensively Managed Ecosystems

One of the most important components of an ecosystem for plant productivity is soil. Soils provision many of the resources and conditions that influence plant productivity and community structure. In particular, soils serve as pools plant nutrients, habitat for plant mutualists such as AMF, and *Rhizobia* that mediate nutrient uptake, and

reservoirs of plant available water (Wild 1993). Management practices can have important impacts on soil biota, chemistry, and physical properties. For example, tillage can increase penetration resistance in soil depths below the plow line, creating a “plow pan” (Rasmussen 1999, Jabro et al. 2009). Also, the use of synthetic inputs can alter biogeochemical cycling as shown by Matson et al. (1998) who found that anhydrous ammonium application in Mexican wheat (*Triticum aestivum* L.) fields strongly accelerated rates of nitrification and volatilization. Also, trampling by grazing livestock or wildlife can decrease soil macroporosity, which in turn, may hamper water infiltration (Bell et al. 2011). Thus, land managers should understand the ramifications of their suite of practices on soil properties to avoid degradation.

Perturbations to soil biota, chemistry and physical properties can feedback on plant productivity and community structure. First, changes to soil physical properties can affect plant productivity by facilitating or inhibiting parts of plant ontogeny. For example, soil bulk density over a threshold value of 2 MPa can impede root exploration which in turn may reduce plant biomass and water infiltration (Wild 1993, Bell et al. 2011). Second, management practices can impact resource availability such as plant available water and nutrient pools. Kahimba et al. (2008) found that in-season cover-cropping with berseem clover (*Trifolium alexandrinum* L.) reduced soil moisture content in oat (*Avena sativa* L.) fields compared with oat fields that were not cover-cropped, which resulted in a 16% decline in total biomass in cover cropped fields. Thus, understanding the effects of that land management practices have on soil feedbacks to

plant communities is critical before implementing new techniques. This is especially true in production systems where such changes may have substantial economic impacts.

Land Management and Ecological Filters

Ecological Filters: An environmental factor or management practice that directs species assemblage by systematically excluding or promoting certain species from a habitat represents an ecological filter determining a system's diversity (Keddy 1992, Funk et al. 2008). In this context, the planned diversity and its associated suite of management practices, represent ecological filters for the associated diversity. Understanding the joint-impact that these anthropogenic ecological filters and environmental variables have on the regional species pool will allow managers to influence community structure favorably (Booth and Swanton 2002, Cardina et al. 2002, Wilby and Thomas 2002, Myers and Harms 2009).

Sheep-Grazing and its Effects on Plant Communities: Re-integrating livestock into croplands may provide several benefits to farmers and ranchers. First, it may offer farmers alternative sources of income such granting leases for ranchers to graze their livestock on high quality forage. Second it could be an effective management strategy for cover crop termination instead of tractor mowing, thus reducing fossil fuel dependence. Third, it may provide an expeditious method of weed management with minimal labor (Popay and Field 1996). Fourth, livestock grazing may aid in nutrient cycling (Thiessen Martens and Entz 2011). However, to successfully implement the re-

integration of targeted sheep grazing into agricultural systems, it is important to understand its biological and environmental effects.

The effect of livestock grazing on plant communities depends on the duration and intensity of grazing (Popay and Field 1996, Frost and Launchbaugh 2006). For example, Yates et al.(2000) found that exotic annual forb cover was 27.5% in intensively sheep-grazed *Eucalyptus* (L' Hér.) woodlands compared with only 0.5% in sparsely-grazed and ungrazed sites. Native perennial forb and shrub cover was only 3.6% in heavily sheep-grazed sites compared with 9.1% in sparsely-grazed and ungrazed sites (Yates et al. 2000). Barger et al. (2004) compared plant communities subjected to different sheep stocking rates (1.3, 2.7,4.0, 5.3 and 6.7 sheep ha⁻¹ yr⁻¹) on an Inner Mongolian Steppe, and found that total vegetation cover generally decreased with increasing grazing pressure. However, this trend was somewhat buffered at intermediate grazing intensities because *Potentilla spp.* (L.) cover replaced *Artemesia frigida* (Willd.) cover. Loeser et al. (2001), however, found that neither species richness nor percent cover of either exotic or native plant species differed among different cattle-grazing regimes (no grazing, low-intensity long-duration, high-intensity short-duration, very-high-intensity very-short-duration).

While the effect of livestock grazing on plant communities is rather variable across ecosystems and among different livestock species, Bakker (1998) noted that grazing tends to favor early successional plant communities, such as species with annual and biennial habits, and short stature. Furthermore, the changes in plant community structure may be dependent on spatial scale. Multiple studies of the effect of grazing

secession showed that at small spatial scales grazing strongly reduced plant species richness, but at larger scales, the reduction in species richness was not as strong. This suggests that grazing have the effect of homogenizing the plant community and secession of grazing may make vegetation patchier (Bakker 1998).

Sheep grazing can have several impacts on soil quality. First, sheep grazing may alter nutrient cycling compared with mineralization of plant detritus. Thiessen Martens and Entz (2011) noted that grazing ruminants can retain up to 25% of the N they consume. However, the remaining N, deposited as urine and feces, is often more labile than plant detritus. Second, sheep trampling could alter soil physical properties such as macroporosity and compaction Franzluebbbers (2007). Bell et al. (2011) however, note that while trampling from grazing livestock may have adverse effects on soil structure and soil water content, those effects are usually evanescent and limited to 0 – 10 cm of below the soil surface.

Cover Crops and Nurse-Crops

A cover crop is a suite of non-marketable plants grown to improve soil quality (Dabney et al. 2001) that can enhance ecosystem services for agriculture both directly by protecting soil from erosion and enhancing nutrient cycling, and indirectly by promoting conservation biocontrol (Altieri 1999, Hartwig and Ammon 2002, Tillman et al. 2012). Cover-crops may improve both the physical and chemical properties of soils through several mechanisms. First, root exploration can increase soil macroporosity and plant growth can increase evapotranspiration. Both of these processes increase saturated hydraulic conductivity (K_{sat}), therefore improving water infiltration (Dabney 1998,

Dabney et al. 2001). However, in xeric environments, this may be a detriment as it would reduce plant-available water. Second, mineralization of the plant litter provided by the cover-crop can increase soil organic matter (Reeves 1994, Hartwig and Ammon 2002, Lal 2004), which in turn, increases the cation exchange capacity of the soil and provides food for soil microorganisms (Wild 1993, Hu et al. 1999). Third, cover-crops may enhance cycling of macronutrients. For example, Kamh et al. (1999) found that the common cover-crop *Lupinus albus* (L.) was capable of uptaking recalcitrant inorganic phosphorus (P) in a P-deficient luvisol, which in turn increased wheat (*Triticum aestivum* L.) P-uptake and yield. Finally, if legumes are included in a cover-crop, biological nitrogen (N) fixation by *Rhizobia* symbionts and subsequent mineralization of plant material can increase N capital (Snapp et al. 2005).

In contrast to cover crops, nurse-crops (a.k.a. relay-crops or companion-crops), are a species with a short life-cycle grown simultaneously with a second, longer-lived species, usually to protect the second species during a vulnerable part of its life cycle (Roslon and Fogelfors 2003). Like cover-crops, nurse-crops can provide a variety of agronomic benefits including weed suppression, soil stabilization, alternative sources of revenue, as well as pest management (Canevari 2000). While recognized mostly for their benefits to soil quality, nurse-crops and cover-crops may also be important components of an integrated pest management strategy. For example, use of nurse-crops or cover-crops can affect several vital rates in the life cycle of a weed. First, their use may reduce the *per capita* seed production of a weed through competitive exclusion (Gallandt et al. 1999). Second, cover-crops and nurse-crops may indirectly reduce seed survival in the

seed bank by providing habitat to seed-predators (Swanton et al. 1999, Snapp et al. 2005, Landis et al. 2005) and by enhancing the rate of microbially-mediated seed decay. Third, detritus from terminated cover-crops may reduce emergence either by preventing light transmittance or through allelopathy (Teasdale et al. 1991, Gallandt et al. 1999).

In addition to seed predators, cover-crops and nurse-crops can provide habitat for beneficial organisms such as parasitoids of phytophagous insects, enhancing the effectiveness of conservation biological control in highly disturbed agroecosystems (Barbosa 1998, Landis and Menalled 1998). Robust populations of these natural enemies may help prevent populations of pestiferous arthropods from reaching the dynamic economic threshold (Altieri and Nicholls 1999).

Research Originality and Need:

Agriculture in the twenty-first century must balance increased demands for food, fuel and fiber with the need to reduce adverse environmental ramifications such as eutrophication of water bodies, decreases in biodiversity, and degradation of soil structure (Foley et al. 2005). To achieve this balance, Reganold et al. (2011) call for transformative innovations that alter the entire management regime in agroecosystems. They contend that the *status quo* of incremental innovations aimed at altering only a single component of the entire management regime will not suffice to achieve agronomic and ecological sustainability. Both re-integrating targeted sheep grazing with cover cropping and nurse cropping as a form of habitat management are examples of such transformative innovations for ecologically-based management in agricultural systems.

However, our understanding the effects of livestock grazing for cover crop termination on associated biodiversity, soil quality, and subsequent yields need further development to promote such an approach for managing agroecosystems successfully (Franzluebbers 2007, Sulc and Tracy 2007)

One major drawback of cover-crops is that farmers cannot generate direct revenue the season in which they are grown. Livestock grazing for cover crop termination may provide alternative sources of income and enhance producer adoption. However, livestock grazing can have adverse effects on soil quality under certain conditions. In particular, the effects of grazing cover crops on soil chemical and physical properties have not been well studied (Kahimba et al. 2008, Thiessen Martens and Entz 2011). While the ecological and agronomic benefits of cover-crops are well documented (e.g., Dabney 1998, Dabney et al. 2001, Hartwig and Ammon 2002, Snapp et al. 2005, Tillman et al. 2012), less is known about using livestock grazing as a method for cover-crop termination (Franzluebbers 2007, Kahimba et al. 2008, Thiessen Martens and Entz 2011). The information that exists primarily focuses on the integration of cover-crops and livestock grazing in large-scale commodity production and addresses the effects of its implementation on soil quality (Hilimire 2011, Bell et al. 2011, Thiessen Martens and Entz 2011).

There is little research on crop performance in integrated crop-livestock agroecosystems, and most of the studies that have investigated crop performance focus on major commodities (Bell et al. 2011). Furthermore, to our knowledge, no study has investigated the impacts of targeted-grazing for cover-crop termination on carabid beetle

communities and only a scant few have investigate its impacts on weed communities (e.g., Davis et al. 2005, Tracy and Davis 2009). Thus, our understanding of the impacts of targeted grazing on horticultural vegetable production and the associated biodiversity of such systems needs further development.

Both nurse cropping and cover cropping are forms of habitat management, a conservation biological control practice. Habitat management aims at providing the necessary resources to maintain viable and effective populations of predators and parasitoids (i.e., natural enemies) of agricultural pests within an agroecosystem (Clark et al. 1997, Landis et al. 2000). To accomplish this goal, land managers minimize detriments to or enhance the quality of resources and conditions for natural enemies in agroecosystems. Habitat management can include altering disturbance regimes to decrease incidental mortality to natural enemy taxa, improving shelter or microclimate to prevent their emigration, and providing alternate food sources to their populations when there is a dearth of prey (Landis et al. 2000). Barbosa and Wratten (1998) argue that habitat management, such as augmenting plant diversity, is an effective means of conservation biological control only if the natural enemy populations have the proper spatial and temporal distribution within an agroecosystem. Thus, it is imperative to evaluate how habitat management practices affect natural enemy community dynamics and how alterations to plant communities, in turn, affect natural enemy habitat selection through space and time.

Habitat management is a relatively nascent concept in agroecology. While there is a burgeoning literature of the benefits of buffer strips and weed zones in

agroecosystems, the benefits of cover cropping as habitat management needs further development (Landis et al. 2000). Similarly, there is a paucity of research on nurse cropping as a form of habitat management in perennial cropping systems. This research attempts to further investigate these topics.

Research Questions, Objectives and Justifications

This research attempts to determine (1) How management practices and environmental factors act as ecological filters that determine within-field levels of biodiversity, and (2) the ramifications that those practices have for associated ecological functions, namely moisture retention, net primary production, crop production and nutrient cycling. Specifically, our research asks three main questions: (1) Do management practices that seek to reduce off-farm synthetic inputs alter the associated biodiversity of agroecosystems?, (2) Do those practices alter the ecological conditions and functions necessary for production, and (3) Does cropping diversity and stability change associated diversity?

We conducted two complementary studies to address these questions. First, we assessed the effects of sheep grazing and mowing as methods of cover crop termination on plant and carabid beetle community structure as well as soil physical and chemical properties in small-scale cropping systems. Second, we compared the weed and carabid communities among an alfalfa (*Medicago sativa* L.) monoculture, an alfalfa – hay barley (*Hordeum vulgare* L.) polyculture, and an adjacent uncultivated hayfield. We selected carabid beetles and plants as our study taxa because of their ubiquity and importance in

agroecosystems. Carabid beetles and plants are useful study organisms because they represent different trophic levels, they have trophic interactions with each other, their populations respond differently to agronomic management practices, and they represent two important suites of associated biodiversity.

Study 1: Ecological Consequences of
Integrating Sheep Grazing for Cover-Crop
Termination in Small Scale Cropping Systems

Objective 1: Assess the impact of cover-crop termination approaches on soil physical and chemical properties including nutrient status, penetration resistance, temperature and moisture.

Justification for Objective 1: Sheep grazing may have important consequences for soil chemical and physical properties such as accelerate nutrient cycling through inputs of labile forms of nutrients in urinate or feces (Thiessen Martens and Entz 2011). Also sheep trampling may compact the soil, thus altering soil aggregation and porosity. These perturbations could, in turn, affect water infiltration and root penetration (Zhao et al. 2012). Furthermore, the termination of cover-crops with sheep grazing or mowing could have important consequences for cash-crop growth in successive seasons, but the extent of these possible legacy effects is largely unknown.

Objective 2: Assess differences in plant and carabid beetle community structure between grazed and mowed cover-crops.

Justification for Objective 2: Targeted sheep grazing and mowing as methods of cover-crop termination represent distinct ecological filters. Mowing may favor one suite of species, while grazing may favor another. Carabid beetles and plants are ubiquitous and economically important in agroecosystems. Carabid beetles are considered beneficial because they are generalist predators on a variety of pestiferous arthropods (Lovei and Sunderland 1996, Sunderland 2002) and many species are seed-predators of weeds (Lee et al. 2001, Menalled et al. 2007). Understanding changes to the carabid community is especially important for ecologically-based management because such changes may have important ramifications for conservation biocontrol of pestiferous organisms.

Weeds are often blamed as an impediment to production because they compete with crops for resources (Aldrich 1987). However, weeds may confer valuable ecological benefits such as habitat for pollinators (Carvalho et al. 2011), and enhanced nutrient cycling (Shennan 2008). Assessing the response of the plant community to the two methods of cover-crop termination will elucidate whether sheep grazing directs plant species assemblages toward more beneficial or more insidious weed species.

Objective 3: Quantify differences in cash-crop yield in the season following cover-cropping between plots terminated with either grazed or mowed treatments.

Justification for Objective 3: Ultimately, economic viability plays an important role in determining whether producers adopt an agronomic practice or not. Sheep grazing may affect important factors for crop yields such as soil quality (Sulc and Tracy 2007,

Bell et al. 2011, Thiessen Martens and Entz 2011) and/or the biological community.

Quantifying crop yield is crucial because it is one of the most important factors determining whether integrating sheep grazing for cover crop termination is economically viable.

Study 2: Effects of Cropping Habitat Heterogeneity on Carabid Beetle Community Structure

Objective 1: Characterize the carabid beetle community structure among different vegetation management systems.

Justification for Objective 1: Vegetation structure and diversity are ecological filters of the associated biodiversity in agroecosystem. Understanding how changes in vegetation structure affect carabid beetle communities will help alfalfa growers choose vegetation management strategies that enhance ecologically-mediated pest suppression.

Objective 2: Identify changes in vegetation structure that influence carabid habitat selectivity.

Justification for Objective 2: Changes in vegetation structure can alter the environmental condition imposed on carabid beetles. Identifying how these condition change in response to altered vegetation structure may elucidate the mechanisms by which habitat management influences carabid beetle habitat selection in alfalfa agroecosystems.

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CHAPTER TWO

INTEGRATION OF SHEEP GRAZING FOR COVER-CROP TERMINATION
INTO MARKET GARDENS: AGRONOMIC CONSEQUENCES OF AN
ECOLOGICALLY-BASED MANAGEMENT STRATEGYIntroduction

Growing concerns about the need to balance food production with conservation of biodiversity has led to an increased interest in reducing the use of off-farm synthetic inputs (Altieri 1999, Foley et al. 2011). However, this approach to farming will only be viable if the agronomic and ecological conditions remain favorable for crop production (Robertson and Swinton 2005). The need to reconcile these apparently disparate goals has precipitated a call for the development of ecologically-based management systems (Matson et al. 1997, Robertson et al. 2008, Reganold et al. 2011). Such systems are those that augment ecological processes or community structure to provide the functions necessary for production and management of pest populations (Magdoff 2007, Altieri et al. 2012). One such practice is the use of cover-crops, a suite of non-marketable plants grown to improve agronomic conditions such as soil quality (Dabney et al. 2001).

Cover-crops may improve both the physical and chemical properties of soils through several mechanisms. Root exploration by cover-crop species can increase soil macro-porosity and plant growth can increase evapotranspiration. Both of these processes increase saturated hydraulic conductivity (K_{sat}), therefore improving water infiltration (Dabney 1998, Dabney et al. 2001). Mineralization of the plant litter provided

by the cover-crop can increase soil organic matter (Reeves 1994, Hartwig and Ammon 2002, Lal 2004), which in turn, increases the cation exchange capacity of the soil and provides food for soil microorganisms (Wild 1993, Hu et al. 1999). Furthermore, cover-crops may enhance cycling of macronutrients. For example, Kamh et al. (1999) found that the common cover-crop white lupine (*Lupinus albus* L.) was capable of uptaking recalcitrant inorganic phosphorus (P) in a P-deficient luvisol, which in turn increased wheat (*Triticum aestivum* L.) P-uptake and yield. Additionally, if legumes are included in a cover-crop, biological nitrogen (N) fixation by *Rhizobia* symbionts and subsequent mineralization of plant material can increase N capital (Snapp et al. 2005).

In addition to the potential benefits to soil quality, cover-crops may be an important component of an integrated pest management strategy. For example, the use of cover-crops can affect several vital rates in the life cycle of a weed. First, cover-crops may reduce the *per capita* seed production of a weed through competitive exclusion (Gallandt et al. 1999). Second, cover-crops may indirectly reduce seed survival in the seed bank by providing habitat to seed-predators (Swanton et al. 1999, Snapp et al. 2005, Landis et al. 2005) and by enhancing the rate of microbially-mediated seed decay (Dabney et al. 1996, Liebman and Davis 2000). Third, detritus from terminated cover-crops may reduce weed emergence either by preventing light transmittance or through allelopathy (Teasdale et al. 1991, Gallandt et al. 1999). Finally, in addition to seed predators, cover-crops can provide habitat for beneficial organisms such as parasitoids of phytophagous insects, enhancing the effectiveness of conservation biological control in

highly disturbed agroecosystems (Barbosa 1998, Landis and Menalled 1998, Altieri and Nicholls 1999).

A major drawback to the use of cover-crops is that producers cannot generate direct revenue the season in which the cover-crop is grown (Sulc and Tracy 2007, Thiessen Martens and Entz 2011). One approach to overcome this challenge may be integration of livestock grazing for cover-crop termination. Integrating livestock may offer several benefits to producers besides a quick method of terminating cover-crops. First, livestock production may provide producers with alternative sources of revenue through the production of food (e.g., meat) and fiber (e.g., wool) as well as grazing leases (Gardner et al. 1991, Franzluebbers 2007, Thiessen Martens and Entz 2011). Second livestock grazing could be a component of an integrated weed management program because it may reduce the number of flowering ramets producing seeds and the associated seed rain from mature fruits (Popay and Field 1996, Meissner and Facelli 1999). Finally, livestock grazing may aid in nutrient cycling through inputs of urine and feces (Bakker 1998, Thiessen Martens and Entz 2011).

Despite these agronomic benefits, at least two potential adverse outcomes could arise from the integration of livestock grazing. First, trampling by livestock could alter soil physical properties such as macroporosity and compaction (Franzluebbers 2007). Bell et al. (2011) however, noted that while trampling from grazing livestock may have adverse effects on soil structure and soil water content, those effects are usually temporary, limited to 0 – 10 cm below the soil surface, and often naturally attenuated by freeze-thaw cycles. Second, livestock consumption of plant matter represents a potential

mass export of nutrients. Thiessen Martens and Entz (2011) noted that grazing ruminants can retain up to 25% of the N they consume but, the remaining N, deposited as urine and feces, is often more labile than plant detritus.

Consumer demand for produce from horticultural market-gardens has grown substantially in recent years. Low and Vogel (2011) note that US sales of local food in 2008 totaled $\$4.8 \times 10^9$ with fruit, vegetable, and nuts comprising the bulk of these sales. Correspondingly, there has been a concomitant resurgence in market-garden vegetable systems after decades of decline (Lyson and Guptill 2004). Consumer preferences, costs, and environmental concerns often prohibit intensive use of off-farm synthetic inputs in these systems. Thus, the development of ecologically-based management practices is especially important for market-garden vegetable production systems. While there has been substantial research on the agronomic consequences of cover-crops (e.g., Dabney 1998, Dabney et al. 2001, Hartwig and Ammon 2002, Snapp et al. 2005, Tillman et al. 2012), most of this research has focused on their use in large-scale commodity production. In contrast, there has been substantially less investigation into cover-crop use in market-garden vegetable production. Furthermore, there is a paucity of research on the effects integrating livestock grazing for cover-crop termination as the research that exists largely focuses on large-scale commodity production (Franzluebbers 2007, Kahimba et al. 2008, Thiessen Martens and Entz 2011).

We compared the agronomic effects of sheep-grazing for cover-crop termination with those of mowing over two consecutive years, 2012 and 2013. Our study consisted of two phases. In the first phase, we assessed the impacts of sheep grazing as a method

of termination on weed pressure and soil quality in the cover-crop. In the second phase of the study, we estimated weed pressure and yield in subsequently grown cash-crops. We had two trials of our experiment, one trial beginning its first phase in 2012 and the second trial beginning its first phase in 2013. Our research asked four main questions: (1) Does sheep grazing affect soil physical and chemical properties differently than mowing, a common approach used to terminate cover-crops? (2) Is there a difference in weed pressure between the two management strategies? (3) Can cover-crops serve as viable forage for sheep?, and (4) Does cash-crop yield differ between the two management strategies in the subsequent year?

Materials and Methods

Study Site

Our study was conducted at Townes Harvest Farm (THF), 1.2 ha certified organic, diversified vegetable farm on the campus of Montana State University – Bozeman (45° 40' N, 111° 4' W). The farm follows a six-year rotation beginning with a cover-crop season (Year 1) and followed by cash-crops in the subsequent five growing season (Years 2 – 6)(Charles Holt, *Pers. comm.*). THF has Turner loam (fine loamy over sandy, mixed, superactive, frigid, typic Agriustoll) soils. The soil texture at THF is a clay loam consisting of 25% sand, 44% silt and 30% clay. THF receives approximately 380 – 480 mm of precipitation annually, and has a mean annual air temperature between 3.9 – 7.2 °C (NRCS 2013).

Cover-Crop Phase Experimental Design

The cover-crop phase followed a single factor, completely-randomized design with two treatment-levels (sheep-grazed and mowed for cover-crop termination) and three replicates per treatment-level. Each replicate consisted of a 10m × 15m rectangular plot. On June 8, 2012 and on June, 25, 2013, we cultivated the soil in all plots and seeded a cover-crop consisting of 56 kg ha⁻¹ buckwheat (*Fagopyrum esculentum* Moench), 23 kg ha⁻¹ beets (*Beta vulgaris* L.), 11 kg ha⁻¹ sweetclover [*Melilotus officinalis* (L.) Lam.], and 68 kg ha⁻¹ pea (*Pisum sativum* L.).

Between August 3, 2012 and August 7, 2012, we terminated the cover-crops at anthesis by either tractor-mowing or sheep grazing. Similar treatments were used to terminate the cover-crops between August 7, 2013 and August 11, 2013. For the sheep-grazing plots, we set up temporary electrical fences charged between 3500 V – 6000 V, stocked each plot with 6 – 11 Rambouillet yearling rams and allowed those sheep to graze *ad libitum* until the cover-crop appeared >90% removed. In each plot, we placed large watering troughs to provide the sheep with supplemental water.

Cash-Crop Phase Experimental Design

In 2013, three seedbeds were tilled to a depth of approximately 25 – 35 cm with a 1.07 m-diameter spader (Celli Co., Flori, Italy) through the plots previously under cover-crop in 2012. The farm manager planted and harvested kohlrabi (*Brassica oleracea* L. var. *gongyloides* L.), spinach (*Spinacia oleraceae* L.), and lettuce (*Lactuca sativa* L.) in these seedbeds, one crop per seedbed, based on his experience (Table 2.1). Due to the farmer's space and equipment requirements, this study followed an unreplicated split-plot

design. To prevent interference with crop yield estimates, each 10 m × 15 m plot was divided in half north-south. Each half was randomly assigned to be used for weed sampling or crop yield sampling. All marketable produce was harvest and weighed to estimate crop yields. Due to heavy rain and subsequent soil crusting, the spinach crop failed in half of our experimental plots and thus yield data were excluded from analysis. However, data exploration revealed that weed densities and biomass had similar values and were as variable as those in kohlrabi and lettuce plots. Thus, we retained these data for analysis.

Soil Quality Estimation

We assessed the impact of cover-crop termination strategy on soil quality by measuring several soil physical and chemical parameters. Soil moisture was measured using 7cm soil moisture data loggers (HOBO U30 Station, Onset Computer Corp., Bourne, MA) placed near the center of each plot to a depth of approximately 7cm. We measured soil temperature by placing four temperature loggers approximately 10cm below the soil surface near the center of each plot (iButton® model DS1921G, Maxim Integrated, San Jose, CA). Temperatures within a plot from all recovered probes were averaged to obtain mean plot temperature through time. On April 28, 2013, soil compaction at the beginning of the cash-crop phase, was assessed at four locations per plot using a soil penetrometer by measuring penetration resistance at four depth ranges: 0-15cm, 15-30cm, 30-45 cm and 45-60cm. Penetration resistance values from the four sampling sites were averaged for each depth within each plot.

To assess nutrient content during the cash-crop phase, two randomly-located soil core samples were collected per plot on April 28, 2013 using a hydraulic auger with a 5cm diameter. We separated the soil from each sample by the same depths as above and combined them into one sample per depth and plot. Samples from each depth within each plot were weighed immediately after sampling to the nearest 0.1g, dried to constant mass in a soil drying oven at 105°C, and re-weighed to obtain an estimate of gravimetric water content. For nutrient analyses, we combined the 15-30 cm, 30-45 cm and 45-60 cm depth into a single subsoil sample. All soil samples were sent to a third party soil analytics laboratory (Agvise Laboratories, Northwood, ND) to be assayed for Olsen P, potassium, calcium, electrical conductivity, cation exchange capacity, organic matter, and pH.

We measured foliar N content of the aboveground plant biomass at anthesis to estimate N-capital of our system in the cash-crop phase. Foliar N is often a more robust metric of N-capital than is soil NO_3^- because plants uptake N over a larger spatial scale than would be captured by a soil sample (Hausenbuiller 1985). Furthermore, usually <1% of soil N is NO_3^- at any point in time, whereas immobilized foliar N in detritus and living plant tissue comprises the largest pools of N in terrestrial ecosystems (Foth and Ellis 1997). Foliar N was estimated as part of the crude protein assay (see Forage Quality section for details) in the cover-crop phase. In the cash-crop phase, we combined all plant species from each treatment-cash-crop combination collected at crop anthesis for biomass estimation. Samples were ground in a plant matter grinder with a 2mm screen (Wiley® Mill, Thomas Scientific Inc., Swedesboro, NJ) and further ground in laboratory

grinding mill (Cyclone Mill, UDY Corporation, Fort Collins, CO). Samples were assayed for foliar nitrogen in a gas chromatograph carbon/nitrogen analyzer (LECO Corporation, St. Joseph, MI).

Forage Quality Estimation

We measured cover-crop forage quality on July 31, 2012 and on August 2, 2013 by collecting all above ground plant material from four randomly placed 0.33m² quadrats randomly placed within each plot and combining biomass from all quadrats. Samples were dried at 60°C for one week, weighed to the nearest 0.1g, and ground to pass a 2mm screen (Wiley[®] Mill, Thomas Scientific Inc., Swedesboro, NJ). Acid and neutral detergent fiber was assayed in an ANKOM 200 Fiber Analyzer (ANKOM Technology, Macedon, NY) following manufacturer protocols (ANKOM Technology 2011a, 2011b). Crude protein was assayed using a LECO LP528 Nitrogen/Protein Analyzer (LECO[®], St. Joseph, MI), correcting for dry matter. To obtain estimates of dry matter, two 1.000 ± 0.01g samples of ground plant material were placed into tins. The mass of the empty tin as well as the mass of the sample and tin combined were recorded. Samples were dried in a drying oven at 100°C for 72hrs. To avoid rehydration after removal from the drying oven, we placed the samples in a desiccator until they were weighed. Dry matter (DM) was calculated as:

$$DM = \frac{m_f}{m_0} \times 100\% \quad (2.1)$$

where, m_f is the final mass of the sample after drying and m_0 is the initial mass of the sample. These metrics were used to obtain dry digestible matter (DDM), dry matter

intake (DMI), and relative feed value (RFV) (Undersander and Moore 2002), which were calculated as:

$$DDM = 88.9 - (0.779 \times ADF) \quad (2.2)$$

$$DMI = \frac{120}{NDF} \quad (2.3)$$

and

$$RFV = \frac{(DDM \times DMI)}{1.29} \quad (2.4)$$

Cover-Crop and Weed Biomass Estimation:

We took biomass samples of all cover-crop and weed species on July 25, 2012 and on August 1, 2013 at anthesis, but prior to cover-crop termination. Post-treatment biomass samples were also collected on September, 7 2012 and on August 30, 2013. Due to a wet fall in the second year of our study, we collected an additional set of biomass data on October 9, 2013 after fall regrowth, but prior to senescence. For biomass data, we again randomly placed four 0.44m × 0.75m quadrats in each plot, cut all plant material flush the soil surface within quadrats and separated it by species. For each species, we combined the biomass collected in the four quadrats within a plot to avoid pseudoreplication. We dried all samples at 60°C to constant mass and weighed them to the nearest 0.1g.

Cash-Crop Phase Weed Density and Biomass Estimation

We estimated weed pressure at crop emergence on June 25, 2013 and at crop anthesis on July 25, 2013. In the randomly selected five-meter weed sampling zone, we

randomly placed two $0.44 \times 0.75\text{m}$ rectangular quadrats with the long edge perpendicular to crop rows. For both the emergence and the anthesis datasets, we counted all ramets of each species within each quadrat. Data from both quadrats for each crop-plot combination were pooled. At emergence, we took all above ground plant biomass from a representative sample of five ramets of each species. If a species had fewer than five ramets, all ramets were collected. These sample were dried to constant mass at 60°C in a drying oven and weighed to the nearest 0.001g . We used these biomass values to compute an allometric estimate of total biomass by species at emergence. At anthesis, we counted the total number of ramets of each species, clipped all aboveground biomass, and pooled it by species. Biomass samples were dried to constant mass at 60°C in a drying oven and weighed to the nearest 0.001g for sample $\leq 9.999\text{g}$ and to the nearest 0.1g for samples $>10.0\text{g}$.

Table 2.1 Planting and harvest dates for the 2013 cash-crop phase at Townes Harvest Farm, Bozeman, MT, United States. Cash-crops were planted in rows through previously grazed or mowed cover-crop treatments.

	Treatment	Crop	Planting Date	Harvest Date
Plot 1	Grazed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	April 23, 2013	July 23, 2013
		Lettuce	April 23, 2013	July 8, 2013
Plot 2	Grazed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	June 6, 2013	Crop Failed
		Lettuce	May 13, 2013	July 23, 2013
Plot 3	Mowed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	April 23, 2013	July 23, 2013
		Lettuce	April 23, 2013	July 8, 2013; July 26, 2013
Plot 4	Mowed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	June 6, 2013	Crop Failed
		Lettuce	May 13, 2013	July 16, 2013
Plot 5	Grazed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	April 23, 2013	July 23, 2013
		Lettuce	April 23, 2013	July 8, 2013; July 26, 2013
Plot 6	Mowed	Kohlrabi	June 6, 2013	August 30, 2013
		Spinach	June 6, 2013	Crop Failed
		Lettuce	May 13, 2013	July 16, 2013

Data Analysis

To evaluate the effect of cover-crop termination method on soil temperature, we used a growing degree day model and a hydrothermal time model. Growing degree-days were calculated as:

$$GDD = \sum_{i=1}^n \left(\frac{T(max)_i - T(min)_i}{2} \right) \quad (2.5)$$

where GDD is the accumulated growing degree days, $T(max)_i$ is the daily maximum soil temperature on day i , and $T(base)$ is a physiological lower threshold temperature.

Growing degree-days are accumulated if $T(max)_i > T(base)$. Because redroot pigweed (*Amaranthus retroflexus* L.) was an abundant and ubiquitous weed in all plots in both years, we used an empirically derived $T(base)$ value for this species of 15.0°C in our model. This value corresponds to the minimum temperature at which *A. retroflexus* begins shoot elongation (Oryokot et al. 1997). Growing degree-day accumulation was compared between treatments with a repeated measures ANOVA.

To compare treatment effects on soil moisture content, we constructed a hydrothermal time model. Hydrothermal time was calculated as:

$$HTT = \sum_{i=1}^n GDD_i(H_i) \quad (2.6)$$

$$\text{for: } \begin{aligned} \theta_i < \theta_{pwp}, & \quad H_i = 0 \\ \theta_i > \theta_{pwp}, & \quad H_i = 1 \end{aligned}$$

where HTT is the accumulated hydrothermal days, GDD_i is the growing degree days accumulated on day i , θ_i is the mean soil water content on day i , and θ_{pwp} is the water content at the permanent wilting point, H_i is the binomial plant water available, and i indexes days of measurement. In this model, H_i takes a value of 1 when θ_i is greater than

the water content at the permanent wilting point. When θ_i is less than the permanent wilting point, H_i is 0. We took the water content at the permanent wilting point to be 20%, a representative value for clay loam soils (Hausenbuiller 1985). Accumulated growing degree-days and hydrothermal days were compared between treatments using a two-sample permutation test. Due to technical difficulties with the soil moisture data loggers, the range of sampling dates differed between years. Thus, we did not compare accumulated hydrothermal time between years.

We compared soil chemical properties and penetration resistance between treatments and among soil depth using a two-way factorial ANOVA. Because we only measured foliar N at anthesis during the cash-crop phase, we compared it between mowed and grazed plots using a two-sample permutation test with 1000 Monte-Carlo iterations. Due to concerns of unequal variance, we compared all forage quality metrics between grazed and mowed plots using Welch's two sample t-test.

We compared the total plant biomass in the cover-crop phase at anthesis between grazed and mowed plot as well as between trials using an ANOVA blocked by trial-year. Once cover-crops were terminated, we tested treatment effects on biomass reduction using ANCOVA with pretreatment *Malva neglecta* (Wallr.) biomass as covariate. ANCOVA was used due to high *M. neglecta* biomass before and after cover-crop termination. Prior to the analysis, a Box-Cox power transformation analysis revealed that a log-transformation of biomass was warranted. The log-response (LR) ratio was calculated as:

$$LR = \ln\left(\frac{M_f}{M_0}\right) = \ln(M_f) - \ln(M_0) \quad (2.7)$$

where M_0 is the pretreatment biomass and M_f is the post-treatment biomass.

Because weed density in the cash-crop phase was sampled at emergence and anthesis, we compared weed density between treatments and cash-crops using a split-plot ANOVA with repeated measures where period was nested within cash-crop rows and cash-crop rows were nested within cover-crop treatment plots. Total weed biomass in the cash-crop phase was only measured at anthesis, and thus treatment and cash-crop effects were tested with a split-plot ANOVA with cash-crop rows nested within cover-crop termination method. Cash-crop yields were compared with a split-plot ANOVA with cash-crop rows nested within cover-crop termination strategy.

All analyses were conducted in R version 3.0.2 (R Development Core Team 2013). Mean separations for significant interactions were performed using Tukey's HSD in the TukeyC package of R (Jeliahovschi and Allaman 2011). Advanced graphics were constructed in the sciplot (Morales et al. 2012) and ggplot2 (Wickham 2009) packages of R.

Results

Soil Quality

Soil temperature in the top 10 cm of soil, as measured by growing degree day accumulation, did not differ between grazed and mowed plots in 2012 ($F = 0.017$; $df = 1,4$; $P = 0.903$; Fig 2.1A). Soil moisture in the top 7 cm was below the permanent wilting point in 2012 for the entire month after cover-crop termination (Fig 2.1B). Thus, neither grazed plots nor mowed plots accumulated hydrothermal days following cover-crop

termination in 2012. Similarly, in 2013 there was no difference in growing degree day accumulation between treatments ($F = 0.16$; $df = 1, 4$; $P = 0.95$; Fig 2.1C). In contrast to 2012, soil moisture in the top 7cm of soil exceeded the permanent wilting point for five days in 2013 following cover-crop termination (Fig 2.1D). However, hydrothermal day accumulation did not differ between treatments ($P = 0.695$, 1000 iterations) as grazed plots accumulated 11.17 ± 0.85 hydrothermal days, whereas mowed plots accumulated 10.58 ± 1.20 hydrothermal days.

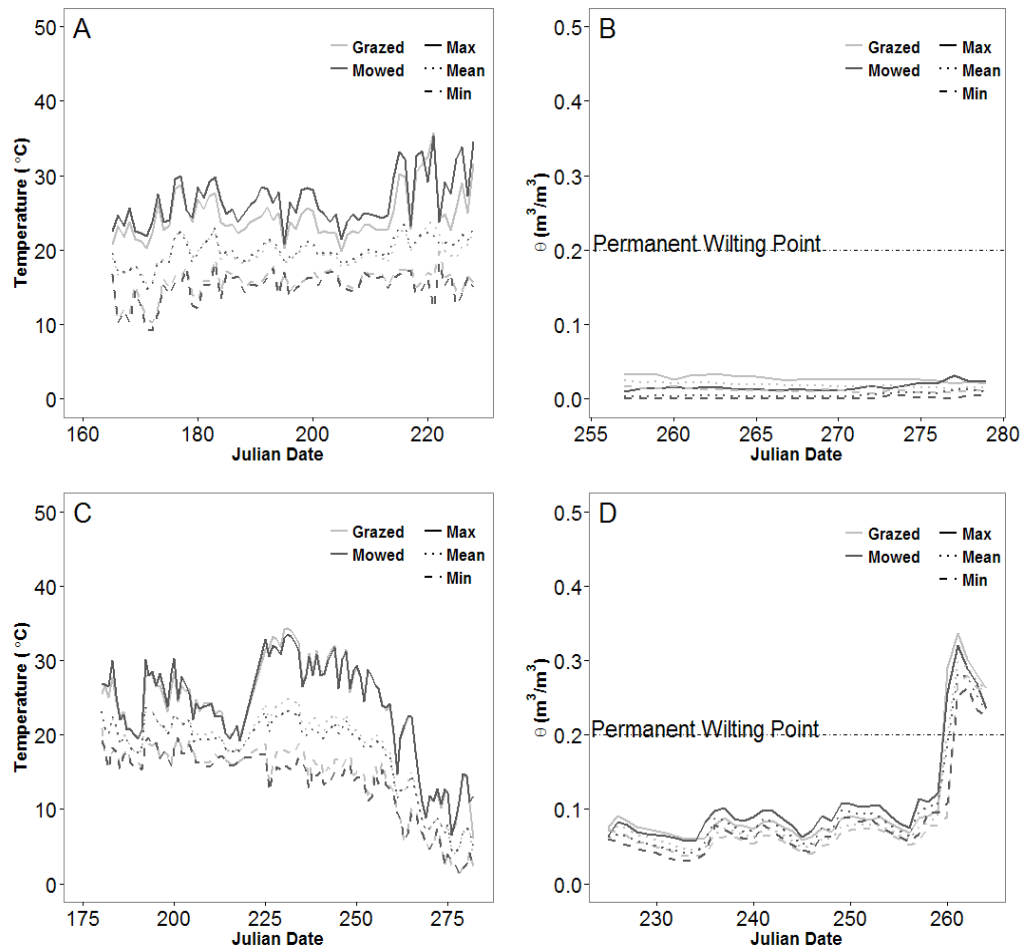


Figure 2.1: Effects of sheep grazing and mowing on (A) soil temperature in 2012, (B) soil moisture in 2012, (C) soil temperature in 2013 and (D) soil moisture in 2013 during the cover-crop phase at Townes Harvest Farm, Bozeman, MT United States.

Soil compaction increased with depth in spring following termination for the 2012 plots ($F = 14.57$; $df = 3, 16$; $p < 0.001$). However, we found no difference in soil compaction between cover-crop termination strategies ($F = 2.08$; $df = 1, 16$; $p = 0.113$). Overall, penetration resistance increased from 11.12 ± 0.48 MPa 0 – 15 cm below the soil surface to 26.98 ± 2.97 MPa 45 – 60 cm below the soil surface. Soil compaction 45 – 60 cm beneath the soil surface was higher than any other depth range ($P < 0.005$); however penetration resistance did not differ among depths from 0 – 45 cm ($P > 0.09$) (Fig 2.2).

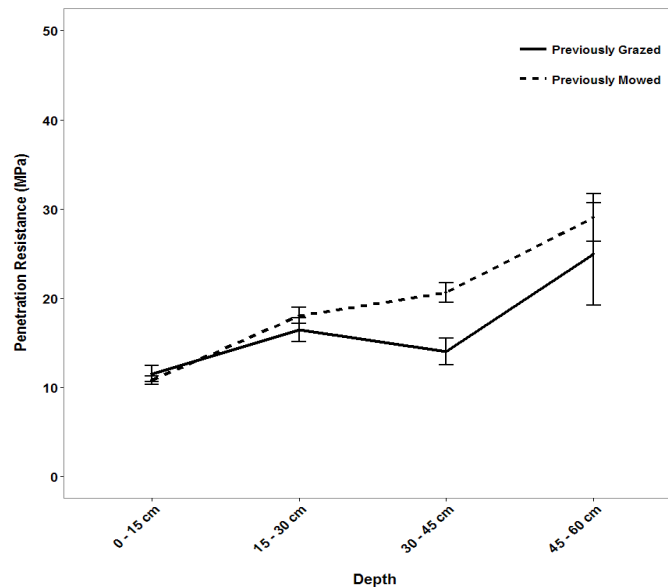


Figure 2.2: Effects of sheep grazing and mowing on soil compaction at Townes Harvest Farm, Bozeman, MT, United States. Values are reported as mean $\pm$ SE.

Soil organic matter and measured plant nutrients (P, K, Mg, and Ca) differed between topsoil and subsoil in at the beginning of the 2013 cash-crop phase (Table 2.2). Soil organic matter, P and K concentrations were greater in the topsoil than in the subsoil

($P < 0.001$), whereas Mg ($P = 0.002$) and Ca ($P = 0.05$) concentrations were greater in the subsoil than in the topsoil. However, none of these metrics of soil chemistry differed between previously grazed and previously mowed plots. In addition, there was no interactive effect of cover-crop termination strategy and soil depth. Foliar N did not differ between previously grazed and mowed plots during the 2013 cash-crop phase ($p = 0.509$, 1000 iterations). Foliar N was $2.93 \pm 0.178\%$ in grazed plots and $3.13 \pm 0.132\%$ in mowed plots.

Table 2.2: Impacts of sheep grazing and mowing on soil chemistry in the 2013 cash-crop phase at Townes Harvest Farm, Bozeman, MT, United States. Mowed and grazed plots refer to treatment in 2012 cover-crop phase. Values are reported as mean $\pm$ SE.

	Topsoil (0-15cm)				Subsoil (15-60cm)			
	Mowed Plots		Grazed Plots		Mowed Plots		Grazed Plots	
Organic Matter (%)	3.70	± 0.06	3.60	± 0.22	2.30	± 0.03	2.30	± 0.19
pH	7.80	± 0.03	7.80	± 0.00	7.90	± 0.03	7.90	± 0.09
Electrical Conductivity (mmhos)	0.37	± 0.02	0.37	± 0.03	0.46	± 0.05	0.43	± 0.02
NO ₃ (PPM)	17.00	± 2.89	16	± 2.09	14	± 2.32	12	± 1.50
P (PPM)	97.00	± 3.51	93	± 8.82	73	± 10.10	65	± 8.19
K (PPM)	850.00	± 40.20	840	± 18.90	550	± 65.90	540	± 42.10
Ca (PPM)	3900.00	± 308.00	4400	± 795.00	6000	± 101.00	5300	± 803.00
Mg (PPM)	510.00	± 12.20	500	± 11.80	590	± 18.20	580	± 28.70
Cation Exchange Capacity (cmol _c kg ⁻¹)	26.00	± 1.72	28	± 3.99	36	± 0.19	33	± 3.81

	Depth		Treatment		Depth $\times$ Treatment	
	F _(1,6)	P	F _(1,6)	P	F _(1,6)	P
Organic Matter (%)	148.00	1.87×10^{-5}	0.08	0.78	0.08	0.78
pH	4.41	0.08	1.59	0.25	0.18	0.69
Electrical Conductivity (mmhos)	4.88	0.07	0.12	0.74	0.12	0.74
NO ₃ (PPM)	1.64	0.25	0.33	0.59	0.10	0.76
P (PPM)	51.00	3.80×10^{-4}	2.72	0.15	0.41	0.55
K (PPM)	177.00	1.12×10^{-5}	0.26	0.63	8.42×10^{-4}	0.98
Ca (PPM)	6.13	0.05	0.02	0.91	1.07	0.34
Mg (PPM)	28.50	0.00	0.35	0.58	0.07	0.81
Cation Exchange Capacity (cmol _c kg ⁻¹)	5.67	0.05	0.03	0.88	1.00	0.36

Forage Quality:

We found no difference in the RFV of the cover-crop between treatments.

Similarly, there was no interactive effect of treatment and year on RFV. There were no

treatment or interactive effects on any of the other forage quality parameters we measured (Table 2.3).

Table 2.3: Forage quality of cover-crops at Townes Harvest Farm, Bozeman, MT, United States. Values are reported as mean $\pm$ SE.

	2012				2013			
	Mowed		Grazed		Mowed		Grazed	
Neutral Detergent Fiber (%)	52.50	$\pm$ 1.24	56.20	$\pm$ 3.65	53.20	$\pm$ 0.64	55.60	$\pm$ 4.04
Acid Detergent Fiber (%)	13.60	$\pm$ 0.82	9.25	$\pm$ 1.06	11.50	$\pm$ 2.30	11.40	$\pm$ 1.07
Crude Protein (%)	14.50	$\pm$ 1.17	13.50	$\pm$ 2.58	20.00	$\pm$ 0.52	19.80	$\pm$ 0.80
Digestible Dry Matter (%)	78.30	$\pm$ 0.64	81.70	$\pm$ 0.82	80.00	$\pm$ 1.79	80.00	$\pm$ 0.83
Dry Matter Intake (%)	2.29	$\pm$ 0.06	2.15	$\pm$ 0.13	2.26	$\pm$ 0.03	2.18	$\pm$ 0.15
Relative Feed Value	139.00	$\pm$ 3.69	136.00	$\pm$ 9.24	140.00	$\pm$ 4.86	135.00	$\pm$ 8.41

	Treatment		Treatment $\times$ Year	
	F _(1,8)	P	F _(1,8)	P
Neutral Detergent Fiber (%)	1.18	0.31	0.05	0.83
Acid Detergent Fiber (%)	2.35	0.16	2.20	0.18
Crude Protein (%)	0.14	0.72	0.06	0.81
Digestible Dry Matter (%)	2.35	0.16	2.20	0.18
Dry Matter Intake (%)	1.05	0.34	0.08	0.79
Relative Feed Value	0.28	0.61	0.03	0.86

Cover-Crop and Weed Biomass:

Total biomass at anthesis in the cover crop phase did not differ between mowed and grazed plots in either trial of our experiment (Figs 2.3A, 2.3B). In 2012, grazing reduced total biomass more than mowing ($F = 13.33$; $df = 1, 7$; $p = 0.0082$). Total biomass in grazed plots was reduced $88.6 \pm 6.07\%$ compared with $75.8 \pm 10.8\%$ in mowed plots. Cover-crop biomass declined more than weed biomass ($F = 42.98$; $df = 1, 7$; $p < 0.001$). However, there was no significant interaction between termination method and plant class ($F = 3.33$; $df = 1, 7$; $p = 0.11$). Grazing reduced cover-crop biomass $97.8 \pm 1.1\%$ and weed biomass $56.5 \pm 18.8\%$. Mowing reduced cover-crop biomass $89.1 \pm 5.1\%$ and weed biomass $34.2 \pm 25.4\%$.

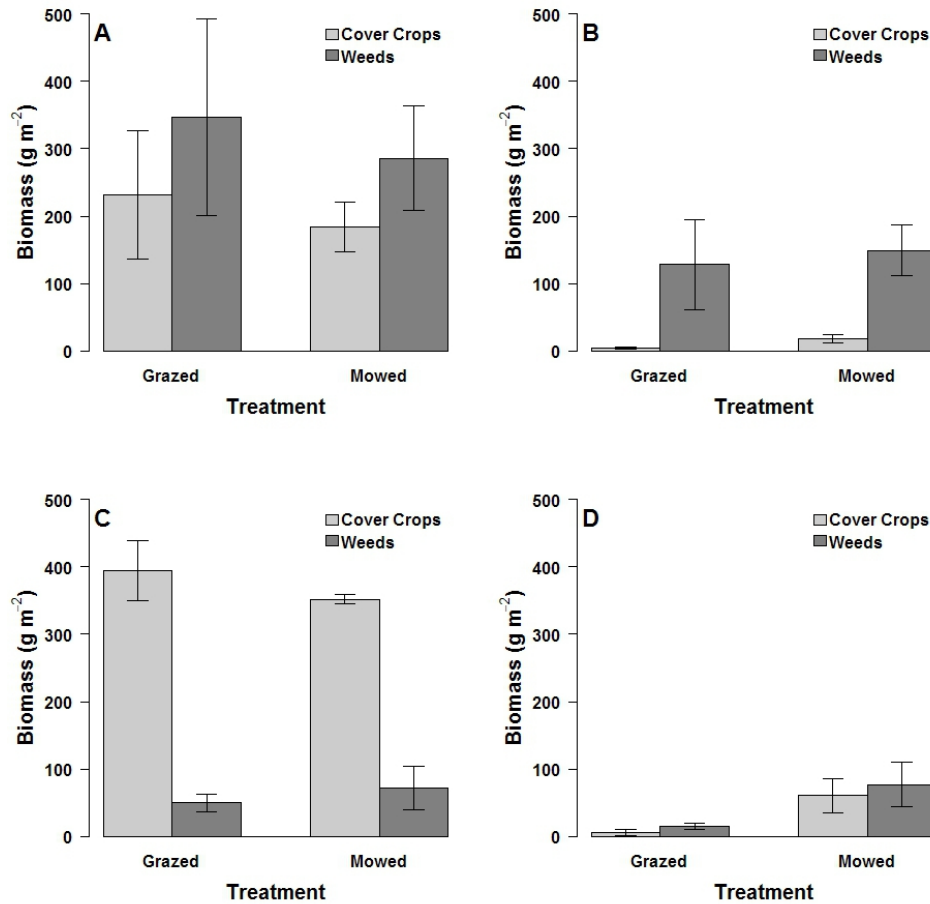


Figure 2.3: Impacts of termination approach (sheep grazing or mowing) on cover crop and weed biomass in (A) 2012 pretreatment (B) 2012 post-treatment, (C) 2013 pretreatment and (D) 2013 post-treatment at Townes Harvest Farm, Bozeman, MT, United States. Error bar are $\pm$ SE.

In 2013, cover-crop biomass was reduced more than weed biomass ($F = 16.89$; $df = 1, 7$; $p = 0.005$), but as in 2013, there was no interaction between termination method and plant class ($F = 1.56$; $df = 1, 7$; $p = 0.252$). Grazing reduced cover-crop biomass $98.3 \pm 1.2\%$ compared with $83.0 \pm 7.1\%$ in mowed plots. While grazing reduced weed biomass $65.8 \pm 9.4\%$, mowing increased weed biomass $36.7 \pm 76.9\%$ (Figs 2.3C, 2.3D). The observed increase in weed biomass in mowed plots is the result of an increase in two

abundant species in one of three mowed plots. In this plot, *M. neglecta* biomass increased from 21.8 g m⁻² at anthesis to 71.5 g m⁻² after cover-crop termination. While there was no *A. retroflexus* from this plot at anthesis; its biomass was 23.6 g m⁻² following cover-crop termination.

Cash-Crop Phase Weed Density and Biomass

In the 2013 cash-crop phase, weed density did not differ between previously grazed and previously mowed plots ($F = 11.21$; $df = 1, 2$; $P = 0.08$; Fig. 2.4A). However, weed density differed among cash-crop rows ($F = 10.61$; $df = 2, 8$; $P = 0.006$). The density of weed seedlings was higher in rows sown with lettuce than in rows sown with kohlrabi (209.72 ± 29.06 ramets m⁻² and 72.85 ± 14.45 ramets m⁻², respectively; $P = 0.004$). Weed density was higher at emergence than at anthesis ($F = 7.39$; $df = 1, 12$; $P = 0.02$, Figs. 2.4A and 2.4B). However, this pattern did not vary among cash-crop rows ($F = 1.42$; $df = 1, 12$; $P = 0.28$). Finally, there was no three-way interactive effect of cash-crop, termination method and sampling period on weed density ($F = 0.97$; $df = 2, 12$; $P = 0.41$).

Because density as a metric for weed pressure may underestimate the competitive effects of larger plants, we also sampled weed biomass at anthesis in the cash-crop phase (Fig 2.4C). Total weed biomass did not differ among cash-crops ($F = 2.265$; $df = 2, 10$, $P = 0.154$) or between previously grazed and mowed plots ($F = 1.661$; $df = 1, 10$; $P = 0.226$). Additionally, there was no interaction between cash-crop and termination approach on total weed biomass at anthesis ($F = 0.449$; $df = 2, 10$; $P = 0.650$).

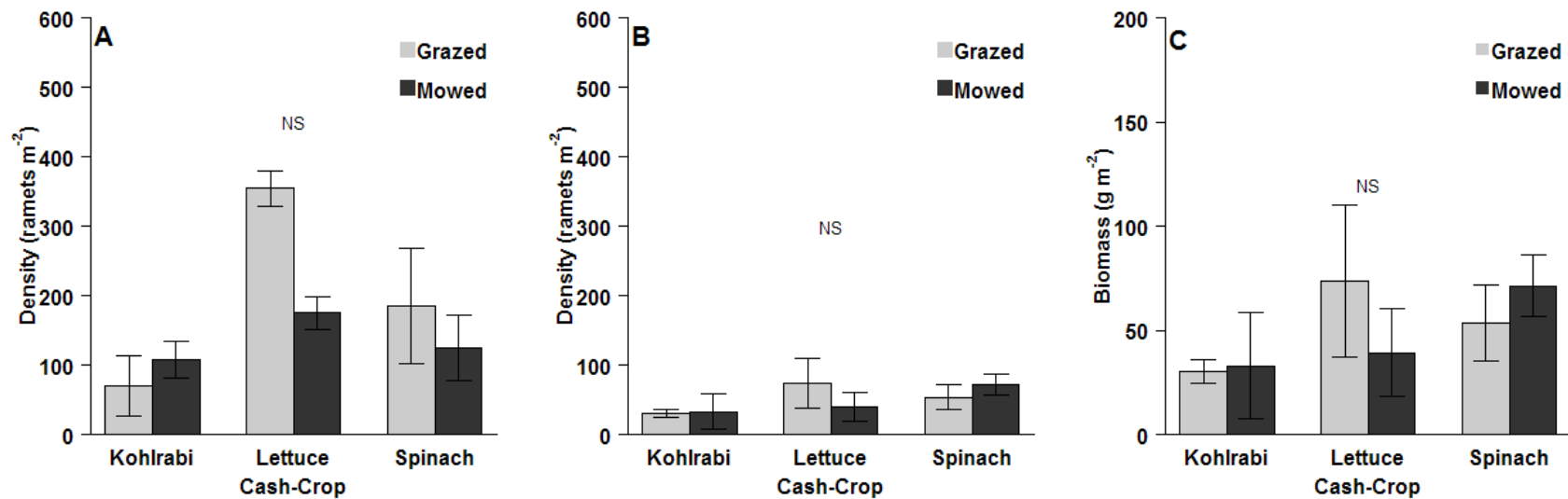


Figure 2.4: Impacts of sheep-grazing and mowing on (A) density of weeds at emergence, (B) density of weeds at anthesis, and (C) biomass of weeds at anthesis in the 2013 cash-crop phase at Townes Harvest Farm, Bozeman, MT, United States. Values are shown as mean $\pm$ SE. “NS” indicates that no groups were significantly different ($P > 0.05$).

Cash-Crop Yields

The spinach crop failed in three of the six replicates, probably due to heavier than normal spring rains in 2013 and subsequent soil crusting (Charles Holt, *Pers. comm.*). Two of the plots had their cover-crops terminated by mowing and one plots had its cover-crop terminated by grazing. Thus, to avoid introducing bias, we excluded spinach yields from our analysis. In lettuce and kohlrabi rows, we found marginally higher yields in mowed plots than in grazed plots ($F = 9.98$; $df = 1,2$; $P = 0.0873$; Fig. 2.5). There was a marginally-significant interactive effect of cash-crop species and termination method on yield ($F = 6.34$; $df = 1,4$; $P = 0.065$), but there was no main effect of cash-crop species on yields ($F = 1.81$; $df = 1,4$; $P = 0.250$). This is likely the result of a marginal difference of lettuce and kohlrabi yields in mowed plots ($P=0.055$; Fig 2.5).

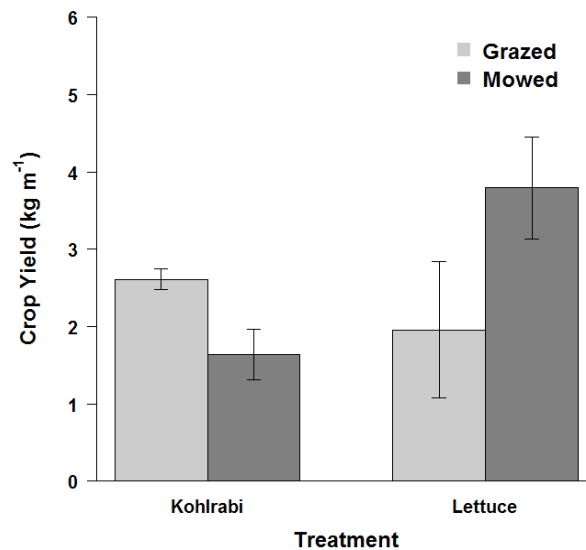


Figure 2.5: Impacts of sheep-grazing and mowing on subsequent cash-crop yields in 2013 at Townes Harvest Farm, Bozeman, MT, United States. Values are reported as mean $\pm$ SE.

Discussion

Soil Quality

Previous research suggests that soil compaction by livestock is limited to the top 10cm of soil, ephemeral, and similar to the compaction caused by farm machinery (Greenwood and McKenzie 2001, Franzluebbers and Stuedemann 2008, Bell et al. 2011, but see Tracy and Zhang 2008). In accordance, we did not detect any differences in penetration resistance between treatments the spring following cover-crop termination. As soil water content increases, the soil load capacity declines, making it more susceptible to compaction (Hamza and Anderson 2005). In our study, sheep grazed during a relatively dry period, which may explain the observed lack of differences between treatments.

There was no difference in growing degree-day accumulation between grazed and mowed plots in either year of the cover-crop phase. This result contrasts with that of Yates et al. (2000) who found that soil temperatures in heavily grazed *Eucalyptus* woodland were higher than in either lightly grazed or ungrazed systems. Our study involved a relatively short duration of grazing and both treatments equally removed living vegetation. As a consequence, both mowed and grazed plots likely had lower rates of evapotranspiration and higher rates of light transmittance compared with their respective pretreatment levels.

We did not detect any differences in hydrothermal time accumulation between grazed and mowed plots. In pastures, light to moderated grazing has been shown to reduce water infiltration (Greenwood and McKenzie 2001). Because plants can uptake

soil water much deeper than 10 cm (Wild 1993) our methods did not necessarily reflect the effects of sheep grazing on total plant available water. Additionally, our plots were grazed during the driest part of the year for southwestern Montana.

Despite distributional differences in soil chemistry between the topsoil and subsoil independent of treatments, and in accordance with previous studies (Marrs et al. 1989, Franzluebbers 2007), we did not observe differences between grazed and mowed plots overall or between depths on soil chemistry. Collins (2003) notes that for most nutrients, ruminants return up to 90% what they consume in their excreta. However, the short-term nature of our study precludes us from formally evaluating the mid- and long-term consequences of repeated mass export of nutrients by sheep grazing.

Forage Quality

We did not detect any differences in forage quality of cover-crops, as measured by the relative feed value (RFV), between treatment plots. Additionally, we did not find an effect of year or an interactive effect of year and treatment on forage quality. These results suggest that the forage quality of our cover-crop was spatially homogeneous and temporally consistent.

The values we obtained for acid detergent fiber (ADF), a metric of indigestible fiber, were lower than reported a maximum ADF value of 290 g kg⁻¹ (29%) for premium quality alfalfa (*Medicago sativa* L.) forage (Bath and Marble 1989, Buxton 1996). Forbes (2007) notes that optimal forage crude protein concentrations for sheep nutrition range between 130 -160 g kg⁻¹ (13-16%). In 2012, crude protein concentrations were within this range for both treatments. However, in 2013, crude protein values were larger

than this optimal range. Excess protein has a few potential adverse health effects on sheep including increased risk of heat stress, pizzelle rot and urolithiasis (Pugh 2002). However, Kyriazakis and Oldham (1993) found that sheep can discriminate the forages they consume to optimize their crude protein intake. Thus, it is unlikely that sheep grazing cover crops would suffer the deleterious effects of excess crude protein intake.

Both years the forage quality (as measured by RFV) fitted within the top two categories as defined by the American Forage and Grassland Council (Hopper et al. 2004). Alfalfa forage of such standards commanded \$77.76 Mg⁻¹ and \$69.37 Mg⁻¹, respectively (Hopper et al. 2004). Based on these values, the cover-crop in the first trial was worth \$435.59 ± 74.60 ha⁻¹ and \$409.69 ± 76.79 ha⁻¹ for mowed and grazed plots, respectively. In the second trial the cover-crop was worth \$276.18 ± 29.57 ha⁻¹ and \$255.30 ± 27.81 ha⁻¹ for mowed and graze plots, respectively.

The cover-crop may not command prices as high as those of hay if the producer grants a grazing lease to a sheep rancher. In a study conducted in the Imperial Valley of California, alfalfa growers granted grazing leases to sheep ranchers for \$0.06 – 0.11 head⁻¹ d⁻¹ (Bell and Guerrero 1997). At these rates and a stocking rate of 80 head ha⁻¹ d⁻¹, a grazing lease would be worth \$24.00 – 44.00 ha⁻¹. Hence, for sheep ranchers purchasing a grazing lease on cover-crops may represent a substantial savings compared with buying hay. Concomitantly, growers would receive a direct source of revenue from their cover-crop, at least partially off-setting the cost of its husbandry.

Cover-Crop and Weed Biomass

The effect of cover-crop termination method on cover-crop and weed species was not uniform. In 2012, sheep grazing reduced total plant biomass more than did mowing. However, in 2013 we found no differences between mowed and grazed plots. Despite these differences, both years cover-crop biomass consistently declined more than weed biomass. In the 2012 trial, weed biomass was greater than cover-crop biomass prior to termination with redroot pigweed (*Amaranthus retroflexus* L.) and common mallow (*Malva neglecta* Wallr.) as the dominant species. *Malva neglecta* has a prostrate growth form and thus may have avoided termination through either grazing or mowing. Despite the erect stems of *A. retroflexus*, many stems of this species were able to resprout following termination. The dominant cover-crop species was buckwheat (*Fagopyrum esculentum* Moench.), which has erect stems. In contrast to *A. retroflexus*, *F. esculentum* stem did not re-sprout after being mowed or grazed (see Chapter 3). These results suggest that grazing and mowing are equally effective at terminating a cover-crop, but the efficacy of these cover-crop termination methods may be variable from year to year and may depend on the species composition of the weed community and the cover-crop.

Cash-Crop Phase Weed Density and Biomass

During the cash-crop phase of this study, weed density declined between emergence and anthesis, probably due to self-thinning (Westoby 1984). Weed density at emergence was higher in rows sown with lettuce that were grazed terminated in 2012 than in any other cash-crop-treatment combination. This may be an artifact of the planting date of lettuce. In two of the three grazed plots, lettuce was planted four weeks earlier

than either kohlrabi or spinach, which may have allowed more weed seeds to germinate and emerge in these rows prior to sampling than in other cash-crops. This research was conducted as an on-farm experiment; thus planting dates were dictated by market needs as well as the farmer's experience and constraints. The lack of complete experimental control is often cited as a major drawback to on-farm research (Molnar et al. 1992). However, such research often offers realistic results, which may be more useful to producers than highly controlled experiments on research farms (Tanaka et al. 2008, Meynard et al. 2012). Despite the higher weed density at emergence in previously grazed lettuce rows, and even though the spinach crop failed in half of our experimental plots, weed density and biomass did not differ between mowed and grazed plots or among cash-crop rows. This suggests other factors are more important in determining weed density and biomass than either legacy effects from the cover-crop method employed or competitive interaction between crops and weeds.

We did not detect any overall differences in weed density between grazed and mowed plots in the 2013 cash-crop phase. In addition, we found no effect of cover-crop termination method on weed biomass at anthesis, suggesting that mowing and grazing represent similar ecological filters (Keddy 1992). In accordance with our results, Tracy and Davis (2009) found that weed biomass did not differ between cattle-grazed oat (*Avena sativa* L.) cover-crops and conventionally-terminated cover-crops in a corn (*Zea mays* L.) cropping system. Both sheep grazing and mowing have the potential to reduce seed rain. However, because sheep may consume weed seeds, they may reduce seed viability (Wallander et al. 1995). By contrast, it seems unlikely that mowing would

affect seed viability. We did not investigate seed rain and viability, and we only quantified weed density biomass over two growing season, thus precluding long-term prediction of weed demography under these two management strategies.

Cash-Crop Yields

Similar to previous studies (Franzluebbers 2007, Hilimire 2011, Bell et al. 2011, Thiessen Martens and Entz 2011), we did not find any detriments to crop yields from integrating livestock into our cropping system. In addition, our results concur with Franzluebbers' (2007) observation that using livestock to terminate cover-crops does not impact subsequent crop yields.

Conclusion

Our study adds to a growing body of literature on the agronomic and economic consequences of integrated crop-livestock systems. We compared the effects of sheep grazing for cover-crop termination with those of mowing on soil quality, forage quality, and cover-crop termination efficacy. In addition, we tested the effects of these two cover-crop termination strategies on weed pressure and crop yield in the subsequent growing season. Our results indicate that sheep grazing was as effective as mowing for cover-crop termination and had no detrimental effects on soil penetration resistance, chemistry, or microclimate. Additionally, weed pressure and cash-crop yield did not differ between treatments. The cover-crop represents a high quality forage that could provide \$24.00 - \$44.00 ha⁻¹ of direct revenue for producers as a grazing lease. Thus, the integration of sheep grazing could make the use of cover-crops more economically

feasible in market vegetable gardens, and not have adverse effects on agronomic conditions. Our study represents one of a very few studies on the integrated crop-livestock regimes in market vegetable gardens. Further research should investigate long term effects on agronomic conditions under repeated grazing.

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CHAPTER THREE

ECOLOGICAL EFFECTS OF INTEGRATING LIVESTOCK INTO
HORTICULTURAL VEGETABLE PRODUCTION ON WEED AND GROUND
BEETLES (COLEOPTERA: CARABIDAE) COMMUNITIESIntroduction

Mounting concerns about the adverse effects of high-input, industrially-managed approaches to food, fiber and more recently energy production has precipitated a call for ecologically-based management in agroecosystems (Altieri et al. 1983, Liebman and Gallandt 1997, Altieri 1999, Robertson and Swinton 2005). In contrast to industrially-based management, which is largely dependent on synthetic inputs for sustained production, ecologically-based management primarily relies on augmenting ecological processes to provide the functions necessary for production (Magdoff 2007). These necessary functions include nutrient cycling, pollination, pest suppression, regulation of soil temperature and moisture, and detoxification of noxious chemicals (Altieri 1999, Altieri and Nicholls 1999). In this context, agroecologists have become increasingly interested in understanding the role that biodiversity plays in ecosystem functions and finding land management practices that direct community structure toward achieving those goals (Altieri and Letourneau 1982, Benton et al. 2003, Shennan 2008).

In agroecosystems, species constitute either the “planned biodiversity” or the “associated biodiversity”. Planned biodiversity consists of the species that a land manager intentionally includes in the system, usually through anthropogenic disturbances

such as seeding, cultivation, harvest and pesticide applications (Matson et al. 1997). Associated biodiversity is the suite of organisms not deliberately included by the land manager, and thus includes species that normally live in the area occupied by the production ecosystem or colonize it from adjacent habitats. Associated biodiversity includes pest, beneficial, and neutral species (Vandermeer and Perfecto 1995, Altieri 1999, Vandermeer et al. 2002). Changes to the associated biodiversity therefore, can have important consequences for weed and insect pest dynamics (Bugg and Waddington 1994), as well as for ecosystem services such as pollination (Keitt 2009, Carvalheiro et al. 2011), weed seed predation (Tooley and Brust 2002, Menalled et al. 2007, Gaines and Gratton 2010), nutrient cycling (Jordan and Vatovec 2004, Magdoff 2007), and crop production (Altieri and Letourneau 1982, Cardinale et al. 2003, Carvalheiro et al. 2011). Both land management practices and planned biodiversity act as ecological filters of the associated biodiversity, systematically favoring some species while excluding others (Keddy 1992, Matson et al. 1997, Funk et al. 2008). Thus, implementing novel land management practices or changing the planned biodiversity in a production ecosystem can have important consequences for the associated biodiversity.

In agroecosystems, those species that comprise the associated plant biodiversity are often considered weeds. Despite their recognition as a major impediment to crop production (Aldrich 1987), weeds can provide a variety of ecological services that would otherwise require the use of synthetic inputs (Jordan and Vatovec 2004). First, weeds may provide habitat for natural enemies of pestiferous arthropods, and thus aid in conservation biocontrol (Landis et al. 2000, 2005) by helping to keep pest insect

populations below the economic threshold (Altieri and Nicholls 1999). Second, weeds may stabilize or enhance pollinator communities. For example, Carvalheiro et al. (2011) found that higher diversity of non-crop plants in agroecosystems and greater proximity to natural habitats increased pollinator species richness in a South African sunflower (*Helianthus annuus* L.) plantation, resulting in increased sunflower yields. Third, several weed species maintain mutualisms with multiple species of arbuscular mycorrhizal fungi (AMF) that can infect crops (Jordan and Vatovec 2004, Vatovec et al. 2007). Feldmann and Boyle (1999) found that weeding non-crop AMF host plants reduced maize (*Zea mays* L.) biomass by 28%. Hence, a major challenge in the implementation of ecologically-based weed management is minimizing the negative effects of competitive exclusion by weeds while reaping the benefits of the ecological services that they provide (Jordan and Vatovec 2004). Understanding how land management practices affect non-crop plant communities can aid in addressing this challenge by helping producers avoid imposing ecological filters that favor particularly insidious weed species.

An important component of the associated arthropod diversity is the carabid beetle family (Coleoptera:Carabidae). Carabid beetles comprise one of the most abundant and diverse families in the Coleoptera order. They are abundant in northern temperate agroecosystems (Lovei and Sunderland 1996) and are important predators of pests such as aphids, slugs, and other beetles (Holland 2002, Sunderland 2002). Most carabid beetle species in the Harpalini and Zabarini tribes are seed predators and may therefore help regulate weed populations (Tooley and Brust 2002, Menalled et al. 2007, Gaines and Gratton 2010). Thus, carabids are often a target of conservation biological control

practices (Clark et al. 1997). Because many carabids have specific habitat preferences and are acutely sensitive to changes in their environment, they have been considered as bioindicator taxa (Lovei and Sunderland 1996). For these reasons, land management practices that alter carabid beetle community dynamics could have important implications in conservation biocontrol.

Integrating crop and livestock production has been proposed as a method of enhancing the economic and environmental sustainability of agroecosystems (Franzluebbbers 2007, Sulc and Tracy 2007, Hilimire 2011, Thiessen Martens and Entz 2011). In particular, grazing livestock on cover-crops may provide alternative sources of revenue for producers, thus making the use of cover-crops more economically feasible. While the ecological and agronomic benefits of cover-crops are well documented (e.g., Dabney 1998, Dabney et al. 2001, Hartwig and Ammon 2002, Snapp et al. 2005, Tillman et al. 2012), less is known about using livestock grazing as a method for cover-crop termination (Franzluebbbers 2007, Kahimba et al. 2008, Thiessen Martens and Entz 2011). The information that exists primarily focuses on the integration of cover-crops and livestock grazing in large-scale commodity production and addresses the effects of its implementation on soil quality (Hilimire 2011, Bell et al. 2011, Thiessen Martens and Entz 2011). Thus, research is need on the integration of livestock grazing for cover-crop termination in horticultural vegetable production, and the ecological consequences of this practice on the associated biodiversity.

To assess the extent to which sheep grazing and mowing act as different ecological filters of associated biodiversity, we conducted a two-year study comparing

their effects on weed and carabid beetle community structure. Our study consisted of two phases. In the first phase, we grew a four species cover-crop and terminated it by either sheep grazing or mowing. In the second phase, we grew three cash-crops in the plots that had a cover-crop the previous year and had been terminated through either grazing or mowing. We conducted two trials of the first phase in 2012 and 2013, and one trial of the second phase in 2013. Our research asks whether weed and carabid beetle communities exposed to sheep grazing shifted to a different community structure compared with those exposed to mowing. Our hypothesis is that these two cover crop termination methods act as distinct ecological filters. Consequently, we predicted that the community structure of weeds and carabids would change following each cover-crop termination approach.

Materials and Methods

Study Site

Our study was conducted at Townes Harvest Farm (THF), a 1.2 ha certified organic, diversified vegetable farm on the campus of Montana State University – Bozeman, Montana (45° 40' N, 111° 4' W). The farm follows a six-year rotation beginning with a cover crop season (Year 1), followed by cash crops in the subsequent five growing season (Years 2 – 6) (Charles Holt, *Pers. Comm.*). THF is underlain with Turner loam (fine loamy over sandy, mixed, superactive, frigid, typic Agriustoll), receives approximately 380 – 480 mm of precipitation annually, and has a mean annual air temperature of 3.9 – 7.2 °C (NRCS 2013). The soil texture at THF is a clay loam consisting of 25% sand, 44% silt and 30% clay.

Experimental Design:

The cover-crop phase followed a single factor, completely-randomized design with two treatment-levels (sheep-grazing and mowing for cover-crop termination) and three replicates per treatment-level. Each replicate consisted of a 10 m × 15 m rectangular plot with at least a 3 m buffer between plots to avoid contamination of weed seeds between plots due to tillage (Liebman et al., 2014). On June 8, 2012 and on June 25, 2013, we cultivated the soil in all plots and seeded a four-species cover-crop consisting of buckwheat seeded at 56 kg ha⁻¹ (*Fagopyrum esculentum* Moench), beets (*Beta vulgaris* L.) seeded at 23 kg ha⁻¹, sweetclover [*Melilotus officinalis* (L.) Lam.] seeded at 11 kg ha⁻¹, and peas (*Pisum sativum* L.) seeded at 68 kg ha⁻¹.

Between August 3, 2012 and August 7, 2012, we terminated the cover-crops at anthesis by either tractor-mowing or sheep grazing. Similar treatments were used to terminate the cover-crops between August 7, 2013 and August 11, 2013. For the sheep-grazing plots, we set up temporary electrical fences charged between 3500 V – 6000 V, stocked each plot with 6 – 11 Rambouillet yearling rams, and allowed them to graze *ad libitum* until the cover-crop appeared >90% removed. In each plot, we placed large watering troughs to provide the sheep with supplemental water.

In 2013, three seedbeds were tilled to a depth of approximately 25 – 35 cm with a 1.07 m-diameter spader (Celli Co., Flori, Italy) through the plots previously under cover-crop in 2012. The farm manager planted and harvested kohlrabi (*Brassica oleracea* L. var. *gongyloides* L.), spinach (*Spinacia oleraceae* L.), and lettuce (*Lactuca sativa* L.) in these seedbeds, one crop per seedbed, based on market needs and his experience (see

Table 2.1). Due to the farmer's space and equipment requirements, the cash-crop phase of the study followed an unreplicated split-plot design. To prevent interference between the weed community assessment and crop yield estimates, each 10 m × 15 m plot was further divided in half north-south. Each half was randomly assigned to be used for weed sampling or crop yield sampling. All marketable produce was harvested and weighed to estimate crop yields. Due to heavy rain and subsequent soil crusting, the spinach crop failed in half of our experimental plots and thus yield data were excluded from analysis. However, data exploration revealed that weed densities and biomass had similar values and were as variable as those in kohlrabi and lettuce plots. Thus, we retained these data for analysis.

Weed Community Sampling:

Cover-Crop Phase: On May 24, 2012 and on June 25, 2013, and prior to soil cultivation, we collected seedling emergence data from four randomly placed 0.44 × 0.75m quadrats in each plot. Seedling emergence data were collected later in 2013 than in 2012 due to cooler spring in 2013. At anthesis, but prior to cover-crop termination, we took biomass samples of all cover-crop and weed species. These data were collected on July 25, 2012 and on August 1, 2013 for the first and second trials, respectively. Post-treatment biomass samples were also collected on September, 7 2012 and on August 30, 2013. Due to a wet fall in 2013, we collected an additional set of biomass data on October 9, 2013 after fall regrowth, but prior to senescence. For biomass data, we cut all plant material flush within four 0.44 × 0.75m quadrat at the soil surface, separated it by

species, and combined samples from the four quadrats. We dried all samples at 60°C to constant mass and weighed them to the nearest 0.1 g.

Cash-Crop Phase: We estimated weed pressure at crop emergence on June 25, 2013 and at crop anthesis on July 25, 2013. Within each previously grazed or mowed plot, we randomly selected a five-meter weed sampling zone and randomly placed two $0.44 \times 0.75\text{m}$ rectangular quadrats with the long edge oriented perpendicular to crop rows. For both the emergence and the anthesis datasets, we counted all ramets of each species within each quadrat. Data from both quadrats for each crop-plot combination were pooled prior to analysis. At emergence, we took all aboveground plant matter from a representative sample of five ramets of each species. If a species had fewer than five ramets, all ramets were collected. These samples were dried to constant mass at 60°C in a drying oven and weighed to the nearest 0.001 g. We used these biomass values to compute an allometric estimate of total biomass by species at emergence. At anthesis, we counted the total number of ramets of each species and clipped all aboveground biomass of each species. Biomass samples were dried to constant mass at 60°C in a drying oven and weighed to the nearest 0.001 g for sample ≤ 9.999 g and to the nearest 0.1 g for samples $>10.0\text{g}$.

Carabid Beetle Community Sampling:

We estimated carabid beetle activity-density, a proxy for species abundance (Thomas et al. 1998), during the cover-crop phase of each trial, by placing three pitfall traps in the center of the each one of our six experimental plots. To construct the pitfall

traps, we dug approximately 20 – 30 cm deep $\times$ 10 cm wide holes using a posthole auger (10 cm diameter) and placed two stacked 0.5 L plastic cups (Solo Cup Company, Lake Forest, IL) in each of those holes. The pitfall trap holes were backfilled until the mouth of the top cup was flush with the soil surface, and the top cup of the pitfall trap was filled approximately one-third full with a propylene glycol-based antifreeze (Arctic Ban[®], Camco Manufacturing Inc., Greensboro, NC). We covered each pitfall trap with a rain cover constructed with 25 cm–diameter clear plastic plates held to the ground with three equally spaced 10 cm bolts. Each rain cover had at least 2 cm between the soil surface and the rim of the clear plastic plates to avoid interfering with ground dwelling arthropod activity.

During the first trial of the experiment, we collected all arthropods caught in the pitfall traps weekly from May 25, 2012 to June 1, 2012, from June 22, 2012 to July 27, 2012, and from August 16, 2012 to October 5, 2012. These three periods represent the carabid community prior to soil cultivation (“precultivation” hereafter), under actively growing cover-crop (“pretreatment” hereafter) and after cover-crop termination (“terminated” hereafter), respectively. During the second trial, we collected all arthropods caught in pitfall traps weekly from May 3, 2013 to May 17, 2013 and from June 7, 2013 to June 21, 2013 for the precultivation period. For the pretreatment period we collected the pitfall traps weekly from June 28, 2013 to August 2, 2013. Pitfall traps were collected from August 16, 2013 and October 4, 2013 for the terminated period. Due to an error, the pitfall traps were not collected on July 21, 2012, and therefore the samples

from July 27, 2012 represented two weeks of collection. To correct for this error, we calculated the mean daily catch rate for each capture period.

At each collection, we placed the catch into either a 9.5×18 cm or an 11.5×23 cm plastic bag (Whirl-Pak®, Nasco Inc., Fort Atkinson, WI) and refilled the pitfall traps with antifreeze. The three pitfall traps within each plot were combined into the same plastic bag, stored in a freezer, and later transferred into 70% ethanol by volume. We identified carabid beetles to species if possible to estimate activity-density following Lindroth (1968). Those beetles that could not be positively identified to species were identified to genus, following (Lindroth 1968), and recorded as a distinct morphospecies. Positively identified species names follow Bousquet (2012).

Data Analysis:

Weed Communities: For the cover-crop and cash-crop phases of the experiment, we compared the weed density, biomass, species richness, diversity, and community structure between grazed and mowed plots. A Box-Cox power transformation analysis revealed that a log-transformation of density and biomass were warranted for the cover-crop phase, but only for biomass in the cash-crop phase. For all analyses, we compared data from the cover-crop and cash-crop phases separately. For each plot at each of our sampling periods within a trial, we estimated α -diversity using Simpson's diversity index ($1 - D$):

$$D = \sum_{i=1}^s p_i^2 \quad (3.1)$$

where p_i is proportion that species i comprises in a community and S is the total number of species in a community (Simpson 1949). We compared species richness and α -diversity between treatments and sampling periods using a repeated measures ANOVA with sampling period as the repeated factor within treatment and treatment blocked by trial.

For each trial, weed community structure for each trial was analyzed using non-metric multidimensional scaling (NMDS). Initial data locations in ordination space were determined by principal coordinates analysis (PCO). We constructed the dissimilarity matrix for our PCO using the Bray-Curtis dissimilarity index:

$$BC_{jk} = \frac{\sum_{i=1}^S 2|a_{ij} - a_{ik}|}{\sum_{i=1}^S a_{ij} + \sum_{i=1}^S a_{ik}} \quad (3.2)$$

where BC_{ij} is the dissimilarity between sites j and k , a_{ij} and a_{ik} are the total biomass of individuals of species i in sites j and k , respectively, and S is the combined total number of species in both communities (*Bray and Curtis 1957, McCune et al. 2002*). Prior to constructing the dissimilarity matrix, the raw data were log-transformed to de-emphasize the effect of dominant species according to:

$$T_{ij} = \ln(M_{ij} + 1) \quad (3.3)$$

where T_{ij} is the log-transformed abundance (biomass or density) of species i in community j and M_{ij} is the raw abundance of species i in community j .

For the cover crop phase, we tested differences in weed community structure by treatment and by sampling date using Permutation Multivariate Analysis of Variance (PERMANOVA) of the dissimilarity matrix (Anderson 2005). The two trials were

analyzed separately. Because the cash-crop phase had both repeated measure and split plot nesting, we conducted separate PERMANOVA tests to test whole-plot, subplot, and repeated measures effects.

Carabid Beetle Communities: We compared total carabid beetle activity-density, species richness, α -diversity (as indexed by Simpson's 1-D), and community structure between grazed and mowed plots. Activity-density and α -diversity was compared between treatments and trials using a repeated measures ANOVA with sampling period nested within treatment. For all other metrics, we pooled data across sampling dates within each period listed in the sampling protocol above. Species richness was compared using a repeated measures ANOVA with period as the repeated factor within treatment and treatments blocked by trial. We compared carabid community structure between grazed and mowed plots with NMDS, using PCO based on a Bray-Curtis dissimilarity matrix for initial positions. Differences in carabid community structure were analyzed among periods and between treatments using PERMANOVA on a Bray-Curtis dissimilarity matrix. Because period of the growing season was nested within treatment, we conducted separate PERMANOVA analyses for main treatment effects and for temporal effects. Additionally, NMDS and PERMANOVA analyses were conducted separately for each trial of the experiment.

All statistics and graphics were performed in R version 3.0.2 (R Development Core Team 2013). Community indices and PERMANOVA were calculated in the vegan package of R (Oksanen et al. 2007). Ordinations were calculated and graphed using the cluster (Maechler et al. 2012), labdsv (Roberts 2007), and vegan (Oksanen et al. 2007)

packages. All other graphics were created using the ggplot2 (Wickham 2009) and sciplot (Morales et al. 2012) packages of R. All post-hoc tests for significant interactions found in the ANOVA were conducted using Tukey's Honestly Significant Difference (HSD) in the TukeyC package (Jeliahovschi and Allaman 2011).

Results

Weed Communities:

Cover-crop Phase: We sampled a total of 11 weeds species in 2012 and 16 weeds species in 2013. Three species [redroot pigweed (*Amaranthus retroflexus* L.), common lambsquarter (*Chenopodium album* L.), and common mallow (*Malva neglecta* Wallr.)] comprised over 90% of the total weed biomass in all plots in 2012. In 2013, five species [prostrate pigweed (*Amaranthus blitoides* S. Watson), *A. retroflexus*, *C. album*, *M. neglecta*, and purslane (*Portulaca oleracea* L.)] comprised over 90% of the total weed biomass in all but one plot. Flower-of-an-hour (*Hibiscus trionum* L.) comprised 40.3% of the total biomass after the cover-crop was terminated in one anomalous plot, but was absent from all other plots in 2013.

Weed density, biomass, α -diversity and species richness did not differ between grazed and mowed plots in either year of the study (Table 3.1). While there were temporal differences in total weed biomass, with more biomass sampled in the pretreatment period than in the terminated period ($P = 0.01$) these differences did not vary between grazed and mowed plots. We found no temporal differences in α -diversity overall or between grazed and mowed plots. In contrast, species richness varied by

period of the growing season, but patterns did not differ between grazed and mowed plots. Specifically, species richness was higher in the pretreatment period than in either the precultivation ($P = 0.03$) or terminated ($P = 0.04$) periods.

In 2012, weed community structure did not differ between grazed and mowed plots (pseudo- $F = 1.89$; $df = 1, 5$; $r^2 = 0.32$; $P = 0.30$; Fig. 3.1A). Weed community structure shifted between the pretreatment and terminated periods (pseudo- $F = 6.35$; $df = 1, 8$; $r^2 = 0.38$; $P = 0.006$). However, within sampling periods, we did not detect any differences in weed community structure between grazed and mowed plots (pseudo- $F = 1.01$; $df = 1, 8$; $r^2 = 0.061$; $P = 0.40$). As in 2012, weed community structure in 2013 did not differ between grazed and mowed plots (pseudo- $F = 1.41$; $df = 1, 5$; $r^2 = 0.26$; $P = 0.20$; Fig. 3.1B). In contrast to our findings in 2012, in 2013 we did not detect a shift in weed community structure between the pretreatment and terminated periods (pseudo- $F = 1.44$; $df = 1, 8$; $r^2 = 0.12$; $P = 0.24$). Additionally, there was no interactive effect of cover-crop termination method and period of the growing season on weed community structure in the second trial of the experiment (pseudo- $F = 1.63$; $df = 1, 8$; $r^2 = 0.13$; $P = 0.18$).

Table 3.1: Impacts of sheep grazing and mowing on weed density, biomass and species richness during the cover-crop phase in 2012 and in 2013 at Townes Harvest Farm, Bozeman, MT, United States. Results are reported as mean $\pm$ SE.

		Grazed Plots						Mowed Plots					
		Emergence		Pretreatment		Post-treatment		Emergence		Pretreatment		Terminated	
		F	P	F	P	F	P	F	P	F	P	F	P
2012	Total Weed Density (ramets m ²)	324.00	± 98.08	–	–	–	–	261.67	± 71.63	–	–	147.92	± 37.57
	Total Weed Biomass (g m ¹)	–	–	344.91	± 144.81	127.32	± 66.34	–	–	283.69	± 77.37	147.92	± 37.57
	Simpson's Diversity (1 - D)	0.57	± 0.07	0.38	± 0.14	0.43	± 0.08	0.48	± 0.08	0.54	± 0.03	0.39	± 0.09
	Species Richness	6.33	± 0.33	4.67	± 0.33	3.00	± 0.58	4.67	± 0.33	6.67	± 1.45	4.67	± 0.67
2013	Total Weed Density (ramets m ²)	11.67	± 3.18	–	–	–	–	6.33	± 1.76	–	–	57.55	± 24.83
	Total Weed Biomass (g m ¹)	–	–	37.50	± 10.17	11.39	± 3.31	–	–	53.90	± 23.91	57.55	± 24.83
	Simpson's Diversity (1 - D)	0.61	± 0.11	0.56	± 0.08	0.49	± 0.09	0.51	± 0.09	0.54	± 0.07	0.40	± 0.12
	Species Richness	4.00	± 0.58	6.67	± 1.20	5.00	± 0.58	2.67	± 0.67	8.33	± 0.33	5.00	± 1.15
		Treatment			Period			Treatment × Period					
		F	df	P	F	df	P	F	df	P			
Total Weed Density		1.35	1,5	0.30	–	–	–	–	–	–			
Total Weed Biomass		3.85	1,5	0.11	9.45	1,10	0.01	2.84	1,10	0.12			
Simpson's Diversity		0.35	1,5	0.58	1.69	2,20	0.21	0.96	2,20	0.40			
Species Richness		1.05	1,5	0.35	6.53	2,20	0.01	3.05	2,20	0.07			

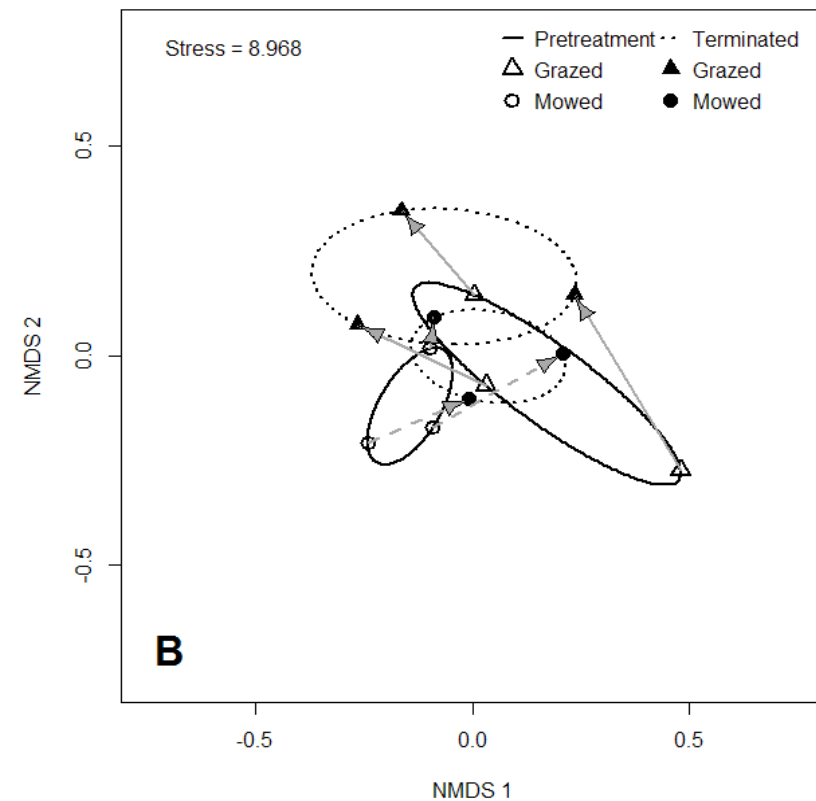
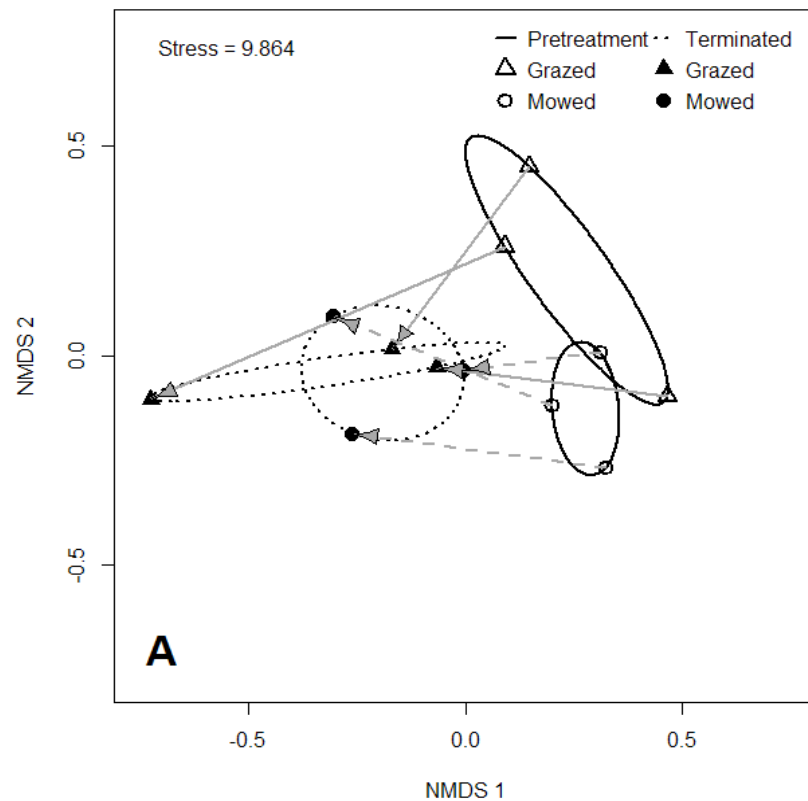


Figure 3.1: Non-metric multidimensional scaling (NMDS) ordination of weed community structure in sheep grazed and mowed plots during the cover-crop phase (A) in 2012 and (B) in 2013 at Townes Harvest Farm, Bozeman, MT, United States. Solid ellipses denote the community structure in the pretreatment period and dotted ellipses denote the community structure in the terminated period. Solid arrows denote the shift in community structure for grazed plots and dashed arrows denote the shift in community structure for mowed plots.

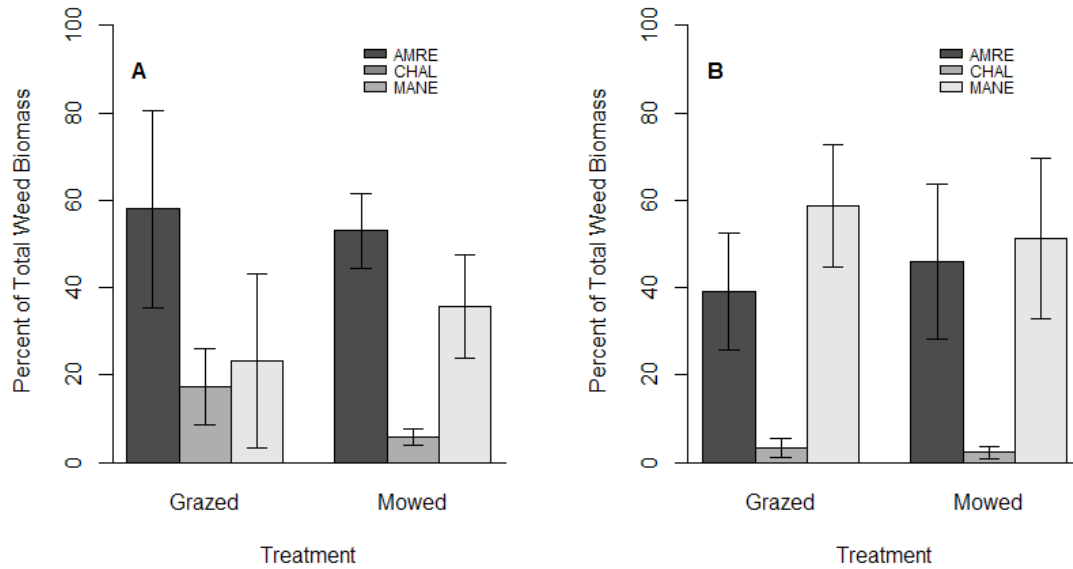


Figure 3.2: Impact of sheep grazing and mowing on relative abundance of the most dominant weed species (A) prior to cover-crop termination and (B) after cover-crop termination in 2012 at Townes Harvest Farm, Bozeman, MT, United States. Species codes are as follows: AMRE = *Amaranthus retroflexus* (L.), CHAL = *Chenopodium album* (L.) and MANE = *Malva neglecta* (Wallr.).

The observed 2012 temporal shifts in weed community structure appeared to be driven by both the decline in weed species richness noted above, as well as the changes in the relative abundance of the most dominant weed species (Fig 3.2). In 2012, *A. retroflexus* comprised $57.9 \pm 22.6\%$ of the total weed biomass prior to cover crop termination in grazed plots and $53.0 \pm 8.7\%$ of the biomass in mowed plots. *Malva neglecta* (Wallr.), by contrast, comprised $23.3 \pm 19.9\%$ of the biomass in grazed plots and $35.7 \pm 11.9\%$ of the biomass in mowed plots (Fig 3.2A). However, following cover-crop termination, *M. neglecta* became the most abundant weed in both grazed and mowed plots, comprising $58.7 \pm 13.9\%$ and $51.2 \pm 18.4\%$ of the biomass in grazed and mowed plots, respectively (Fig 3.2B).

Cash-Crop Phase: We sampled 24 weed species in the cash-crop phase. Three of these species were volunteer crop species including buckwheat (*Fagopyrum esculentum* Monech), sweetclover (*Melilotus officinalis* L.), and tomato (*Solanum lycopersicum* L.). There were four dominant species, comprising >85% of the total biomass: *A. retroflexus* (22.0%), *M. neglecta* (25.7%), Canada thistle (*Cirsium arvense* (L.) Scop.) (20.8%) and henbit (*Lamium amplexicaule* L.) (20.1%).

We did not detect any overall differences in weed density, biomass, α -diversity, or species richness between grazed and mowed plots (Table 3.2). Weed density differed among crops, with higher density in lettuce rows than in kohlrabi rows ($P = 0.01$). Additionally, weed density was greater at emergence than at anthesis ($P = 0.02$). However, the observed differences weed density among cash-crops did not vary by cover crop termination method or through time. While total weed biomass did not vary among crops, biomass was greater at anthesis than at emergence ($P < 0.001$). These temporal differences in weed biomass varied with cover crop termination method and cash crop. Weed biomass in grazed plots at emergence was greater in lettuce and spinach rows than in kohlrabi rows ($P < 0.001$ and $P = 0.007$, respectively). While there were no overall differences in α -diversity among crops or between emergence and anthesis, we found that diversity was greater in spinach rows than in kohlrabi rows in mowed plots at emergence ($P = 0.02$). Species richness differed among cash-crop rows, with greater richness in lettuce ($P = 0.02$) and spinach ($P = 0.03$) rows than in kohlrabi rows. However, that pattern did not vary between mowed and grazed plots or between emergence and anthesis.

Table 3.2: Legacy impacts of sheep grazing and mowing for cover-crop termination on weed biomass, density, α -diversity, and species richness in the cash-crop phase at Townes Harvest Farm, Bozeman, MT, United States. Values are reported mean $\pm$ SE.

		Grazed Plots			Mowed Plots		
		Kohlrabi	Lettuce	Spinach	Kohlrabi	Lettuce	Spinach
Emergence	Biomass (g m ⁻²)	0.13 ± 0.11	16.90 ± 8.28	3.95 ± 1.82	26.80 ± 25.68	10.50 ± 4.98	3.12 ± 2.55
	Density (ramets m ⁻²)	70.70 ± 43.43	355.00 ± 25.89	185.00 ± 82.85	108.00 ± 26.39	175.00 ± 23.18	125.00 ± 46.49
	Diversity (1 – D)	0.41 ± 0.18	0.61 ± 0.06	0.47 ± 0.22	0.27 ± 0.15	0.61 ± 0.12	0.70 ± 0.07
	Species Richness	3.67 ± 0.67	8.33 ± 0.33	7.67 ± 2.40	6.00 ± 1.00	8.00 ± 1.73	7.33 ± 0.88
Anthesis	Biomass (g m ⁻²)	19.90 ± 3.63	48.70 ± 23.97	35.40 ± 12.12	21.80 ± 16.98	26.00 ± 13.84	47.20 ± 9.77
	Density (ramets m ⁻²)	5.00 ± 0.58	6.00 ± 1.53	8.33 ± 0.67	5.33 ± 0.33	6.33 ± 0.67	6.00 ± 0.58
	Diversity (1 – D)	0.35 ± 0.14	0.58 ± 0.04	0.60 ± 0.04	0.69 ± 0.04	0.62 ± 0.01	0.58 ± 0.04
	Species Richness	5.00 ± 0.58	6.00 ± 1.53	8.33 ± 0.67	5.33 ± 0.33	6.33 ± 0.67	6.00 ± 0.58

		Treatment		Crop		Treatment × Crop		Period		Treatment × Period		Crop × Period		Treatment × Crop × Period	
		F _(1,2)	P	F _(2,8)	P	F _(2,8)	P	F _(1,12)	P	F _(1,12)	P	F _(1,12)	P	F _(2,12)	P
	Biomass (g m ⁻²)	0.86	0.45	3.70	0.07	1.70	0.24	32.75	<0.001	3.29	0.09	3.47	0.06	5.58	0.02
	Density (ramets m ⁻²)	11.21	0.08	10.60	0.01	2.94	0.11	7.39	0.02	1.48	0.25	1.42	0.28	0.97	0.41
	Diversity (1 – D)	1.88	0.30	2.80	0.12	0.17	0.85	1.16	0.30	0.70	0.42	1.32	0.30	3.77	0.05
	Species Richness	0.00	>0.9	7.18	0.02	1.88	0.21	1.20	0.29	0.83	0.38	1.30	0.31	0.53	0.60

Overall, during the cash-crop phase, weed community structure did not differ between previously grazed and mowed plots (pseudo-F = 1.92; df = 1, 4; P=0.20; Fig. 3.3). By contrast, weed community structure differed among cash crops (pseudo-F = 2.23; df = 2, 12; $r^2 = 0.21$; P = 0.02). However, these differences in weed community structure by cash-crop did not vary by cover-crop termination method (pseudo-F = 0.89; df = 2, 12; $r^2 = 0.09$; P = 0.57). Weed community structure shifted between emergence and anthesis (pseudo-F = 3.26; df = 1, 24; $r^2 = 0.08$; P < 0.001); but these shifts did not differ between previously grazed and mowed plots (pseudo-F = 1.02; df = 1, 24; $r^2 = 0.03$; P = 0.43), by cash-crop (pseudo-F = 0.82; df = 2, 24; $r^2 = 0.04$; P = 0.65) or by cash-crop within previously grazed or mowed plots (pseudo-F = 0.03; df = 2, 24; $r^2 = 0.03$; P = 0.89).

As noted above, the observed temporal shifts in community structure were driven by differences in the biomass between emergence and anthesis. In particular, the biomass of *C. arvensis* pooled across termination methods and crops declined between emergence and anthesis from $45.4 \pm 14.4 \text{ g m}^{-2}$ to $21.7 \pm 6.9 \text{ g m}^{-2}$. By contrast, *A. retroflexus* biomass increased from $23.9 \pm 5.7 \text{ g m}^{-2}$ to $35.8 \pm 6.3 \text{ g m}^{-2}$ between emergence and anthesis. The differences in community structure between cash-crops were likely driven by greater weed species richness in lettuce rows than in kohlrabi rows, as noted above.

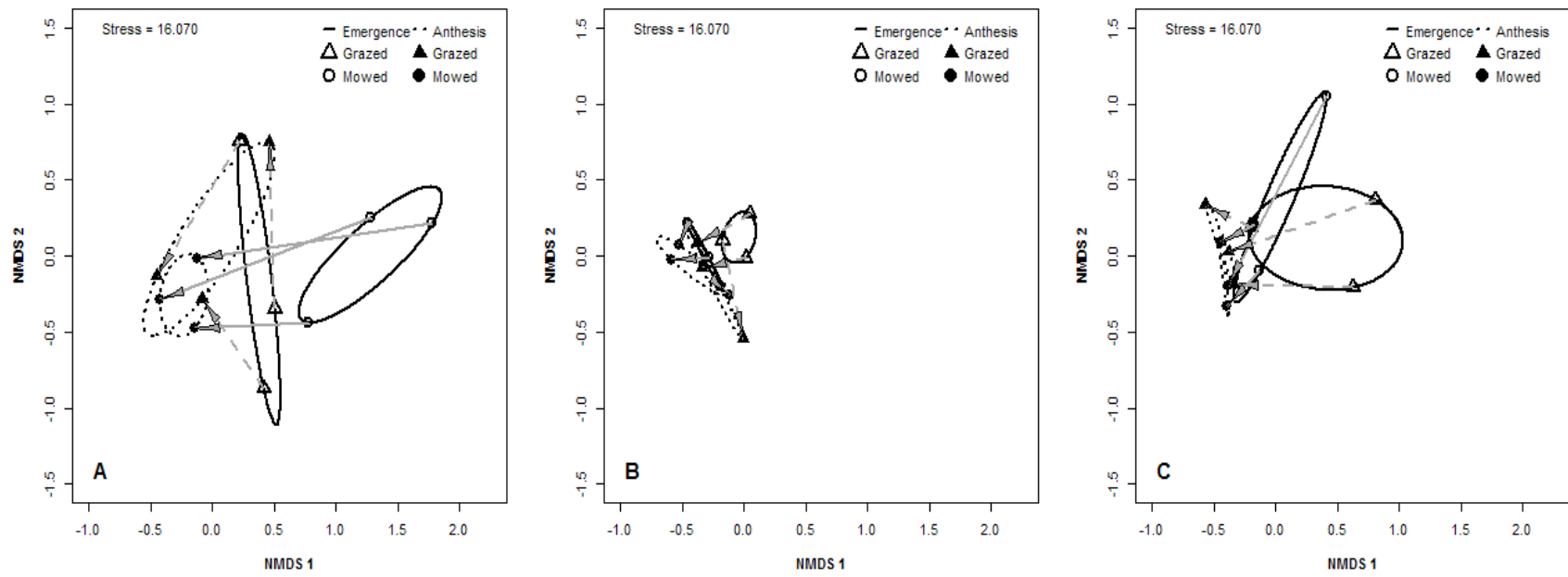


Figure 3.3: Non-metric multidimensional scaling (NMDS) ordination of weed community structure in previously sheep grazed and mowed plots during the 2013 cash-crop phase (A) in kohlrabi (B) lettuce, and (C) spinach rows at Townes Harvest Farm, Bozeman, MT, United States. Solid ellipses denote communities at emergence and dotted ellipses denote the community structure at anthesis. Solid arrows denote the shift in community structure for grazed plots and dashed arrows denote the shift in community structure for mowed plots.

Carabid Beetle Communities

We collected a total of 2132 carabid beetles from 33 species in 2012 and 2127 beetles from 39 species in 2013. In 2012, over 80% of all beetles collected were members of six species: *Pterostichus melanarius* (Illiger) (n = 972; 45.6% of all carabids), *Poecilus scitulus* (LeConte) (n = 263; 12.3%), *Amara patruelis* (Dejean) (n = 165; 7.7%), *Amara thoracica* (Hayward) (n = 160; 7.5%), *Harpalus amputatus* (Say) (n = 140; 6.6%), and *Bembidion rupicola* (Kirby) (n = 109; 5.1%). In 2013, over 80% of all beetles collected were members of five species: *P. melanarius* (n = 1149; 53.9%), *A. patruelis* (n = 235; 11.0%), *H. amputatus* (n = 136; 6.4%), *A. thoracica* (n = 105; 4.9%), and *Bradycellus congener* (LeConte) (n = 95; 4.5%).

We did not detect any differences in activity-density, species richness or α -diversity of carabid beetles between grazed and mowed plots (Table 3.3). However, both activity-density, and species richness varied by period of the growing season. Carabid activity-density was higher in the precultivation and pretreatment periods than in the terminated period ($P < 0.001$ and $P = 0.001$, respectively). However, activity-density did not differ between the precultivation and pretreatment periods ($P = 0.93$). Species richness was higher in the precultivation period than in the terminated period ($P = 0.004$). Species richness in the pretreatment period did not differ with that in the precultivation ($P = 0.25$) or the terminated periods ($P = 0.12$). These temporal changes in total activity-density and species richness did not differ between mowed and grazed plots. In contrast to activity-density and species richness, we did not detect any temporal changes in α -diversity.

Table 3.3: Impacts of sheep-grazing and mowing on carabid beetle activity-density, species richness, α -diversity during the cover-crop phase in 2012 and 2013 at Townes Harvest Farm, Bozeman, MT, United States.

		Grazed						Mowed					
		Precultivation		Pretreatment		Terminated		Precultivation		Pretreatment		Terminated	
2012	Total Activity Density (beetles day ⁻¹)	5.95	± 1.63	8.33	± 2.91	0.38	± 0.05	6.00	± 0.87	5.69	± 0.56	0.90	± 0.13
	Species Richness	9.33	± 0.33	9.67	± 1.20	2.67	± 0.33	7.33	± 1.33	8.33	± 2.67	5.00	± 0.58
	α -Diversity (1 – D)	0.89	± 0.00	0.89	± 0.01	0.61	± 0.06	0.86	± 0.02	0.83	± 0.08	0.79	± 0.02
2013	Total Activity Density (beetles day ⁻¹)	3.62	± 0.50	3.24	± 0.91	0.81	± 0.25	3.10	± 1.44	2.76	± 1.08	1.10	± 0.05
	Species Richness	9.67	± 1.76	4.33	± 1.76	4.00	± 1.00	8.33	± 2.96	5.00	± 0.58	6.33	± 0.33
	α -Diversity (1 – D)	0.89	± 0.02	0.55	± 0.28	0.72	± 0.06	0.85	± 0.05	0.79	± 0.02	0.84	± 0.01
		Treatment		Period		Treatment × Period							
		F _(1,5)	P	F _(2,20)	P	F _(2,20)	P						
	Total Activity Density (beetles day ⁻¹)	0.96	0.37	13.54	<0.001	0.62	0.55						
	Species Richness	0.03	0.86	6.99	0.01	1.66	0.22						
	α -Diversity (1 – D)	2.18	0.20	2.25	0.13	1.16	0.33						

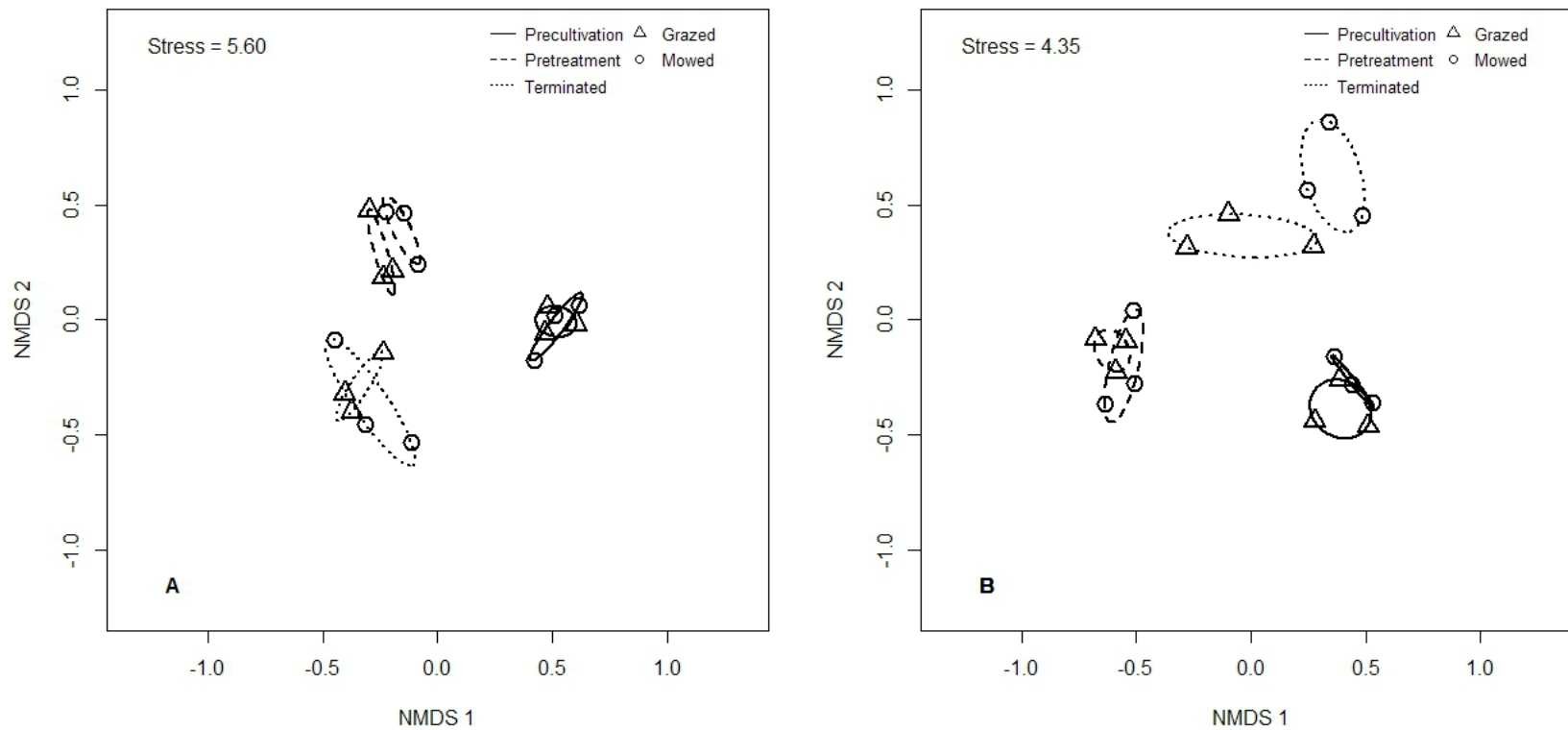


Figure 3.4: NMDS ordination of the impacts of sheep grazing and mowing during cover-crop phase on carabid beetle community structure in (A) 2012 and (B) 2013 at Townes Harvest Farm, Bozeman, MT, United States. Solid ellipses inscribe beetle communities in the precultivation period, dashed ellipses inscribe those in the pretreatment period, and dotted ellipses inscribe those in the terminated period.

Overall, carabid beetle community structure in 2012 did not differ between grazed and mowed plots (pseudo-F = 0.38; df = 1,4; r^2 = 0.09; P = 0.90; Fig 3.3A). By contrast, we observed strong temporal shifts in carabid beetle community structure among periods of the growing seasons in 2012 (pseudo-F = 11.34; df = 2,12; r^2 = 0.63; P < 0.001). However, these temporal dynamics did not differ between mowed and grazed plots (pseudo-F = 0.48; df = 2,12; r^2 = 0.03; P = 0.92). Similarly, in 2013 overall carabid beetle community structure was similar in grazed and mowed plots (pseudo-F = 0.55; df = 1,4; r^2 = 0.12; P = 0.80; Fig 3.3B), but there were temporal shifts in carabid community structure (pseudo-F=18.46; df = 2,12; r^2 = 0.69; P < 0.001). As in 2012, these temporal dynamics in carabid beetle community structure did not differ between mowed and grazed plots (pseudo-F = 1.43; df = 2,12; r^2 = 0.05; P = 0.21).

These temporal shifts in carabid beetle community structure are likely a result of a marked fluctuation in the activity-density of *P. melanarius*. Both years, activity-density of this beetle increased precipitously in the pretreatment period, but declined following cover crop termination. We noted a concomitant decline in *A. patruelis* activity-density with the increase in *P. melanarius* activity density both years in both grazed and mowed plots. Conversely, as *P. melanarius* activity-density declined following cover crop termination, *A. thoracica* activity-density increased (Fig. 5).

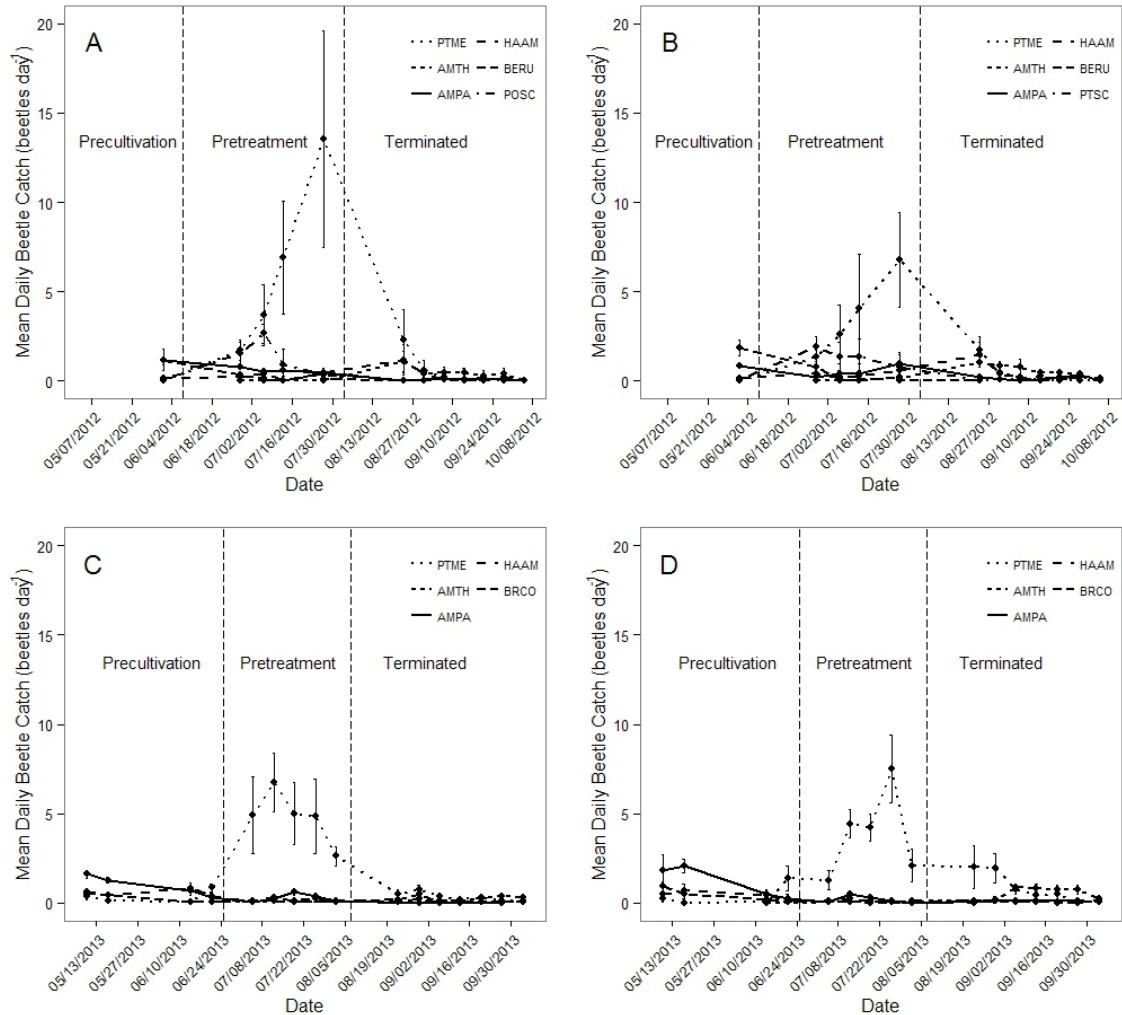


Figure 3.5: Dynamics of activity-density of dominant carabid beetle species during the cover-crop phase in (A) 2012 grazed plots (B) 2012 mowed plots, (C) 2013 grazed plots and (D) 2013 mowed plots at Townes Harvest Farm, Bozeman, MT, United States. Species codes are as follows: PTME = *Pterostichus melanarius* (Illiger); AMTH = *Amara thoracica* (Hayward); AMPA = *Amara patruelis* (Dejean); HAAM = *Harpalus amputatus* (Say); POSC = *Poecilus scitulus* (LeConte); BRCO = *Bradycellus congener* (LeConte); BERU = *Bembidion rupicola* (Kirby).

Discussion

In contradiction to our hypothesis, neither weed nor carabid beetle community structure differed between plots in which cover-crops were terminated by sheep grazing

or by mowing. The lack of differences were consistent through both the cover-crop and cash-crop phases of this study, suggesting that integrating targeted sheep grazing as an approach to terminate cover-crops in horticultural vegetable production systems does not have immediate or short-term legacy impacts different than those of mowing. However, in accordance with previous studies (e.g., Sergeeva 1994, Chen and Willson 1996, Thomas et al. 2002, Lososová et al. 2004, Davis et al. 2005), we observed strong temporal shifts in both weed and carabid beetle communities.

Community assembly theory predicts that a series of ecological filters selectively favors or excludes species from the regional pool in a local community (Keddy 1992, Funk et al. 2008, Myers and Harms 2009). Two local communities that share a common regional species pool, but are subjected to a different set of ecological filters, will have dissimilar community structures (Funk et al. 2008). By this logic, if two management practices act as distinct ecological filters, then the resultant community structure should be dissimilar. Because we did not observe differences in either weed or carabid community structure between graze-terminated and mow-terminated plots, our results suggest that management practices act as similar ecological filters of these two suites of associated biodiversity.

As expected, we observed shifts in the weed community between emergence and anthesis in the cash-crop phase (Lososová et al. 2003, 2004, Davis et al. 2005), but not between previously grazed and mowed plots. The variation in weed community structure among crops could be an artifact of when the cash-crops were planted. Because cash-crop rows were subjected to disturbances such as tillage and seedling transplanting at

different times, some species may have emerged earlier in cash-crop rows with earlier planting dates than in cash-crop rows with later planting dates. These disturbance, therefore represent extraneous ecological filters to those tested in this study. As noted in Chapter 2, this was on-farm study, and cash-crop planting dates were dictated by the farm manager's experience and labor constraints. While a lack of experimental control has been noted as a drawback to on-farm research (Molnar et al. 1992), such research programs often provide more realistic results (Tanaka et al. 2008, Meynard et al. 2012).

To our knowledge, this is the first study to investigate the impacts of integrated livestock grazing in horticultural vegetable market garden on associated plant and insect biodiversity. However, studies of grazing impact on plant community structure and studies of integrated crop-livestock production in commodity production may allow for some comparisons. Tracy and Davis (2009) compared weed biomass and species composition among two integrated cattle/grain production systems [Oat (*Avena sativa* L.) followed by winter forage cover-crop mixture and corn (*Zea mays* L.) followed by corn residue] and one non-integrated cropping systems (continuous corn monoculture). They found that while cover-crops and crop residues produced for forage reduced weed biomass and alter weed community composition compared with continuous corn monoculture, cattle grazing had no effect on either weed biomass or community composition. Similarly, Loeser et al. (2001) found that livestock grazing had negligible short-term impacts on plant community structure in semi-arid grasslands. These studies concur with our findings that livestock grazing does not alter weed community structure

in the subsequent growing season and that other aspects of management are stronger ecological filters of weed diversity.

One particular concern with our study is that it only investigates short-term changes in weed community structure (immediately following grazing and in the subsequent growing season). Renne and Tracy (2013) note that disturbance events such as grazing can have long-term impacts on the seedbank or can interact with future disturbance to alter weed community structure. They stress that these ecological legacies of disturbance are not immediately manifested aboveground. Indeed, weed species richness, seed production and density all increased when livestock grazed on previously disturbed sites compared with undisturbed sites (Renne and Tracy 2013). Similarly, Miller et al. (In Press) found that sheep-grazing during fallow for weed and crop residue management favored perennial weed species especially dandelion (*Taraxicum officinale* L.). Thus, future work should investigate longer-term impacts of grazing on the successional trajectory of weed species in horticultural vegetable production.

We did not detect any difference in carabid community structure between mowed and grazed plots. However, we observed strong temporal shifts in carabid beetle community structure. The observed changes in carabid community structure could be the result of a number of drivers such as differences in the phenology among carabid species (Niemelä et al. 1992, Sergeeva 1994, Lovei and Sunderland 1996), habitat alteration as a result of agronomic practices (Lovei and Sunderland 1996, Holland and Luff 2000, Luff 2002), interspecific competition (Niemelä 1993, Holland and Luff 2000) or an interaction of these factors. Our study did not isolate these factors and therefore precludes any

inferences on which of these drivers is responsible for the observed temporal shifts.

Future research should investigate the relative impact of the ecological filters to help land managers implement practices that structure the carabid community favorably.

Gardner et al. (1997) found that sheep grazing in heather (*Calluna spp.* Salisb.) moorlands reduced the canopy height and biomass. These environmental changes, in turn, directed carabid assemblages toward species with preferences for sparse vegetation. Petit and Usher (1998) reported that intensive sheep grazing of adjacent hedgerows in Scottish agroecosystems was associated with a shift to communities dominated by carabid species preferring open vegetation and characteristic of grasslands. Conversely, ungrazed hedgerows were dominated by carabid species preferring densely-vegetated habitats and characteristic of forests. In our study, the similarity between grazed and mowed plots suggest that these methods of cover crop termination act as of carabid communities. Thus, integrating sheep grazing for cover-crop termination in horticultural vegetable production should not affect within-season changes in carabid beetle community dynamics differently than mowing.

The ecological and agronomic benefits derived from the use of cover-crops are well documented (e.g., Dabney 1998, Dabney et al. 2001, Hartwig and Ammon 2002, Snapp et al. 2005, Tillman et al. 2012), but their use has been limited, primarily because they do not provide a direct source of revenue during the season in which they are grown. Integrating livestock for cover-crop termination could provide an alternative source of revenue for producers directly through the production of fiber (wool) or meat, or indirectly through grazing leases, thus making the use of cover-crops more economical

(Sulc and Tracy 2007, Thiessen Martens and Entz 2011). Overall, our results suggest that producers are unlikely to experience changes in associated biodiversity if they switch from terminating cover-crops with mowing to termination by sheep grazing. Furthermore, integrating sheep grazing for cover-crop termination may help land managers reduce their need for off-farm synthetic inputs and their reliance on fossil fuels.

Conclusion

Integrating sheep grazing for cover-crop termination could be an economically- and agronomically-beneficial practice in horticultural vegetable production (Chapter 2). The use of cover-crops and their termination represents an integrated, ecologically-based weed management strategy (Liebman and Gallandt 1997). However, mowing and sheep grazing could potentially direct ecological communities differently. We tested this hypothesis by comparing weed and carabid beetle community structure between grazed and mowed plots both during the cover-crop season and the subsequent cash-crop season. We found that despite temporal shifts in both weed and carabid beetle community structure, these ecological communities did not differ between grazed and mowed plots. Thus, our results suggest that grazing and mowing act as similar ecological filters of both weed and carabid beetle communities.

While long-term impacts of repeated sheep grazing could direct weed communities toward dominance of perennial weeds (Miller et al. in press), we did not observe these trends. Also despite known strong habitat preferences of carabid beetles, we found no difference in carabid beetle community structure between grazed and

mowed plots. Future work should determine whether these shifts are driven by phenology, habitat changes or inter-specific competition.

To our knowledge this is the first study to investigate the impacts of integrated livestock grazing on the community dynamics of associated biodiversity in horticultural vegetable production. Our results suggest that integrating sheep grazing for cover-crop termination could provide several economic and agronomic benefits while not having deleterious effects on weed and carabid beetle communities. Further research is needed to investigate possible long-term legacy effects of integrated grazing in such systems.

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CHAPTER FOUR

IMPACTS OF CONTRASTING ALFALFA (*MEDICAGO SATIVA* L.)
PRODUCTION SYSTEMS ON THE DRIVERS OF CARABID BEETLE
(COLEOPTERA:CARABIDAE) COMMUNITY DYNAMICS

Introduction

Growing concerns about the environmental consequences of chemically-based pest control strategies has precipitated a call for the development of integrated, ecologically-based pest-management programs (Altieri et al. 1983, Matson et al. 1997, Robertson and Swinton 2005). Instead of relying primarily on synthetic inputs, these programs are based on augmenting ecological processes to stabilize or manage pest populations (Liebman and Gallandt 1997, Magdoff 2007, Altieri et al. 2012). Conservation biological control, in which a producer manipulates the ecological conditions in his/her system to enhance populations of natural enemies, is one such strategy (Barbosa 1998). Habitat management is a subset of conservation biocontrol that includes altering disturbance spatio-temporal regimes to decrease natural enemy mortality, improving shelter or microclimatic conditions to prevent their emigration, or providing refugia to which they can escape during management-imposed disturbance (Landis et al. 2000).

Carabid or ground beetles (Coleoptera:Carabidae) are an important group of natural enemies of common agricultural pests such as aphids, slugs, and other beetles (Holland 2002, Sunderland 2002). They comprise one of the most abundant and diverse

families of beetles and are abundant and ubiquitous in northern temperate agroecosystems (Lovei and Sunderland 1996). Many carabid beetle species, especially those in the Zabrinini and Harpalini tribes, are seed predators and may help regulate weed populations (Tooley and Brust 2002, Menalled et al. 2007, Gaines and Gratton 2010). For these reasons, carabids are often regarded as target species of conservation biocontrol. However, many carabid species have very specific habitat preferences and are highly sensitive to changes in their environment (Lovei and Sunderland 1996). Thus, habitat management practices could have important ramifications for carabid beetle conservation in highly disturbed agricultural systems.

Alfalfa (*Medicago sativa* L.) is one of the most common forage crop species in the semi-arid western United States (Putnam et al. 2000). In 2011, Montana alone produced 4.0×10^6 Mg of alfalfa on 8.1×10^5 ha for gross revenue in excess of $\$4.3 \times 10^8$, making it the third largest crop by revenue and area harvested in the state after spring and winter wheat (*Triticum aestivum* L.) (NASS 2013). A major threat to alfalfa production is herbivory by insect pests such as the alfalfa weevil (*Hypera postica* Gyllenhal), aphids (Hemiptera: Aphididae), and cutworms (Lepidoptera: Noctuidae) (Summers 1998, Brewer and Hoff 2002, Salisbury 2004). For example, herbivory by the alfalfa weevil alone can result in yield losses of up to 30 – 40% in the Intermountain West of the United States (Salisbury 2004).

In contrast to most other major commodities in the region, alfalfa is a perennial crop, thus providing temporally stable habitat for insect pests as well as their natural enemies, including carabids (Summers 1998). Therefore, habitat management to enhance

natural carabid communities in alfalfa could be an important ecologically-based component of an integrated pest management strategy (Clark et al. 1997). Specifically, increasing plant diversity at both the within-field (α -diversity) and between-field (β -diversity) scales may help assemble a more diverse array of natural enemies and thereby enhance biological control (Altieri and Letourneau 1982, Altieri 1999, Benton et al. 2003, Letourneau et al. 2011).

Barbosa and Wratten (1998) argue that habitat management is only an effective means of conservation biological control if the natural enemy populations have the proper spatial and temporal distribution within an agroecosystem. Thus, understanding the community dynamics of target natural enemies and how those dynamics relate to changes in the environment is imperative for proper habitat management. Nurse-cropping (a.k.a. relay-cropping or companion-cropping), in which one species with a short life-cycle is grown simultaneously with a second, longer-lived species, is a method by which to increase vegetative α -diversity in agroecosystems (Roslon and Fogelfors 2003). Nurse-cropping can provide a variety of agronomic benefits including weed suppression, soil stabilization, alternative sources of revenue, as well as pest management (Canevari 2000). Uncultivated areas within farmlands can increase β -diversity as they may provide refugia or alternative habitats to natural enemies (Lee et al. 2001, Lee and Landis 2002, Gaines and Gratton 2010).

While many studies conducted in agroecosystems have compared carabid community structure among habitat types (e.g., Kromp 1989, Östman et al. 2001, MacLeod et al. 2004, Lövei et al. 2006, Menalled et al. 2007, Gaines and Gratton 2010),

few have directly investigated the temporal dynamics of or the influence of vegetative architecture on carabid communities (but see Gardner et al. 1997). Increased understanding of the drivers of carabid community dynamics can help inform better habitat management practices in alfalfa production for carabid conservation. In this study, we assessed carabid beetle community dynamics and its relationship with vegetative architecture in three alfalfa production systems: monoculture alfalfa, alfalfa nurse-cropped with barley (*Hordeum vulgare* L.) and uncultivated areas. Our first objective was to relate carabid activity-density with vegetative architecture as well as time within the growing season to understand the drivers of carabid community dynamics. Our second objective was to develop a predictive model of the most abundant species of carabids as a function of vegetative architecture.

Materials and Methods

Site Description

This research was conducted on the Sieben Ranch in Helena, Montana, United States (WGS84 46° 41.40' N, 112° 0.02' W). The site is underlain with Thess-Series loam (fine loamy over sandy or sandy skeletal, superactive, frigid, Aridic, Calciusteps), receives approximately 250 – 355 mm of precipitation annually, and has a mean annual air temperature of 2.8 – 7.2 °C (NRCS 2013).

Study Design

We conducted our study over the 2012 and 2013 growing season. Each year, our study consisted of three sites each with adjacent systems of monoculture alfalfa, alfalfa

nurse-cropped with hay barley (“barley nurse-crop” hereafter) and an uncultivated refuge consisting of a variety of forbs and grasses (see Table 4.1). At each site, we set up two subsample plots within each system to assess carabid beetle community structure using pitfall traps. Subsample plot consisted of three pitfall traps arranged in an equilateral triangle with 10 m sides. The subsample plots were at least 100 m from any field boundary and were spaced 100 m apart. To construct the pitfall traps, we dug approximately 20 – 30 cm deep $\times$ 10 cm wide holes with a post-hole auger and placed two stacked 0.5 L plastic cups (Solo Cup Company, Lake Forest, IL) in each of those holes. We backfilled the pitfall trap holes until the mouth of the top cup was flush with the soil surface and filled the top cup of the pitfall trap approximately one-third full with propylene glycol-based antifreeze (Arctic Ban[®], Camco Manufacturing Inc., Greensboro, NC). Each pitfall trap was covered with a rain cover constructed from a 25 cm diameter clear plastic plate held to the ground with three equally spaced 10 cm bolts. All rain covers had at least 2 cm between the soil surface and the rim of the clear plastic plates to avoid interfering with ground dwelling arthropod activity.

To accommodate for farming activities, pitfall traps installation and removal dates varied among systems and between years (Fig 4.1). Early in the growing season, we installed the pitfall traps at each subsample in the uncultivate refuge and monoculture alfalfa systems. Once the barley nurse-crop was seed, we installed pitfall traps into the barley nurse crop fields. Pitfall traps from all monoculture alfalfa fields were removed to allow the producer to harvest. Pitfall traps we reinstalled in the monoculture alfalfa fields following harvest. In 2012, we removed the pitfall traps from all barley nurse-crop fields

to allow the producer to harvest and did not reinstall them for the remainder of the growing season. Uncultivated refuge pitfall traps were removed both years to allow the producer to stack baled hay. In 2012 these pitfall traps were not reinstalled for the remainder of the growing season, but in 2013 we reinstall after the produce finished baling activities.

Table 4.1: Vegetation cover and plant community structure in uncultivated refuge systems at in 2012 and 2013 Sieban Ranch, Helena, MT, United States.

		2012			2013		
Stand Cover	Live Vegetation	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
	Thatch	35%	45%	35%	45%	40%	50%
	Bare ground	5%	10%	15%	50%	20%	20%
		60%	45%	50%	10%	40%	30%
Species Cover	<i>Medicago sativa</i> (L.)	19%		39%	15%	45%	21%
	<i>Descurania sophia</i> (L.) Webb ex Prantl	36%	3%	40%	1%	5%	5%
	<i>Descurania pinnata</i> (Walter) Britton	14%					1%
	<i>Bromus inermis</i> (Leyss.)	31%	85%	21%	67%	31%	66%
	<i>Dactylis glomerata</i> (L.)		7%	1%	2%	4%	6%
	<i>Poa pratensis</i> (L.)		1%		15%	1%	
	<i>Melilotus officinalis</i> (L.)		5%				
	<i>Cirsium vulgare</i> (L.)					1%	
	<i>Taraxicum officinale</i> (L.)						1%
	<i>Cardaria draba</i> (L.) Desv.					4%	
	<i>Cirsium arvensis</i> (L.)					10%	

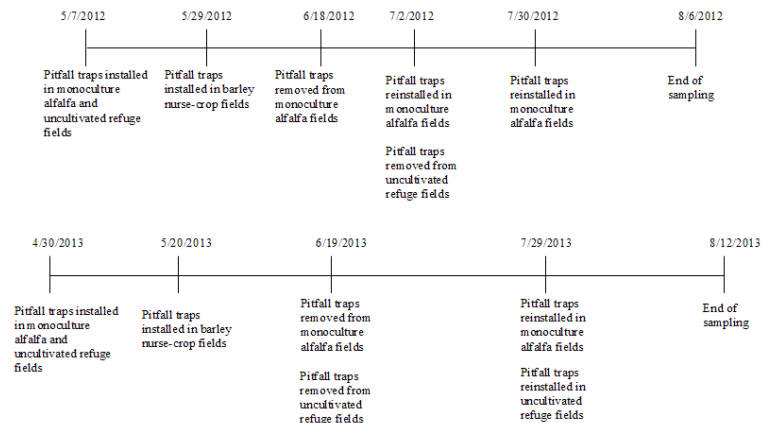


Figure 4.1: Pitfall trap installation and removal dates for carabid beetle sampling in 2012 and 2013 at Sieban Ranch, Helena, MT, United States.

While installed, each week we collected all arthropods caught in the pitfall traps by placing them in an 11.5×23 cm plastic bag (Whirl-Pak[®], Nasco Inc., Fort Atkinson, WI). Following collection, all pitfall traps were replenished with antifreeze for sampling the subsequent week. We sorted all subsamples for carabid beetles, transferred them to 70% by volume ethanol and identified them to species in the laboratory following Lindroth (1968). All species names follow Bousquet (2012).

One limitation of pitfall trapping is that the probability of capturing a beetle depends on both how many beetles are in a given area and how much those beetles are moving (Luff 2002). Thus, pitfall trapping confounds activity and density. Entomologists, therefore, refer to values obtained from pitfall trapping as “activity-density,” and treat those values as metrics of relative abundance (Kromp 1989). Additionally, because in our study beetles were free to disperse between fields, our results reflect habitat selection rather than changes in carabid populations *per se* (Lee *et al.* 2001). While these limitation have been well documented in the literature, pitfall trapping remain one of the most efficient methods for sampling carabid beetles (Greenslade 1964, Kromp 1989, Spence and Niemelä 1994, Lee *et al.* 2001, Luff 2002).

Each time pitfall traps were collected, we measured the vegetation canopy height and percent cover for each subsample. Canopy height was estimated by randomly placing a meter stick at five locations in each subsample and recording the height of the tallest plant. The five measurements were averaged prior to data analysis. Percent cover was measured by randomly tossing a 0.5 m² wire hoop in each subsample and visually estimating the percent bare ground within the hoop.

Our study was conducted as on-farm research and, sampling intensity and timing varied among vegetation types to allow for farm operations. While a lack of investigator control has been noted as a drawback to on-farm research, (Molnar et al. 1992), such research programs often provide more realistic results (Tanaka et al. 2008, Meynard et al. 2012). Thus, while we suggest that readers exercise caution when interpreting our results, we believe they are an informative and realistic assessment of carabid community dynamics as a function of habitat management.

Data Analysis

We analyzed the effects of vegetation canopy height and percent bare ground on carabid beetle community structure using multivariate fuzzy set ordination (MFSO) on a Bray-Curtis dissimilarity matrix (Roberts 1986). Prior to constructing the dissimilarity matrix, the raw data were log-transformed to de-emphasize the effect of dominant species according to:

$$T_{ij} = \ln(a_{ij} + 1) \quad (4.1)$$

where T_{ij} is the log-transformed activity-density of species i in community j and a_{ij} is the raw abundance of species i in community j . Bray-Curtis dissimilarity was calculated as:

$$BC_{jk} = \frac{\sum_{i=1}^S 2 |T_{ij} - T_{ik}|}{\sum_{i=1}^S T_{ij} + \sum_{i=1}^S T_{ik}} \quad (4.2)$$

where BC_{jk} is the dissimilarity between sites j and k , T_{ij} and T_{ik} are the log-transformed activity-density of species i in sites j and k , respectively, and S is the combined total number of species in both communities (Bray and Curtis 1957, McCune et al. 2002).

Two major advantages MFSO over constrained ordination methods such as canonical correspondence analysis (CCA) and redundancy analysis (RA) are that MFSO ordination axes correspond directly to environmental gradients and that it detrends autocorrelated predictors to avoid confounding effects of non-independent environmental gradients (Roberts 2009).

We compared carabid community structure among vegetation types using a permutation multivariate analysis of variance (PERMANOVA) on a log-transformed Bray-Curtis dissimilarity matrix of species activity-densities with 9999 Monte Carlo iterations. Because we sampled the same plots on multiple dates, we used the Julian date of collection as a covariate in the PERMANOVA. Canopy height and canopy cover are autocorrelated with Julian date, and these covariates were not included in the analysis. For each year, PERMANOVA tests for overall differences in carabid community structure by vegetation type and for temporal shifts in carabid community structure were conducted separately. In addition, these analyses were conducted separately for each year of our study.

To assess the overall effects of habitat management on carabid communities, we compared mean weekly carabid activity-density, total species richness, and α -diversity among vegetation types from data pooled across all sampling dates. A Box-Cox power transformation analysis indicated that a log-transformation was warranted for activity-density. These metrics were compared using ANOVA with vegetation type blocked by site and $\alpha = 0.05$. We quantified α -diversity using Simpson's Diversity Index ($1 - D$):

$$D = \sum_{i=1}^S p_i^2 \quad (4.3)$$

where p_i is proportion that species i comprises in a community and S is the total number of species in a community (Simpson 1949).

We compared canopy height and percent bare ground among monoculture alfalfa, barley nurse-crop and uncultivated refuge fields using ANCOVA with Julian date as a covariate. An omnibus ANCOVA was conducted separately for each year to test for main effects. Pairwise ANCOVA models were constructed to compare slope differences between vegetation types. Due to concerns of spurious inference, we ignored intercept differences because planting dates varied among the three vegetation types.

Finally, to investigate habitat preferences among the most common carabids, we created a predictive model for the activity-density of the three species with the greatest total number of specimens collected within each vegetation system (*Pterostichus melanarius* Illiger, *Agonum placidum* Say, and *Agonum cupreum* Dejean). Candidate predictors of activity-density included canopy height, Julian date of the sampling period, and percent bare ground. Our models of activity-density were constructed using quasi-Poisson regression due to concerns of overdispersion (Maindonald and Braun 2006). Model selection was performed by comparing reduction in residual deviance (ΔD) among candidate models beginning with a full model of all three predictors and dropping one predictor at a time. Data from both 2012 and 2013 were pooled prior to constructing the predictive models to allow for more generalizable models.

All statistics and graphics were performed in R version 3.0.2 (R Development Core Team 2013). Community indices and PERMANOVA were calculated in the vegan

(Oksanen et al. 2007) labdsv (Roberts 2007) packages of R. Ordinations were calculated and graphed using the cluster (Maechler et al. 2012) fso (Roberts 2010) and rgl (Adler and Murdoch 2008) packages. All other graphics were created using the ggplot2 (Wickham 2009) and sciplot (Morales et al. 2012) packages. Post-hoc tests for significant interactions found from ANOVA were conducted using Tukey's Honestly Significant Difference (HSD) in the TukeyC package (Jeliahovski and Allaman 2011).

Results

We captured a total of 15106 carabid beetle specimens from 59 species in 2012 and 12336 specimens from 47 species in 2013. Over 85% of all beetles caught in 2012 were members of just six species: *Pterostichus melanarius* (Illiger) (n = 9144, 60.5% of all beetles captured), *Agonum placidum* (Say) (n = 2080, 13.8%), *Agonum cupreum* (Dejean) (n = 972, 6.4%), *Bradycellus congener* (LeConte) (n = 383, 2.5%), *Agonum cupripenne* (Say) (n = 316, 2.1%), and *Harpalus amputatus* (Say) (n = 298, 2.0 %). In 2013 over 90% of all specimens were members of just three species: *P. melanarius* (n = 7975, 64.6%), *A. placidum* (n = 2625, 21.3%) and *A. cupreum* (n = 589, 4.7%). The activity-densities of *P. melanarius* and *A. placidum*, our two most frequently captured species, were greatest in the barley nurse-crop fields in both 2012 and 2013. The activity-density of our third most commonly collected species, *A. cupreum*, was greatest in monoculture alfalfa fields in 2012, but was greatest in nurse-crop barley in 2013 (Table 4.2).

Based on species composition and activity-density, the PERMANOVA indicated that carabid community structure differed among vegetation systems in 2012 sampled (pseudo-F = 4.25; df = 2, 6; $r^2 = 0.59$, $P = 0.007$, Table 4.2). In addition, there were strong temporal shifts the carabid community in the three studied systems (pseudo-F = 11.17, df = 1, 74; $r^2 = 0.10$; $P < 0.001$). The MFSO revealed that variation in canopy height among three vegetation systems in 2012 was primarily responsible for these differences observed in carabid community structure. Points that are closer in ordination space have community structures that more closely resemble each other, whereas those farther apart in ordination space have more dissimilar community structures. Axis values of MFSO are the fuzzy set membership of each sample to the corresponding environmental gradient. Membership values reflect the estimated value of the environmental gradient based on the dissimilarity of a given community to the communities on either extreme of the gradient (Roberts 1986). While canopy height had only a marginally significant impact on carabid community structure in 2012 ($r^2 = 0.63$, $P = 0.10$), it was the strongest ecological filter structuring carabid communities as that ordination axis had the greatest spread of communities. Communities with the same apparent canopy height had different apparent dates in the ordination, suggesting that date growing season modified the effect of canopy height on carabid community structure ($r^2 = 0.05$; $P = 0.01$). Finally, percent bare ground (estimated by ground cover) modified the impacts of canopy height and date within the growing season on carabid communities, with uncultivated refuge systems having higher apparent bare ground than

either barley nurse-crop or monoculture alfalfa systems at similar values of apparent canopy height and apparent date in the ordination ($r^2 = 0.03$; $P = 0.01$).

In 2013, carabid community structure also differed among the three vegetation types in 2013 (pseudo-F = 5.98; df = 2,6; $r^2 = 0.67$; $P = 0.005$, Table 4.2). As in 2012, there were temporal shifts in carabid community structure within each vegetation type (pseudo-F = 10.94; df = 1,65; $r^2 = 0.11$; $P = 0.0001$). Similar to our observations in 2012, the MFSO showed that variation in canopy height among the three vegetation systems was the main driver of the observed differences in carabid communities (Fig 4.2B). Despite having only a marginally significant effect, canopy height again was the strongest ecological filter affecting carabid communities as this ordination axis accounted for the greatest amount of variation in community structure ($r^2 = 0.50$; $P = 0.07$). Date of the growing season modified the impact of canopy height on carabid community structure, so that communities were dissimilar on different dates despite having the same apparent canopy height ($r^2 = 0.07$; $P = 0.02$). In contrast to the results observed in 2012, percent bare ground did not modify the effects of either canopy height or date of the growing season on carabid community structure, as there was little variation along this ordination axis ($r^2 = 0.007$; $P = 0.55$).

Table 4.2: Mean weekly carabid beetle captures from May 2012 – August 2012 and from May 2013 – August 2013 in monoculture alfalfa, barley nurse-crop and uncultivated refuge fields at Sieban Ranch, Helena, MT, United States.

	2012			2013		
	Alfalfa	Nurse-Crop	Refuge	Alfalfa	Nurse-Crop	Refuge
<i>Agonum cupreum</i> (Dejean)	63.1	41.6	1.0	26.7	50.1	0.3
<i>Agonum cupripenne</i> (Say)	22.4	11.5		4.9	12.4	
<i>Agonum placidum</i> (Say)	24.2	229.6	0.1	9.4	318.8	1.1
<i>Amara apricaria</i> (Paykull)		0.1				
<i>Amara cupreolata</i> (Putzeys)	8.8	2.5	3.1	14.6	3.8	7.5
<i>Amara familiaris</i> (Duftschmid)						0.1
<i>Amara farcta</i> (LeConte)	4.6	2.8	20.0	1.3	1.4	2.3
<i>Amara idahoana</i> (Casey)	0.1					
<i>Amara littoralis</i> (Dejean)	14.8	2.3	12.1	7.0	2.3	4.0
<i>Amara obesa</i> (Say)	0.4	0.9	0.8	0.6	0.4	13.9
<i>Amara quenseli</i> (Schönherr)	0.7	0.3	0.9			0.5
<i>Amara thoracica</i> (Hayward)	0.8	0.3	0.1	0.1	0.1	
<i>Anisodactylus harrisi</i> (LeConte)			0.1			0.1
<i>Bembidion bimaculatum</i> (Kirby)		0.1				
<i>Bembidion concolor</i> (Kirby)					0.1	
<i>Bembidion nigripes</i> (Kirby)				0.1		
<i>Bembidion nitidum</i> (Kirby)	0.1	20.9	2.6	0.1	1.5	0.3
<i>Bembidion obscurellum</i> (Motschulsky)	0.1	0.4	0.1			
<i>Bembidion quadrimaculatum dubitans</i> (LeConte)	3.3	13.0	1.5	2.4	3.1	0.1
<i>Bembidion rapidum</i> (LeConte)	1.9	4.1	0.1		0.1	
<i>Bembidion rupicola</i> (Kirby)	0.3	0.5	0.1	0.4		
<i>Bembidion timidum</i> (LeConte)		0.1				
<i>Bembidion versicolor</i> (LeConte)	2.3	3.0	1.0	2.4	1.4	
<i>Bradycellus congener</i> (LeConte)	35.1	0.8	3.3	4.3		0.4
<i>Bradycellus neglectus</i> (LeConte)	0.1					
<i>Bradycellus nigerrimus</i> (Lindroth)		0.3				
<i>Calosoma cancellatum</i> (Eschscholtz)	0.1	0.9		0.1	0.9	
<i>Calosoma lepidum</i> (LeConte)	0.3	0.5			1.1	0.1
<i>Calosoma obsoletum</i> (Say)		0.5			0.8	
<i>Carabus nemoralis</i> (Müller)	0.1		0.1			0.5
<i>Chlaenius impunctifrons</i> (Say)	0.2	0.3		0.1		
<i>Chlaenius purpuricollis</i> (Randall)				0.1		
<i>Chlaenius sp.</i> (Bonelli)					0.1	
<i>Chlaenius tomentosus</i> (Say)		0.1				
<i>Cicindela purpurea audobonii</i> (LeConte)		0.1				
<i>Clivina fossor</i> (L.)	0.5	0.4				
<i>Clivina impressifrons</i> (LeConte)	0.2					
<i>Harpalus affinis</i> (Schrank)		0.1				
<i>Harpalus amputatus</i> (Say)	7.2	16.6	11.6	3.9	4.4	2.6
<i>Harpalus desertus</i> (LeConte)	0.2	0.8	6.0		0.1	0.1
<i>Harpalus erraticus</i> (Say)	0.1					
<i>Harpalus fraternus</i> (LeConte)	0.5	7.4	0.5	0.1	1.1	0.6
<i>Harpalus fuscipalpis</i> (Sturm)	0.2	3.8	14.6	0.3	0.4	3.0
<i>Harpalus nigrirarsis</i> (Sahlberg)	0.6	0.9	0.6	0.1	0.1	6.9
<i>Harpalus opacipennis</i> (Haldeman)	0.1	1.6	1.4		0.1	0.8
<i>Harpalus pensylvanicus</i> (DeGeer)	0.3				0.3	
<i>Harpalus reversus</i> (Casey)	0.3	3.8	3.1	0.1	1.1	0.4
<i>Harpalus somnulentus</i> (Dejean)	0.4	0.5	1.5	0.4	4.0	1.6
<i>Harpalus sp.</i> (Latreille)					0.1	
<i>Harpalus ventralis</i> (LeConte)	0.4	1.3	0.1		0.3	0.9
<i>Lebia guttula</i> (LeConte)	0.1					
<i>Lebia solea</i> (Hentz)			0.1	0.3		0.8
<i>Loricera pilicornis</i> (F.)	5.1	0.8	0.1	2.1	0.1	
<i>Microlestes linearis</i> (LeConte)	6.0	4.1	6.9	1.0	1.3	6.5
<i>Notiophilus simulator</i> (Fall)	0.1		0.1			
<i>Piosoma setosum</i> (LeConte)		0.3	0.1			
<i>Poecilus corvus</i> (LeConte)	1.3	0.3		1.4	2.4	
<i>Poecilus lucublandus</i> (Say)	2.8	1.0		1.9	2.6	
<i>Poecilus scitulus</i> (LeConte)		0.1			0.1	
<i>Pterostichus adstrictus</i> (Eschscholtz)	5.3	0.4	0.1	0.7	0.1	0.1
<i>Pterostichus corvinus</i> (Dejean)	0.3					
<i>Pterostichus melanarius</i> (Illiger)	338.6	692.6	27.1	75.6	922.0	8.8
<i>Selenophorus pedicularius</i> (Dejean)			0.1			
<i>Trachypachus inermis</i> (Motschulsky)	0.1					

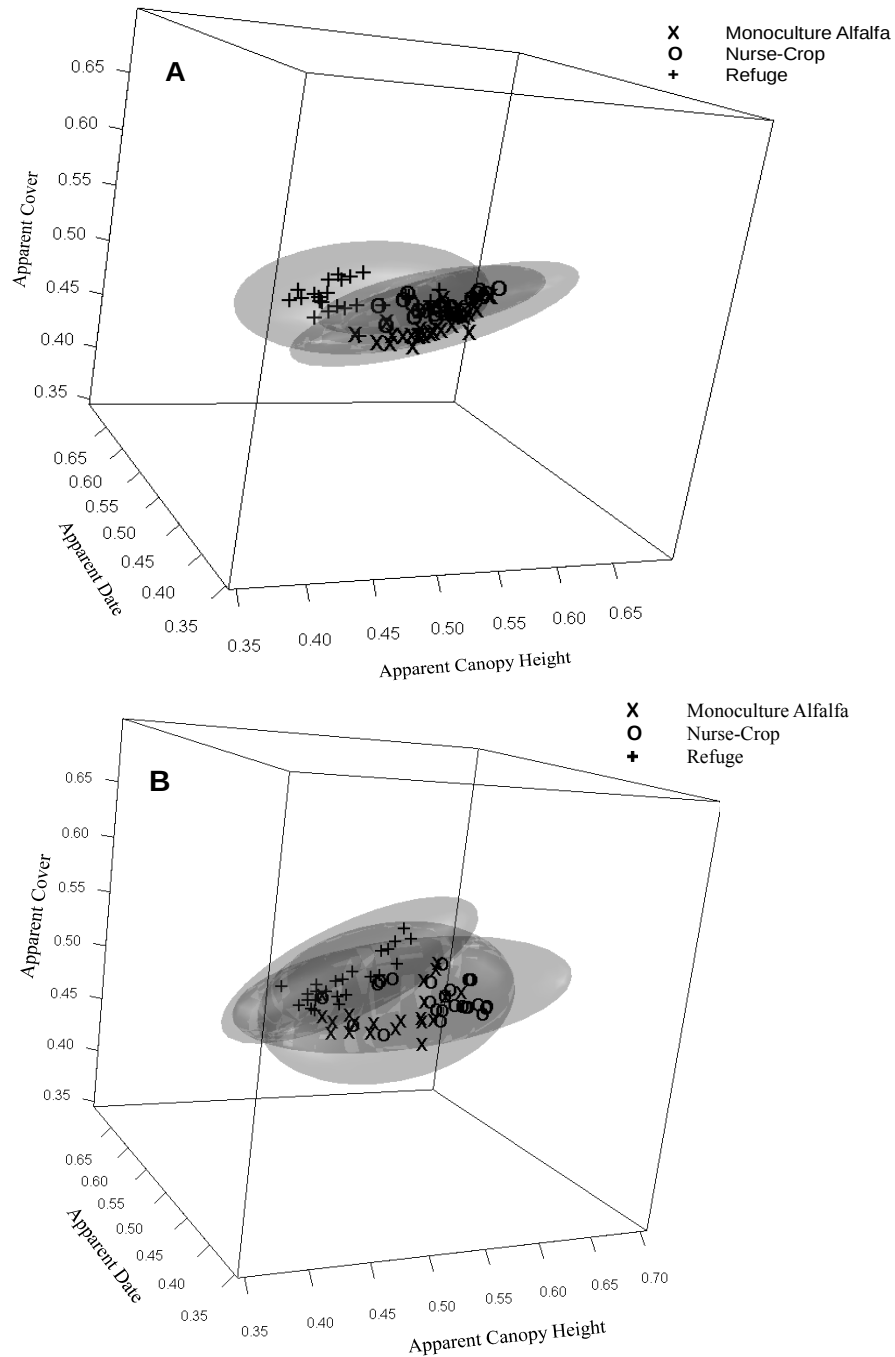


Figure 4.2: Influence of canopy height, date of the growing season, and percent bare ground on carabid beetle community dynamics in monoculture alfalfa, barley nurse-crop and uncultivated refuge fields between (A) May 2012 and August 2012 and (B) May 2013 and August 2013 at Sieban Ranch, Helena, MT, United States.

Carabid beetle activity-density differed among vegetation systems in both 2012 and 2013 (Table 4.2). In 2012, activity-density was greater in barley nurse-crop systems than in refuge systems ($P = 0.02$, Fig 4.3A), but it did not differ between barley nurse-crop and monoculture alfalfa systems ($P = 0.56$). Activity-density was marginally greater in monoculture alfalfa systems than in uncultivated refuge areas ($P = 0.06$) in 2012. In 2013, carabid activity-density was greater in barley nurse-crop systems than in either monoculture alfalfa systems ($P = 0.03$) or uncultivated refuge areas ($P = 0.008$), but it did not differ between monoculture alfalfa systems and uncultivated refuge areas ($P = 0.23$, Fig. 4.3D). Carabid species richness did not differ among vegetation systems in either 2012 (Table 4.2, Fig 4.3B) or 2013 (Table 4.2, Fig. 4.3E). While α -diversity did not differ among the three vegetation systems in 2012 (Table 4.2, Fig. 4.3C), we found in 2013 that uncultivated refuge areas had higher diversity than in either barley nurse-crop ($P < 0.001$, Table 4.3, Fig 4.3F) or monoculture alfalfa systems ($P < 0.001$). Monoculture alfalfa systems, in turn, had higher α -diversity than did barley nurse-crop systems ($P < 0.001$).

Table 4.3: ANOVA table of impact of vegetation systems on carabid beetle communities at Sieban Ranch, Helena, MT, United States.

		F	df	P
2012	Ln[Activity-Density (beetles week ⁻¹)]	11.03	2,4	0.02
	Species Richness	2.46	2,4	0.2
	α -diversity (1 – D)	4.64	2,4	0.09
2013	Ln[Activity-Density (beetles week ⁻¹)]	19.53	2,4	0.008
	Species Richness	1.65	2,4	0.3
	α -diversity (1 – D)	3037	2,4	<0.001

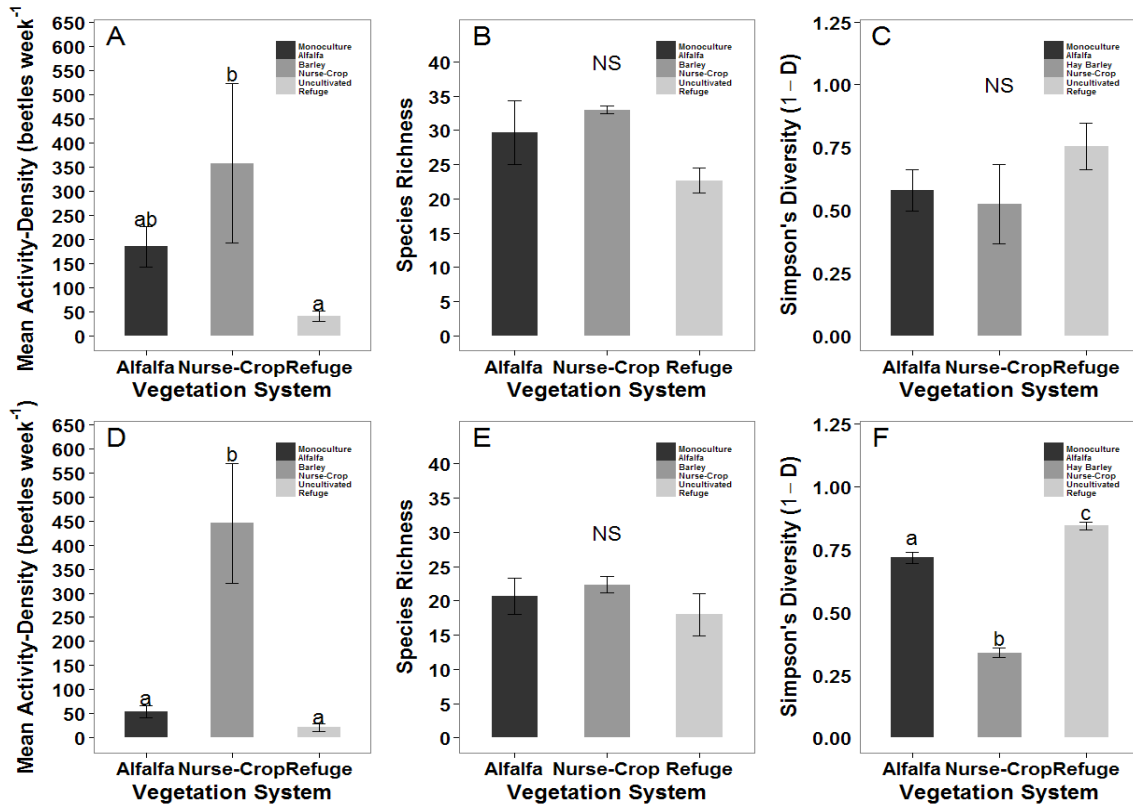


Figure 4.3: Impacts of vegetation system on carabid beetle (A) activity-density in 2012 (B) species richness in 2012 (C) α -diversity indexed by Simpson's Diversity (1 - D) in 2012, (D) activity-density in 2013, (E) species richness in 2013, and (F) α -diversity in 2013 in monoculture alfalfa, barley nurse-crop and uncultivated refuge areas at Sieban Ranch Helena, MT, United States. Lower case letters indicate means comparisons. Bars with the same lower case letters are not significantly different ($P > 0.05$). "NS" indicates that none of the means differed significantly ($P > 0.05$) from each other.

Changes in canopy height during the growing season differed among monoculture alfalfa, barley nurse-crop, and uncultivated refuge systems in both 2012 ($F = 71.45$; adjusted $r^2 = 0.82$; $df = 5, 72$; $P < 0.001$, Fig. 4.4A) and 2013 ($F = 28.79$; adjusted $r^2 = 0.67$; $df = 5, 63$; $P < 0.001$, Fig. 4.4B). In 2012 and 2013, we found that the canopy increased height faster in barley nurse-crop systems than in either monoculture alfalfa ($t = 8.49$, $P < 0.001$ and $t = 5.93$, $P < 0.001$, respectively) or in uncultivated refuge systems ($t = 7.23$, $P < 0.001$ and $t = 8.28$, $P < 0.001$, respectively). During both years of this

study, there was no difference in the rate of change in canopy height between monoculture alfalfa or uncultivated refuge systems ($t = 0.19$, $P = 0.85$ and $t = -0.53$, $P = 0.60$ for 2012 and 2013, respectively).

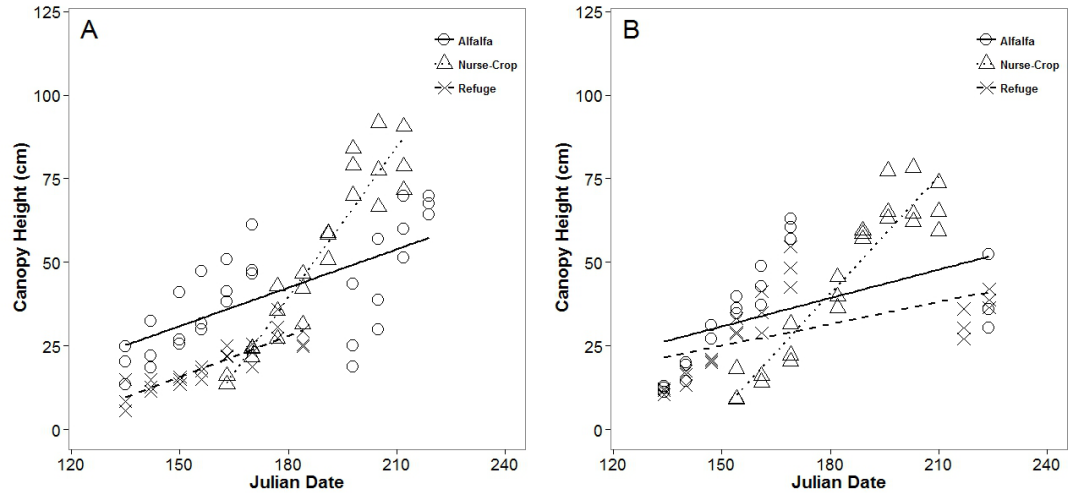


Figure 4.4: Comparison of changes in canopy height during the (A) 2012 and (B) 2013 growing seasons among monoculture alfalfa, barley nurse-crop and uncultivated refuge systems at Sieban Ranch, Helena, MT United States.

Changes in percent bare ground varied among our three systems in 2012 ($F = 13.68$; $df = 5, 72$; $P < 0.001$, Fig. 4.5A) and in 2013 ($F = 33.66$; $df = 5, 63$; $P < 0.001$, Fig. 4.5B). In 2012, the canopy closed faster, as indexed by change in percent bare ground, in barley nurse-crop systems than in either monoculture alfalfa ($t = 5.90$, $P < 0.001$) or uncultivated refuge systems ($t = -4.23$, $P < 0.001$). Likewise, canopy closure was faster in the barley nurse-crop than in either of the other two systems in 2013 (monoculture alfalfa: $t = -8.00$, $P < 0.001$; uncultivated refuge: $t = -5.92$, $P < 0.001$). However, we did not detect a difference in the rate of canopy closure between monoculture alfalfa systems and uncultivated refuge areas in either year (2012: $t = 1.68$, $P = 0.09$; 2013: $t = -0.97$, $P = 0.40$).

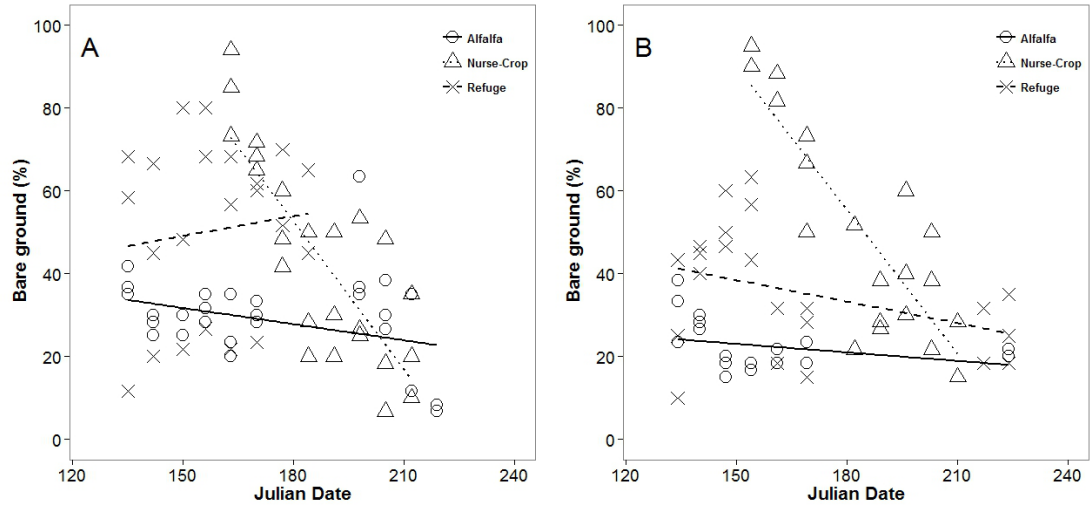


Figure 4.5: Comparison of percent bare ground during the (A) 2012 and (B) 2013 growing seasons among monoculture alfalfa, barley nurse-crop and uncultivated refuge fields at Sieban Ranch, Helena, MT United States.

In monoculture alfalfa systems, we found that *P. melanarius* activity-density (AD_{PTME}) was best explained by:

$$AD_{PTME} = e^{(-3.07 + 0.032D + 0.023H)} \quad (4.4)$$

where D is the date of the growing season and H is the canopy height. For this species, percent bare ground was not an important predictor of AD_{PTME} in monoculture alfalfa systems after accounting for Julian date and canopy height, and was dropped from the model ($\Delta D = 35.46$; $df = 47, 48$; $P = 0.42$). Interestingly, canopy height, date of the growing season, and percent bare ground were not important predictors of AD_{PTME} in barley nurse-crop systems ($P > 0.40$), despite the fact that AD_{PTME} was greatest in those fields. Similarly, none of these environmental variables explained AD_{PTME} in uncultivated refuge areas ($P > 0.50$).

The activity-density of *A. cupreum* (AD_{AGCU}) in monoculture alfalfa systems was best explained according to:

$$AD_{AGCU} = e^{(5.11 + 0.034H - 0.028D + 0.037B)} \quad (4.5)$$

where H is the canopy height, D is the Julian date, and B is the percent bare ground ($\Delta D = 253.17$; $df = 47, 50$; $P < 0.001$). In barley nurse-crop systems, canopy height and percent bare ground were important predictors of AD_{AGCU} ($\Delta D = 386.57$; $df = 45, 47$; $P = 0.003$), but Julian date was not an important predictor after accounting for these two variables ($\Delta D = 0.43$; $df = 44, 45$; $P = 0.91$). Thus in barley nurse-crop systems, AD_{AGCU} was best predicted by:

$$AD_{AGCU} = e^{(-1.73 + 0.046H + 0.043B)} \quad (4.6)$$

In uncultivated refuge areas, percent bare ground and Julian date best predicted AD_{AGCU} ($\Delta D = 16.03$; $df = 45, 47$; $P = 0.02$), but canopy height was not an important predictor after accounting for the other two variables ($\Delta D = 1.28$; $df = 44, 45$; $P = 0.44$). The best model for AD_{AGCU} in uncultivated refuge area was:

$$AD_{AGCU} = e^{(7.02 - 0.050B - 0.044D)} \quad (4.7)$$

Canopy height and percent bare ground were important predictors of *A. placidum* activity-density (AD_{AGPL}) in monoculture alfalfa systems ($\Delta D = 177.22$; $df = 48, 50$; $P < 0.001$), but Julian date of the growing season did not improve model fit after accounting for the other two predictors ($\Delta D = 1.29$; $df = 47, 48$; $P = 0.72$). Thus, the best model for the activity-density of this species was:

$$AD_{AGPL} = e^{(-1.41 + 0.050H + 0.040B)} \quad (4.8)$$

In barley nurse-crop systems, Julian date was the best predictor of AD_{AGPL} ($\Delta D = 1875.3$; $df = 46, 47$; $P < 0.001$), but neither canopy height or percent bare ground further explained AD_{AGPL} after accounting for date of the growing season. AD_{AGPL} was best predicted by:

$$AD_{AGPL} = e^{(-3.33+0.04D)} \quad (4.9)$$

A. placidum was rarely captured in uncultivated refuge areas. Accordingly, none of the measured environmental variables were important predictors of its activity-density in uncultivated refuge areas.

Discussion

In this study, we sampled a total 64 carabid species, and in agreement with previous studies conducted in agroecosystems (Thiele 1977, Holland and Luff 2000, Luff 2002), we observed that communities were dominated by a small subset of species. Specifically, most of the sampled carabids were members of the *Amara*, *Agonum*, *Bembidion*, *Harpalus*, and *Pterostichus* genera, as is typical of temperate agricultural systems in the Northern Hemisphere (Luff 2002, Clark et al. 1997, Petit and Usher 1998, Lee et al. 2001, Gaines and Gratton 2010).

Community assembly theory predicts that a series of ecological filters selectively favors or excludes species from the regional pool in a local community (Keddy 1992, Funk et al. 2008, Myers and Harms 2009). Two local communities that share a common regional species pool, but are subjected to a different set of ecological filters, will have dissimilar community structures (Funk et al. 2008). Thus, differences in vegetative architecture, crop species and agronomic practices can result in different carabid community structures between crop fields. Holland and Luff (2000) suggested that timing of crop husbandry, rather than the crop species identity, may be the more important filter of carabid diversity in agricultural landscapes. Nevertheless, our results suggest that vegetation type acts as an ecological filter of carabid communities as we

found that species composition and community structure differed among monoculture alfalfa, barley nurse-crop and uncultivated refuge systems. Specifically, *A. placidum* and *P. melanarius* activity-densities were highest in barley nurse-crop fields, but *Amara littoralis* (Dejean) and *Amara cupreolata* (Putzeys) had the lowest activity-density in those fields.

In agreement with previous research on drivers of carabid assembly (Gardner et al. 1997, Ribera et al. 2001, Pakeman and Stockan 2014), we found that carabid community structure shifted in response to both vegetation structure and time within the growing season. Specifically, the dominant species in barley nurse-crop and monoculture alfalfa systems were *P. melanarius* and *A. placidum*, which are both polyphagous, nocturnal species (Lindroth 1968, Luff 2002, Bousquet 2012). By contrast, uncultivated refuge fields were dominated by seed predator species in the genera *Amara* and *Harpalus* (Tooley and Brust 2002). In our study, canopy height had the strongest impact on carabid community structure. Julian date modified the effect of canopy height, but only to a small extent. Percent bare ground had a variable effect between 2012 and 2013.

Our results agree with previous observations that carabids are sensitive to the microclimate of their habitat, particularly to temperature and humidity (Thiele 1977, Evans 1983, Thomas et al. 2002). While we did not specifically measure these variables, the rate of evapotranspiration in plant communities at the stand level is proportional to green biomass (Larcher 2003), and greater vegetative cover may buffer against daily temperature fluctuation, reducing the risk of desiccation (Thomas et al. 2002). Thus, taller plant stands may be more humid, and as a result, carabid communities may shift to

a composition of more hygrophilic species. By contrast, shorter plant stands may favor more xerophilous species. Alternatively, taller plant communities provide more shade, and therefore may increase the active period of nocturnal species (Baker and Dunning 1975, Hance 2002). Interestingly, the dynamics of two most common species in our study suggest the latter as the dominant mechanism of community assembly. *Agonum placidum* is a xerophilous species, whereas *P. melanarius* is a hygrophilous species (Lindroth 1968). Yet both species had the highest activity-densities in barley nurse-crop fields, which suggests that humidity was not the major driver of habitat selection by these two dominant species. Both species, however, are nocturnal and would likely benefit from longer active period that increased canopy height would provide (Baker and Dunning 1975, Hance 2002).

Barley nurse-crop systems had greater total activity-density of carabid beetles, particularly our two dominant species *P. melanarius* and *A. placidum*, than did monoculture alfalfa systems. This result agrees with previous research that polycultures enhance carabid populations (Kromp 1999, Holland and Luff 2000, Hance 2002). However, despite greater plant phylogenetic diversity in the uncultivated refuges, we found lower carabid activity-density in those systems than in barley nurse-crop systems. This suggests that increasing plant species richness alone is not a sufficient habitat management practice for enhancing carabid populations. The structural heterogeneity hypothesis, which posits that vegetation structural heterogeneity rather than plant phylogenetic diversity is a more important factor in carabid habitat selection (Dennis et al. 1998, Siemann 1998, Brose 2003, Pakeman and Stockan 2014) helps explain the

observed results. In agreement with this hypothesis, we found that the greatest carabid activity-density was in barley nurse-crops, which also had the highest canopy growth and closure (as indexed by decrease in percent bare ground) rates.

Our results suggest that land managers may be able to enhance carabid species richness and total abundance by creating a heterogeneous vegetation structure, and nurse-cropping in particular may be particularly effective to achieve this goal. However, species composition is often a more important driver of ecosystem services such as biological control compared with species richness or evenness because *per capita* consumption rates differ among species of carabids (Straub and Snyder 2006). Thus, land managers should implement habitat management to favor a particular suite of natural enemy species rather than increasing arthropod diversity *per se* (Landis et al. 2000). Such a strategy requires predictability in the response of targeted species. Our predictive models offer strategies for targeting the most common predatory species sampled in this study.

In alfalfa, the activity-density *P. melanarius* increased with canopy height as well as Julian date, which could be explained by its autumn breeding biology and its preference for dense vegetation (Lindroth 1968). Thus, land managers seeking to conserve populations of this species, a known predator of aphids (Hemiptera:Aphidae) (Dixon and McKinlay 1992, Sunderland 2002), in monoculture alfalfa may wish to delay cutting until late in the growing season. We found the highest mean activity-density of this carabid in barley nurse-crop fields. Thus, incorporating a nurse-crop in production

systems may be an effective strategy for increasing *P. melanarius* abundance, especially when establishing an alfalfa crop from seed.

In all three systems, we found that the activity-density of *A. cupreum*, a documented predator of cutworm eggs (Lepidoptera:Noctuidae) (Frank 1971), responded to the percent bare ground. Interestingly, *A. cupreum* activity-density increased with increasing bare ground in both monoculture alfalfa and barley nurse-crop fields, but decreased with increasing bare ground in the uncultivated refuge. This suggests that *A. cupreum* does not have a monotonic response to canopy cover, but rather prefer an intermediate optimum level of canopy cover. In barley nurse-crop field, the activity-density of *A. cupreum* increased with canopy height and percent bare ground. Thus, land manager may increase row spacing to enhance the abundance of this species in nurse-crop fields.

Finally, the activity-density *A. placidum*, a predator of cutworm eggs (Frank 1971), increased with both increasing canopy height and bare ground in monoculture alfalfa fields. One reason that *A. placidum* may prefer both tall canopies as well as open ground is that it is a nocturnal, xerophilous species (Lindroth 1968). Open vegetation may provide more xeric conditions, but taller canopies may increase its active period (Baker and Dunning 1975, Hance 2002). In barley nurse-crop fields, however, neither metric of vegetation structure was an important predictor of *A. placidum* activity-density. Thus, this species may prefer habitats of mixed grasses and legumes over plant communities with less functional diversity. A habitat management strategy for bolstering populations of *A. placidum* would thus be to plant polycultures of alfalfa and Poaceous

crop species when possible. In monoculture alfalfa, land manager may wish to reduce seeding density when establishing the crop to enhance *A. placidum* populations.

Conclusion

We conducted a two year study investigating the drivers of carabid community dynamics and the effects of vegetation structure on the habitat preferences of common carabid species under contrasting habitat management practices. Our results indicate that carabid communities vary among monoculture alfalfa, barley nurse-crop and uncultivated refuge fields. Barley nurse-crop fields had greater total carabid activity-density and species richness than either of the other two systems, which suggests that nurse-cropping may be an effective habitat management strategy to enhance carabid populations.

We found that carabid communities shifted in response to changes in vegetation structure. Canopy height in particular appears to be a strong driver of carabid diversity in the studied systems. Land managers seeking to enhance the populations of carabid beetles should consider changing seed row spacing or swathing dates to favor the putative habitat preferences of these species.

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CHAPTER FIVE

SUMMARY OF FINDINGS AND FURTHER RESEARCH

Agriculture in the twenty-first century must balance increased demands for food, fuel, and fiber with the need to reduce adverse environmental ramifications such as eutrophication of water bodies, decreases in biodiversity, and degradation of soil structure (Foley et al. 2005). To achieve this balance, Reganold et al. (2011) call for transformative innovations that alter the entire management regime in agroecosystems. They contend that the *status quo* of incremental innovations aimed at altering only a single component of the entire management regime will not suffice to achieve agronomic and ecological sustainability. Here, we have investigated two ecologically-based management practices to help bring such changes to fruition. In our first study, we investigated the agronomic and ecological effects of integrating sheep grazing for cover crop termination. In our second study, we investigated the use of nurse crops as a habitat management practice for conservation of carabid beetles. Both practices have the potential to be important components in ecologically-based management and reduce reliance on off-farm synthetic inputs.

Integrating sheep grazing for cover-crop termination could be an economically- and agronomically-beneficial practice in horticultural vegetable production. The use of cover-crops and their termination through targeted grazing represents an integrated, ecologically-based weed management strategy (Liebman and Gallandt 1997). We compared the effects of sheep grazing for cover-crop termination with those of mowing

on soil quality, forage quality, and cover-crop termination efficacy. In addition, we tested the effects of these two cover-crop termination strategies on weed pressure and crop yield in the subsequent growing season. Sheep grazing was as effective as mowing for cover-crop termination and had no detrimental effects on soil penetration resistance, chemistry, or microclimate. Additionally, weed pressure and cash-crop yield did not differ between cover-crop termination methods. The cover-crop represents a high quality forage that could provide \$24.00 - \$44.00 ha⁻¹ of direct revenue for producers as a grazing lease. Thus, the integration of sheep grazing could make the use of cover-crops more economically feasible in market vegetable gardens, and not have adverse effects on agronomic conditions.

One concern with any novel land management practice is that it could potentially alter ecological communities, which in turn, may have important consequence for ecosystem services in production systems such as pest management. Thus, we also investigated the ecological consequences of integrating sheep grazing for cover-crop termination by comparing weed and carabid beetle community structure between grazed and mowed plots. We found that despite temporal shifts in both weed and carabid beetle community structure, they did not differ between grazed and mowed plots. Our results suggest that grazing and mowing act as similar ecological filters of both weed and carabid beetle diversity.

Our study adds to a growing body of literature on the agronomic consequences of integrated crop-livestock systems, and represents one of a very few studies on integrated crop-livestock regimes in market vegetable gardens. To our knowledge, this is the first

study to investigate the impacts of integrated livestock grazing on the community dynamics of associated biodiversity in horticultural vegetable production. The results of this study suggest that integrating sheep grazing for cover-crop termination could provide several economic and agronomic benefits while not have deleterious effects on weed and carabid beetle communities. However, more research is needed to see if these patterns hold in other regions and climates. Furthermore, there is a major need to investigate grazing for cover-crop termination in larger production systems. Finally, while we briefly investigated the potential marketable value of the cover-crop we used, a full economic assessment of this strategy is imperative.

Other studies of integrating sheep grazing into cropping systems have found that these practices could direct weed communities toward dominance of perennial weeds (Miller et al. in press, Renne and Tracy 2013). While we did not observe that trend, our study only assessed the legacy effect of sheep grazing in the growing season immediately following the cover crop. Further research is needed to investigate possible long term legacy effects of integrated grazing in such systems on weed communities.

In addition to our study of integrating sheep-grazing for cover crop termination, we conducted a two year study examining the drivers of carabid community dynamics and the effects of vegetation structure on the habitat preferences of common carabid species under contrasting habitat management practices. Our results indicate that carabid communities vary among monoculture alfalfa, barley nurse-crop and uncultivated refuge fields. Barley nurse-crop fields had greater total carabid activity-density and species

richness than either of the other two systems, which suggests that nurse-cropping may be an effective habitat management strategy to enhance carabid populations.

We found that carabid communities shifted in response to changes in vegetation structure. Canopy height in particular appears to be a strong driver of carabid diversity in the studied systems. Land managers seeking to enhance the populations of carabid beetles should consider changing seed row spacing or swathing dates to favor the putative habitat preferences of these species. However, we did not investigate how these changes to carabid communities feedback to pest population dynamics. This is an important avenue for future research, as the success of implementing habitat management for carabid beetle conservation depends on whether populations of these generalist predators are sufficient to keep pest populations below the dynamic economic threshold.

Anthropocentric needs for fuel, fiber, food, and timber will continue to grow as global population increases. To meet these needs while simultaneously enhancing the economic and environmental sustainability in production systems, researchers and land managers must find ecologically-based management practices that make these ecosystems more resilient to stressors such as climate change and perturbations such as pest outbreaks. Consequently, agroecologists have become increasingly interested in understanding the role that biodiversity plays in ecosystem functions and finding land management practices that direct community structure toward achieving those goals (Altieri and Letourneau 1982, Benton et al. 2003, Shennan 2008). Our studies add to a growing body literature on the impacts of land management on associate biodiversity agroecosystems. However, community dynamics are often site-specific and temporally

variable. We hope that research on biodiversity and ecological services in production systems continues to flourish and our studies will aide in that pursuit.

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