

IMPACTS OF DRYLAND FARMING SYSTEMS ON BIODIVERSITY, PLANT-
INSECT INTERACTIONS, AND ECOSYSTEM SERVICES

by

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DEDICATION

To my parents, my family, and Montana friends

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ABSTRACT

Farming system impacts the structure and functioning of associated biodiversity and plant-insect interactions. However, the extent of these impacts is largely unknown in drylands of the Northern Great Plains, an important region for cereal, pulse, oilseed, and forage production. Using three complementary studies, I compared the impacts of conventional and organic systems on associated biodiversity (weeds, bees, insect pests, and parasitoids), bee-flower networks, and bumblebee colony success.

First, I assessed stem cuts by and parasitism on *Cephus cinctus* (wheat stem sawfly) in spring and winter wheat cultivars grown in conventional and organic fields. I found that organic fields had less *C. cinctus* infestation and more braconid parasitoids of *C. cinctus*, indicating an increased pest regulation in organic system. I compared *C. cinctus* preference and survival on Kamut with Gunnison and Reeder wheat cultivars and found the lowest *C. cinctus* oviposition and survival in Kamut, suggesting that Kamut is a potential genetic source for this pest.

Second, I assessed the impacts of conventional and organic systems on forb and bee communities. I found greater forb diversity and more connected bee-flower networks in organic fields, but bee communities did not differ between systems. Comprising only 12% of the landscape, natural habitat did not affect small-bodied bees in either system but had a positive effect on large-bodied bees at the scale of 2000 m radius. These results indicate that an increased forb diversity and bee-flower interaction in organic fields is not enough to offset the negative effects of landscape homogeneity on bees.

Third, I compared *Bombus impatiens* colony success, worker condition, and colony-collected pollen between farming systems. I found greater growth rate, brood cells, and pollen species richness in *B. impatiens* colonies as well as lower wing wear and greater body lipid mass in workers from organic fields, than in conventional fields. The greater colony success and better worker conditions could be a proxy for better ecosystem services provided by organic fields.

Overall, my studies show that organic farming supports greater associated biodiversity, more complex bee-flower networks, and better biodiversity-based ecosystem services in the Northern Great Plains.

CHAPTER ONE

INTRODUCTION

Farming Systems and their Role as Ecological Filters

Modern industrialized crop production relies on intensive management practices, including the use of substantial off-farm inputs such as pesticides and fertilizers in the majority of conventional systems and mechanical soil disturbance such as tillage in the organic systems, to control pest populations, maintain soil fertility, and prepare fields for planting. While the practices of using synthetic pesticides and fertilizers in conventional systems provide valuable agronomic and economic benefits to humankind, they are also major drivers of declines in local and regional biodiversity, selection for pesticide resistance, greenhouse gas emissions, and eutrophication (Krebs, 1999; Hole et al., 2005; Kirchmann et al., 2008; Gelfand et al., 2010; Tilman et al., 2011; Duru et al., 2015). Organic farming, however, can also result in several environmental detriments, including soil erosion and increased N₂O and other greenhouse gas emissions associated with the use of animal manures, but the incorporation of crop rotations and cover cropping can ameliorate these detriments (Cavigelli et al., 2013). Also, previous studies have reported that on average, organic systems yield 25-50% less than conventional ones, mainly because the former tend to have lower soil N and P capital (Hole et al., 2005; Kirchmann et al., 2008). However, due to higher prices, profitability is higher and less variable in organically managed agroecosystems than in conventionally managed systems (Crowder et al., 2015; Reganold and Wachter, 2016; Ponisio et al., 2015).

Given the environmental impacts of current conventional and organic agricultural systems and their vulnerabilities to increasingly extreme climatic variation, there is a renewed interest in developing alternative, more environmentally sensitive and resilient farm management systems. Ecologically-based diversified farming system is one alternative that augments ecological processes to provide the resources and conditions necessary for sustained production using on-farm practices like green manuring, crop rotation, intercropping, and crop-livestock integration (Hole et al., 2005). For example, Davis et al (2012) reported either similar to or greater crop yield and profit of farming systems that relied on ecologically-based practices such as crop rotations and crop mixtures, than those in industrially managed systems that relied on large amounts of agrochemical inputs. Similarly, ecosystem services such as pollination and pest regulation provided by ecologically-based diversified systems can be greater than those of current industrialized farming systems (Syswerda and Robertson, 2014).

Farming systems act as distinct ecological filters of biodiversity, selectively favoring some taxa while excluding others from the regional pool of species (Keddy, 1992; Booth and Swanton, 2002; Funk et al., 2008; Smith et al., 2015). For example, conventional and organic systems rely on different arrays of management practices, or ecological filters, to control weeds (i.e. synthetic herbicides in the former and a suite of tactics in the later including tillage, cover cropping, crop rotation, increasing crop density, and solarization) resulting in a characteristic plant composition associated with each system (Keddy, 1992, Funk et al., 2008). The biodiversity structure and functioning associated with management systems may, in turn, influence ecosystem services (Brittain et al., 2010; Cardinale et al., 2006, 2012).

Biodiversity, Ecosystem Functioning, and Ecosystem Services

Ecosystem functions are the ecosystem properties such as nutrient cycling and energy flow resulting from interactions among organisms and the abiotic environment (Hooper et al., 2005). Ecosystem services are also the subset of ecosystem functions valuable to humanity including food, fiber and energy production, air and water purification, climate regulation, pollination, and pest regulation (Kirchmann et al., 2008; Mace et al., 2012; Power, 2010; Quijas et al., 2010; Vandermeer et al., 2002). Increased biodiversity enhances ecosystem resistance and resilience to perturbations such as invasive species, diseases, and soil disturbances, as well as stressors such as climate change (known as the diversity-stability hypothesis; Hautier et al., 2015; Tilman et al., 2014, 2006). Also, increased biodiversity buffers against interruptions in ecosystem functioning following disturbances through compensatory effects of multiple species with redundant functions as a result of niche overlap (known as the insurance hypothesis; Hooper et al., 2005; Vandermeer et al., 2002; Yachi and Loreau, 1999). Recently, ecologists have considered functional diversity (diversity of organisms based on their functional roles in ecosystem functioning) more important to maintain ecosystem processes and services than just biodiversity *per se* (Cadotte et al., 2011; Gagic et al., 2015; Moonen and Bàrberi, 2008; Tilman et al., 1997; Tilman, 2001).

These ecological principles that we learned from natural systems can also be applied to the design and ecologically-based management of sustainable agroecosystems so that the farm managers benefit from enhanced biodiversity (Gaba et al., 2015).

Ecologically-based management capitalizes on the synergistic effects of biodiversity and

ecosystem function, consequently increasing ecosystem stability (Gross et al., 2014; McNaughton, 1977). Except in small-scale farming systems, diversified agroecosystems are relatively rare in the NGP, but the potential exists to complement crop species, which can share and use resources more effectively (Callaway, 1995; Brooker et al., 2015; Li et al., 2014). Hence, research is needed in the NGP to assess how biodiversity in agroecosystems could support better ecosystem services such as pest regulation or pollination (Kang et al., 2015; Loreau et al., 2001; Vandermeer et al., 2002).

Biodiversity in agroecosystems includes planned diversity and associated biodiversity. While planned diversity consists of crop species that the farm manager selects for a specific production goal, associated biodiversity is not intentionally included in the system and is composed of pestiferous, beneficial, and neutral organisms (Altieri, 1999; Swift et al., 2004; Vandermeer et al., 2002). Planned diversity may alter the community structure of associated biodiversity (and vice versa), interactions among the constituent taxa, and their functioning. These changes in the associated biodiversity can have important ramifications for the provisioning of ecosystem services such as pest regulation, pollination, and crop production (Brittain et al., 2010; Cardinale et al., 2006). For example, if the suite of imposed management practices favors pestiferous species, growers may experience decreases in marketable yields, due to ecosystem dis-services. On the other hand, if management practices favor an associated biodiversity dominated by beneficial organisms, growers may reap the benefits of enhanced ecosystem services such as biological control (Cardinale et al., 2003; Landis et al., 2000), pollination (Carvalho et al., 2011), and nutrient cycling (Jordan and Votaw, 2004). Farm managers, through various farming practices such as crop rotation, multiple-cropping, or

cover cropping can create spatial and temporal habitat heterogeneity to enhance the associated biodiversity (Altieri, 1999; Benton et al., 2003; Gaba et al., 2015). The taxa of associated biodiversity on which my dissertation focuses include weeds, *Cephus cinctus* Norton, 1872 (wheat stem sawfly), parasitoids of *C. cinctus* [*Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae)], and bees (Hymenoptera: Apoidea, Apiformes).

Weeds

Weeds are often considered impediments to agricultural production due to their impacts on crop yields and interference with farming practices (DeDecker et al., 2014). In particular, managing populations of perennial weeds such as *Cirsium arvense* (L.) Scop (Canada thistle) and *Taraxacum officinale* Weber (dandelion) is especially challenging for organic farmers (Carr et al., 2013; Gruber and Claupein, 2009; Sans et al., 2011) who are required to avoid the use of synthetic herbicides (Albrecht, 2005; Cavigelli et al., 2008; Halde et al., 2015). Weeds however, may provide valuable ecosystem services by increasing soil organic matter, facilitating nutrient cycling, serving as propagule pools of arbuscular mycorrhizal fungi and symbiotic bacteria such as *Rhizobia* (Jordan and Vatovec, 2004), and providing food and habitat for pollinators (Gabriel and Tschardt, 2007; Carvalheiro et al., 2011) and natural enemies (Bengtsson et al., 2005; Siemann, 1998; Kremen and Miles, 2012).

Since the diverse soil microbial communities in organic systems facilitate greater resource partitioning between competing crops and weeds (Smith et al., 2010), crop yield may not necessarily decrease even with high weed abundance in these systems (See

Benaragama et al., 2016; Johnson et al., 2017). Greater resource partitioning, in turn, allows for enhanced crop-weed coexistence as they may no longer need to compete for the same pool of soil resources (Johnson et al., 2017; Loreau and Hector, 2001; Schoener, 1974). Hence, rather than due to the competition with weeds, the yield losses in organic farming, compared to conventional, may have been resulted from lower soil fertility (Benaragama et al., 2016).

Cephus cinctus and its Braconid Parasitoids

Cephus cinctus, wheat stem sawfly, is a major pest of grain crops in the NGP (Weiss and Morrill, 1992; Shanower and Holmer, 2004; Nansen et al., 2005), causing USD\$350 million in economic losses to wheat growers in this region annually (Bekerman, 2011; Beres et al., 2011a). *Cephus cinctus* adult females, after their emergence in late spring through early summer, oviposit in stems of wheat or other grasses, mainly in the most recently elongated internodes (Weiss and Morrill, 1992; Perez-Mendoza and Weaver, 2006). Developing *C. cinctus* larvae consume parenchyma tissue and breach vascular bundles when they bore through the stem nodes to reach new tissue in adjacent internodes. Their feeding disrupts the photosynthetic capacity of infested culms or “stems” (Macedo et al. 2005, Delaney et al. 2010), reducing plant height, seed head development, seed weight, and grain quality (Morrill et al., 1992; Perez-Mendoza et al., 2006). Once the infested plant matures, *C. cinctus* larvae move to lower parts of the stem where they encase themselves in a hibernaculum to overwinter in diapause, after notching the stem above (Holmes, 1975). The dry and notched stem dislodges, creating a readily identifiable cut stem that results in yield loss because of the

reduced harvest efficiency (Beres et al., 2011b; Nansen et al., 2005). While yield losses resulting from *C. cinctus* lodging have high economic importance to *Triticum aestivum* L. (wheat) growers, there has been limited success in controlling this pest.

Bracon cephi and *B. lissogaster* are the only parasitoids that consistently attack *C. cinctus* in *T. aestivum*, reducing the survival and abundance of pest (Morrill et al., 1998; Runyon et al., 2002; Weaver et al., 2005; Buteler et al., 2008). Both species of parasitoids are specialists, idiobiont (preventing further development and kill the host), and ectoparasitoids (living externally on host), with two generations per year (Nelson and Farstad, 1953). Once the adult parasitoids locate *C. cinctus* larvae, they insert their ovipositor through the grass stems in which the larvae reside, paralyze the host, and deposit eggs (Nelson and Farstad, 1953). These eggs develop into larvae, which feed on the juvenile life stage of their host and emerge through a hole on wheat stems as adults (Nelson and Farstad, 1953). Industrial management practices can have negative impacts on populations of these parasitoids. For example, soil disturbance from tillage can kill (Runyon et al., 2002) and toxicity from herbicide applications may eliminate the weeds that potentially provide food and shelter to parasitoids. However, reducing tillage, avoiding unnecessary pesticide application, and diversifying cropping systems can help conserve these parasitoids (Runyon et al., 2002; Weaver et al., 2004), ultimately controlling *C. cinctus* and increasing wheat yield (Buteler et al., 2008).

Bees

Bees are a major clade within the Hymenoptera, depending solely on pollen and nectar for energy (Michener, 2007). There are ~20,000 described bee species in the world

and at least 5,000 of them occur in North America (Ascher and Pickering, 2014; Michener, 2007), but very little is known about the ecology of most bee species. Bees are the most important group of pollinators globally (Corbet et al., 1991; Klein et al., 2007; Winfree et al., 2008), pollinating more than 70% of animal-pollinated plants (Gabriel et al., 2010; Kevan, 1999; Kremen et al., 2002, 2007; Moisset and Buchmann, 2011; Steffan-Dewenter et al., 2005). With one third of the leading global crop species requiring animal vectors for pollination, global declines in bee abundance and diversity have marked ecological and economic implications for many commercially-important crops (Klein et al., 2007, Brown and Paxton, 2009; Potts et al., 2010, 2016), but we lack the knowledge on status of pollinators and their interactions with plants in the NGP.

A suite of anthropogenic stressors and perturbations contribute to declines in bee biodiversity including reduced regional floral resources, landscape simplification, habitat fragmentation, and exposure to parasites [e.g., *Varroa destructor* Anderson & Trueman, 2000 (varroa mites) in *Apis mellifera* Linnaeus, 1758 (honey bees)] and pathogens (Goulson et al., 2008, 2015; Potts et al., 2010). Modern agricultural practices further drive declines of bee diversity, including mortality from exposure to toxins such as insecticides (Kirchmann et al., 2008; Féon et al., 2010; Whitehorn et al., 2012; Kessler et al., 2015; Rundlöf et al., 2015) and soil disturbances from tillage (Shuler et al., 2005; Williams et al., 2010). Generally, organic systems support greater bee abundance and richness than conventional systems (Lichtenberg et al., 2017), but these effects can be mediated by landscape structure (Carrié et al., 2017; Steffan-Dewenter et al., 2002). To my knowledge, no previous study has formally evaluated the impact of farming system and landscape structure on bee communities in the NGP.

Plant-insect Interactions

Insects can interact with plants positively as mutualistic pollinators, negatively as herbivores and parasites, or neutrally (Odum and Barrett, 1971). Both mutualistic and parasitic interactions coevolve in adapting to their environments (Darwin, 1862; Mello and Silva-Filho, 2002; Muchhala and Thomson, 2009; Odum and Barrett, 1971). Bee-flower networks, which exemplify mutualistic plant-insect interactions, are composed of pairwise links of interacting plants and pollinators (Bascompte et al., 2003), thus reflecting the structure and function of a community (Bascompte and Jordano, 2007; Montoya et al., 2006; Tylianakis et al., 2008). In bee-flower networks, nestedness measures the degree to which specialist species interact with a subset of more generalist species (Bascompte et al., 2003; Nielsen and Bascompte, 2007). The increase in pairwise links or species interactions and nestedness within a given bee-flower network supports robustness (network resilience towards external disturbances) of these networks (Piazzon et al., 2011).

Landscape simplification, soil disturbances, declines in plant α -, β -, and γ -diversity, and exposure to pathogens and pesticides can impact the structure of pollinator communities, and in turn bee-flower networks (Goulson et al., 2015, 2008; Kremen and Miles, 2012; Potts et al., 2010). Concomitant with global declines in pollinator populations and diversity (Potts et al., 2010) and zoophilously pollinated plants (Biesmeijer, 2006), connectedness of pollination networks have been compromised (Burkle et al., 2013).

In agricultural settings, weeds may provide food and habitat for pollinators (Gabriel and Tscharntke, 2007; Carvalheiro et al., 2011), but due to herbicide use, conventional systems are almost weed-free so may not support bees and bee-flower networks. Also, many insect pollinators are highly sensitive to synthetic insecticides and fungicides (Féon et al., 2010; McArt et al., 2017) used in conventionally managed systems, so the heavy use of these inputs can decrease pollinator populations and richness (Otieno et al., 2011; Whitehorn et al., 2012), destabilizing pollination networks. However, since organic farms in the NGP and elsewhere do not use synthetic pesticides and often support a greater diversity of weed species (Polnac et al., 2008; Wortman et al., 2010), they may support greater pollinator abundance and species richness, and more stable and complex bee-flower networks with more connected interactions (Kehinde and Samways, 2014; Kremen and Miles, 2012; Power and Stout, 2011). Changes in weedy forb and pollinator community structure in agricultural landscapes can increase or decrease these network complexities (Gabriel and Tscharntke, 2007; Pocock and Memmott, 2012). Additionally, increases in the abundance of insect-pollinated forbs may represent a positive feedback loop for the successional trajectory of forb communities, in which greater forb abundance increases pollination efficiency, and in turn, further increases the forb abundance (Gabriel and Tscharntke, 2007; Hald, 1999). However, no studies have been done in the NGP regarding the effects of farming systems on bee-flower networks.

Ecosystem Services

Ecosystem services are the suite of ecosystem functions that are useful to humanity (Montoya et al., 2012). These services can be divided into four major categories: (i) provisioning: food, fiber, timber, fuel, and genetic resource production; (ii) regulating and mitigating: pollination, disease and pest regulations, water quality, soil development, climate stability, and greenhouse gas sequestration; (iii) supporting: nutrient and water cycling, and soil fertility; and (iv) aesthetic and cultural: spiritual and recreational benefits from rural views and landscapes (Assessment, 2005; Haines-Young and Potschin, 2012; Robertson et al., 2014; Swinton, 2007, but see Boyd and Banzhaf, 2007; Schröter et al., 2014; Wallace, 2007). Diversified agroecosystems support many agronomically beneficial insects including bees, carabid beetles, and braconid parasitoids, providing important biodiversity-based ecosystem services, such as pest regulation and pollination (Altieri, 1999; Kremen and Miles, 2012; Landis, 2017; Lichtenberg et al., 2017).

Biodiversity-based Ecosystem Services

The relationship between biodiversity and ecosystem services is complex but usually positive (Harrison et al., 2014; Mace et al., 2012), involving multiple trophic levels (de Bello et al., 2010). Furthermore, the evidence of biodiversity-ecosystem service relationships especially in agroecosystems are not well understood, and these inherently complex relationships depend on crop characteristics, associated biodiversity, and spatial and temporal scale (Graves et al., 2017; Ricketts et al., 2016; Tilman et al., 1997). Enhancing biodiversity helps to foster the resilience of ecosystem services, as high

diversity is hypothesized to buffer against negative perturbations (Biggs et al., 2012; Hooper et al., 2005; Srivastava and Vellend, 2005). Therefore, losses in the associated biodiversity could affect agroecosystem functioning and services (Loreau et al., 2001; Vandermeer et al., 2002). For example, agricultural landscapes with low biodiversity cannot provide ecosystem services such as pest regulation without parasitoids, or pollination without bees. Hence, in any agricultural landscapes, first it is important to know about parasitoids and bees that can be used as proxies or indicators of ecosystem services in certain ecosystems, yet no previous research has been conducted in this aspect in the dryland agroecosystems of the NGP. I did not specifically measure direct pest regulation and pollination services in my dissertation, but I focused on the proxies of biodiversity-based ecosystem services such as parasitoids (proxy for pest regulation) and bee –flower interactions (i.e., flower visits), colony success, bee abundance, and diversity (proxies for pollination services) (see Boyd and Banzhaf 2007; Ricketts et al. 2008).

Pest Regulation

With an annual economic value of \$4.5 billion in the United States only (Losey and Vaughn, 2006), pest regulation through biological control by beneficial insects is an important ecosystem service for agriculture (Landis, 2017; Power, 2010). Biological control of *Cephus cinctus* by its braconid parasitoids, *B. cephi* and *B. lissogaster*, is an example of the pest regulation services in agroecosystem, as it reduces pest damage to wheat crops (Morrill et al., 1998, Weaver et al., 2005, Buteler et al., 2008, 2015). Enhancing biological control, by increasing the growth, reproduction, and survival of natural enemies in agricultural landscapes helps to effectively regulate crop pests

(Duncan et al., 2015; Landis et al., 2000; Naranjo et al., 2015). Additionally, it may reduce the need for pesticide applications, and consequently reduce producer expenditures (Tooley and Brust, 2002). Reducing pesticide use may also reduce non-target mortality, leaching, and the evolution of pesticide-resistant populations. Relatively undisturbed, uncultivated lands and perennial crop fields support more for conservation biological control, than regularly disturbed, cultivated lands, and annual crop fields (Landis et al., 2000).

Pollination

Pollination is a vital ecosystem services for agriculture (e.g., Klein et al., 2007; Kremen et al., 2002; Lautenbach et al., 2012; Losey and Vaughn, 2006; Vanbergen and Initiative, 2013) with an estimated worldwide annual economic value of more than \$215 billion (Gallai et al., 2009). The United States lacks an updated comprehensive valuation of pollination services but, as an example, 1.6 million colonies of *Apis mellifera* are required to pollinate the 130 million *Prunus dulcis* (Mill.) D.A. Webb (almonds) trees in California's Central Valley, which represents \$11 billion of California's economy annually and supports ~100,000 jobs (CAB, 2016).

There is a global demand for pollination services. In the past half century, there has been a 300% increase in the proportion of zoophilously pollinated crops grown in agroecosystems worldwide (Aizen and Harder, 2009), hence increasing the demand for pollination. However, human labor cannot replace pollinators' services and meet the pollination demand in a cost-effective way. For example, due to the declines in bee pollinators resulting from land-use intensification, pesticide use, invasive species, and

climate change, farmers in Sichuan, China adopted hand pollination in apple crops in late 1980s (Partap and Ya, 2012; Teichroew et al., 2017). However, due to the 1000% increase in human labor cost between 2001-2011 and with the reduced pollination efficiency of hand pollination compared with mellitophilous pollination, farmers in 50% of the villages in Maoxian County, Sichuan, had shifted from apple to other fruits or vegetables (Partap and Ya, 2012). Hence, promoting pollinators is the only option to meet the demand of global pollination.

Landscape Effects on Biodiversity

Landscape heterogeneity modifies biodiversity and ecosystem service provisioning (Landis, 2017; Werling et al., 2014). Flowering crops and weeds in arable lands may provide food resources to beneficial insects such as bees, braconid parasitoids, and generalists predators for a limited duration, but uncultivated natural habitats are required to provide nesting ground, season-long food resources, and refugia from disturbances (Bohart, 1972; Danner et al., 2016; Hagen and Kraemer, 2010; Landis et al., 2005; Lee et al., 2001; Requier et al., 2015). Hence, conservation of beneficial insects through habitat management within and around croplands enhances pollination and pest regulation. For example, increasing the proximity of farms to native plants in natural habitats can enhance pollinator communities on farms, which in turn may improve crop yields (Brittain et al., 2010; Féon et al., 2010; Morandin et al., 2007). Specifically, landscape-level heterogeneity of plant communities, can impact pollinator visitation rates in agricultural landscapes (Carvalho et al., 2011; Garibaldi et al., 2011; Ricketts et al., 2008), but we lack this knowledge in the NGP.

Several studies have shown the importance of uncultivated natural habitats on beneficial insects in the agricultural landscapes. Kremen et al. (2004) found that native bee abundance and diversity increased more strongly with the proportion of natural habitat than with a specific type of farming system (conventional and organic) in *Citrullus lanatus* var. *lanatus* (Thunb) Matsum. & Nakai (watermelon) farms of California. Similarly, Carvalheiro et al (2011) found that the frequency of flower visitation by *A. mellifera* in a South African *Helianthus annuus* L. (sunflower) plantation declined 61% for every 1000m of distance from plantations to native plant communities. Additionally, Morandin and Winston (2006) calculated that maximal crop yield and profit in *Brassica napus* L. (canola) can be achieved when 30% of the land surrounding crop fields is occupied by native plant communities and uncultivated lands. Nonetheless, due to the conversion of natural habitats into row crop production systems, bee abundance between 2008 and 2013 has been declined in 23% of the key US agricultural regions (Koh et al., 2016).

Significance of the Study

Predators and parasitoids help to control pest population in agricultural systems of the NGP and provisioning food resources such as pollen and nectar (from forbs) is essential for their survival and reproduction (Isaacs et al., 2009; Klein et al., 2004; Pywell et al., 2005). Diversified farming systems and landscape heterogeneity could offset the negative effects of resource-poor monoculture-based cereal production on these beneficial insects. Therefore, the ecological role of associated biodiversity in agricultural

landscapes is important (Altieri, 1999; Duru et al., 2015; Isaacs et al., 2009) in providing ecosystem services like pest regulation, ultimately reducing the need for synthetic inputs.

In addition, *Triticum aestivum*, a dominant crop in many section of the NGP, does not require animals for pollination, but other crops commonly found in the region such as *Medicago sativa* L. (alfalfa), *B. napus*, *H. annuus*, or *Carthamus tinctorius* L. (safflower) require pollinators for sustained production. Also, native pollinators are required for the reproduction of wild native forbs and aid in their conservation in already intensified agricultural landscapes. Hence, pollinators and plant-pollinator interaction networks are important, but, we still lack the knowledge and status of these beneficial insects in the highly simplified landscapes of the NGP.

Globally, there is a paucity of research regarding the impacts of dryland farming systems on associated biodiversity across trophic levels, plant-insect interaction networks, and biological control services provided by agroecosystems. Previous studies that separately assessed the impact of farming system on associated biodiversity including weeds, pollinators and their services, bee-flower networks, or pest regulation were conducted in Europe (Brittain et al., 2010; Hole et al., 2005; Tscharrntke et al., 2005; also see Kremen and Miles, 2012), California (Kremen et al., 2004, 2002; Williams et al., 2010), and the mid-western US (Isaacs et al., 2009; Isaacs and Kirk, 2010; Spiesman et al., 2017). However, there is a dearth of such research in the NGP, a leading region in the production of *T. aestivum*, and *Hordeum vulgare* L. (barley), *Lens culinaris* Medik. (lentils), *M. sativa*, and *C. tinctorius*. Also, previous studies in the NGP have reported higher weed abundance and diversity in organic fields (Pollnac et al., 2008) than in conventional fields, but no research has assessed whether higher within-field floral

diversity translates into greater abundance and diversity of bees and more complex bee-flower networks in the NGP and how farming systems interact with landscape context to impact bee communities. Also, no knowledge exists on whether higher within-field floral diversity translates into greater bee colony success and better worker condition. My research fills these knowledge gaps by assessing the impacts of dryland farming systems on the associated biodiversity of multiple taxa across trophic levels including weeds, *C. cinctus*, and braconid parasitoids, bees, bee-flower interactions, and arthropod-mediated (pest regulation and bee colony success) ecosystem services.

Research Objectives

1. Determine how conventional and organic farming systems and *T. aestivum* cultivars affect *C. cinctus* infestation and parasitism on *C. cinctus*.
2. Assess the impacts of conventional and organic farming systems on forb and bee communities.
3. Evaluate the effects of percent natural habitat on small-and large-bodied bee abundance.
4. Compare floral resources and pollen composition collected by *B. impatiens* (bumble bee) workers between conventionally and organically managed systems.
5. Compare *Bombus impatiens* colony success and individual worker condition between conventionally and organically managed farming systems.

In chapter II of my dissertation, I address objective 1 by comparing infestation of and parasitism on *C. cinctus* in *T. turgidum* ssp. *turanicum* (Kamut), and other wheat

cultivars grown in no-till conventional and tilled organic fields in north-central Montana. Additionally, I compare *C. cinctus* preference and survival on Kamut and two spring wheat cultivars in a greenhouse experiment to determine whether Kamut is resistant against *C. cinctus*.

I address objectives 2 and 3 in chapter III by assessing the impacts of conventional and organic farming on associated biodiversity including forbs and bees and the associated bee-forb interaction networks. I also assess how the bee abundance is affected by landscape structure, particularly by the proportion of natural habitat.

I address objectives 4 and 5 in chapter IV, by assessing floral resources, and by using *B. impatiens* as a model organism to compare bee colony success and worker condition between conventional and organic systems. I also assess the pollen composition collected by bee workers between two farming systems.

Finally, in chapter V, I provide a summary of my overall dissertation work and future directions.

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CHAPTER TWO

FARMING SYSTEM AND WHEAT CULTIVAR AFFECT INFESTATION OF AND
PARASITISM ON *CEPHUS CINCTUS* IN THE NORTHERN GREAT PLAINSIntroduction

Cephus cinctus Norton, Hymenoptera: Cephidae (wheat stem sawfly), is a major pest of grain crops in the Northern Great Plains of the US and Canada (Nansen et al., 2005a; Shanower et al., 2004; Weiss and Morrill, 1992). Every year, *C. cinctus* causes \$45 - 80 million in economic losses to wheat growers in Montana and \$350 million across the Northern Great Plains (Bekerman, 2011; Beres et al., 2011a). After emergence of adults in late spring through early summer, *C. cinctus* females oviposit in stems of wheat or other grasses, mainly in the most recently elongated internodes (Perez-Mendoza and Weaver, 2006; Weiss and Morrill, 1992). Developing *C. cinctus* larvae consume parenchyma tissue and breach vascular bundles when they bore through the stem nodes to reach new tissue in adjacent internodes. This feeding disrupts plant's photosynthetic capacity of the infested stem, reducing its height, seed head development, seed weight, and grain quality (Macedo et al., 2005; Morrill et al., 1992; Perez-Mendoza et al., 2006). Once the infested plant matures, *C. cinctus* larvae move to the lower part of the stem where they encase themselves in a hibernaculum to overwinter in diapause, after notching the stem above (Holmes, 1975; Macedo et al., 2005). The dry and notched stem breaks and lodges, creating a readily identifiable cut stem. Lodging due to stem cutting results in

yield loss because of the reduced harvest efficiency (Beres et al., 2011a; Nansen et al., 2005b).

Cephus cinctus was first reported as a pest of wheat in 1895 (Ainslie, 1920). This opportunistic species expanded its host range from native grasses to spring wheat about a decade after this crop was first grown in large areas of western North America (Ainslie, 1920; Beres et al., 2011a; Criddle, 1923). Then a second shift of documented host plant use in Montana occurred because of its ability to complete development in earlier maturing winter wheat (Morrill and Kushnak, 1996), a phenomenon that has recently been reported for areas experiencing *C. cinctus* outbreaks further south (Irell and Pears, 2014; Lesieur et al., 2016). *Cephus cinctus* has the ability to utilize both spring and winter wheat, and Montana has a large proportion of land planted to either winter or spring wheat, which is unique among neighboring states and provinces that experience recurring losses due to *C. cinctus*. Due to the warming climate in the Northern Great Plains (Lanning et al., 2010), there may be changes in seasonal phenology of *C. cinctus* as well as in agronomic practices used to grow spring and winter wheat crops. However, we lack evidence for a phenological synchrony between *C. cinctus* and winter wheat.

There has been limited success in controlling *C. cinctus* in agricultural systems though researchers have spent decades investigating the efficacy of cultural (Morrill et al., 1998; Weaver et al., 2004), chemical (Holmes and Peterson, 1963; Skoog and Wallace, 1964), and biological control (Beres et al., 2011a,c; Morrill et al., 1998; Runyon et al., 2002). The type of farming system can affect *C. cinctus* abundance. For example, compared to tilled fields where stubble is incorporated into the soil, no-till wheat followed by chemical fallow has more stubble that provides more habitats for *C. cinctus*

overwintering and potential colonization of adjacent wheat fields (Beres et al., 2011b). In organic cropping systems, greater abundance and diversity of weeds (Pollnac et al., 2008; Romero et al., 2008) can potentially provide more food and shelter for parasitoids of *C. cinctus* than fields conventionally managed where weeds are sprayed with herbicides. As a result of increased parasitoid pressure, *C. cinctus* survival and abundance can be reduced (Buteler et al., 2008; Morrill et al., 1998; Runyon et al., 2002; Weaver et al., 2005). While tillage kills *C. cinctus* larvae overwintering within wheat stems by burying the wheat stubble (Morrill et al., 1993), it may also disproportionately kill parasitoids of *C. cinctus* if they over-winter belowground (Beres et al., 2011b; Runyon et al., 2002; Weaver et al., 2004).

Bracon cephi (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) are the only parasitoids that commonly attack *C. cinctus* in *Triticum aestivum*, reducing its survival and abundance (Morrill et al., 1998; Runyon et al., 2002; Weaver et al., 2005). Both parasitoid species are specialists (*C. cinctus* is the only host), idiobiont (prevent further development and kill the host) ectoparasitoids (live externally on host), with two generations per year (Nelson and Farstad, 1953). Once the adult parasitoids locate *C. cinctus* larvae, they insert their ovipositor through the grass stems in which the larvae reside, paralyze the host, and deposit eggs (Nelson and Farstad, 1953). These eggs develop into larvae, start feeding on the juvenile life stage of their host and, after killing their hosts at pupation, emerge through a hole on wheat stems as adults (Nelson and Farstad, 1953).

Increased resistance of wheat to *C. cinctus* has been accomplished by developing solid-stemmed cultivars that reduce egg deposition and decrease survival of

eggs and larvae (Beres et al., 2007, 2011a; Buteler et al., 2015; Varella et al., 2017). However, solid-stem wheat cultivars often yield less than the traditional hollow stemmed cultivars (Beres et al., 2011a; DePauw et al., 1994, 1998, but see Sherman et al., 2015), and limit parasitism of *C. cinctus* (Rand et al., 2012, but see Weaver et al., 2004; Wu et al., 2013) because penetration of the stem and host location is more difficult for parasitoids (Fischer et al., 2003); effectiveness of hollow-stemmed wheat is also dependent on the availability of preferred alternative hosts (Keren et al., 2015). Further incorporation of genetic diversity of Triticeae is necessary to increase resistance to climate, disease, and pests like *C. cinctus* while maintaining yields (Cook et al., 2017; Mondal et al., 2016; Varella et al., 2015).

Kamut wheat (*Triticum turgidum*, *ssp. turanicum* McKey), commonly known as Khorasan wheat (hereafter, Kamut) is a tetraploid cultivar closely related to durum wheat (*Triticum turgidum* *ssp. durum*) that is grown in dryland organic farming systems in Montana, USA and Saskatchewan, Canada (Grausgruber et al., 2005). Believed to be grown in Khorsana region of Persia 4,000 years ago (Ikanovic et al., 2014), Kamut is registered under the trademark of Kamut International to be grown only under organic conditions (QK-77: USDA; Bordoni et al., 2017; Quinn et al., 1999; Sacks et al., 2005). Anecdotal accounts have indicated that *C. cinctus* infestation and stem cutting is lower in Kamut than in other wheat cultivars grown under different farming systems, such as no-till chemically managed (hereafter, conventional) systems (Quinn R, 2015, pers. comm.). To our knowledge, there has not been a systematic evaluation to determine if reduced infestation occurs in Kamut fields managed organically compared to no-till chemically

managed wheat fields, and, if differences exist, whether it is a result of wheat cultivar or the farming system under which it is grown.

The aim of this study was to determine how conventional and organic farming systems and the seasonality of the wheat crop (i.e. spring versus winter wheat) affected *C. cinctus* infestation and parasitism of *C. cinctus* larvae. We surveyed *C. cinctus* infestation and presence of specialist larval parasitoids among cultivars of spring and winter wheat grown in conventional fields and in tilled organic fields (hereafter, organic) in the Northern Great Plains. To further assess *C. cinctus* preference and survival in Kamut, we compared Kamut to two spring wheat cultivars with known differences in *C. cinctus* preference under greenhouse conditions. We hypothesized that the effects of farming system on *C. cinctus* infestation depends on the seasonality of the wheat crop and the type of wheat cultivars. Specifically, (i) because *C. cinctus* phenology overlaps more with winter wheat, rates of infestation would be greater in winter wheat than in spring wheat cultivars; (ii) because different tillage regimes reduce available stubble, and more weeds provide habitat for parasitoids, wheat stems from organic fields would have less *C. cinctus* infestation and a greater numbers of specialist larval parasitoids, resulting in less *C. cinctus* stems cut than in conventional fields; and (iii) based on farmers' observations in field settings, *C. cinctus* infestation and survival in Kamut would be lower than other spring wheat cultivars.

Materials and Methods

Cephus cinctus Infestation, Cut Stems, and Parasitoids in Field Conditions

Site Description. To assess if *C. cinctus* infestation varies by farming system or seasonality of wheat cultivar, we recorded *C. cinctus* incidence in spring wheat, and winter wheat stubble collected in conventional and organic wheat fields in Big Sandy, Montana, USA (48.036° N, 110.014° W; elevation 960 m). Big Sandy is located in Montana's Golden Triangle, important dryland wheat producing region in the Northern Great Plains and primarily composed of small grain and pulse crop fields (Miller et al. 2011; Pollnac et al. 2008). The 94-year mean annual precipitation for Big Sandy is 325 mm, and the mean annual maximum and minimum temperatures are 14.8⁰ C and -1.2⁰ C, respectively (Table A1). Big Sandy is underlain with a Telstad-Joplin loam (fine loamy, mixed, Aridic Argiboroll) with a pH of 7.9 - 8.2 (Miller et al., 2011).

Field Selection and Cropping History. Each year between 2013 and 2015, we conducted an on-farm study by selecting three conventional fields with spring wheat and three adjacent organic Kamut fields. Kamut is licensed (trade name: Kamut®) to be grown only in organic systems, thus there were no conventional fields of Kamut to be sampled. Conventional spring wheat fields were planted and harvested at the same times as organic Kamut fields. In 2013 and 2014 the variety grown in conventional spring wheat fields was Clearfield, a Jedd cultivar, and in 2015 the cultivar was Vida. These cultivars are known to be low to moderately susceptible to stem cutting (3-15% infested) by *C. cinctus* (Heo et al., 2016; Lanning et al., 2012). In 2014 and 2015, three

conventional winter wheat fields planted with the cultivar Yellowstone, and three organic winter wheat fields planted with spelt wheat (*Triticum aestivum* subsp. *spelta* L.) were selected. These winter wheat cultivars are moderately susceptible (~20%) to *C. cinctus* infestation (Berg et al., 2017; Wallace and McNeal 1966). All fields were located within 5 km of each other and their sizes ranged from 25 ha to 70 ha (Tables A2 and A3). Since 1989 organic fields have been certified by the Organic Crop Improvement Association International and by the United States Department of Agriculture organic certificate standards since 2003. All conventional (spring and winter wheat) fields follow a two-year winter wheat – chemical fallow rotation and all organic fields follow a multi-year continuous rotation of crops or cover crops (Tables A2 and A3). In conventional fields, the fallow phase was treated with glyphosate at rates ranging from 1,121 g ai ha⁻¹ to 1,682g ai ha⁻¹ five times a year between crop termination and seeding in the following fall. In organic fields, crop residues and cover crops were incorporated by chisel and/or disk tilling. In all fields, the producers were responsible for the rotation of crops or cover crops, frequency and intensity of tillage, timing of seeding, pesticide and fertilizer applications, and harvesting.

Wheat Sampling. In each field, stems were sampled at five locations evenly spaced along a 55 m transect that was randomly oriented in the field. All transects were at least 150 m from any field border. At each of the five locations along each transect, 30 cm of the wheat row was sampled. All winter wheat samples consisted of the roots and stems of post-harvest stubble, while spring wheat samples consisted of the whole plants taken just prior to harvest. In spring wheat and Kamut fields, sampling was conducted

during the first week of August in 2013, 2014, and 2015, and each winter wheat field was sampled during the first week of August 2014 and the first week of March 2016, after the 2015 harvest. All samples were stored in large plastic barrels and brought to the laboratory for dissection, where the number of wheat stems infested with *C. cinctus* was recorded. We also recorded presence of *C. cinctus* larvae, presence of frass (larval excrement), and the presence of fungal pathogens on larvae or pre-pupae. Number of *C. cinctus* parasitoids was recorded by noting the presence of either an intact cocoon or a vacated cocoon with an emergence hole. The only known parasitoids to attack *C. cinctus* in these wheat fields are *Bracon cephi* and *B. lissogaster*, but we did not specifically identify individuals of these two congeneric specialists in our study.

Cephus cinctus Oviposition Preference and Survival in Greenhouse Conditions

Insect Material. To assess preference of *C. cinctus* on wheat cultivars, adult female and male individuals were reared in laboratory conditions from field-collected wheat (Yellowstone winter wheat) stubble containing larvae in overwintering diapause. To facilitate the completion of larval diapause under laboratory conditions, stubble was maintained in cold storage (0–4 °C) for at least 3.5 to 4 months. The stubble was later placed in plastic boxes (70 cm x 35 cm x 20 cm) held at room temperature (22–27 °C) until the adult *C. cinctus* emerged. By opening the boxes daily, we collected the newly-emerged male and female *C. cinctus* adults and retained them in 2-liter Mason glass jars for 2-3 hours until they were used in the experiments. To provide adults with substrates to grasp and move around before experiments, 2-3 narrow wooden sticks were also placed inside each jar.

Plant Material. A total of 300 pots (13 cm x 13 cm x 13.5 cm) were filled with Montana State University greenhouse soil mix containing equal parts by volume of a sterilized silty loam, washed concrete sand, and Canadian sphagnum peat moss. Three spring wheat cultivars (Gunnison, Kamut, and Reeder) were planted twice a week from February 27th to April 1st 2015 to ensure availability of plants during the study period. Three plants of each cultivar were grown in separate pots under a 14-h photoperiod of natural sunlight and supplemental artificial light (GE Multi-Vapor Lamps model MVR1000/C/U, GE Lighting, General Electric Company, Cleveland, OH) at 22 °C and ambient humidity (20 to 40%). Pots were watered as needed and were fertilized, twice each week with Peters General Purpose Fertilizer (20-20-20; J.R. Peters, Allentown, PA) at 100 ppm in aqueous solution.

Choice Tests. In this choice test, the three spring wheat cultivars were simultaneously presented to *C. cinctus* in two combinations: (i) Kamut with Gunnison, a less preferred spring wheat cultivar, and (ii) Kamut with Reeder, a preferred spring wheat cultivar. We did not include a combination of Gunnison and Reeder for choice test because *C. cinctus* preferences for these two cultivars have already been assessed (Heo et al., 2014; Weaver et al., 2009).

Choice tests were conducted inside screened cages (91.4 cm x 66.7 cm x 91.4 cm with 530 µm mesh openings; BioQuip Products, Rancho Dominguez, CA, USA). We conducted a total of 33 trials over six weeks. Each cage contained a Kamut pot, paired with a pot of either Gunnison or Reeder. Since *C. cinctus* lays eggs on elongating stems (Buteler et al., 2009; Weiss and Morrill, 1992), all plants used in choice tests were at

Zadoks growth stage 32–33, when two to three nodes were detectable (Zadoks et al., 1974). Ten females and five males of *C. cinctus* were released in each cage to allow mating and oviposition for three days. Within three days, *C. cinctus* females had completed oviposition, and the pots were removed from cages and stems were dissected to count *C. cinctus* eggs.

No-choice Test. The no-choice test was conducted using the same cultivars as the choice test. The tests were conducted in transparent plastic tubes (767 ml volume, 4.5 cm diameter x 62 cm height with 5 small holes covered by mesh for aeration). The no-choice test had two parts; each conducted using a different cohort of wheat plants. The first part measured the rate of oviposition to determine if, given no choice, *C. cinctus* deposited differing numbers of eggs in the tested wheat cultivar. The second part measured survival of larvae by assessing if the larvae were able to cut stems after the wheat had fully ripened and senesced.

In the oviposition preference portion of the no-choice experiment, we conducted three trials of each cultivar twice a week between April 10th and May 24th, 2015 by releasing four females and two males of *C. cinctus* inside each plastic tube that contained a single plant of one of the wheat cultivars. Female *C. cinctus* were allowed to mate and oviposit over a three-day period. All wheat plants used in this test were at Zadoks growth stage 32–33 (Zadoks et al., 1974). After three days, each plant was removed from the tube, and stems were dissected to count *C. cinctus* eggs.

To assess *C. cinctus* survival in the second portion of the no-choice test, we conducted three trials between April 10th and May 24th, 2015. Wheat cultivars and their

growth stages, as well as the number of male and female *C. cinctus* used and duration of treatment, were the same as in the no-choice oviposition preference experiment.

However, after allowing *C. cinctus* to lay eggs for three days, plants remained in the greenhouse until maturity or until stems were cut by *C. cinctus* mature larvae.

Subsequently, we dissected stems following the same protocol as described in the field study section. When stems were left to mature, obligate cannibalism by *C. cinctus* larvae (Buteler et al., 2009, 2015), meant stems with multiple larvae could not be observed, therefore we recorded only presence or absence of *C. cinctus* larvae (Nansen et al., 2005b; Perez-Mendoza et al., 2006).

Data analysis

In the field study, we assessed the proportions of *C. cinctus* infested wheat stems, cut stems, and *C. cinctus* larvae with parasitoids by fitting logistic regression models in response to farming system, the seasonality of the wheat crop, and the interaction of the seasonality of the wheat crop and farming system. To determine if the models were confounded by spatial autocorrelation, we first examined the distribution of fields and the correlation of proportion of stems infested by *C. cinctus* based on distances among fields. Finding no correlation of *C. cinctus* infestation in relation to distance, we proceeded to fit logistic regression models. The factor levels of cropping systems were organic and conventional, and the factor levels of the seasonality of the wheat crop were spring wheat and winter wheat. The logistic regression models were fit as generalized linear models with a binomial distribution and logit link. However, when the response contained many zeros and the model was overdispersed, we used the quasi-binomial error distribution. To

assess significance of the predictor variables, we conducted analysis of variance (ANOVA) using likelihood ratio tests (Chi-squared). To evaluate differences among treatment levels, we conducted post-hoc ranked Tukey tests using the “multcomp” package (Hothorn et al., 2008) in R version 3.3.1 (R Development Core Team, 2016).

To model the number of *C. cinctus* eggs per stem in response to wheat cultivar, a generalized linear model with a Poisson distribution and log link was used, and significance of the predictor variable was assessed using likelihood ratio tests and post-hoc Tukey tests. The proportion of stems cut by *C. cinctus* obtained in the greenhouse choice, no-choice oviposition preference, and no-choice survival tests were modeled using logistic regression in response to wheat cultivar. ANOVA using a likelihood ratio test was conducted to determine if wheat cultivar accounted for variation in proportion of stems infested and post-hoc Tukey tests were used to compare variation among wheat cultivars. All statistical analyses were performed in R.

Results

Cephus cinctus Infestation, Cut Stems, and Parasitoids in Field Conditions

The number of stems infested by *C. cinctus* varied between the seasonality of the wheat crop and between conventional and organic farming systems (Table 2.1; the seasonality of the wheat crop $\times$ farming system, χ^2 (2, 29) = 20962, $p < 0.001$). In the three years of samples collected, less than 0.1% (± 0.1 SE) of stems were infested by *C. cinctus* in organic Kamut fields and the largest proportion of infested stems occurred in conventional winter wheat fields ($37\% \pm 1.1$ SE; Fig. 2.1a and Table 2.1). In conventional

spring wheat fields, 4% (± 1.0 SE) of stems were infested by *C. cinctus* and in organic winter wheat fields 20% (± 1.3 SE) of stems were infested by *C. cinctus* (Fig. 2.1a and Table 2.1).

Table 2.1. Number of stems infested with *Cephus cinctus*, *C. cinctus* infested stems that had parasitoids, stems cut by *C. cinctus*, and total number of stems observed among the different seasonality of the wheat grown under no-till conventional and tilled organic farming systems in Big Sandy, Montana between 2013 and 2015.

Cultivar*	Farming system	Infested stems	Parasitoids	Cut stems	Total stems observed
Spring wheat	Conventional	50	18	17	1135
	Organic	1	0	0	850
Winter wheat	Conventional	684	37	359	1835
	Organic	195	54	48	969

* Spring wheat cultivars: Jedd and Vida in conventional fields; Kamut in organic fields. Winter wheat cultivars: Yellowstone in conventional fields; spelt in organic fields.

The incidence of cut wheat stems by *C. cinctus* recorded in field conditions jointly varied among spring wheat and winter wheat cultivars and by farming system (Fig. 2.1b; the seasonality of the wheat crop $\times$ farming system, χ^2 (3, 470) = 493, $p < 0.001$). While no stems were cut by *C. cinctus* in organic Kamut fields (Fig. 2.1b), 1.5% (± 0.35 SE) of the stems were cut by *C. cinctus* in conventional spring wheat fields (Fig. 2.1b and Table 2.1) and the greatest incidence of stems cut by *C. cinctus* was recorded in conventional winter wheat (Table 2.1 and Fig. 2.1b) where 20% (± 0.93 SE) of stems were cut by *C. cinctus*. In contrast, in organic winter wheat fields only 5% (± 0.70 SE) of stems were cut by *C. cinctus* (Fig. 2.1b).

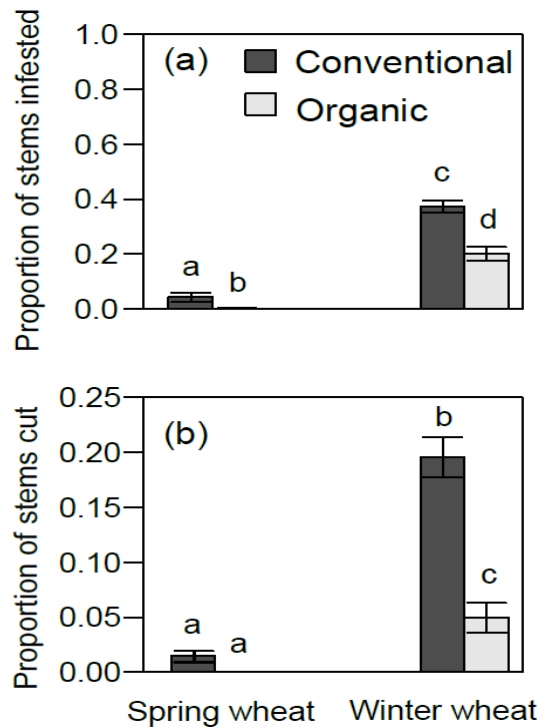


Figure 2.1. Proportion of (a) wheat stems infested with *Cephus cinctus*, and (b) wheat stems cut by the *C. cinctus* in response to the seasonality of the wheat crop (spring wheat and winter wheat) and farming system (conventional and organic). Error bars indicate the standard error; letters indicate significant differences among factor levels ($P < 0.001$ in all cases). Spring wheat cultivars in conventional fields were Jedd and Vida and in organic fields were Kamut. Winter wheat cultivar in conventional fields was Yellowstone and in organic fields was spelt.

The proportion of stems infested by *C. cinctus* sampled from winter wheat fields that had parasitoids differed between conventional and organic farming systems (χ^2 (1, $N=877$) = 265, $p < 0.001$). In conventional fields, only 5% (± 0.01 SE) of the infested stems were parasitized while 27% (± 0.03 SE) of the infested stems in organic winter wheat fields were parasitized (Table 2.1). Of the 50 stems infested by *C. cinctus* in conventional spring wheat fields, 36% (± 0.07 SE) had parasitoids present, which did not differ from organic winter wheat (pairwise, $z = -1.22$, $p = 0.56$; Table 2.1) but it was larger

than the proportion of parasitized stems sampled in conventional winter wheat (pairwise, $z = -6.7$, $p < 0.001$, Table 2.1). There was no difference in the number of *C. cinctus* that had visible fungal hyphae in response to farming system; 5% (± 0.02) of the *C. cinctus* larvae had hyphae in both the conventional and organic winter wheat fields [χ^2 (1, $N=877$) = 0.004, $p=0.8$].

Cephus cinctus Oviposition Preference and Survival in Greenhouse Conditions

When exposed to three different cultivars simultaneously in a choice test, the number of eggs deposited differed among the cultivars (Fig. 2.2; χ^2 (2, 424) = 248, $p < 0.001$). *Cephus cinctus* had the least preference for Kamut (Fig. 2) as this wheat cultivar had the fewest number of eggs per stem (0.13 eggs $\pm$ 0.05 SE). On Gunnison, an average 0.43 eggs per stem (± 0.12 SE) were deposited, and Reeder had the greatest number of eggs at 1.61 per stem (± 0.4 SE).

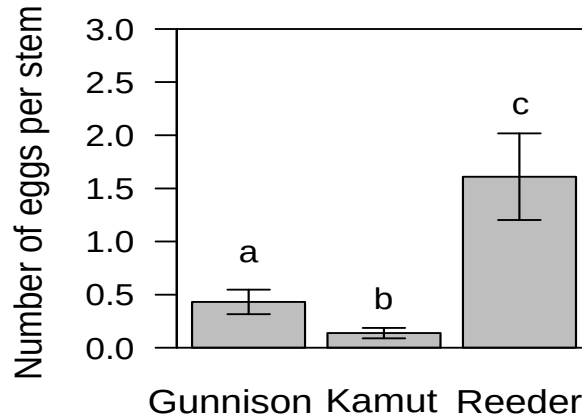


Figure 2.2. Number of *Cephus cinctus* eggs deposited per stem on wheat cultivars in choice tests performed under greenhouse conditions. Error bars represent the standard error; letters indicate differences among wheat cultivars ($P < 0.001$).

When *C. cinctus* was exposed to only a single wheat cultivar, in a no-choice test, the number of eggs deposited in a stem varied among cultivars (Fig. 2.3; χ^2 (2, $N=173$) = 164, $p < 0.001$). The number of *C. cinctus* eggs in Kamut was significantly lower than in the other cultivars (mean = 0.68 ± 0.25 SE; $p < 0.001$), but the number of eggs deposited in Gunnison and Reeder did not differ (mean = 3.6 ± 1.2 SE, and mean = 3.4 ± 1 SE, respectively, $p = 0.48$; Fig. 2.3a).

In no-choice tests, wheat stem cuts, an estimate of *C. cinctus* survival, differed among cultivars (Fig. 2.3b; χ^2 (2, $N=132$) = 132, $p < 0.001$). Kamut had the smallest proportion of wheat stems cut by *C. cinctus* ($6\% \pm 4.0$) compared with Gunnison ($34\% \pm 6.9$) or Reeder ($38\% \pm 6.9$). There was no difference in the number of stems of Gunnison or Reeder that were cut by *C. cinctus* in no-choice tests ($p = 0.70$; Fig. 2.3b).

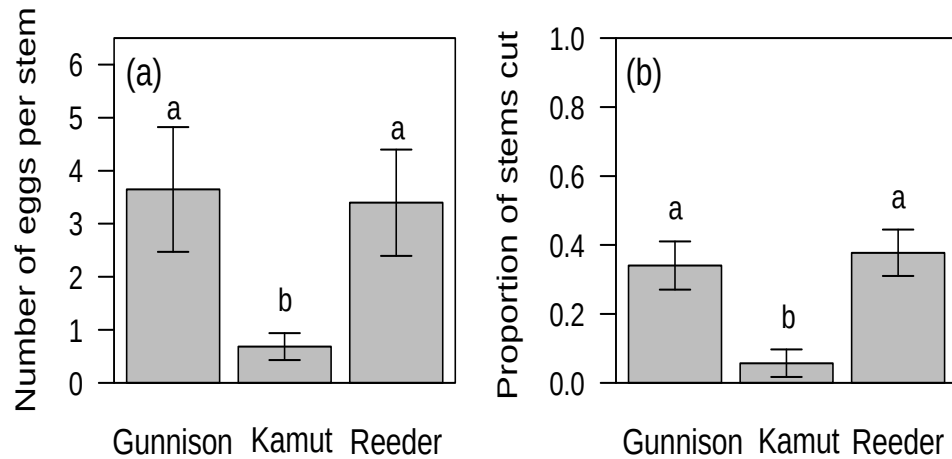


Figure 2.3. (a) The number of *Cephus cinctus* eggs deposited in different cultivars when exposed to only one cultivar at a time. (b) The proportion of stems cut by the *C. cinctus* on three cultivars of wheat when exposed to one cultivar at a time. Error bars represent the standard error; letters indicate differences among wheat cultivars ($P < 0.001$ in all cases).

Discussion

Cephus cinctus Infestation, Cut Stems, and Parasitoids in Field Conditions

In this study, the damage to wheat by *C. cinctus* larvae and the presence of parasitoids that killed *C. cinctus* larvae varied in response to the seasonality (spring or winter wheat cultivars) of the wheat crop and farming system. Spring wheat was observed to have lower infestation of *C. cinctus*, compared to winter wheat, and conventional winter wheat had a greater proportion of stems infested than organic winter wheat, which had more specialist larval parasitoids of *C. cinctus*. To our knowledge this is the first study to confirm that Kamut was less preferred by adult *C. cinctus*. This study highlights the interaction of different farming management systems and multiple trophic levels that include wheat cultivars, *C. cinctus*, and the insect specialists that parasitize and

kill *C. cinctus* larvae.

In our study, winter wheat in conventional fields had the highest rates of infestation and proportion of wheat stems cut by the *C. cinctus*, which partially reflects a preference for the larger and more succulent stems of winter wheat (Buteler and Weaver, 2012; Morrill and Kushnak, 1996,1999). The greater *C. cinctus* injury in winter wheat relative to spring wheat could also reflect climate warming in the Northern Great Plains, causing a greater phenological synchrony between winter wheat and *C. cinctus* (Lanning et al., 2010). Winter wheat seeds are sown in October (before winter starts) and so the post winter stems are mature enough in late-May when the majority of *C. cinctus* adult emerge. However, the spring wheat cultivars are seeded in April and May and do not reach the infestable stage of stem elongation until after the wheat stem sawfly adult flight has begun. This reduces numbers that might infest spring wheat and adults foraging in fields prior to stem elongation must move to other host plants, which are typically winter wheat. Since winter wheat yields more than spring wheat (McVay et al., 2010; Montana Agricultural Statistics, 2016), this phenological shift of *C. cinctus* could have major implications on the economic losses associated with winter wheat damage, as well as to the potential risk of *C. cinctus* outbreaks in the face of climate change (Lesieur et al., 2016).

The greater incidence and number of stems cut by *C. cinctus* in conventional winter wheat can be partially attributed to the amount of undamaged and unburied wheat stubble left in fields compared to organic systems (Beres et al., 2011a; Morrill et al., 1993). Although tillage is considered detrimental to *C. cinctus* parasitoids (Runyon et al., 2002; Weaver et al., 2004), our results did not support this as we observed a greater

number of parasitoids in tilled organic winter wheat compared to no till conventional winter wheat fields. The greater incidence of parasitoids in organic winter wheat fields was associated with a lower incidence of stems cut by *C. cinctus*, thereby reducing crop injury. Greater weed abundance and diversity as well as crop diversification in organic fields might have provided more food for parasitoids, ultimately reducing *C. cinctus* incidence (Altieri, 1999; Buteler et al., 2008; Morrill et al., 1993; Weaver et al., 2004). The greater weed diversity in organic fields in a landscape that is dominated by cultivated croplands (Adhikari S et al., unpublished) could provide critical refuge and food for parasitoids which ultimately enhances the biological control of pests like *C. cinctus* (Landis, 2017; Landis et al., 2000, but see Winqvist et al., 2011). Hence, in the highly simplified agricultural landscapes that dominate the driest sections of the Northern Great Plains, diversified farming system may provide ecosystem services that enhance beneficial insects like parasitoids and strengthen pest suppression (Crowder et al., 2010; Landis et al., 2000; Tschumi et al., 2016).

Beneficial insect communities that suppress pests could also be enhanced by conserving semi-natural habitat patches, or by increasing habitat and food resources through supplemental flowering plants strips. For example, plant species such as *Medicago sativa* L., *Heterotheca villosa* (Pursh) Shinnars, *Achillea millefolium* L., and *Solidago mollis* Bartlett observed in the semi-natural habitats of our study area (Adhikari S et al., unpublished), could be the potential food resources for parasitoids, but understanding of the extent to which these habitats contribute floral and nesting resources to beneficial insects is lacking. In addition, the level of *C. cinctus* infestation in wheat may also depend on other alternative host grasses such as *Bromus tectorum* (Keren et al.,

2015) present in crop fields or in the semi-natural habitats. Hence, more studies are needed on how the effects of landscape composition and farming system influence *C. cinctus* infestation and its parasitism, especially in the face of climate change.

A main limitation of the field research was that Kamut is licensed only to be planted in organic systems, and was therefore not used in conventional systems that used herbicides and fungicides. In our field observations, Kamut had less infestation and a lower number of stems cut compared to the other wheat cultivars grown in conventional fields. As it is not grown in conventional fields, we could not compare Kamut in the field conditions between two farming systems. The wheat cultivar planted in conventional spring fields of 2013 and 2014 was Jedd (a high yielding hollow stemmed Clearfield spring wheat) and in 2015 was Vida (a semi-dwarf, hollow-stemmed hard red spring wheat), and neither is considered resistant to *C. cinctus*. To overcome the limitation, we conducted choice and no-choice experiments in greenhouse settings.

Cephus cinctus Oviposition Preference and Survival in Greenhouse Conditions

Cephus cinctus oviposition preference was known to be low for Gunnison and high for Reeder (Heo et al., 2014; Weaver et al., 2009), but was unknown for Kamut. When given a choice between Kamut and either Gunnison or Reeder, *C. cinctus* did not oviposit in Kamut stems. Even in the few instances where *C. cinctus* laid eggs in Kamut, survival and development into overwintering larvae was negligible. Hence, the number of cut stems in Kamut was very low (6%), whereas more than one third of total stems were cut in both Gunnison and Reeder, supporting farmers' observations and our field trial results of low infestation rates of Kamut in organic fields.

In the no-choice test, when *C. cinctus* was exposed to only one wheat cultivar, Kamut had the lowest number of eggs. Interestingly, there was no difference in oviposition between Gunnison and Reeder, despite field records that indicated a lower preference for Gunnison (Heo et al., 2014, 2016). The same distinction was observed for comparisons of Reeder and Conan, another less preferred cultivar (Weaver et al., 2009). While this study did not evaluate the eco-physiological mechanisms responsible for the low *C. cinctus* oviposition in Kamut, it is potentially due to the amounts of certain volatile compounds, as studies have shown that semiochemicals play a key role in the location of host plants by female *C. cinctus* (Piesik et al., 2008; Varella et al., 2017; Weaver et al., 2009). It is also possible that Kamut's thick and pith-filled stems, as observed in other cultivars (Kong et al., 2013; Wallace and McNeal, 1966) or the interaction of chemical and morphological characteristics played a role in limiting *C. cinctus* oviposition behavior in Kamut.

Conclusion

Kamut, a tall wheat cultivar with large grain size, demonstrated greater resistance to *C. cinctus* than the other wheat cultivars commonly used in Montana small grain production. Our field and greenhouse trials suggest that Kamut is more resilient in the face of pest pressure, particularly in organically managed systems and indicate that future studies should explore the semiochemicals, stem structure, and genotypes of Kamut which could provide specific mechanisms of resistance to *C. cinctus* (Grausgruber et al., 2005; Quinn, 1999; Stallknecht et al., 1996). For example, solidness, caused by the wheat genotype, might have strongly affected *C. cinctus* infestation and its parasitism in

Kamut (Rand et al., 2012; Wu et al., 2013). Similarly, as different geographical and microclimatic conditions may also provide different environment (favorable or unfavorable) for *C. cinctus* populations (Lesieur et al., 2016; Lestina et al., 2016), data is required for *C. cinctus* from other areas where Kamut is grown. Our study provides evidence that diversified organic farming systems, with the likely provisioning of more food resources through the variety of weeds and crop diversification, supported more parasitoids and reduced *C. cinctus* infestation. Organic production does encompass the components identified for *C. cinctus* integrated pest management in wheat (Beres et al., 2011a), but other cultural methods including trap crops, crop rotations, habitat management, cover crops, and reduced fallow fields can also be used in the field to minimize *C. cinctus* infestation in both conventional and organic wheat production (Landis et al., 2000; Morrill et al., 2001; Runyon et al., 2002; Weaver et al., 2004).

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CHAPTER THREE

DRYLAND FARMING SYSTEMS AND LANDSCAPE COMPOSITION INFLUENCE
FORB AND BEE COMMUNITIESIntroduction

Bees (Hymenoptera: Apoidea, Apiformes) provide billions of dollars of pollination services to valuable crops across the globe (Kleijn et al., 2015). However, a suite of anthropogenic stressors, including agricultural intensifications, reduced regional floral resources, landscape simplification, pesticide toxicity, and exposure to parasites and pathogens are driving the declines in bee abundance and diversity (Klein et al. 2007, Potts et al., 2010, 2016; Goulson et al., 2015; Koh et al. 2015, Landis 2017). These reductions in bee abundance and diversity (Potts et al., 2010; Garibaldi et al., 2011), in turn, influence the bee-flower networks (Burkle et al., 2013), negatively impacting ecosystem functioning and food security (Vanbergen, 2013).

Compared to conventional farming, organic farming follows more frequent crop rotation, avoids synthetic herbicides, and results in higher weed abundance and diversity (Pollnac et al., 2008; Romero et al. 2008; Benaragama et al., 2016 a, b). Via plant-mediated bottom-up effects (Scherber et al., 2010; Han et al., 2015), the changes in weed abundance and composition influence beneficial insect communities including bees (Nicholls and Altieri, 2013; Smith et al., 2008) and pollination networks (Pocock and Memmott, 2012; Power and Stout, 2011). Previous studies conducted in the Northern Great Plains (NGP), a key agricultural region of conventional and organic small grain,

pulse, and oilseed crop productions (Johnston et al., 2002; Miller et al., 2002, 2011), have shown higher weed abundance and diversity in organic systems compared to conventional ones (Benaragama et al., 2016 a, b; Pollnac et al., 2008), but the extent to which these differences in weed communities are associated with a greater abundance and diversity of pollinators and more complex bee-flower networks is largely unknown.

Studies conducted in diversified landscapes have shown positive effects of percent natural habitat or landscape heterogeneity, on farmland biodiversity (Tews et al., 2004; Fahrig et al., 2011), including plants (Rader et al., 2014), bee pollinators (Kennedy et al., 2013; Boscolo et al., 2017; Senapathi et al., 2017), and pollination networks (Ferreira et al., 2013; Moreira et al., 2015), but little knowledge on these effects exist in extremely simplified landscapes in dryland sections of the NGP. Mass-flowering crops and forbs present within crop fields provide food resources to beneficial insects during a short time interval (Morandin and Winston, 2006), but surrounding natural habitats (uncultivated habitats) provide greater season-long food resources, nesting substrate, and refugia for longer periods (Landis et al., 2005; Danner et al., 2016). Hence, reduction in percentage natural habitat also reduces pollination services (Kremen et al., 2004; Morandin and Winston, 2006; Deguines et al., 2014) and pest control (Rusch et al., 2016) in the crop fields.

Farming systems and percent natural habitat in agricultural landscapes influence bee communities (Holzschuh et al., 2007; Winqvist et al., 2012) and their pollination services (Nicholson et al., 2017), but the effects depend on landscape scale and complexity (Steffan-Dewenter et al., 2002; Carrié et al., 2017). For instance, Holzschuh et al. (2007) found that when compared with conventional fields, the effect of organic

farming of cereals in Germany on bee diversity was stronger in less complex landscapes that had limited natural habitats than in more complex landscapes. Similarly, Nicholson et al. (2017), in a study of highbush blueberry farms in Vermont, USA, found that more intensively managed farming further worsens the negative effects of limited natural habitat on bees and their pollination services. However, in contrast to these previous studies that were conducted in relatively more diversified agroecosystems, understanding about the interacting effects of farming system and percent natural habitat on bee communities is lacking for the drylands of the NGP, a highly simplified yet important agricultural region

The effects of percent natural habitat on bee communities may depend on bee sizes (Benjamin et al., 2014; Torné-Noguera et al., 2014; Forrest et al., 2015). Due to their short distance flight capacities, the foraging ranges of small-bodied bees are limited (radius of less than 500m from their nesting habitat) (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007). This limitation may make small-bodied bees more vulnerable to the impact of landscape simplification (Jauker et al., 2013; Benjamin et al., 2014) compared to large-bodied bees that have larger flight capacities and foraging ranges (Westphal et al., 2006; Greenleaf et al., 2007). Theoretically, an agricultural landscape that has limited natural habitat should have stronger negative effects on small-bodied bees than on large-bodied bees (De Palma et al., 2015, but see Rader et al., 2014; Forrest et al., 2015). Hence, in the extremely simplified landscapes of the NGP, we expect lower abundances of small-bodied bees compared to abundances of large-bodied bees, but there is currently no empirical evidence testing this theoretical expectation.

To our knowledge, no previous study has formally assessed the joint impact of dryland farming systems and percent natural habitat on forb and bee communities, and bee-flower networks in highly simplified agricultural landscapes. Over three years, we conducted an on-farm study in the NGP near Big Sandy, MT, USA to test the influence of conventional vs. organic farming on forb (i.e., broad-leaf weeds and volunteer broadleaf forbs) and bee communities. We also assessed how the amount of natural habitat within various distances from crop fields might mediate the effects of farming system on the abundances of small-bodied and large-bodied bees. We hypothesized that: (i) because of the higher crop rotation diversity and avoidance of synthetic herbicides, organically-managed tilled wheat fields (hereafter, organic system) would have greater forb flower density and species richness than chemically-managed no-till wheat fields (hereafter, conventional system); (ii) greater floral density and species richness in organic fields would be positively correlated with greater abundance and diversity of bees, and (iii) the percentage natural habitat would be positively associated with the abundances of both small- and large-bodied bees, but the positive effects of percent natural habitat on bees would be stronger in conventional fields than in organic fields.

Materials and Methods

Site Description and Cropping History

We conducted our study on conventional and organic wheat farms near Sandy, Montana, USA (48.036°N, 110.014°W; elevation 960m). Big Sandy is located in Montana's Golden Triangle, an important dryland wheat producing region in the NGP,

and primarily composed of small grain producing agricultural lands (Miller et al., 2011; Pollnac et al., 2008). The 94-year mean annual precipitation for Big Sandy is 325 mm, and the mean annual maximum and minimum temperatures are 14.8°C and -1.2°C, respectively (Table A1). Big Sandy is underlain with a Telstad-Joplin loam (fine loamy, mixed, Aridic Argiboroll) with a pH of 7.9 - 8.2 (Miller et al., 2011).

In each year from 2013 to 2015, we selected three conventionally-managed no-till spring wheat (*Triticum aestivum* L.: Clearfield® cultivar of ‘Jedd’ in 2013 and 2014, and ‘Vida’ cultivar in 2015) fields and three adjacent organically-managed tilled “Kamut” wheat (*Triticum turgidum*, ssp. *turanicum* McKey) fields. Field sizes ranged from 25 to 70 ha, and all organic fields were certified by the Organic Crop Improvement Association International since 1989 and by the United States Department of Agriculture organic certificate standards since 2003 (Seth Goodman, *Pers. Comm*). Conventional fields followed a spring wheat and chemical fallow rotation, and organic fields followed a multi-year continuous rotation of crops or cover crops (Table A2). In conventional fields, the fallow phase was treated with multiple applications of glyphosate (*Roundup*®) at rates ranging from 1,121 g active ingredient ha⁻¹ to 1,682 g active ingredient ha⁻¹ between crop termination and seeding. In organic fields, crop residues and cover crops were incorporated by chisel and/or disk tilling. Also, disk plow was used as needed to manage forbs in the organic fields. Specific agronomic management practices were at the grower’s discretion (Table A3).

Forb and Bee Community Sampling

Each year, we established a randomly oriented 55 m transect located at least 150 m from any field border within each field. At each of three randomly selected points along this main transect, we established three perpendicular 25 m sub-transects. On three dates (June, July, and August) spanning the growing season in each year, we quantified forb communities by visually estimating percent cover of each forb species within a 0.5 × 1 m quadrat placed perpendicular to each sub-transect at every 1m interval. The percent cover data was used to calculate forb richness, forb species evenness, and forb community composition. Additionally, to estimate forb flower density, we also counted the number of flowers per individual forb plant within each quadrat.

We assessed bee communities using plastic pan traps (250 ml), one of the most efficient methods of sampling pollinator communities (Westphal et al., 2008), on each of the three times that we sampled forb communities in each year. Having a very short growing season in our study area and also due to logistical constraints, we assume that three sampling dates are enough to cover temporal variability in bee communities. To sample bee groups that are attracted to different colors, we used blue, yellow, and white, as these colors are effective to passively capture diverse bee groups (Lebuhn et al., 2013). We alternated traps of each color, placing them 5 m apart at crop canopy height along the main transects described above (N = 12 total pan traps per transect on a sampling day). After 24 hours in the field, bees were collected from traps and stored in a freezer until their further processing.

Bees were identified to family following Goulet and Huber (1993); to genus following (Michener et al., 1994); and, when possible, to species following Ascher and

Pickering (2014), dichotomous keys, and identification guides. Approximately 78% (85 of 109 bee taxa) of total bee taxa were identified to species and the rest identified to subgenus (mainly *Lasioglossum* (*Dialictus*) spp.) or morpho-species. All bee taxa are referred to as “bee species” throughout the analysis. We preserved voucher specimens in the Montana Entomological Collection at Montana State University, Bozeman, MT. Of the bees collected in our samples, the vast majority were “wild” (i.e., non-managed) bees. Of the managed species, we assume that all *Apis mellifera* were from managed colonies and all of the *Bombus impatiens* originated from experimental colonies involved in another study (Adhikari et al., unpublished). Finally, using digital calipers, we measured intertegular distance, a standard proxy of body size, foraging distance (Cane, 1987; Greenleaf et al., 2007), and proboscis length (Cariveau et al. 2016) of 10 individuals of each species and used the average value for further analysis (e.g., comparison between conventional and organic systems).

Bee-Flower Networks

To assess the impact of farming system on bee-forb interactions, we also walked for 20 minutes along each of the 25m sub-transects used above to record the identity and frequency of bee-flower interactions. We collected all flower visiting bees using a hand net to determine their taxonomic identities. In the rare cases (~10) when it was not possible to capture the bee, we identified it based on morphology (body size, color, wings, abdomen, etc.) and recorded it as a functional group. We performed these observations three times (June-August) in each field in each year (54 total hours of observations) between 08:00 and 16:25 under sunny, warm (mean temperature: 29 ± 0.3

°C, $n = 231$), and calm (mean wind speed: $5 \pm 0.2 \text{ m s}^{-1}$, $n = 231$) conditions. Voucher bee specimens collected during observations were stored in freezer, processed, and identified, as above. However, due to no or extremely few bee-forb interactions in conventional fields, we did not perform any quantitative analysis to test the effects of farming system on network characteristics.

Data Analysis for Forb and Bee Communities

For each field, we calculated forb flower density, forb species richness, and forb evenness as well as bee abundance, bee species richness, and bee species evenness. We calculated species richness as the total number of species present. Species evenness was calculated using Pielou's evenness index (Pielou, 1966; Whittaker, 1972)

For all our analysis, we first created a correlation matrix among all response variables for respective questions, to determine whether any of them were linearly related. If any response variables were strongly correlated ($r > 0.6$), we selected the most representative ones and included with other uncorrelated response variables in Multivariate Analysis of Variance (MANOVA).

To test the effect of farming system on forb flower density, forb species richness, bee abundance, and bee species richness, we used generalized linear mixed-effects models with Poisson distribution. To meet the assumptions of normality and homogeneity of variance, the variables were log-transformed as required. Also, to test the effects of farming system on forb species evenness and bee species evenness, we used linear mixed-effect models. In all mixed-effect models, farming system was treated as a fixed effect while year and field were treated as random effects, with month nested within

field, and field nested in year. Given that there was no main effect of year on the metrics mentioned above, we pooled all three years in our analysis.

The effects of conventional and organic farming on forb and bee community composition were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) on a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957; McCune and Grace, 2002) and visualized with Non-metric Multidimensional Scaling (NMDS) ordination. Community dispersion (β -diversity) between conventional and organic farming systems was tested using the “betadisper” function. After the “adonis” test of PERMANOVA, for post-hoc tests, we used the “pairwise.perm.manova” function and reported false discovery rate (“fdr”) adjusted p-value (Benjamini and Hochberg, 1995; Hervé, 2017). Following significant PERMANOVAs, we used similarity percentage analysis (Clarke, 1993) or “simper” (Oksanen et al., 2016), to determine which species contributed the most to the observed dissimilarity in community composition between farming systems. Also, following significant PERMANOVAs between farming systems, to identify indicator species for both conventional and organic fields, we performed the indicator value analysis or “IndVal” (Dufrêne and Legendre, 1997; Cáceres and Legendre, 2009). Indicator species analysis identifies the key species in a particular site based on its relative abundance (specificity) and relative frequency (fidelity) (Bakker, 2008; Dufrêne and Legendre, 1997). Only species with P -value < 0.05 were considered as indicator species, by using permutation tests ($n_{\text{perm}} = 999$).

Percent Natural Habitat and its effects on
Small-and Large-bodied Bee Abundance

For each of the 18 fields sampled, we acquired cloud-free Landsat 8 images (30m × 30m resolution) from the United States Geological Survey and used ArcGIS 10.2.

Using ArcMap and V-LATE 2.0 beta (Vector-based Landscape Analysis Tools Extension), a Landscape Ecology ArcGIS extension, we classified the areas of patches within images and calculated the percent natural habitat (all uncultivated and undisturbed lands) within four concentric circles of 250 m, 500 m, 1000 m, and 2000 m radii from the center of each sampled field. Because small-bodied bees fly short distances and large-bodied bees fly further (Gathmann and Tschardt, 2002; Greenleaf et al., 2007), we chose the aforementioned radii to test for the spatial scales at which percent natural habitat influences bee abundance. Previous studies conducted to assess landscape effects on bees have also chosen similar radii (see, Steffan-Dewenter et al., 2002; Kremen et al., 2004; Holzschuh et al., 2006; Nicholson et al., 2017). We also used ground observation, Google Earth Pro, and USDA-National Agriculture Imagery Program to crosscheck the land use types.

To compare the proportion of natural habitat between conventional and organic fields within the specified circles, we utilized generalized linear mixed models- automatic differentiation model builder (“glmmADMB”), with beta distribution (see, Fournier et al., 2012 and Skaug et al. 2016). To evaluate the effects of percent natural habitat on large- and small-bodied bee abundances, following Benjamin et al. (2014), all sampled bees were divided into “large-bodied” (intertegular distance ≥ 2.5 mm) bees and “small-bodied” (intertegular distance < 2.5 mm) bees. To meet the assumptions of normality and

homogeneity of variance, large-bodied and small-bodied bee abundances were log-transformed. Using mixed-effects models, we tested the effect of percent natural habitat within 500 m, 1000 m, and 2000 m radii of each field on large- and small-bodied bee abundances. However, we could not include the 250 m radius because the majority of crop fields (14 out of 18 fields) had 0% natural habitat within this radius. To determine whether the effects of percent natural habitat on small- and large-bodied bees, tested in mixed effect models, were stronger in conventional fields compared to organic fields, we calculated marginal R^2 (variance explained by fixed factor alone) and conditional R^2 (variance explained by fixed and random factors) from mixed effect models (Johnson, 2014; Nakagawa and Schielzeth, 2013), using “MuMIn”.

All statistical analyses and graphics were conducted with R 3.2.4 (R Development Core Team, 2016). We used “lme4” (Bates et al., 2015), “nlme” (Pinheiro et al. 2016), “glmmADMB” (Fournier et al., 2012; Skaug et al. 2016), and “MuMIn” (Barton, 2017) packages for mixed-effect models, and “lsmeans” (Lenth, 2016) for multiple comparisons. Multivariate analyses, PERMANOVA post-hoc tests, and ordination graphics were conducted using “labdsv” (Roberts, 2016), “vegan” (Oksanen et al., 2017), and “RVAideMemoire” (Hervé, 2017) packages. We produced all other graphics using the “ggplot2” (Wickham, 2009) and ‘sciplot’ (Morales, 2017) packages.

Results

Forb Communities

Of the 38 forb species recorded over the 3-year period of our study, we observed 14 of them in the conventional fields and 37 in the organic fields (Table B1). Forb flower density was, on average, 3.9 times greater in organic fields than in conventional fields (Fig. 3.1A; $F = 16.8$; $df = 1, 16$; $P = 0.001$). Forb species richness was 3.5 times greater in organic fields than in conventional fields (Fig. 3.1B; $F = 44.3$; $df = 1, 16$; $P = <0.0001$). However, there was no effect of farming system on forb species evenness (Fig. 3.1C; $F = 0.69$; $df = 1, 16$; $P = 0.42$).

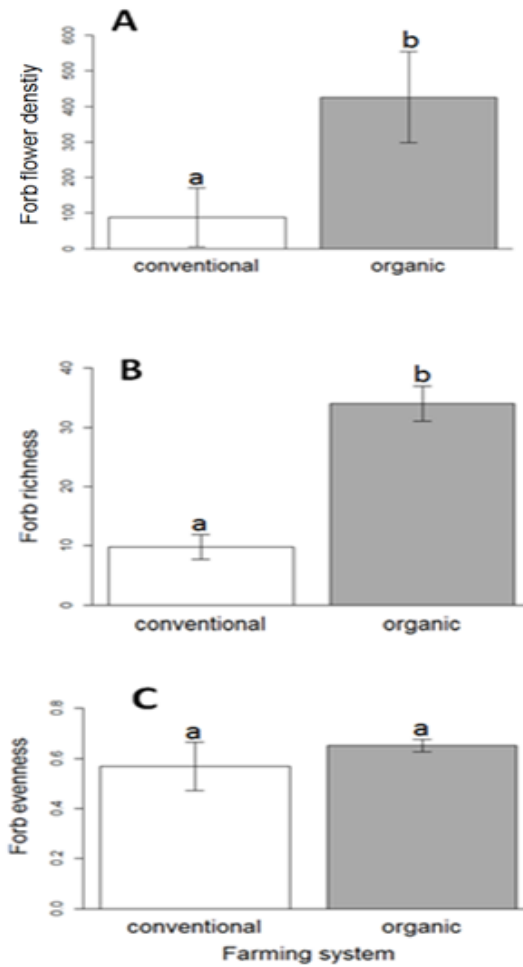


Figure 3.1. Effects of conventional and organic farming system on (A) forb flower density, (B) forb species richness, and (C) forb species evenness. Error bars represent the standard errors of the mean, while letters above bar diagrams indicate significant differences between systems ($P < 0.01$ in all cases, except evenness).

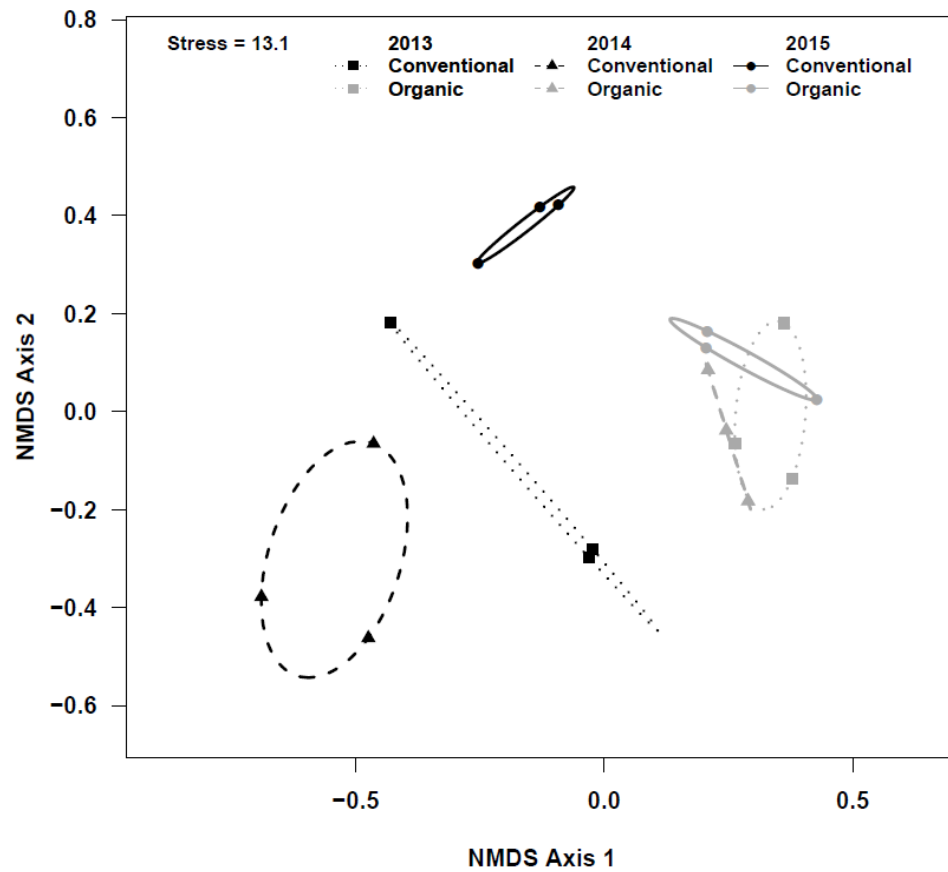


Figure 3.2. Non-metric multidimensional scaling (NMDS) ordination of weed forb communities observed in conventional and organic wheat fields. Dotted ellipses inscribe communities in 2013, dashed ellipses inscribe communities in 2014, and solid ellipses inscribe communities in 2015.

As hypothesized, forb community composition differed between conventional and organic fields (Fig. 3.2; pseudo- $F = 6.9$; $df = 1, 16$; $r^2 = 0.30$; $P = 0.001$). Forb community dispersion was greater across conventional fields than across organic fields ($F = 35.2$; $df = 1, 16$; $P = <0.0001$). There was no temporal shift observed in forb community composition (pseudo- $F = 0.41$; $df = 2, 51$; $r^2 = 0.02$; $P = 0.08$) through the growing season (June, July, and August) in either farming system. *Thlaspi arvense*, *Salsola kali*, *Carthamus tinctorius*, *Polygonum convolvulus*, *Pisum sativum*,

Chenopodium album, *Medicago sativa*, and *Amaranthus retroflexus* contributed 72% to the observed dissimilarity in forb community composition between the two farming systems; these species were more abundant on organic farms. Despite the differences in forb community composition between the two farming systems, indicator species analysis did not reveal any indicator forb species for either conventional or organic fields.

Bee Communities

We collected 8,710 bee specimens, representing 109 species taxa in 25 genera and five families, from pan traps (Table B2). The five most abundant bee taxa for both conventional and organic systems were *Lasioglossum (Dialictus)* spp., *Agapostemon texanus* (Cresson), *Eucera hamata* (Bradley), *Agapostemon femoratus* Crawford, and *Agapostemon virescens* (F.). Bee sizes (intertegular distances) ranged from 0.7 mm (*Perdita fallax* Cockerell) to 5.9 mm (*Bombus nevadensis* Cresson). About 81% of the bee taxa were ground nesting bees, representing 99.9% of the total specimens captured (Table B2). While approximately 79% of total bees were small-bodied bees (intertegular distance < 2.5 mm), bee species collected from organic fields ($2.35 \text{ mm} \pm 0.04 \text{ mm}$) were 5% larger ($F = 3.8$; $df = 1, 16$; $P = 0.07$) than the bee species collected from conventional fields ($2.25 \text{ mm} \pm 0.04 \text{ mm}$), though this result was not significant.

Surprisingly, we did not detect any differences in bee abundance, species richness, or evenness between conventional (158 ± 31 bees/sampling, 25 ± 2 species/sampling, and 0.85 ± 0.02 , respectively) and organic (165 ± 33 bees/sampling, 27 ± 3 species/sampling, and 0.80 ± 0.02 , respectively) systems ($F = 0.56$; $df = 1, 14$; $P = 0.47$, $F = 0.19$; $df = 1, 14$; $P = 0.67$, and $F = 3.55$; $df = 1, 14$; $P = 0.08$, respectively).

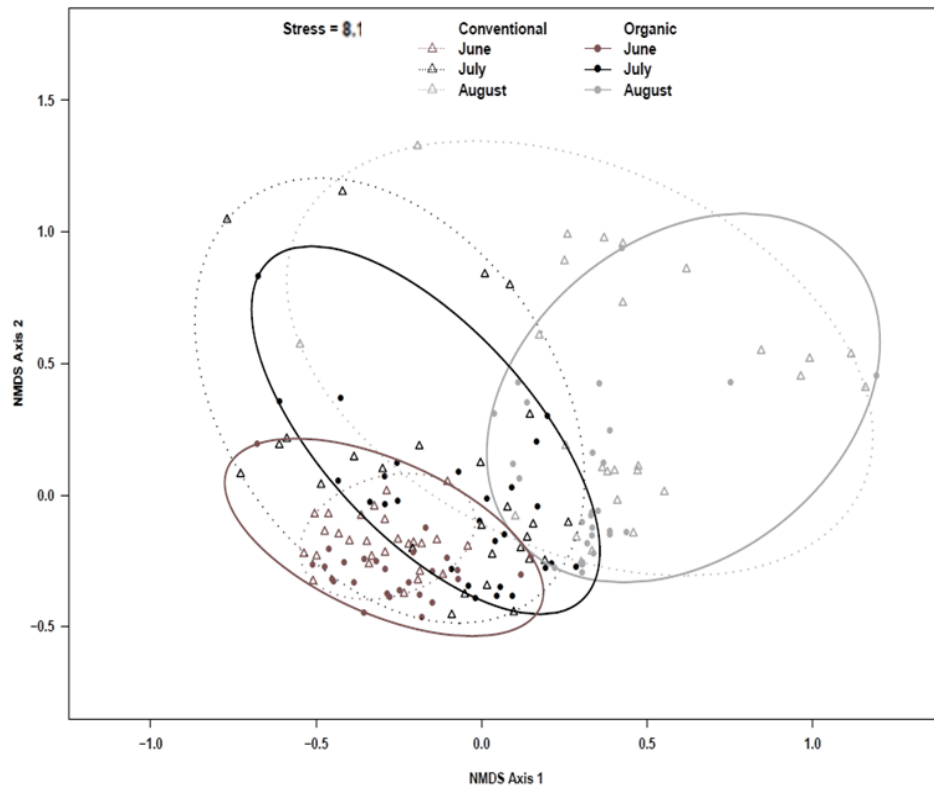


Figure 3.3. Non-metric multidimensional scaling (NMDS) ordination of bee communities observed across June, July and August in conventional and organic wheat fields. Due to the non-significant effects of year, values were pooled across three years (2013 -2015). Dotted ellipses inscribe communities in conventional fields and solid ellipses inscribe communities in organic fields.

Across the three years of sampling, we observed no differences in bee community composition between conventional and organic fields in June ($P = 0.18$) or July ($P = 0.49$). However, composition between the farming systems differed in August (Fig. 3.3; pseudo- $F = 10.7$; $df = 4, 156$; $r^2 = 0.21$; $P = 0.001$). In both farming systems, we observed a temporal shift in bee community composition (Fig. 3.3; pseudo- $F = 29.9$; $df = 2, 159$; $r^2 = 0.27$; $P = 0.001$) through the growing season, where each sampling month (June, July, and August) was different from each other ($P = 0.001$, for all pairwise combinations). *Lasioglossum* (*Dialictus*) *Melissodes agilis*, *Melissodes pallidisignata*, *Halictus ligatus*,

and *Melissodes lupina* contributed 75 % of the total observed dissimilarity in bee community composition between the two farming systems in August. Also, indicator species analysis revealed that *M. pallidesignata* was indicative of conventional systems, whereas *Andrena* sp.1 and *Anthidium porterae* Cockerell were indicative of organic systems (Table B3). Twenty bee species were indicative of bee communities in June, two species (*Anthophora occidentalis* Cresson and *Bombus fervidus* (F.)) were indicative in July, and four species (*Melissodes agilis* Cresson, *Melissodes coreopsis* Robertson, *Melissodes pallidesignata* Cockerell, and *Melissodes menuachus* (Cresson) were indicative in August (Table B3).

Bee-Flower Networks

Bee-forb networks were either absent or extremely simplified (i.e., single forb species visited by a single bee taxon) in conventional fields in all three years (Fig. B1). In contrast, because of greater forb flower density and diversity, bee-forb networks were more complex (i.e., more bee-forb interactions) in organic fields (Fig. B1).

Percent Natural Habitat and its effects on Small-and Large-bodied Bee Abundance

The landscape in which this study was embedded was highly dominated by croplands (84% of the total area within 2000m radii from each field), compared to a low proportion of natural habitat (12%within 2000m radii ; Fig. B2 and Table B4). Percent natural habitat within 500 m and 1000 m of the conventional fields was 3.7 times and 2 times greater (Fig. B2; $\chi^2 = 4.5$; df = 1; $P = 0.04$ and $\chi^2 = 10.6$; df = 1; $P = 0.001$, respectively) than those of the organic fields, but no difference within 2000 m ($\chi^2 = 3.04$;

df = 1; $P = 0.08$). Percent natural habitat did not affect small-bodied bee abundance in either farming system in any of the analyzed distances (Fig. 3.4A-C; 500 m: $F = 0.27$; df = 1, 16; $P = 0.61$, 1000 m: $F = 0.21$; df = 1, 16; $P = 0.65$, and 2000 m: $F = 2.23$; df = 1, 16; $P = 0.15$). Similarly, we found no effect of percent natural habitat on large-bodied bee abundance in either farming system in the 500 m circle (Fig. 3.4D; $F = 0.15$; df = 1, 16; $P = 0.7$) or in 1000 m (Fig. 3.4E; $F = 2.5$; df = 1, 16; $P = 0.14$). However, percent natural habitat within 2000 m positively affected large-bodied bee abundance (Fig. 3.4F; $F = 11$; df = 1, 16; $P = 0.004$) in both conventional and organic fields; but the effects of natural habitat on large-bodied bee abundance were not stronger in conventional (conditional $R^2 = 0.93$, marginal $R^2 = 0.46$), compared to organic (conditional $R^2 = 0.93$, marginal $R^2 = 0.41$) fields.

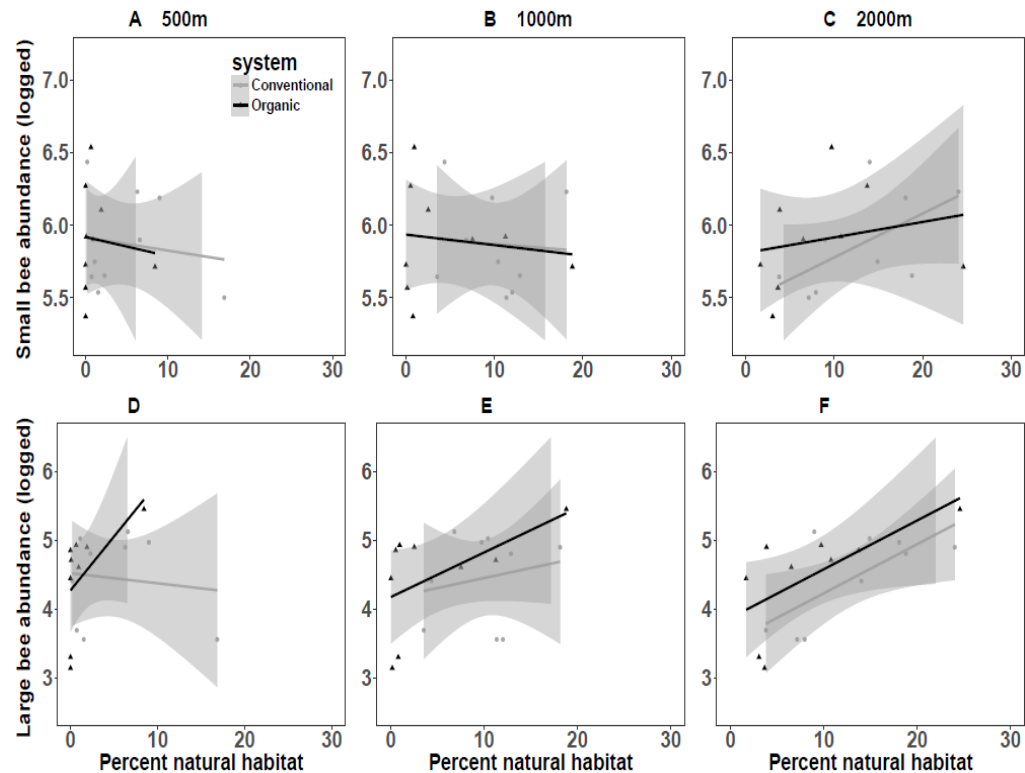


Figure 3.4 (A-F): Relationship between small bee (<2.5 mm ITD) and large bee (≥ 2.5 mm ITD) abundance and percent natural habitat within the circles of 500 m, 1000 m, and 2000 m. Circles were drawn from the centers of each conventional and organic wheat field, where the transects were established to trap bees. Shade bands around lines are the 95% confidence interval.

Discussion

We observed greater forb flower density and species richness in organic fields compared to conventional fields, but there were no differences in the abundance, species richness, species evenness, or community composition of bees between two systems. This agricultural landscape in the NGP has very limited natural habitats; in both farming systems, percent natural habitat within 2000 m did not influence small-bodied bees but positively affected large-bodied bee abundance. Finally, compared with organic fields, we recorded few to no bee-forb interactions in conventional fields. Together, these results

indicate that adopting organic farming in the highly simplified agricultural landscapes, such as in the drylands of the NGP, helps enhancing within-field forb communities and bee-flower interactions but the current extent of organic fields is not enough to support more bees, than on the conventional fields. Yet, surprisingly high bee diversity in the resource-poor landscape (i.e. very limited natural habitats and within-field floral resources) of the NGP has few ecological implications; (i) how do bees sustain their population in these landscapes, and (ii) are these very simple bee-flower networks stable against the future disturbances? Our findings also have management implications that, in addition to organic farming, landscape diversification (by increasing natural habitats, cover crops, and crop rotations), helps to support and conserve bee populations and bee-flower networks.

Forb Communities

Consistent with Pollnac et al. (2008), our results showed that, compared to conventional fields, organic fields in the NGP had greater forb flower density and species richness, suggesting to provide more food resources to beneficial insects (Vaughan et al., 2004; Bretagnolle and Gaba, 2015), influence forb-insect interactions, and support biodiversity and ecosystem services (DiTommaso et al., 2016; Jordan and Vatovec, 2004). These differences in forb communities between conventional and organic fields could result from the different ecological filters imposed by the two farming systems (Funk et al., 2008; Smith et al., 2015). Specifically, the continuous use of selective herbicides, such as auxin-regulating herbicides, in conventional small grain fields in the NGP would exclude dicotyledonous species (Grossmann, 2009), ultimately decreasing

forb floral resources available to pollinator communities (Nicholls and Altieri, 2013). We found greater variability in forb community composition among years in conventional fields compared with those in organic fields, which is consistent with the study, performed by Menalled et al. (2001) in the annual row cropping systems in Michigan. This higher year-to-year variation in forb community composition (i.e., beta-diversity) in our conventional fields may suggest inconsistencies or inefficiencies in weed control tactics among different conventional growers across years.

Bee Communities

Several possibilities exist to explain the lack of difference in bee abundance, richness, and composition between our conventional and organic fields, though previous studies have demonstrated that organic farming supports greater floral and bee diversity when compared to conventional (Hole et al., 2005; Holzschuh et al., 2007; Krauss et al., 2011). First, it is possible that plant species are more strongly affected by farm management system at the field- or farm-scale, but more mobile species like bees respond at a larger landscape scale (Gabriel et al. 2010). Thus, farming system may not have as strong an effect on bees as we expected. Second, we see a possibility that because there are so few flowers in conventional fields, the pan traps may have served as ‘magnets’ for bees that would not normally have flown over those fields, and perhaps individuals from the same pool of bees were lured equally to both conventional and organic fields. Third, in our study, a vast majority of bees were solitary bees that are less sensitive to the disturbances imposed by tillage in organic fields, compared with social bees (Williams et al., 2010; Winfree et al. 2009). In addition to solitary bees, many social bee species such

as bumble bees and some halictids could adapt to nest in the disturbed grounds or field margins (Kim et al. 2006; Osborne et al. 2008). Few previous studies have indicated that increased soil disturbance due to tillage in organic fields reduces the habitat suitability for ground-nesting bees (Sardiñas et al., 2016; Shuler et al., 2005; Steffan-Dewenter, 2002; Williams et al., 2010), but our findings showed that, despite tillage, organic fields did not support fewer ground nesting bees than did no-till conventional fields. Hence, bees were probably flying further distances and nesting in more disturbed lands than previously thought so that we did not detect any differences in bee communities between conventional and organic fields.

We collected a surprisingly high number of bee species (109 taxa) from both conventional and organic fields, despite the extensive monoculture-based cereal system, limited natural habitat, and windy climate in the NGP. One potential contributor to this high bee species richness, particularly ground-nesting bees, could be the sandy soil in this landscape, which - due to the increased drainage - is favorable for bee nesting (Cane, 1991). Second, perhaps an agricultural mosaic landscape composed of conventional fields (not tilled and therefore providing nesting ground), organic fields (providing floral resources), and natural habitat (providing both season-long floral resources and nesting ground) together may provide adequate resources to support diverse bee assemblages. Hence it would be interesting to investigate how bees are using different resources across the landscape and between farming system in the NGP.

Bee community composition between the two systems differed only in August, where *M. pallidesignata* was indicative of conventional fields, and *Andrena* sp.1 and *A. porterae* were indicative of organic fields. There are limited studies done on biology,

ecology, or phenology of *M. pallidesignata*, so it is not clear why this species was more abundant and indicative of the resource-poor and less disturbed conventional fields, but it has been observed preferring sandy soil for its nesting and is known as an oligolege (collecting pollen from a limited genus only) of the family Asteraceae (LaBerge , 1961; Thorp and Chemsak, 1964). Similarly, the biology of *Andrena* sp.1 is also not known, but this genus is ground nesting often in open bare soil and mostly oligolege to polylege with peak abundance in early summer (Ascher and Pickering, 2017; North American Native Bee Collaborative, 2017). Lastly, though many species in the genus *Anthidium* are cavity nesting, *A. porterae* is described as ground nesting and pebble-gathering (in the nest plug) species, visiting a wide range of flowers and mostly active from June to September (Gonzalez and Griswold 2013). Nevertheless, these known traits are not enough to explain why the three bee species were indicative of conventional or organic farms.

Bee-Flower Networks

We recorded fewer bee-flower interactions (i.e. less connected bee-flower networks) in conventional fields compared to those in organic fields, due to the low forb flower density and forb richness available to visit for bees in these fields. Our results are partly consistent with Kehinde and Samways (2014), who compared insect-flower networks between conventional and organic vineyards in South Africa and found that, despite the similarities in insect and plant species richness between the two systems, the higher number of interactions that existed in organic vineyards were due to their greater forb abundance. Power and Stout (2011) also found more connected and “larger” insect-flower networks in Irish organic dairy farms with greater floral and bee abundance than

in conventional farms. Bee-flower networks in organic fields could have been affected by the surrounding natural habitats or field margins, but we did not sample any bee-flower interactions in these areas that might have higher floral abundance and diversity than in the fields. Yet, the size and connectedness of bee-flower networks in organic fields in the NGP were relatively less connected compared with networks observed in grasslands and other more botanically diverse natural and human-managed systems (Kehinde and Samways, 2014; Pocock and Memmott, 2012; Power and Stout, 2011; Tucker and Rehan, 2017; Welts, 2017), suggesting that the simplified agricultural landscapes of the NGP maintains a relatively impoverished bee-flower networks, even with a high diversity of bee taxa.

Percent Natural Habitat and its Effects on Small-and Large-bodied Bee Abundance

The landscape in the drylands of the NGP is heavily dominated by crop fields and limited amount of natural habitat. Previous studies assessing bee abundance and diversity in agricultural landscapes have been primarily conducted in diversified systems and heterogeneous landscapes, but little knowledge exists on the extent to which percent natural habitat impacts bee communities in very simplified landscapes such as in the NGP. All of our studied fields contained only 12% natural habitat within a 2000 m radius of their center, whereas, a study by Morandin and Winston (2006) in Canadian canola (*Brassica napus* L.) reported 30% of the land within 750m of the field edges is required to be uncultivated to sustain pollinators (also see, Fahrig, 2003; Jauker et al., 2013; Kremen et al., 2004; Steffan-Dewenter et al., 2002). Provided that other conditions are similar with their system, our landscape, dominated by wheat crops that does not offer

floral resources (while canola offers), may require even higher percent of natural habitat to sustain pollinators. While within-field forbs may provide food resources for pollinators, their relatively short flowering period may not be enough to provide enough resources for bees, hence natural habitats may be needed to secure ground for nesting substrate and season-long food resources (Danner et al., 2016; Holland et al., 2017). Nevertheless, the combination of limited natural habitat in the NGP and strikingly high bee diversity (>109 bee taxa) are contradictory, suggesting that other possible mechanisms, including landscape structure and composition, soil, and climatic factors, are driving bee population dynamics. Hence, our results of high bee diversity in windy climate, disturbed lands, low natural habitat, and low within-field plant diversity suggests that the bees in this system are uniquely adapted to flying in windy conditions, nesting in disturbed habitats, and foraging in resource-limited lands in the NGP landscape.

Our results suggest that in the highly simplified landscape of the NGP, the abundance of small-bodied bees is not enhanced by natural habitat at either smaller or larger spatial scales, probably because the, small-bodied bees may not respond to increases in natural habitat beyond their short foraging range, irrespective of farming system (Benjamin et al., 2014). Several studies have shown that the foraging range of small bodied-bees is limited to a radius of less than 500 m from their nesting habitat (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007), and can be as limited as 90 m (Wright et al., 2015, but see Castilla et al. 2017). Also, these authors indicated that with a short distance flight capacity, small bees are trapped near the field edges (Benjamin et al., 2014), making them more vulnerable to the impact of landscape simplification (Belfrage et al., 2005; Jauker et al., 2013). However, most of the bees (~79%) that we collected

were small-bodied bees and were trapped from the center of all fields, but how these small-bodied bees are sustained in the center of large, resource-constrained conventional fields with little nearby natural habitat, is unknown. Perhaps the results from previous studies done in other landscapes with more abundant floral resources underestimate the flight capacity of small bees that may be adapted to, or with no other choice to, fly greater distances (for example, see Castilla et al. 2017), but this could be an interesting subject for future studies.

In contrast to our results for small-bodied bees, the abundance of large-bodied bees increased with natural habitat at the largest spatial scale considered (within 2000 m radii of crop field centers) in both farming systems. These results agree with previous research showing that large-bodied bee populations, due to their longer foraging range, respond positively to increases in natural habitat (Greenleaf et al., 2007; Westphal et al., 2006). Large-bodied bees, in the simplified landscape of the NGP, may have been adapted to fly greater distances, as they can show extreme foraging plasticity to visit relatively consistent floral patches in the landscape (Jha and Kremen 2012). However because of its low amounts, the effects of percent natural habitat on large-bodied bees may not be detectable at smaller spatial scales such as at the field or farm scale (i.e. within 500m and 1000m radii, in our case). In addition, because large-bodied bees, due to their larger flight capabilities, respond more at larger spatial scales, may not respond to the smaller spatial scales. Despite a significantly greater forb flower density and forb richness in organic fields than in conventional fields, the effects of percent natural habitat on large-bodied bee abundance was not different between farming systems, possibly

suggesting that the effect of organic farming on bee abundances depends on the landscape context.

Conclusions

We conclude that in a highly simplified agricultural landscape that has very limited natural habitat, dryland organic farming in the NGP maintains greater flower density and forb richness and more connected bee-flower networks, compared to conventional farming, whereas both farming systems equally support a high bee abundance and diversity. Our results have raised several questions about how diverse bee communities can be sustaining in such a highly simplified and seemingly depauperate agricultural landscape in the NGP with limited natural habitat. In addition, are the simple bee-flower networks sustainable toward future disturbances? Nevertheless, our results suggest that, in addition to increase in diversified organic farms in the drylands of the NGP, probably having more natural habitats intermixed with crop fields in the landscape, may help further enhancing weed diversity, improving complexity of forb-bee networks, and possibly sustaining these bee communities. The NGP harbors several wild flowers and recently has many crops such as alfalfa (*Medicago sativa* L.), safflower (*Carthamus tinctorius* L.), sunflower (*Helianthus annuus* L.), and canola (*Brassica napus* L.) expanding, that would support to and benefited from these bee communities.

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CHAPTER FOUR

COMPARED TO CONVENTIONAL, DRYLAND ORGANIC FARMING ENHANCES
FLORAL RESOURCES AND BUMBLE BEE COLONY SUCCESSIntroduction

Pollination is a vital ecosystem service for agriculture (e.g., Kremen et al., 2002; Losey and Vaughan, 2006; Klein et al., 2007; Lautenbach et al., 2012; Vanbergen and the Insect Pollinators Initiative, 2013), with an estimated worldwide annual economic value of more than \$215 billion (Gallai et al., 2009). Approximately one third of the leading global crop species require animal vectors, particularly bees (Hymenoptera: Apoidea, Apiformes), for pollination (Kevan, 1999; Kremen et al., 2002; Steffan-Dewenter et al., 2005; Gabriel et al., 2010; Moisset and Buchmann, 2011). Thus, global declines in bee abundance and diversity have marked ecological and economic implications for the pollination of many economically-important crops (Brown and Paxton, 2009; Potts et al., 2010, 2016).

Modern agricultural intensification and its consequences, including reduced plant diversity, habitat degradation, pesticide applications, landscape simplification, and reduced availability of floral resources, are major drivers of bee population and community declines (Goulson et al., 2008; Potts et al., 2010). For example, bees are highly sensitive to the pesticides (Féon et al., 2010; Kessler et al., 2015 ; Rundlöf et al., 2015) used in most conventional farming systems (Kirchmann et al., 2008; Whitehorn et al., 2012). Herbicide applications targeting dicot species in conventional systems reduce

forb abundance and diversity and influence the spatial and temporal availability of forb-based resources (Pollnac et al., 2008, 2009; Romero et al., 2008). These effects of conventional farming can ultimately reduce colony development and fitness of eusocial bees such as honey bees (Apidae: *Apis mellifera* L.) and bumble bees (Apidae: *Bombus* spp.), and the pollination services they provide (Bernauer et al., 2015; Gill and Raine, 2014; Stanley et al., 2015). By contrast, organic production systems do not use synthetic pesticides and have a greater abundance and diversity of weeds (Kremen and Miles, 2012; Menalled et al., 2001; Power and Stout, 2011) that can provide floral resources to beneficial insects including native bees and bumble bees (Hole et al., 2005; Holzschuh et al., 2006). However, ground nesting bees, such as bumble bees, are highly sensitive to tillage (Shuler et al., 2005; William et al., 2010), which is common in organic systems.

Bumble bees, with more than 250 species worldwide (Williams, 1994), are important pollinators in natural and agricultural ecosystems (Goulson, 2010; Williams and Osborne, 2009). Although their life cycle is similar to other social bees, all individuals of bumble bee colonies, except newly inseminated queens, die before winter (Goulson, 2010). Also, compared with many other bee species, bumble bees are more massive, have longer tongues, and are capable of buzz-pollination (Willmer, 2011). These traits make bumble bees more efficient pollinators of many crops than are honey bees (Willmer et al. 1994; Javorek et al. 2002), and, as a result, more than one million commercial bumble bee colonies are used annually to pollinate fruit and vegetable crops in greenhouse and field production worldwide (Goulson and Hughes, 2015). Hence, their key role in pollination has prompted research on bumble bee reproduction and colony

growth in the recent years (Cnaani et al., 2002; Goulson et al., 2002; Williams et al., 2012; Crone and Williams, 2016; Spiesman et al., 2017).

In addition to the environmental factors like pesticides, parasites, and floral resources (Whitehorn et al., 2012; Goulson et al., 2015), bumble bee colony success is related to the success of workers at foraging, storing food, regulating colony temperature, and defending the colony, as well as the success of the entire colony in rearing reproductives that mate and (in the case of new queens) overwinter (Alford, 1969; Dorhaus and Chittka, 2004; Goulson, 2010). These components of colony success can potentially be impacted by farm-management systems and landscape characteristics. For example, a bumble bee colony located in an area with plentiful food resources can grow faster and more successfully defend against predators, pathogens, and parasites than those situated in resource-poor environments (Carter and Dill, 1991; Westphal et al., 2006; Goulson et al., 2015). As the density and proximity of floral resources to the colony declines, worker bumble bees have to travel greater distances to obtain sufficient pollen and nectar, which can reduce the quantity of resources returned to the hive (Walther-Hellwig and Frankl, 2000). In addition to pollen quantity, greater pollen quality (i.e., pollen collected from numerous plant species) provides healthier diets to bumble bee colonies compared to pollen collected from few plant species (Goulson et al., 2002; Tasei and Aupinel, 2008; Kleijn and Raemakers, 2008). Hence, availability of diverse floral resources in any agricultural landscape is critical for bumble bee colony success.

In resource-poor landscapes (for example, conventional wheat fields that are relatively free of weed-based nectar and pollen resources), the developing bumble bee reproductives may have less access to caloric resources, and limiting food resources lead

to decreased lipid reserves and reduced body sizes when they become adults (Gathmann et al., 1994; Gathmann and Tschardtke, 2002; Couvillon and Dornhaus, 2010). Reduced body sizes and lipid reserves can, in turn, be negatively associated with the ability of workers to forage effectively and perform basic physiological processes (Alford, 1969; Arrese and Soulages, 2010), though smaller workers may be less vulnerable to starvation when resources become scarce (Couvillon and Dornhaus, 2010). Adult bumble bee lipid reserves vary as a function of food consumption and metabolic activity, with lipid content increasing after they feed and declining after long flights (Alford, 1969; Paes de Oliveira and Da Cruz Landim, 2003). Hence, the lipid content and subsequent performance, of adult bee foragers is likely influenced by food resource availability around bee colonies. Knowing the food resource availability and its role on worker lipid content between conventional and organic farming, particularly in the dryland agroecosystems, is important, as these farming systems use different management tactics or “ecological filters” of biodiversity.

Compared to conventional farming systems, weedier organic fields with greater floral resources and more diverse pollen may require fewer or shorter foraging visits, potentially resulting in less collision with vegetation during flower visits and greater preservation of bumble bee wings (Carter, 1992; Mueller and Wolf-mueller, 1993; Foster and Cartar, 2011). Wing wear in bumble bees is important because damage can reduce their ability to forage or to escape predation, resulting in early mortality (Mountcastle et al., 2016, but see Haas and Cartar, 2008; Roberts and Cartar, 2015). Because they have been active for more days, older workers often have greater wing wear than younger workers, and thus wing wear can also be indicative of their age (O’Neill et al., 2015).

However in the resource-poor conditions, even the younger workers may be expected to fly a long period of time, wearing their wings more quickly. Hence, it is essential to know how conventional and organic farming systems in the drylands affect floral resources and wing wear of bees, which ultimately affect the bee mortality and colony development.

To our knowledge, no research has evaluated the role of dryland farming systems on bumble bee colony success and worker condition via floral resources. Drylands are arid and semi-arid areas with low precipitation, highly variable temperature, and low soil fertility; hence their average primary productivity can be lower compared to more mesic regions (Parr et al. 1990; Reynolds et al. 2007; Millennium Ecosystem Assessment 2005). Yet, covering about 40% of Earth's land surface, drylands are key agricultural production region globally (Parr et al. 1990; Reynolds et al. 2007). Drylands of the Northern Great Plains (NGP), important region of conventional and organic small grain, pulse, and oilseed crop productions (Johnston et al., 2002; Miller et al., 2002, 2011), supports several commonly grown crops (such as: *Medicago sativa* L., *Carthamus tinctorius* L., and *Brassica napus* L.) and wild flowers which require pollinators for seed set (Levin et al., 1966; Corbert et al., 1991; Morandin and Winston, 2005; Cecen et al., 2008). Previous studies in the NGP and elsewhere have reported higher weed abundance and diversity in organic compared to conventional fields (Pollnac et al., 2008; Romero et al., 2007), but the degree to which the higher within-field forb abundance and diversity in organic fields promotes bumble bee colony success is not known. The highly simplified landscape context (i.e., very limited natural habitat and floral resources in the surrounding area), in which both conventional and organic farming take place in the NGP (Table B4; Fig. B2) provides a unique opportunity to isolate the effects of conventional

vs. organic farming on bee colony success. In addition, we used fields of spring wheat (*Triticum aestivum* L.), a main crop in the NGP which does not offer nectar or pollen rewards that are attractive to bees, in order to further isolate the effects of conventional and organic farm management practices on bee colony success and worker condition.

Hence, to assess the role of dryland farming systems, via floral resources, on colony success and worker condition of bumble bees, we placed mini-colonies of *Bombus impatiens* (Cresson, 1863) in conventional and organic spring wheat fields in the NGP. We hypothesized that: (i) organic fields would have greater forb flower density and forb richness, which in turn, would be positively correlated with bee colony success variables; (ii) compared to weed-free conventional fields, organic fields with more floral resources would have greater *B. impatiens* colony success; (iii) because *B. impatiens* may need to fly longer distances and forage more frequently in conventional fields than in organic fields to gather food resources, worker body lipid reserves would be lower and wing wear would be greater in conventional fields; and (iv) richness and evenness of pollen, which is stored in the bee colonies as an important diet for brood, would be greater in colonies placed in organic fields compared to those in conventional fields.

Materials and Methods

Site Description and Cropping History

We conducted a two-year (2014 and 2015) on-farm study comparing floral resources, *B. impatiens* colony success, and worker condition in conventional and organic small grain row-crop production systems in Big Sandy, Montana, USA (48.036° N, 110.014° W; Altitude 960m). Big Sandy is located in Montana's "Golden Triangle", an

important region of dryland agriculture in the NGP, and dominated by cereal grain, pulse, hay, and oilseed production (Miller et al., 2011). Big Sandy is underlain with a Telstad-Joplin loam (fine loamy, mixed, Aridic Argiboroll) with a pH of 7.9 - 8.2 (Miller et al., 2011). The long term (94-year) mean annual precipitation for Big Sandy is 325 mm, and the mean annual maximum and minimum temperatures are 14.8°C and -1.2°C, respectively (Table A1). Both mean annual maximum and minimum temperatures in 2015 were higher (15.7°C and 1.3°C, respectively) than in 2014 (13.7°C and 0.2°C). Also, total annual precipitation was lower in 2015 (301 mm) compared to 2014 (342 mm), making 2015 drier and hotter than both the long-term average and 2014.

Each year in 2014 and in 2015, we selected three conventionally-managed no-till spring wheat (*Triticum aestivum* L.) fields (a Clearfield® cultivar of ‘Jedd’ in 2014 and ‘Vida’ in 2015) and three nearby, tilled and organically-managed ‘Kamut’ (*Triticum turgidum*, ssp. *turanicum* McKey, a close relative of durum; see details in Adhikari et al., submitted) wheat fields. All fields used in 2014 were different from those used in 2015 for both conventional and organic systems. Field sizes ranged from 25 to 70 ha. All organic fields have been certified by the Organic Crop Improvement Association International since 1989 and have also met United States Department of Agriculture organic certificate standards since 2003 (Miller et al., 2011; Seth Goodman, *Pers. Comm*). Conventional fields followed a reciprocal rotation of spring wheat and chemical fallow, and organic fields followed a multi-year continuous rotation of crops or cover crops (Table A2). In conventional fields, the fallow phase was treated with multiple applications of glyphosate (*Roundup*®) at rates ranging from 1121 to 1682 g active

ingredient ha^{-1} between crop termination and seeding. In organic fields, crop residues and cover crops were incorporated by chisel and/or disk tilling. Also, disk plowing was used as needed to manage the high density of weeds in the organic fields. Agronomic management was at growers' discretion (Table A3).

Floral Resources

To quantify floral resources (i.e., forb flower density and forb species richness) from conventional and organic fields, we established a randomly oriented 55m transect at the center of each field (at least 150m from any border) in each year. At each of three randomly selected points along this main transect, we established three perpendicular 25m sub-transects. To measure forb flower density, we counted the number of flowers of each plant species within a perpendicular $0.5 \text{ m} \times 1 \text{ m}$ quadrat at every meter interval along each sub-transect (75 total quadrats per field) three times over the course of each growing season (i.e., once each in June, July, and August). Having a very short growing season (mainly mid-June to mid-August) in our crop fields and also due to logistical constraints, we assume that three sampling dates are enough to cover temporal variability in weed communities. In the same sub-transects, we calculated forb species richness as the total number of species present from those forbs that had open flowers. These measures of floral resources were used as response variables (the effects of farming systems on floral resources) and as predictor variables (the effects of floral resources on bee colony success).

Bombus impatiens Colony Success and its
Relationship with Floral Resources

To assess the impact of conventional and organic farming systems on bee colony success, we established five mini-colonies of *B. impatiens* in each of the three organic and three conventional fields in each year. We used *B. impatiens* (an eastern North American species) as a model organism because it was the only commercially available bumble bee species. Colonies (and supplemental pollen to feed the colonies during transportation) were obtained from Koppert Biological Systems, Howell, MI. Workers were allowed to forage in fields from June 19 to August 12 in 2014 and from June 23 to August 10 in 2015. All *B. impatiens* hive boxes (35 cm × 30 cm × 23 cm) initially consisted of one queen and 30 workers. Each of these hives had a built-in queen excluder to avoid any escape of queens and to prevent entry by any invading queens from other colonies, thus retaining the colony founder. To calculate relative colony growth over the course of the season, we recorded the weight of each colony to the nearest 0.001 g before placing in the field and again immediately after the colonies were retrieved from the field.

To reduce environmental stress that might occur when *B. impatiens* colonies are placed directly on the soil surface where it is sometimes wet and hot, we placed each colony on a raised platform (50 cm off the ground). We also covered each colony with a hard plastic roof separated from the top of the colony to allow for air flow and *B. impatiens* activity (Fig. C1). To prevent ground-dwelling arthropod, especially ant, invasion, we applied a band of insect adhesive Tangle Guard® Banding Material (Tanglefoot®, Scotts Miracle-Gro Co., Marysville, OH, United States) around the base of

the platform. When forbs in wheat fields senesced in early to mid-August, the colonies were retrieved from the field. To ensure that all foraging workers were present in the colony before retrieval, the entrance door of each hive was closed at night and the colonies were collected early on the following day. After retrieval, colonies were stored in the freezer for further analysis.

We quantified several metrics of *B. impatiens* colony success, including colony relative growth rate (RGR), colony fecundity, and resource storage. RGR was calculated as:

$$\text{RGR} = \frac{(W_2 - W_1)/W_1}{t_2 - t_1} \quad (1)$$

where, W_1 and W_2 represent initial weight and final weights of *B. impatiens* colonies and t_1 and t_2 represent the initial and the final days that the colonies were out in the field, respectively (Spiesman et al. 2017). Bee colonies were in the field for slightly different numbers of days in each year (i.e., 55 days in 2014, and 49 days in 2015). To estimate fecundity at the time when colonies were retrieved from the field, we counted the number of adult female workers, males (drones), and the new queens (gynes) in the hive as well as brood cells (all occupied) still containing eggs, larvae, and pupae (Goulson et al., 2002). To estimate resource storage, we counted non-brood cells: pollen pots and honey pots or nectar stores. Status of brood cells correlates with future adult *B. impatiens* production (workers and reproductives), whereas non-brood cells like pollen pots and nectar stores may indicate the future food stock for brood later in the same year. For each colony, we also calculated the average worker mass by summing the weights of worker bees per colony.

Bombus impatiens Worker Condition

Lipid Content and Wing Wear. To estimate worker body condition at the time of colony retrieval, we extracted lipids and assessed wing wear of individual workers. We measured worker lipid content from the 2015 colonies using a petroleum ether lipid extraction method previously used for the solitary bee *Megachile rotundata* F. (O'Neill et al., 2011, 2015), adjusted for the larger body size of *B. impatiens*. We were unable to conduct lipid extraction of workers from the 2014 colonies because they were not stored at a low enough temperature to prevent lipid degradation. We randomly selected a maximum of 18 workers from each colony for lipid extraction. If a colony had fewer than 18 workers, we conducted lipid analysis on all workers from that colony. We placed each worker in a separate 20 ml scintillation glass vial, dried it at 55°C in a drying oven, and measured the final dry mass. We then added 18 ml petroleum ether to each worker to extract lipids. After 15 days, we decanted the ether (which contained extracted lipids) and let any remaining ether evaporate. We then immediately re-weighed each worker to obtain its dry mass after lipid extraction. We calculated the proportion of total body lipid content (LC) of each worker as:

$$LC = \frac{W1 - W2}{W1} \quad (2)$$

Where W1 = initial or pre-extraction dry body mass, and W2 = post-extraction dry body mass (O'Neill et al., 2015). Note that, although the extraction technique does not target only lipids stored in fat bodies, as in (O'Neill et al., 2015), we assume LC is highly

correlated with the latter, thus reflecting the amount of lipids that workers reserved for metabolic activities.

After extracting lipids, the same 18 individuals of *B. impatiens* workers from each colony were used to visually assess their wing wear under a dissection microscope at 40X magnification. We assumed that the process of lipid extraction did not affect wing wear measures of the workers. Following Mueller and Wolf-Mueller (1993) and O'Neill et al. (2015), we used a wing wear index to score damage to the forewing margin on each wing by ranking them from 0 to 6, where 0 = wing margin entirely intact; 1 = wing margin with only 1–2 nicks; 2 = wing margin with 3–10 nicks; 3 = wing margin partially intact but heavily serrated, with >10 nicks; 4 = wing margin completely serrated but excisions less than half the width of the distal sub-marginal cell; 5 = wing margin completely serrated, but with excisions more than half yet less than the entire width of the distal sub-marginal cell; and 6 = wing margin completely serrated but with excisions greater than the width of the distal sub-marginal cell. Scores for the right and left wings were averaged to compute a single wing-wear value for each *B. impatiens* worker. To isolate the effects of flight on wing wear from other events, we excluded any wings with anomalous damage (~10% of total *B. impatiens* workers selected for study), including large single incisions and missing sections of wing. Finally, using a digital caliper, we measured intertegular distance, a standard proxy of overall worker body size (Cane, 1987; Greenleaf et al., 2007; Hagbery and Nieh, 2012), of each individual selected for measurement of lipid content and assessment of wing wear. We assumed that the process of lipid extraction did not affect intertegular distances of the workers.

Identity of Pollen Stored by *B. impatiens* Workers. In order to compare the diversity of pollen types collected and stored by worker bees between the two farming systems, we studied the composition of pollen sampled from pollen pots during the dissection of colonies in each year. Since the colonies were kept in the field throughout the flowering season, we assumed that this pollen reflected the diversity of flowering plants that were collected by foraging workers over the growing season. We made a homogeneous mixture of each pollen sample and used five random sub-samples from each to prepare slides using fuchsin dye following Kearns and Inouye (1993). To quantify pollen types, we used five spatially separate points in the field of view (Fig. C2) under 100X (or 400X for smaller pollen) using light microscopy (Nikon Eclipse 50I, Nikon Instruments Inc., Melville, NY, USA) and counted and identified all pollen grains under that field of view. Pollen abundance and identity were pooled across the five points for each slide. We identified most of the pollen (~71% across samples) to species by using a reference collection of pollen collected from all common forbs and shrubs within a 5 km radius of our study fields (Table C1), photographs, other available resources (Faegri and Iversen, 1989; Kapp et al., 2000; Hesse et al., 2009, PalDat, 2015), and consulting with experts. The remaining unidentified pollen grains were identified to either genus or family based on their size, shape, and morphology. We calculated pollen species richness as the total number of species present. Similarly, pollen species evenness was calculated using Pielou's evenness index (Pielou, 1966; Whittaker, 1972).

Data Analysis

For all our analysis, we first created a correlation matrix among all response variables for respective questions, to determine whether any of them were linearly related. If any response variables were strongly correlated ($r > 0.6$), we selected the most representative ones and included with other uncorrelated response variables in Multivariate Analysis of Variance (MANOVA).

To determine the effects of farming system (conventional vs. organic) on forb flower density and species richness, we used generalized linear mixed-effects models with Poisson distribution. To meet normality and equal variance assumptions, response variables were log-transformed, as needed. For *B. impatiens* colony success, we tested the effects of farming system (i.e., conventional vs. organic) on relative growth rates of *B. impatiens* colonies using a linear mixed-effects model. We compared the number of workers, queens, males, brood cells, nectar stores, and pollen pots between farming systems using a generalized linear mixed-effects model with Poisson distribution because these were count data. In all mixed-effect models, field and colony identity were random effects, and farming system and year were fixed effects. Year was treated as a fixed effect instead of a random effect because we had only two years of data, and there was significant variation in colony variables between the two years. In addition, we used all colony success variables that were affected by farming system in the above analysis (i.e., relative growth rate, number of brood cells, and nectar stores, as response variables) to test their relationship with floral resources (forb flower density and forb species richness), by fitting a mixed model Multivariate Analysis of Covariance (MANCOVA)

with farming system, flower density, and forb richness as fixed effects and fields as random effects.

To determine the effects of farming system on *B. impatiens* worker condition, we compared workers' body lipid content using a linear mixed-effects model with field and colony identity as random effects and farming system as fixed effects. Due to the ordinal nature, we compared wing-wear index data between conventional and organic systems using a cumulative link mixed model (CLMM). For the CLMM, we conducted analysis of variance (ANOVA) using likelihood ratio tests and reported the Chi-squared value.

After determining that these two variables were not linearly related, we compared colony-collected pollen species richness and evenness across farming systems, using a generalized linear mixed-effects model (with Poisson distribution) and a linear mixed-effects model, respectively. Farming system and year were treated as fixed effects and field was treated as random effects in both models. Differences in pollen species composition between conventional and organic farming systems were assessed using Permutational Multivariate Analysis of Variance (PERMANOVA) on a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957; McCune and Grace, 2002) and visualized with Non-metric Multidimensional Scaling (NMDS) ordination.

Generalized linear mixed effect models for colony success variables were performed in SAS (version 9.4, SAS Institute Inc., Cary, North Carolina) but all other analyses were performed using R 3.2.4 (R Development Core Team, 2016). We used R packages “lme4” (Bates et al., 2015), “nlme” (Pinheiro et al., 2016), and “ordinal” (Christensen, 2015) for mixed-effect models and “lsmeans” (Lenth, 2016) for multiple comparisons. Multivariate analyses and ordination graphics were conducted using

“labdsv” (Roberts, 2007) and “vegan” (Oksanen et al., 2007) packages in R. We produced all other graphics using the “ggplot2” (Wickham, 2009) and ‘sciplo’ (Morales et al., 2012) packages in R.

Results

Floral Resources

Out of 18 total blooming forb species recorded over a 2-year period of our study, we observed three of them in conventional fields and 16 in organic fields (Table C2). Organic fields had greater forb flower density (27 times more in 2014 and 3 times more in 2015) and forb species richness (15 times more in 2014 and 4 times more in 2015) than in conventional fields (Fig. 4.1A; $F = 8.2$; $df = 1, 8$; $P = 0.02$ and Fig. 4.1B; $F = 10.1$; $df = 1, 8$; $P = 0.01$, respectively). Forb flower density and forb species richness were greater in 2015 (8 times more and 2 times more, respectively) than in 2014 (Fig. 4.1A; $F = 15.8$; $df = 1, 8$; $P = 0.004$ and Fig. 4.1B; $F = 15.9$; $df = 1, 8$; $P = 0.004$, respectively).

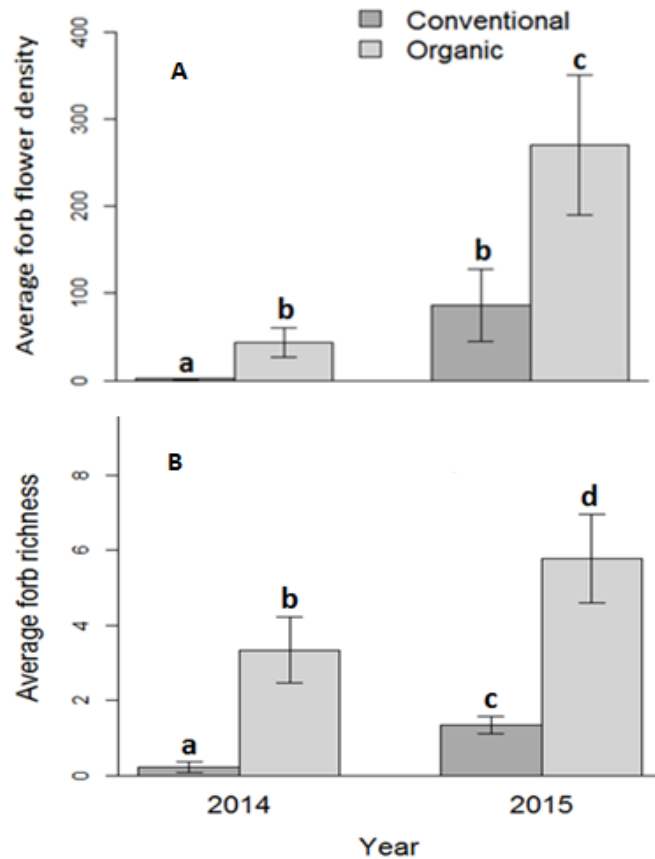


Figure 4.1 (A-B). Differences in forb communities between conventional and organic farming system in 2014 and 2015. A. Forb flower density (no. of flowers/month/field). B. Forb richness. Error bars represent the standard errors of the mean, while letters above bar diagrams indicate significant differences between systems ($P < 0.02$, in all cases).

Bombus impatiens Colony Success and its Relationship with Floral Resources

The numbers of workers, nectar stores, pollen pots, and average mass of *B. impatiens* workers were positively correlated, with the relative growth rate (Table C3). Compared to conventional fields, colonies in organic fields had greater relative growth rate (by 17% in 2014 and by 150% in 2015), average number of brood cells (by 28% in 2014 and by 56% in 2015), and average number of nectar stores (by 29% in 2014 and by

50% in 2015) per colony (Table 4.1). By contrast, percentage of empty cells per colony was 33% greater in 2014 and 60% greater in 2015 in conventional fields than in organic fields (Table 4.1). We did not detect differences in the number of workers, queens, males, and pollen pots between conventional and organic fields (Table 4.1).

Table 4.1. *Bombus impatiens* colony success parameters in conventional and organic farms at Big Sandy, MT. Analysis were done with linear or generalized linear mixed effect models, where farming systems and year were treated as fixed effects and the individual fields were treated as random effects. Significant P-values ($P \leq 0.05$) are bolded. There was no significant System by Year interactions for any of the variables.

Bee colony Variables	2014		2015		DF	System F value	Analysis		Year F value	P value
	Conventional Mean $\pm$ SE	Organic Mean $\pm$ SE	Conventional Mean $\pm$ SE	Organic Mean $\pm$ SE			P value	DF		
RGR ($\text{g g}^{-1} \text{wk}^{-1}$)	0.052 $\pm$ 0.003	0.061 $\pm$ 0.003	0.006 $\pm$ 0.002	0.015 $\pm$ 0.002	1,11.5	6.93	0.02	1,11.5	203	<0.001
Number of queens	1.8 $\pm$ 0.4	1.0 $\pm$ 0.1	1 $\pm$ 0	1 $\pm$ 0	1,12.8	2.41	0.15	1,12.8	2.41	0.15
Number of males	5.7 $\pm$ 1.2	5.1 $\pm$ 1.29	3.9 $\pm$ 1.1	2.8 $\pm$ 0.7	1,7.1	0.38	0.56	1,7.1	3.61	0.099
Number of workers	118.7 $\pm$ 10.2	125.3 $\pm$ 10.1	31.1 $\pm$ 3.3	33.5 $\pm$ 2.6	1,8.6	0.32	0.59	1,8.6	132	<0.001
Number of nectar stores	271.0 $\pm$ 24.0	349.2 $\pm$ 29.2	75.2 $\pm$ 11.3	112.9 $\pm$ 6.1	1,7.9	5.67	0.045	1,7.9	64.27	<0.001
Number of pollen pots	15.4 $\pm$ 6.3	19.0 $\pm$ 4.8	2.8 $\pm$ 0.9	4.8 $\pm$ 1.3	1,8	2.55	0.15	1,8	18.87	0.003
Number of brood cells	84.1 $\pm$ 11.3	107.5 $\pm$ 14.0	110.1 $\pm$ 11.9	171.6 $\pm$ 21.8	1,7.9	6.75	0.03	1,7.9	8.52	0.02
% empty cells	15.9 $\pm$ 1.7	12.0 $\pm$ 1.5	36.2 $\pm$ 6.8	22.6 $\pm$ 3.7	1,56	4.02	0.049	1,56	10.75	0.002

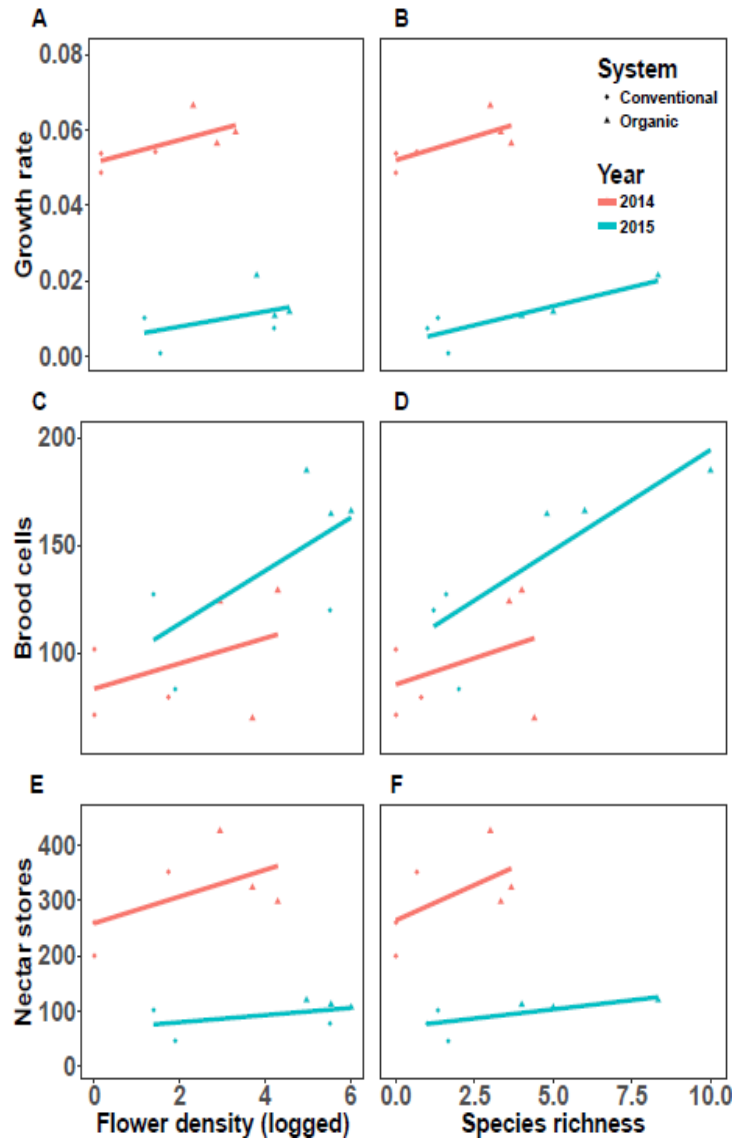


Figure 4.2 (A-F). Relationship between (A) relative growth rate and forb flower density, (B) relative growth rate and forb species richness, (C) total brood cells and forb flower density, (D) total brood cells and forb richness, (E) nectar stores and forb flower density, and (F) nectar stores and forb richness (n=12).

There were also differences in colony success between years. Specifically, relative growth rate was 447% greater in 2014 than in 2015 (Table 4.1). The number of workers (by 278%), and the numbers of nectar stores (by 230%), were also greater in 2014 than in 2015 (Table 4.1). By contrast, there were greater numbers of brood cells (by

47%) and percentage of empty cells per colony (111%) in 2015 than in 2014 (Table 4.1), at the time of colony retrieval. We did not detect differences in the number of queens and males between years (Table 4.1).

Overall, forb flower density and species richness were positively associated with colony relative growth rate (Fig. 4.2A; $F = 42$; $df = 1, 8$; $P = 0.0002$ and Fig. 4.2B; $F = 15$; $df = 1, 8$; $P = 0.004$, respectively) and with number of brood cells (Fig. 4.2C; $F = 9.8$; $df = 1, 8$; $P = 0.01$ and Fig. 4.2D; $F = 9.8$; $df = 1, 8$; $P = 0.01$, respectively). However, forb flower density was only marginally positively associated and forb species richness was not associated with nectar cells (Fig. 4.2E; $F = 5.2$; $df = 1, 8$; $P = 0.05$ and Fig. 4.2F; $F = 1.1$; $df = 1, 8$; $P = 0.32$, respectively).

Bombus impatiens Worker Condition

Table 4.2. Mean wing wear index and lipid content of *Bombus impatiens* workers (n=449) sampled from colonies located in either conventional or organic farms at Big Sandy, MT. Significant P-values ($P \leq 0.05$) are bolded. ^c Proportion of total body lipid content (LC). [†] Chi-squared value was from the likelihood ratio test of cumulative linked mixed model.

Variables	Conventional	Organic	Analysis		
	Mean $\pm$ SE	Mean $\pm$ SE	DF	Test statistic	P value
^c LC	0.048 $\pm$ 0.003	0.055 $\pm$ 0.004	1,28	$F = 3.4$	0.07
Wing Wear Index	3.02 $\pm$ 0.13	2.06 $\pm$ 0.10	1, 13	[†] $\chi^2 = 6.5$	0.01

Lipid Content and Wing Wear. The proportion of body lipid in workers was 15% greater from organic fields, compared with those from conventional fields (Table 4.2), but the effect of farming system was only marginally significant. Consistent with our

hypothesis, workers sampled from colonies placed in conventional fields had 47% higher mean wing-wear compared with those from organic fields (Table 4.2).

Identity of Pollen Stored by *B. impatiens* Workers. We identified 45 plant taxa from 10,978 total grains of pollen collected from pollen pots in *B. impatiens* colonies (Table C4). Pollen richness was similar between the two farming systems in 2014 but was 67% greater in organic fields than in conventional fields in 2015, hence an interaction between farming system and year (Table 4.3). Pollen evenness did not differ between farming systems or by year (Table 4.3).

Pollen community composition did not differ between colonies kept in conventional and organic fields in either year (PERMANOVA, pseudo- $F = 0.88$; $df = 1, 10$; $r^2 = 0.08$; $P = 0.26$). However, pollen community composition in 2014 was different from 2015 (PERMANOVA, pseudo- $F = 5.96$; $df = 1, 10$; $r^2 = 0.37$; $P = 0.002$; Fig. 4.3).

Table 4.3. Mean pollen richness and evenness. Pollen was collected from *B. impatiens* colonies while they were dissected in the lab. Analysis were done with linear or generalized linear mixed effect models, where farming systems and year were treated as fixed effects and the individual fields were treated as random effects. Significant P-values ($P \leq 0.05$) are bolded.

Fixed	2014		2015		Analysis								
Effect					System			Year			System $\times$ Year		
Variables	Conventional	Organic	Conventional	Organic	DF	F	P	DF	F	P	DF	F	P
	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE		value	value		value	value		value	value
Richness	5.07 $\pm$ 0.65	4.33 $\pm$ 0.45	5.93 $\pm$ 0.67	9.93 $\pm$ 0.69	1,8	10.52	0.01	1,8	22.46	0.002	1,8	9.70	0.01
Evenness	0.58 $\pm$ 0.07	0.50 $\pm$ 0.06	0.59 $\pm$ 0.08	0.70 $\pm$ 0.05	1,8	0.01	0.91	1,8	1.39	0.27	1,8	0.95	0.36

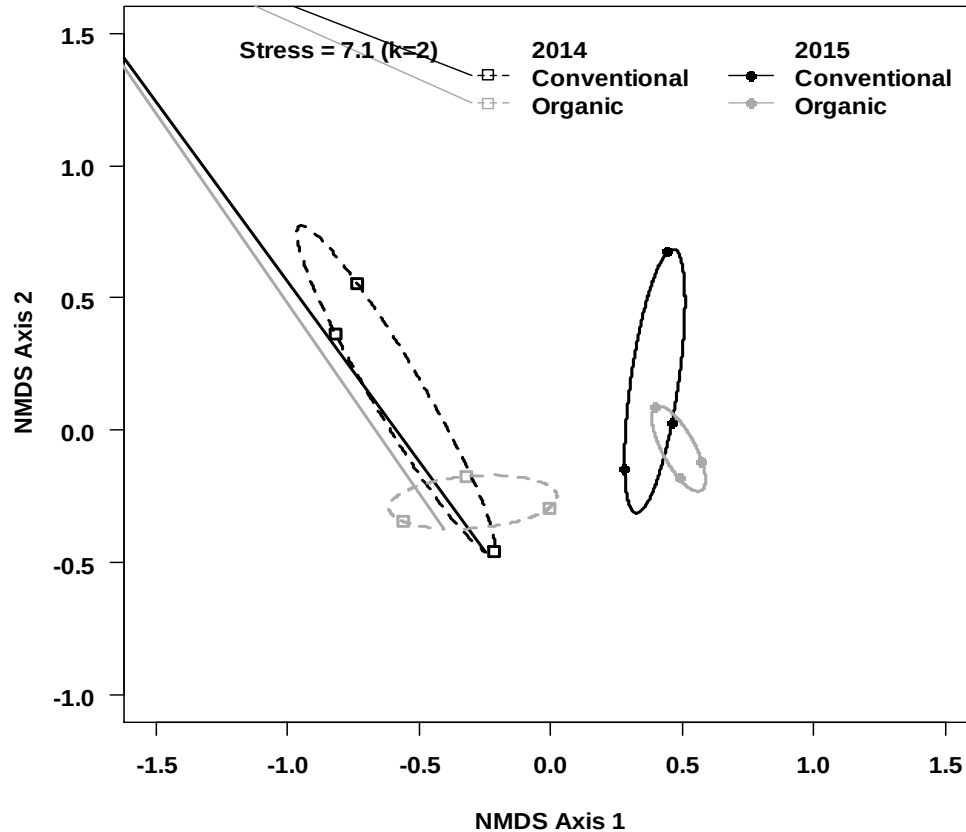


Figure 4.3. Non-metric multidimensional scaling (NMDS) ordination of pollen collected from pollen pots of *Bombus impatiens* colonies (colony-collected) in 2014 and 2015. Dotted ellipses and filled circles inscribe communities in 2014 and solid ellipses and filled circles inscribe communities in 2015. Black represents conventional fields and gray represents organic fields.

Discussion

Our results indicate that, via increased floral resources, dryland organic farming enhances *B. impatiens* colony success and individual worker condition in the highly simplified agricultural landscapes of the NGP. Compared to virtually weed-free conventional fields, weedier organic fields provided more pollen and nectar resources for

B. impatiens workers, potentially reducing both metabolic investment in and mechanical wear from flight. Hence, adoption of diversified farming in dryland agroecosystems could provide biodiversity-based ecosystem services, through enhanced floral resources, bee colony success, and worker condition.

Floral Resources and *Bombus impatiens* Colony Success

Floral resources (forb flower density and forb richness) was greater in organic fields than in conventional fields, which was partially consistent with previous studies (Pollnac et al., 2008; Romero et al., 2007) that assessed weed cover and diversity but not floral resources *per se*. Though no previous study in the NGP evaluated if the increase in forb abundance and richness translates into a greater floral resources, and in turn enhances bee colony success, we showed that the measures of colony success were greater in organic than in conventional fields, likely due to higher floral resources in organic fields; and that regardless of farming system, floral resources were positively associated with colony success. In addition, higher number of brood cells (i.e., eggs, larvae, and pupae) in the colonies placed in organic fields, compared to conventional fields; likely suggest that these colonies have greater potentials to increase adult bumble bees later in the season. Therefore, some of the biodiversity-based indirect ecosystem services that organic farming provides via floral resources may not be realized immediately or will become apparent over time if differences between conventional and organic fields remain consistent.

Previous studies have considered the importance of surrounding natural habitats for securing season-long food resources for bee colonies (Danner et al., 2016; Holland et al., 2017), but the landscape in our study area had very limited natural habitats (Adhikari et al., unpublished) that could contribute floral resources necessary to facilitate bee colony growth. Hence, bumble bee colonies in our study had low growth rates compared to other studies (Goulson et al., 2002; Williams et al., 2012; Spiesman et al., 2017) that were performed in more complex agricultural landscapes with higher floral resources. Additionally, in contrast to previous studies (e.g., Bowers, 1986; Beekman and Van Stratum, 1998; Pelletier and McNeil, 2003; Williams et al., 2012), greater floral resources in our organic fields did not result in a concomitant increase in the number of *B. impatiens* reproductives (males, workers, and gynes), likely suggesting that floral resources in organic fields were nevertheless limiting. Specifically, while within-field floral resources in organic fields supported greater colony growth rates than in conventional fields, perhaps the relatively short flowering period of forbs in crop fields was not enough to provide sufficient resources to produce reproductives and to complete the bee life cycle, particularly during early and late seasons (Goulson et al., 2008; Mallinger et al., 2016; Walther-Hellwig and Frankl, 2000). Hence, it appears that the natural habitats essential for bee colony growth were limiting in the simplified landscape in which this study took place.

Bee colony success significantly varied across years that had different climatic conditions. Specifically, the positive effects of organic farming on colony success variables were mainly evident in 2014, the cooler and wetter year, whereas these effects were smaller or absent in 2015, the hotter and drier year. Greater number of brood cells

but lower numbers of adults and lower colony growth rates were observed in 2015 compared in 2014 in both farming systems, indicating lower colony success in 2015 due to less favorable weather conditions. Interestingly, bee colonies had higher percentages of empty cells in 2015, especially in conventional fields, possibly indicating food-scarcity. The direct and indirect negative effects of adverse climatic conditions on worker foraging performance have been reported in previous studies (Corbet et al., 1993; Kwon and Saeed, 2003; Rathcke and Lacey, 1985), but additional studies are needed to better understand the interacting effects of climatic variables, farming systems, and landscape composition on bee colony success over time.

Bombus impatiens Worker Condition

The marginally greater percent lipid content observed in workers from colonies placed in organic fields compared to those in conventional fields may suggest a trend towards greater energy reserves. The lower lipid content of workers in conventional fields may reflect increased flight times, since lipid stores are used for activities such as flight (Arrese and Soulages, 2010) and workers likely needed to fly further (i.e., outside of field margins) to reach adequate floral resources. The lower lipid content of workers in conventional fields may be explained by the lower forb flower density, forb species richness, and pollen richness in those fields, possibly due to longer flights needed to locate food resources. By contrast, workers in organic fields likely did not have to fly as far to find adequate food resources, allowing them to conserve body lipid reserves. While bumble bee workers generally forage close to their nests (Osborne et al., 2008; Walther-Hellwig and Frankl, 2000), they can fly several kilometers to obtain floral resources if

closer options are limiting (Goulson et al., 2002), and such long flights compromise their energy reserves (Cresswell et al., 2000). Hence, due to shorter flights in organic fields, bee workers can save and reserve their energy stores as lipid, but we need more studies to determine how the amount of these stores translates into greater bee colony success and better worker condition.

The mechanism underlying the greater observed wing wear in workers from colonies placed in conventional fields than those in organic fields is unknown, but likely indicates more intense foraging activities, including collision with vegetation (shown to be important by Foster and Carter, 2011) or longer and more frequent foraging flights. Foster and Carter (2011) did not find any link between wing wear and flight distance, possibly because their study was done in relatively resource-rich conditions (in a wildlife sanctuary in Canada) where even the longest flights of bees were likely not as far as those in the resource-constrained landscape of our study. Given that we found evidence of lower pollen availability in conventional fields, greater wing collision with vegetation may have occurred if workers had to visit more flowers to gather the same amount of pollen compared to workers foraging in relatively more resource-rich organic fields. Regardless of the ultimate causes, higher wing wear in workers of colonies placed in conventional fields may suggest a greater risk of predation and earlier mortality, a reduction in peak acceleration during flight maneuvering, or an inability to forage further afield (Cartar, 1992; Johnson and Cartar, 2014; Mountcastle et al., 2016, but see Roberts and Cartar, 2015).

Because pollen is an essential food resource for bee colonies (the primary protein source to feed queens' offspring), the amount of stored pollen in a colony provides

information on workers' foraging success (Liolios et al., 2015; Marchand et al., 2015; Nicholls and Hempel de Ibarra, 2017). Hence, our results of higher pollen richness in the colonies of organic fields in 2015 may indicate that these colonies were providing healthier diets to their brood (Goulson et al., 2002; Tasei and Aupinel, 2008; Kleijn and Raemakers, 2008), whereas low pollen storage in the colonies of conventional fields, may indicate that these colonies may suffer from increased developmental mortality (Dornhaus and Chittka, 2005; Rotheray et al., 2017). Similarly, the stored pollen in a colony may provide information on the abundance of flowering species in the surrounding landscape (Liolios et al., 2015; Marchand et al., 2015), such that alfalfa (*Medicago sativa* L.) was the most abundant plant taxa in our pollen analyses (Table C4) and also one of the most abundant species blooming in organic fields and in the surrounding landscape. Nevertheless, since we did not see any differences in pollen species richness between farming systems in 2014, the year to year variation was possibly due to the different climatic factors between two years (2014 was cooler and wetter year).

Overall pollen species community composition between conventional and organic fields, however, were similar, maybe because the use of dicot-specific herbicides in conventional fields reduced weedy forb density, forcing workers to forage fly further afield, perhaps even as far as our organic fields. Bumble bees are capable of flying several kilometers to forage if required (Goulson et al., 2002), but it is uncertain if or how long their populations could be sustained in resource-poor landscapes that require them to do so. In addition, given the fact that many of the plant species found in our pollen samples were not present in our plant community samples, bees in both treatment areas

may have been visiting flower outside of the crop fields to find pollen, especially when the resources in crop fields were inadequate.

Conclusions and Management Implications

Though several studies have reported higher biodiversity in organic fields (Holes et al. 2005; Tuck et al., 2014), it was not known if the increase in within-field floral resources could support higher bumble bee colony success. We showed that in the simplified and resource-limited agricultural landscape of the NGP, compared to conventional fields, organic fields support greater floral resources contributing to an increased bumble bee colony success and worker condition. Since the dryland farming systems are understudied, despite their key roles in global agricultural production, the outcomes of our research will contribute to the broader literature on the plant-mediated effects of dryland farming system on bee colony success and worker condition, that we didn't know before. However, additional studies are still required to know whether these within-field food resources in the simplified and resource-challenged landscapes are sufficient to maintain populations of native bumble bee species of the NGP, particularly during the critical phases of colony establishment and offspring production. Although almost no insecticides are used in the conventional fields, the extensive use of dicot-specific herbicides kills forbs and limits food resources to the wild native bees. Our study indicates that through diversified organic farming and limited use of selective herbicides, higher quality food resources can be provided to wild native bees, enhancing their colony success.

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CHAPTER FIVE

SUMMARY OF FINDINGS AND FURTHER RESEARCH

While the suite of agronomic practices associated with modern agriculture efficiently control many pest populations, maintain short-term soil fertility, and secure high crop yields, the global scientific community has long warned of the declines in biodiversity resulting from those practices. Biodiversity plays a critical role in providing ecosystem services including food, fiber, energy, air and water purification, climate regulation, nutrient cycling, pollination, and biological control of pests (Vandermeer et al. 2002; Kirchmann et al. 2008; Mace et al., 2012; Robertson et al. 2014). By diversifying agroecosystems with ecologically-based management practices, we can enhance the associated biodiversity including weeds and insects.

Despite the agronomic and economic importance of the Northern Great Plains (NGP hereafter) region in the production of conventional and organic small grain, pulse, oilseed, and forage production, the impacts of farming management systems on the biodiversity and proxies of ecosystem services such as bee-flower interactions, bee colony success, and parasitoid abundances, had been relatively unexplored. To fill this research gap, I conducted three studies to assess the impacts of conventional and organic row crop production on associated biodiversity and biodiversity-based ecosystem services in dryland agroecosystems of the NGP.

My first study investigated how agricultural management systems and wheat cultivars affected *Cephus cinctus* infestations and the populations of its braconid parasitoids. I found that *C. cinctus* infested more wheat stems in conventional fields than

in organic fields. Correspondingly, organic fields had fewer cut stems and more braconid parasitoids than did conventional fields. Increased weed abundance in organic fields may be driving the increased abundance of braconid parasitoids compared with those in conventional fields. My results from this study underscore the importance of diversifying associated biodiversity in agroecosystems to enhance populations of beneficial insects like parasitoids that regulate pest populations, thus reducing crop damage. Similarly, I found that *C. cinctus* oviposition, survival, and stem logging were lowest in the Kamut wheat cultivar compared with those in the Gunnison and Reeder cultivars. Hence, my study furthers the growing body of literature suggesting that managing fields organically and using pest-resistant wheat cultivars like Kamut can enhance natural pest regulation in dryland agroecosystems of the NGP.

My second study assessed the impacts of conventional and organic farming systems on forb and bee communities. Additionally, I investigated how landscape composition, particularly percent natural habitat in the surrounding landscape, affected small-and large-bodied bee abundances in these agroecosystems. I found that forb community structure differed between conventional and organic farming systems. In particular, organic fields had greater forb flower density and species diversity than conventional fields, suggesting that these two management systems and their associated practices represent distinct community assembly ecological filters. Specifically, the repeated use of dicotyledon-selective herbicides in conventional fields eliminated forbs, while frequent tillage in organic fields selected annual forbs and grasses.

Despite these differences in weed communities, bee abundance, richness, and diversity did not differ between the two management systems. However, the bee-flower

networks in conventional fields were either absent or extremely simple compared to those in organic fields. Surprisingly, organic fields did not support fewer ground nesting bees than did conventional fields, despite tillage and its corresponding soil disturbances. The percent natural habitat in our study area averaged only 12 % of the landscape within a 2000m radius of the center of our fields, suggesting that the landscape is not suitable to wild native bees for foraging and nesting. However, we collected more than 109 bee taxa from our study area, indicating that the landscape mosaic composed of undisturbed conventional fields (providing nesting ground), organic fields (providing floral resources), and natural habitats (providing both nesting and floral resources), is favorable to support bees. Similarly, percent natural habitat did not influence small-bodied bees but positively affected large-bodied bee abundance in both farming systems, but only at the largest spatial scale of 2000 m circle.

In conclusion, my second study demonstrated that in a homogenous landscape that has very limited percent natural habitat, even though organic fields had greater flower density and richness than the conventional fields, they had still very low numbers of flowers and forbs compared to more natural systems, and therefore these organic fields could not support more bees, compared to the conventional fields. In other words, in simplified agricultural landscapes, the greater within-field forb abundance and diversity may enhance bee-flower interactions but not necessarily bee abundance and diversity. An important question to address would be the relative role of food resource availability and habitat suitability in and around both conventional and organic fields in preserving bee populations in the dryland agroecosystems of the NGP. We also need to enhance our

understanding of bee population dynamics and foraging range of solitary and wild native bees in the fragmented and simplified agricultural landscapes such as in the NGP.

My third study compared floral resources, *Bombus impatiens* colony success, and worker condition between conventionally and organically managed farming systems in the NGP and the identity of plant species that were represented in worker-collected pollen between the two systems. I found greater forb flower density and richness in organic fields, compared to conventional fields, reflecting a greater diversity in phenology that could buffer against food scarcity to bees. I also found that forb flower density and forb richness were positively associated with colony growth and brood cells in both farming systems. In addition, colony relative growth rate, number of nectar stores, and number of brood cells were all greater in organic systems than in conventional systems. However, despite greater forb flower density and species richness in organic fields, the number of reproductive offspring including number of queens, workers, and males did not differ between the two systems. *Bombus impatiens* workers from conventional fields had greater wing wear and less body lipid mass than did workers from organic fields, likely suggesting that the workers from conventional fields had to visit more flowers and/or travel farther to obtain sufficient food when foraging compared with workers in organic fields. Pollen species richness was greater in organic fields, but diversity and plant species identified from pollen did not differ between two farming systems, possibly indicating that bees from both fields were foraging in similar places, irrespective of their nest locations. Overall, these results indicate that, by increasing *B. impatiens* colony success and individual worker condition, via greater floral resources, organic systems can provide better biodiversity-based indirect or secondary ecosystem

services in the highly simplified agricultural landscapes of the NGP. However, the extent to which these services are enough to sustain bee populations, particularly during the critical phases of colony establishment and offspring production is still unknown.

Overall, my studies show that organically managed farms support more associated biodiversity including forb weeds and braconid parasitoids, and lower *Cephus cinctus* populations than do conventionally managed farms. These results imply that organic farming, with enhanced floral resources as well as increased disturbances of crop residue, may support natural pest regulation in agroecosystems, a valuable ecosystem service. My studies also demonstrate increased *B. impatiens* colony success and worker condition in organic systems, which, for certain crops and wild flowers can be a good proxy for the enhanced pollination services. In addition, despite the similarities in bee abundance and diversity between systems, bee-forb interaction networks are more complex in organic fields compared to conventional fields, potentially making these agroecosystems more resilient toward disturbances. Soil disturbances due to tillage in organic fields remain a strong limiting factor for ground nesting bees and soil fertility and future researcher may investigate methods for decreasing the need for tillage in organic systems.

Future Directions

The ecological role of associated biodiversity in agricultural landscapes is important (Altieri, 1999; Duru et al., 2015; Isaacs et al., 2009) in providing ecosystem services like pest regulation via parasitoids or pollination services via native pollinators, but, until my work, we lacked the knowledge and status of these beneficial insects in the highly simplified landscapes of the NGP, a globally key agricultural region in the

production of small grains, pulses, forage crops, and oil seeds. Previous studies in the NGP reported higher weed abundance and diversity in organic fields (Pollnac et al., 2008) than in conventional fields, but no research had assessed whether higher within-field floral diversity translates into greater abundance and diversity of bees and more complex bee-flower networks and how farming systems interact with landscape context to impact bee communities. In addition, no knowledge existed on whether higher within-field floral diversity translates into greater bee colony success and better worker condition. My research filled these knowledge gaps by assessing the impacts of dryland farming systems on the associated biodiversity of multiple taxa across trophic levels including weeds, *C. cinctus*, and braconid parasitoids, bees, bee-flower interactions, and arthropod-mediated (pest regulation and bee colony success) ecosystem services. My study findings also added to a growing body of literature regarding effects of percent natural habitat on bee abundances between conventional and organic farms.

My study findings have several future implications. The results of my first study suggest that Kamut, a subspecies of durum wheat and licensed to be grown only in organic systems, may be a genetic lineage that confers potentially novel forms of *C. cinctus* resistance. In addition to using pest-resistant wheat cultivars like Kamut, managing fields organically can enhance natural pest regulation in dryland agroecosystems of the NGP. My second study, showing surprisingly high bee diversity in the resource-poor landscape (i.e. very limited natural habitats and floral resources) of the NGP, raises future questions on how long the bees and bee-flower networks can sustain against future disturbances in these resource-constrained landscapes. My third study, showing greater floral resources and increased bumble bee colony success and worker

condition in organic fields even in the resource-limited agricultural landscape, clearly suggests growers in the NGP and elsewhere that if they have crops requiring pollinators, they can benefit by increasing in acreage of organic fields. Overall, all these studies have management implications that, in addition to increase in organic farming, landscape diversification (by increasing natural habitats, cover crops, and crop rotations), helps to support and conserve parasitoid and bee populations and enhance bee-flower networks.

My findings of increased associated biodiversity and biodiversity-based ecosystems services in the organic farms, compared to conventional, may encourage growers to adopt organic farming, yet, given the environmental impacts of these modern row crop productions and their vulnerabilities to increasingly extreme climate variation, growers and their management practices need to become more environmentally sensitive and resilient. To address these needs, development of ecologically-based management in diversified agroecosystems, and in particular enhancement of biodiversity-based ecosystem services in future agricultural production systems will help. As my study findings shows, greater plant diversity increases natural enemy populations, including parasitoids and predators of crop pests (Landis et al 2000, 2017, Marshall and Moonen 2002, Lundgren et al. 2009) and enhances natural pest regulation (Losey and Vaughan, 2006), thereby reducing the need for heavy reliance on pesticide applications. Reducing insecticide and herbicide use will concomitantly reduce non-target mortality, leaching, and the evolution of resistant populations. Moreover, relying on ecological processes rather than industrial inputs may eventually reduce future risk in agricultural production (Altieri 1999, Gaba et al. 2015), such as disease out-breaks and yield variability. Further studies on impacts of ecologically-based farming systems that rely on ecological

processes as well as the biodiversity-based ecosystems services provisioned by these systems will add knowledge toward the goal of sustainable agriculture.

My study in the NGP showed a very limited natural habitat (12%), despite their importance for nesting, season-long food resources, and refugia for bees as well as other beneficial insects such as natural enemies of pests (Landis et al. 2005, Requier et al. 2015, Danner et al. 2016). Due to the conversion of natural habitats into row crop production, bee abundance between 2008 and 2013 has been declined across 23% of US land including key agricultural regions (Koh et al. 2016). Thus, conservation strategies for bees and other beneficial insects may include allocating 20-30% of agricultural landscape to uncultivated habitats by increased adoption of the Natural Resources Conservation Services' (NRCS) Conservation Reserve Program (CRP), planting native flowers in hedgerows, and including forb crops in crop rotations. These conservation strategies can help enhance beneficial insects' nesting and foraging habitat, consequently bolstering their populations, and will help growers further reap the benefits of pollination and pest regulation.

Growers may have concerns about increased expenses or reduced crop yields, and thus be reluctant to transition to diversified farming systems, adopt ecologically-based management practices, leave their lands uncultivated, or plant native forbs. Therefore, local, state, and federal policies that compensate growers who choose to adopt these new practices and conservation strategies (Robertson et al. 2014) will accomplish the goal of convincing growers to increasing ecologically-based farming systems. Examples of these publicly funded incentives for growers include the NRCS CRP, which compensates growers for leaving a portion of their land uncultivated and the Soil and Water

Conservation Districts, which manages and protects all land and water resources. As an example, we have seen consumer willingness to pay a premium for organic products; hence they could also pay extra in order to get better ecosystem services from beneficial insects with the adoption of ecologically-based diversified agroecosystem.

Beneficial insects provide billions of dollars of pest regulation and pollination services to our valuable crops (Losey and Vaughan, 2006; Gallai et al. 2009) and in the past half century, there has been a 300% increase in the proportion of zoophilously pollinated crops grown in agroecosystems worldwide (Aizen and Harder 2009). Yet, many times, consumers are unaware of the role that insects play in agriculture. Thus, to further public support for arthropod conservation in agroecosystems, education and outreach programs should target consumers, and inform them of the ecosystem services associated that the arthropod diversity provides. Despite all the challenges, adopting ecologically-based practices and diversifying farming systems are necessary steps for the sustainable future of global agriculture in the face of climate change.

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APPENDICES

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2

Table A1. Precipitation and temperature data for Big Sandy, MT, USA

Months	Total Precipitation (mm)				Mean Temperature Maximum (C)				Mean Temperature Minimum (C)			
	2013	2014	2015	LTA ***	2013	2014	2015	LTA	2013	2014	2015	LTA
Oct -April*	87	95	87	103	6.7	4.9	7.94	6.0	-5.7	-8.0	-4.8	-8.0
May	135	38	33	55	21.4	20.8	19.7	21.3	6.0	4.9	5.2	4.7
June	105	82	53	68	25.2	22.5	28.4	25.3	10.3	8.5	10.8	8.8
July	43	84	82	35	29.4	30.9	29.9	31.2	13.3	13.7	13.1	11.8
August	36	78	10	32	30.4	28.7	29.5	30.1	13.0	13.7	12.4	10.4
September	43	25	40	32	25.3	22.4	23.2	23.7	9.8	7.0	5.9	5.2
Annual**	426	342	301	325	14.4	13.7	15.7	14.8	0.2	0.2	1.3	-1.2

* Oct - April period includes data from October through December of the previous year and January through April of current year.

** Annual includes January through December of the same year.

*** LTA (Long Term Average of 94 years) is from 09/01/1921 to 01/16/2015

Source: Western Regional Climate Center, Desert Research Institute, Reno, NV, USA (<http://www.wrcc.dri.edu>).

Table A2. Crop rotation in conventional (C) and organic (O) spring wheat fields between 2013 and 2015 in Big Sandy, MT, USA. All fields were sampled in ‘Year 5’ of the crop phases. Specific information on winter wheat fields was not available.

Year	Systems	Fields	Crop rotation phases				
			Year 1	Year 2	Year 3	Year 4	Year 5
2013	Conventional	C1-C3	Spring wheat (<i>Triticum aestivum</i> L.)	Chemical fallow	Spring wheat	Chemical fallow	Spring wheat
	Organic	O1	Buckwheat (<i>Fagopyrum esculentum</i> Moench)	Spring pea	Barley (<i>Hordeum vulgare</i> L.)	Safflower (<i>Carthamus tinctorius</i> L.)	Kamut (<i>Triticum turanicum</i>)
		O2	Pea (<i>Pisum sativum</i> L.)	Kamut			
		O3	Alfalfa (<i>Medicago sativa</i> L.)	Alfalfa	Spring pea Winter wheat (<i>Triticum aestivum</i> L.)	Safflower Spring pea	Jakubz. (var. Kamut) Kamut Kamut
2014	Conventional	C4-C6	Spring wheat	Chemical fallow	Spring wheat	Chemical fallow	Spring wheat
	Organic	O4	Pea	Kamut	Spring pea	Safflower	Kamut
		O5	Pea	Kamut	Spring pea	Safflower	Kamut
		O6	Safflower	Pea	Barley/alfalfa	Spring pea/alfalfa	Kamut
2015	Conventional	C7	Spring wheat		Spring wheat	Chemical fallow	Spring wheat
		C8	*CRP land	Chemical fallow	CRP land	Chemical fallow	Spring wheat
		C9	CRP land	CRP land	CRP land (terminated)	Chemical fallow	Spring wheat
	Organic	O7	Alfalfa	Alfalfa	Alfalfa	Spelt (<i>Triticum spelta</i> L.)	Kamut
		O8	Alfalfa	Alfalfa	Alfalfa		Kamut
		O9	Barley/alfalfa	Alfalfa	Winter wheat	Spelt Spring pea	Kamut

Sources: Organic farm manager: Seth Goodman, 2013-2015; Conventional farmers: Mark/Patti Gasvoda, JR Labuda, and Frank/Lis Maxwell, 2013-2015. *CRP = Conservation Reserve Program.

Table A3: Agronomic management details for conventional and organic spring wheat fields between 2013 and 2015 at Big Sandy, MT, USA. Specific information on winter wheat fields was not available.

Year	Farming system	Field	Pesticide name	Pesticide rate (g ai ha ⁻¹)	Adjuvants (% in tank mix)	Fertilizer (kg ha ⁻¹)	Wheat cultivar	Row spacing seeding density [yield (kg/ha)]	Farming history
2013	Conventional	C1-C3	Imazamox Propiconazole Glyphosate Octanoic acid est. of bromoxynil + 2-ethylhexyl ester of MCPA	336 269 1682 1121	Non-ionic surfactant (1%)	160 (55N-20P-0K-5S)	Clearfield-Jedd	30cm drill 15kg/ha [2,355]	Chemical fallow/cropping for >20 years
	Organic	O1-O3	-	-	-	Pea/alfalfa	Kamut wheat	18cm chisel plow 28kg/ha [1,211]	24 years
2014	Conventional	C4-C6	Glyphosate 2,4-D LV6	1121 841	N/A	78 (20N-20P-10K-5S)	Clearfield Jedd	30cm drill 15kg/ha N/A	Since 1919
	Organic	O4-O6	-	-	-	Pea/alfalfa	Kamut wheat	18cm chisel plow 28kg/ha [808]	25 years
2015	Conventional	C7-C8	Triasulfuron 2,4-D Propiconazole	22 701 175	-	181 (55N-20P-0K-0S)	Vida	30cm drill 15kg/ha [808]*	C7-C8: CRP until 2014 C9: same as in C1:C3
		C9	Glyphosate	1121	N/A	78 (20N-20P-10K-5S)	Vida	30cm drill 15kg/ha [N/A]	Chemical fallow/cropping for >20 years
	Organic	O7-O8	-	-	-	Alfalfa	Kamut wheat	18cm chisel 28kg/ha [336]	26 years
		O9	-	-	-	Pea/alfalfa	Kamut wheat	18cm chisel [28]**	3 years

Note: All of our conventional fields were chemical fallow the season prior to our study except for C7 and C8, which were CRP (Conservation Reserve Program) for the previous 20 years. These fields were treated with glyphosate (Roundup®) at a rate of 3,786g of active ingredient ha⁻¹ in 2014 fall to break CRP with cultivator that had front row of twisted spikes on it. The producer disked each field twice in the fall of 2014 and prior to seeding in the spring of 2015. All organic fields were cultivated with a chisel plow for seeding and for weed management but a disk plow was also used occasionally to manage the high density weeds. * Low yield was due to hail, drier year, and being a first crop out of CRP. ** Due to hail and drier year. Sources: Organic farm manager: Seth Goodman (2013-2015); Conventional farmers: Mark/Patti Gasvoda (2013, 2015), JR Labuda, (2015) and Frank/Lis Maxwell (2014).

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER 3

Table B1. Complete list of forbs taxa (weeds and volunteer crops) with their relative proportions and floral abundances observed in conventional and organic wheat fields between 2013 and 2015.

Forb taxa	Overall percent composition		Floral abundance	
	Conventional	Organic	Conventional	Organic
<i>Amaranthus blitoides</i> S. Watson	0.001	0.010	0	12
<i>Amaranthus retroflexus</i> L.	0.000	0.651	0	130
<i>Arabidopsis thaliana</i> (L.) Heynh.	0.000	0.001	0	0
<i>Artemisia frigida</i> Willd.	0.000	0.013	0	0
<i>Bassia scoparia</i> (L.) A.J. Scott	0.094	0.195	0	6
Brassicaceae	0.000	0.058	0	5
<i>Buglossoides arvensis</i> (L.) I.M. Johnst.	0.000	0.006	0	0
<i>Carthamus tinctorius</i> L.	0.000	0.956	0	24
<i>Chenopodium album</i> L.	0.000	10.28	0	1541
<i>Chenopodium murale</i> L.	0.000	0.002	0	0
<i>Cirsium arvense</i> (L.) Scop.	3.532	0.002	14	0
<i>Descurainia pinnata</i> (Walter) Britton	0.001	0.041	0	10
<i>Descurainia sophia</i> (L.) Webb ex Prantl	0.000	0.016	0	1
Fabaceae	0.000	0.006	0	0
<i>Fagopyrum esculentum</i> Moench	0.000	0.041	0	3
<i>Helianthus annuus</i> L.	0.010	3.762	0	106
<i>Lactuca serriola</i> L.	0.169	0.595	0	0
<i>Lens culinaris</i> Medik.	0.000	0.203	0	0
<i>Medicago lupulina</i> L.	0.000	0.014	0	2
<i>Medicago sativa</i> L.	1.231	4.811	12	134
<i>Melilotus officinalis</i> (L.) Lam.	0.000	0.098	0	4
<i>Monolepis nuttalliana</i> (Schult.) Greene	0.000	0.001	0	0
<i>Pisum sativum</i> L.	0.000	1.499	0	25
<i>Polygonum aviculare</i> L.	0.016	0.199	0	14
<i>Polygonum convolvulus</i> L.	0.177	9.276	0	96
<i>Salsola kali</i> L.	3.764	50.03	765	1291
<i>Salvia reflexa</i> Hornem.	0.136	0.019	0	0
<i>Silene latifolia</i> Poir.	0.000	0.001	0	0
<i>Sinapis arvensis</i> L.	0.000	3.090	0	105

Table B1 continued

Forb taxa	Overall percent composition		Floral abundance	
	Conventional	Organic	Conventional	Organic
<i>Sisymbrium altissimum</i> L.	0.000	0.060	0	6
<i>Solanum triflorum</i> Nutt.	0.000	0.002	0	0
<i>Taraxacum officinale</i> F.H. Wigg.	0.469	0.051	0	3
<i>Thlaspi arvense</i> L.	0.000	1.817	0	311
<i>Tragopogon dubius</i> Scop.	0.011	0.000	0	0
<i>Trifolium</i> sp.	0.000	0.003	0	0
Unknown (dicot) sp.	0.000	1.116	0	2
<i>Vaccaria hispanica</i> (Mill.) Rauschert	0.000	0.866	0	3
<i>Vicia americana</i> Muhl. ex Willd.	0.002	0.597	0	0
Total	9.613	90.387	791	3834

Source for verification of scientific names and authorities: <http://plants.usda.gov/>

Table B2. Complete list of bee taxa collected between 2013 and 2015 from conventional and organic fields. [†]ITD (Inter tegular length) was the average value of five (or maximum available if <5) randomly selected individuals for each taxon.

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Agapostemon femoratus</i> Crawford	210	79	119	148	86	129	771	8.85	Ground	2.3
<i>Agapostemon texanus</i> Cresson	142	184	326	472	248	282	1654	18.99	Ground	2.0
<i>Agapostemon virescens</i> (F.)	104	75	195	111	44	38	567	6.51	Ground	2.5
<i>Andrena amphibola</i> (Viereck)	0	2	1	0	0	1	4	0.05	Ground	2.6
<i>Andrena geranii</i> Robertson	0	0	0	0	0	1	1	0.01	Ground	1.7
<i>Andrena imitatrix</i> Cresson	0	0	0	1	0	0	1	0.01	Ground	2.6
<i>Andrena lupinorum</i> Cockerell	2	1	1	2	1	1	8	0.09	Ground	3.0
<i>Andrena medionitens</i> Cockerell	0	3	0	0	0	0	3	0.03	Ground	1.9
<i>Andrena nivalis</i> Smith	0	1	0	0	0	0	1	0.01	Ground	2.9
<i>Andrena prunorum</i> Cockerell	7	14	24	33	15	13	106	1.22	Ground	2.8
<i>Andrena</i> sp. 1 (F.)	0	5	0	2	0	0	7	0.08	Ground	2.0
<i>Andrena</i> sp. 2 (F.)	0	0	0	0	0	1	1	0.01	Ground	1.1
<i>Andrena</i> sp. 3 (F.)	0	0	1	0	0	2	3	0.03	Ground	2.1
<i>Anthidium porterae</i> Cockerell	0	3	0	0	0	4	7	0.08	Others	3.8
<i>Anthidium tenuiflorae</i> Cockerell	5	1	3	1	0	0	10	0.11	Others	2.7
<i>Anthidium utahense</i> Swenk	0	2	1	0	0	0	3	0.03	Others	3.0
<i>Anthophora affabilis</i> Cresson	15	12	1	4	0	0	32	0.37	Ground	4.2
<i>Anthophora occidentalis</i> Cresson	4	2	3	7	5	4	25	0.29	Ground	4.4
<i>Anthophora urbana</i> Cresson	0	0	1	3	0	0	4	0.05	Ground	2.9

Table B2 continued

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Anthophora walshii</i> Cresson	1	0	0	1	0	1	3	0.03	Ground	4.3
<i>Apis mellifera</i> Linnaeus	0	0	1	3	2	4	10	0.11	Others	3.4
<i>Ashmeadiella buconis</i> (Say)	0	0	1	0	0	0	1	0.01	Others	2.3
<i>Bombus appositus</i> Cresson	0	1	0	0	0	0	1	0.01	Ground	5.1
<i>Bombus auricomus</i> (Robertson)	0	1	0	0	0	0	1	0.01	Ground	5.0
<i>Bombus centralis</i> Cresson	0	0	0	0	0	1	1	0.01	Ground	3.5
<i>Bombus fervidus</i> (F.)	0	0	1	3	1	5	10	0.11	Ground	5.3
<i>Bombus griseocollis</i> (DeGeer)	0	2	3	8	1	5	19	0.22	Ground	5.4
<i>Bombus huntii</i> Greene	0	0	0	2	1	0	3	0.03	Ground	3.7
<i>Bombus impatiens</i> Cresson	0	0	0	0	0	2	2	0.02	Ground	4.1
<i>Bombus nevadensis</i> Cresson	6	2	2	2	1	0	13	0.15	Ground	5.9
<i>Bombus rufocinctus</i> Cresson	1	4	3	3	1	1	13	0.15	Ground	4.0
<i>Colletes fulgidus</i> Swenk	0	0	1	0	0	0	1	0.01	Ground	3.1
<i>Colletes kincaidii</i> Cockerell	0	0	1	1	0	0	2	0.02	Ground	3.0
<i>Colletes lutzi</i> Timberlake	0	0	0	1	0	0	1	0.01	Ground	1.5
<i>Colletes</i> sp. 1 (Latreille)	1	0	0	0	0	0	1	0.01	Ground	2.8
<i>Diadasia australis</i> (Cresson)	1	2	0	0	0	0	3	0.03	Ground	3.0
<i>Diadasia diminuta</i> (Cresson)	0	1	0	0	0	0	1	0.01	Ground	2.1
<i>Dianthidium curvatum</i> (Smith)	0	0	1	5	2	0	8	0.09	Others	3.0
<i>Dianthidium pudicum</i> (Cresson)	0	0	0	3	0	0	3	0.03	Others	2.3
<i>Dufourea</i> sp. (Lepeletier)	0	0	1	1	0	0	2	0.02	Ground	1.6
<i>Dufourea trochantera</i> Bohart	1	0	0	0	0	0	1	0.01	Ground	1.3

Table B2 continued

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Eucera actiosa</i> (Cresson)	1	1	0	0	0	0	2	0.02	Ground	4.0
<i>Eucera aragalli</i> (Cockerell)	0	2	0	0	0	0	2	0.02	Ground	3.8
<i>Eucera hamata</i> (Bradley)	246	151	74	248	18	87	824	9.46	Ground	3.8
<i>Eucera</i> sp. 1 (Scopoli)	0	2	1	3	1	2	9	0.1	Ground	3.8
<i>Eucera</i> sp. 2 (Scopoli)	0	0	1	2	0	0	3	0.03	Ground	3.5
<i>Eucera speciosa</i> (Cresson)	1	1	1	1	0	1	5	0.06	Ground	3.7
<i>Halictus confusus</i> Smith	137	112	117	32	28	14	440	5.05	Ground	1.5
<i>Halictus farinosus</i> Smith	4	3	0	6	1	3	17	0.2	Ground	2.3
<i>Halictus ligatus</i> Say	33	46	63	46	14	12	214	2.46	Ground	1.7
<i>Halictus rubicundus</i> (Christ)	59	48	122	42	17	23	311	3.57	Ground	1.8
<i>Halictus</i> sp. (Latreille)	0	0	1	0	0	3	4	0.05	Ground	1.5
<i>Halictus tripartitus</i> Cockerell	49	4	3	4	0	0	60	0.69	Ground	0.8
<i>Hoplitis albifrons</i> (Kirby)	0	0	0	0	1	0	1	0.01	Others	2.7
<i>Hoplitis grinnelli</i> (Cockerell)	0	0	0	1	0	0	1	0.01	Others	1.7
<i>Hoplitis pilosifrons</i> (Cresson)	0	6	0	2	0	0	8	0.09	Others	1.5
<i>Hoplitis producta</i> (Cresson)	0	1	0	0	0	0	1	0.01	Others	1.8
<i>Lasioglossum (Evylaeus) Curtis</i>	2	4	0	0	0	0	6	0.07	Ground	1.3
<i>Lasioglossum aberrans</i> (Crawford)	3	2	5	7	4	0	21	0.24	Ground	1.7
<i>Lasioglossum egregium</i> (Vachal)	0	3	4	16	2	3	28	0.32	Ground	2.1
<i>Lasioglossum heterorhinum</i> (Cockerell)	1	0	0	1	0	0	2	0.02	Ground	1.9
<i>Lasioglossum leucozonium</i> (Schrank)	1	3	1	1	2	1	9	0.1	Ground	2.3
<i>Lasioglossum olympiae</i> (Cockerell)	1	4	9	44	5	9	72	0.83	Ground	2.2

Table B2 continued

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Lasioglossum paraforbesii</i> McGinley	25	53	103	116	23	22	342	3.93	Ground	2.0
<i>Lasioglossum s str sp 1</i> Curtis	1	0	0	0	0	0	1	0.01	Ground	1.8
<i>Lasioglossum s str sp 2</i> Curtis	0	0	1	0	0	0	1	0.01	Ground	2.4
<i>Lasioglossum sisymbrii</i> (Cockerell)	32	71	7	26	6	3	145	1.66	Ground	1.7
<i>Lasioglossum trizonatum</i> (Cresson)	0	2	0	2	0	0	4	0.05	Ground	2.5
<i>Lasioglossum zonulum</i> (Smith)	3	2	1	11	1	0	18	0.21	Ground	2.5
<i>Lasioglossum (Dialictus) spp.</i> Curtis	214	536	704	363	318	394	2529	29.04	Ground	1.1
<i>Lasioglossum (Sphecogastra)</i> Curtis	0	1	0	0	0	0	1	0.01	Ground	2.0
<i>Megachile anograe</i> Cockerell	0	0	0	0	0	1	1	0.01	Others	4.0
<i>Megachile brevis</i> Say	2	0	1	1	0	0	4	0.05	Others	2.7
<i>Megachile circumcincta</i> (Kirby)	0	0	1	0	0	0	1	0.01	Others	3.0
<i>Megachile dentitarsus</i> Sladen	3	4	0	0	2	0	9	0.1	Others	4.1
<i>Megachile perihirta</i> Cockerell	1	0	0	0	0	1	2	0.02	Others	3.7
<i>Melecta pacifica</i> Cresson	0	0	0	1	0	0	1	0.01	Ground	3.5
<i>Melissodes agilis</i> Cresson	20	12	11	14	5	1	63	0.72	Ground	2.6
<i>Melissodes bicolorata</i> LaBerge	0	0	1	0	0	0	1	0.01	Ground	2.5
<i>Melissodes communis</i> Cresson	3	1	3	1	1	0	9	0.1	Ground	2.4
<i>Melissodes coreopsis</i> Robertson	2	0	7	4	3	0	16	0.18	Ground	1.9

Table B2 continued

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Melissodes desponsa</i> Smith	0	0	0	1	0	0	1	0.01	Ground	3.0
<i>Melissodes humilior</i> Cockerell	0	0	0	1	0	0	1	0.01	Ground	2.4
<i>Melissodes lupina</i> Cresson	13	9	4	13	3	10	52	0.6	Ground	2.3
<i>Melissodes menuachus</i> Cresson	0	2	0	1	2	0	5	0.06	Ground	2.6
<i>Melissodes pallidisignata</i> Cockerell	3	0	14	3	0	0	20	0.23	Ground	2.7
<i>Melissodes perlusa</i> Cockerell	9	3	4	0	0	0	16	0.18	Ground	2.9
<i>Melissodes perpolita</i> LaBerge	0	0	2	0	0	0	2	0.02	Ground	1.3
<i>Melissodes rivalis</i> Cresson	3	2	3	1	0	0	9	0.1	Ground	3.0
<i>Melissodes</i> sp. 1 (Latreille)	0	0	0	0	1	8	9	0.1	Ground	2.9
<i>Melissodes</i> sp. 2 (Latreille)	0	0	1	0	0	1	2	0.02	Ground	2.4
<i>Melissodes</i> sp. 3 (Latreille)	0	1	0	0	2	0	3	0.03	Ground	2.8
<i>Melissodes</i> sp. 4 (Latreille)	2	0	0	1	1	1	5	0.06	Ground	1.7
<i>Melissodes</i> sp. 5 (Latreille)	0	0	0	0	4	0	4	0.05	Ground	2.3
<i>Nomada articulata</i> Smith	0	1	0	0	0	0	1	0.01	Ground	1.8
<i>Nomia universitatis</i> Cockerell	1	0	0	0	0	0	1	0.01	Ground	2.4
<i>Osmia odontogaster</i> Cockerell	1	0	0	0	0	0	1	0.01	Others	1.8
<i>Osmia</i> sp.1 (Panzer)	1	1	0	2	0	0	4	0.05	Others	2.4
<i>Osmia</i> sp.2 (Panzer)	1	0	0	0	0	0	1	0.01	Others	2.1
<i>Osmia trevoris</i> Cockerell	18	13	11	0	1	0	43	0.49	Others	2.4
<i>Panurginus beardsleyi</i> (Cockerell)	1	0	0	0	0	0	1	0.01	Ground	1.8
<i>Perdita albipennis</i> Cresson	0	2	0	0	4	3	9	0.1	Ground	1.6
<i>Perdita fallax</i> Cockerell	0	0	0	2	2	5	9	0.1	Ground	0.7
<i>Perdita lingualis</i> Cockerell	0	0	0	0	4	0	4	0.05	Ground	1.9
<i>Perdita</i> sp. (Smith)	0	0	0	1	0	1	2	0.02	Ground	1.0
<i>Sphecodes</i> sp.1 (Latreille)	0	0	1	0	0	0	1	0.01	Ground	1.1

Table B2 continued

Bee taxa	2013		2014		2015		Total	Percent	Nesting	ITD [†] (mm)
	Conventional	Organic	Conventional	Organic	Conventional	Organic				
<i>Sphecodes</i> sp.2 (Latreille)	3	2	1	0	0	0	6	0.07	Ground	2.0
<i>Sphecodes</i> sp.3 (Latreille)	0	1	0	0	0	0	1	0.01	Ground	1.4
<i>Stelis</i> <i>lateralis</i> Cresson	0	1	0	0	0	0	1	0.01	Others	1.6
Total	1400	1510	1974	1838	884	1104	8710	100	NA	NA

Table B3. Indicator bee taxa and their indicator values across farming systems and months between 2013 and 2015. Only the taxa with $P < 0.05$ are listed.

Variables		Indicator species	Indicator value	p-value
System	Conventional	<i>Melissodes pallidesignata</i>	0.33	0.02
	Organic	<i>Andrena</i> sp.1	0.27	0.04
Month	June	<i>Anthidium porterae</i>	0.27	0.03
		<i>Halictus rubicundus</i>	0.86	0.001
		<i>Eucera hamata</i>	0.85	0.001
		<i>Lasioglossum paraforbesii</i>	0.85	0.001
		<i>Lasioglossum sisymbrii</i>	0.79	0.001
		<i>Halictus ligatus</i>	0.72	0.001
		<i>Andrena prunorum</i>	0.71	0.001
		<i>Anthophora affabilis</i>	0.56	0.001
		<i>Lasioglossum olympiae</i>	0.53	0.001
		<i>Lasioglossum egregium</i>	0.51	0.001
		<i>Halictus tripartitus</i>	0.44	0.002
		<i>Lasioglossum aberrans</i>	0.43	0.005
		<i>Halictus farinosus</i>	0.42	0.007
		<i>Andrena lupinorum</i>	0.39	0.001
		<i>Andrena</i> sp.1	0.33	0.01
		<i>Lasioglossum zonulum</i>	0.33	0.02
	July	<i>Eucera</i> sp.1	0.32	0.02
		<i>Eucera speciosa</i>	0.30	0.01
		<i>Andrena amphibola</i>	0.27	0.03
		<i>Lasioglossum trizonatum</i>	0.27	0.05
		<i>Sphecodes</i> sp.1	0.27	0.04
		<i>Anthophora occidentalis</i>	0.55	0.001
		<i>Bombus fervidus</i>	0.34	0.01
		<i>Melissodes agilis</i>	0.71	0.001
	August	<i>Melissodes coreopsis</i>	0.43	0.003
		<i>Melissodes pallidesignata</i>	0.43	0.001
		<i>Melissodes menuachus</i>	0.30	0.01

Table B4. Mean total area covered by four land use class types (“Cropland”, “Natural habitat”, “Water”, and “Others”) from nine conventional and nine organic fields at Big Sandy, MT. Area was calculated within the radii of 2km from the centers of each field where the transects were established to collect forbs and bees between 2013 and 2015. Mean and standard error values are in square kilometers.

Land use class types (Area %)	Conventional (Mean $\pm$ SE)	Organic (Mean $\pm$ SE)
Cropland (84.1%)	3.03 $\pm$ 0.65	3.01 $\pm$ 0.65
Natural habitat (12.3%)	0.52 $\pm$ 0.14	0.37 $\pm$ 0.13
Water (3.3%)	0.12 $\pm$ 0.05	0.13 $\pm$ 0.06
Others (0.3%)	0.01 $\pm$ 0.004	0.01 $\pm$ 0.003

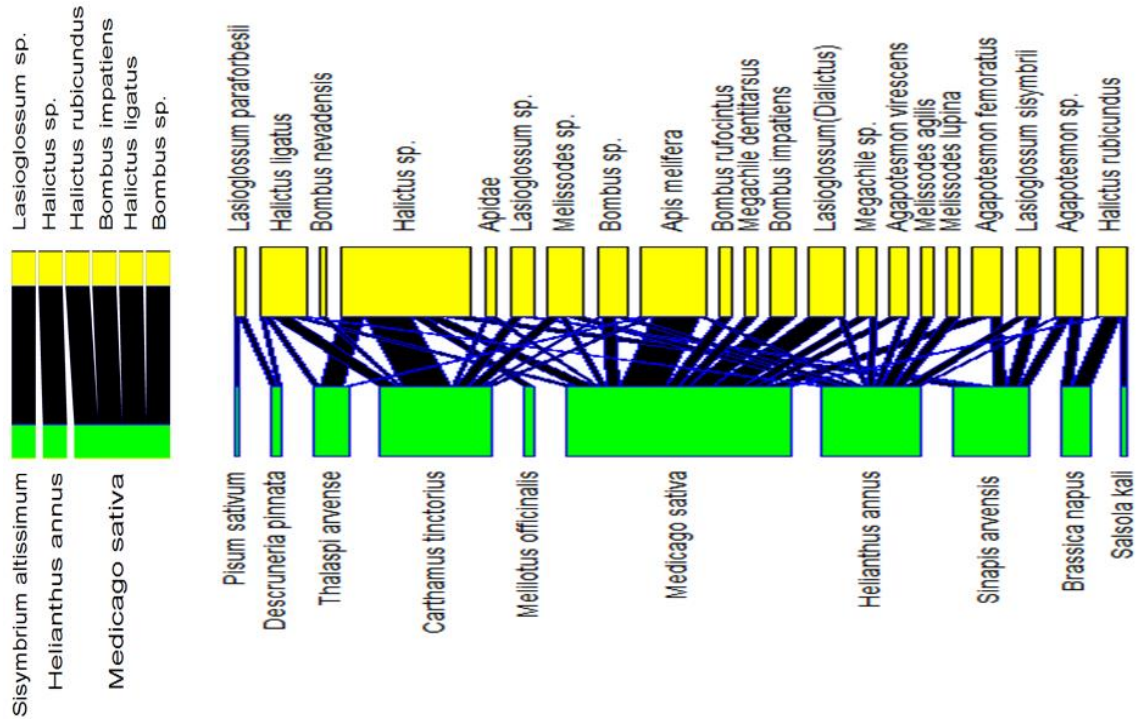


Figure B1. Comparison of bee-forb networks between conventional (left) and organic (right) wheat fields. The top yellow horizontal bars represent bee taxa and the bottom green horizontal bars represent forb species in the networks. The black-blue lines connecting bee taxa and forb species represent interaction links (visits) and the thickness of these lines corresponds to the strength of the interactions between two species. Note: All observation data were pooled across months, fields and years and constructed the bee-forb networks in each system, to show the general patterns of which bee and forb species were present in the landscape during the course of our study.

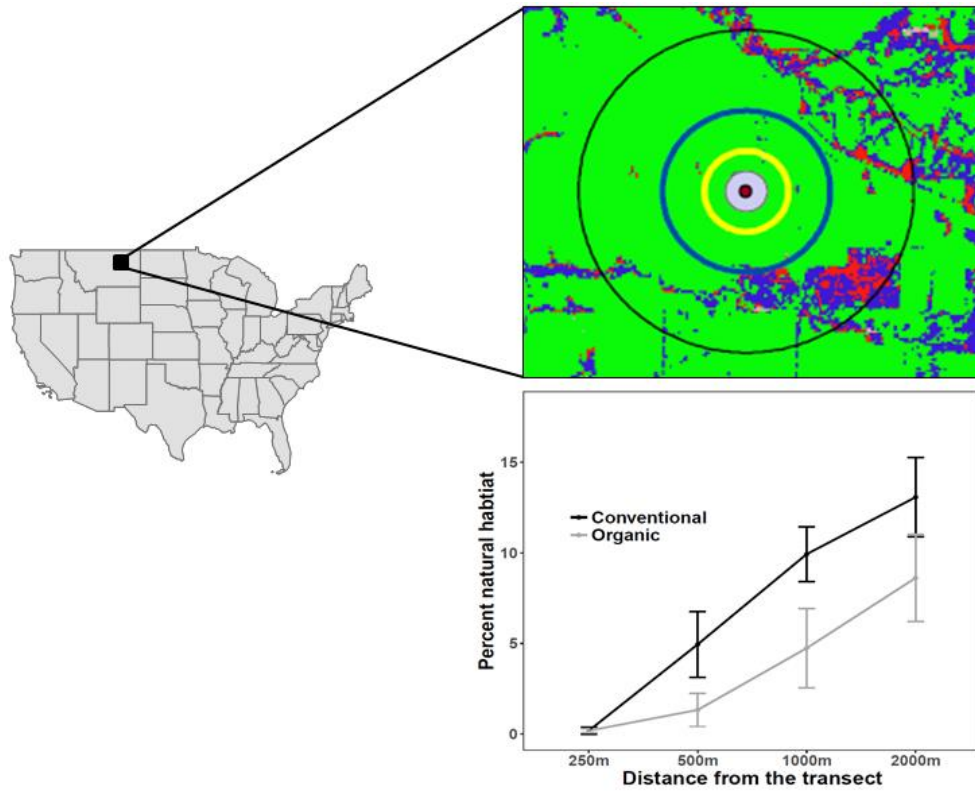


Figure B2. One of the 18 fields (top right) at Big Sandy, MT with 4 circles (250 m, 500 m, 1000 m, and 2000 m) that were used for landscape analysis. Percent natural habitat (mean $\pm$ SE) within each of those four circles across all conventional and organic fields (Bottom right). All 18 fields were used to study forb and bee communities between 2013 and 2015.

APPENDIX C

SUPPORTING INFORMATION FOR CHAPTER 4

Table C1. List of forb species collected for pollen reference collection from Big Sandy in 2014 and 2015.

S.N.	Name	Family
1	<i>Achillea millefolium</i> L.	Asteraceae
2	<i>Amaranthus retroflexus</i> L.	Amaranthaceae
3	<i>Anagallis arvensis</i> L.	Primulaceae
4	<i>Artemisia ludoviciana</i> Nutt.	Asteraceae
5	<i>Artemisia vulgaris</i> L.	Asteraceae
6	<i>Brassica napus</i> L.	Brassicaceae
7	<i>Carthamus tinctorius</i> L.	Asteraceae
8	<i>Caryopteris clandonensis</i> hort. ex Rehder	Verbenaceae
9	<i>Chenopodium album</i> L.	Chenopodiaceae
10	<i>Cirsium arvense</i> (L.) Scop.	Asteraceae
11	<i>Cirsium vulgare</i> (Savi) Ten.	Asteraceae
12	<i>Consolida ajacis</i> (L.) Schur	Ranunculaceae
13	<i>Convolvulus arvensis</i> L.	Convolvulaceae
14	<i>Conyza canadensis</i> (L.) Cronquist	Asteraceae
15	<i>Dasiphora fruticosa</i> (L.) Rydb.	Rosaceae
16	<i>Descurainia pinnata</i> (Walter) Britton	Brassicaceae
17	<i>Equisetum arvense</i> L.	Equisetaceae
18	<i>Fagopyrum esculentum</i> Moench	Polygonaceae
19	<i>Gnaphalium</i> sp. (Herb Linn)	Asteraceae
20	<i>Grindelia squarrosa</i> (Pursh) Dunal	Asteraceae
21	<i>Helianthus annuus</i> L.	Asteraceae
22	<i>Heterotheca villosa</i> (Pursh) Shinnars	Asteraceae
23	<i>Juniperus communis</i> L.	Cupressaceae
24	<i>Lactuca tatarica</i> (L.) C.A. Mey. var. <i>pulchella</i> (Pursh) Breitung	Asteraceae
25	<i>Liatris punctata</i> Hook.	Asteraceae
26	<i>Linum lewisii</i> Pursh	Linaceae
27	<i>Lygodesmia juncea</i> (Pursh) D. Don ex Hook.	Asteraceae
28	<i>Machaeranthera pinnatifida</i> (Hook.) Shinnars	Asteraceae
29	<i>Medicago sativa</i> L.	Fabaceae
30	<i>Melilotus officinalis</i> (L.) Lam.	Fabaceae
31	<i>Oenothera suffrutescens</i> (Ser.) W.L. Wagner & Hoch	Onagraceae
32	<i>Parnassia palustris</i> L.	Saxifragaceae
33	<i>Pisum sativum</i> L.	Fabaceae
34	<i>Polygonum convolvulus</i> L.	Polygonaceae
35	<i>Prunella vulgaris</i> L.	Lamiaceae
36	<i>Ratibida columnifera</i> (Nutt.) Wooton & Standl.	Asteraceae
37	<i>Rosa multiflora</i> Thunb.	Rosaceae
38	<i>Salsola kali</i> L.	Amaranthaceae
39	<i>Sisymbrium altissimum</i> L.	Brassicaceae
40	<i>Solidago mollis</i> Bartlett	Asteraceae
41	<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	Malvaceae
42	<i>Taraxacum officinale</i> F.H. Wigg.	Asteraceae
43	<i>Thlaspi arvense</i> L.	Brassicaceae
44	<i>Tragopogon dubius</i> Scop.	Asteraceae
45	<i>Vaccaria hispanica</i> (Mill.) Rauschert	Caryophyllaceae
46	<i>Verbena bracteata</i> Cav. ex Lag. & Rodr.	Verbenaceae

Source for verification of scientific names and authorities: <http://plants.usda.gov/>

Table C2. List of forb plant taxa (weeds and volunteer crops) with their flower density counted in Big Sandy, MT. Forb plant taxa were quantified by visually estimating percent cover and counting their flowers using 0.5 m × 1 m quadrat at every meter interval along each of the three 25 m transects from each field (six conventional and six organic fields in total) in June, July, and August in 2014 and 2015. There were 25 forb plant taxa in total, but only 18 of them displayed flowers during our study period.

Forb taxa	2014		2015			
	Conventional	Organic	Conventional	Organic	Total	Percent
<i>Amaranthus retroflexus</i> L.	0	22	0	2	24	0.66
<i>Carthamus tinctorius</i> L.	0	9	0	7	16	0.44
<i>Chenopodium album</i> L.	0	24	0	1096	1120	31.01
<i>Cirsium arvense</i> (L.) Scop.	14	0	0	0	14	0.39
<i>Descurainia pinnata</i> (Walter) Britton	0	0	0	5	5	0.14
<i>Fagopyrum esculentum</i> Moench	0	0	0	3	3	0.08
<i>Helianthus annuus</i> L.	0	0	0	104	104	2.88
<i>Bassia scoparia</i> (L.) A.J. Scott	0	4	0	0	4	0.11
<i>Melilotus officinalis</i> (L.) Lam.	0	0	0	4	4	0.11
<i>Medicago sativa</i> L.	0	3	12	120	135	3.74
<i>Pisum sativum</i> L.	0	23	0	1	24	0.66
<i>Polygonum aviculare</i> L.	0	0	0	14	14	0.39
<i>Polygonum convolvulus</i> L.	0	13	0	34	47	1.30
<i>Salsola kali</i> L.	0	274	765	1009	2048	56.70
<i>Sisymbrium altissimum</i> L.	0	0	0	6	6	0.17
<i>Taraxacum officinale</i> F.H. Wigg.	0	0	0	3	3	0.08
<i>Thlaspi arvense</i> L.	0	18	0	20	38	1.05
<i>Vaccaria hispanica</i> (Mill.) Rauschert	0	1	0	2	3	0.08
Total	14	391	777	2430	3612	100

Source of verification of scientific names and authorities: <http://plants.usda.gov/>

Table C3. Overall relationship between relative growth rate and other colony variables.

Colony variables	Test statistics (t)	DF	<i>P</i> -value	Pearson's r
Number of workers	12.56	58	<0.001	0.86
Number of non-brood cells	11.44	58	<0.001	0.83
% empty cells	-4.99	58	<0.001	-0.55
Number of honey pots	11.85	58	<0.001	0.84
Number of pollen pots	3.8	58	<0.001	0.45
Body mass of workers (g)	9.5	58	<0.001	0.78

Table C4. List of plant species identified from pollen collected off of the bee colonies that were deployed in conventional and organic farms at Big Sandy, MT. Out of 46 total plants collected from the field for reference collection, only 30 of them were found to be garnered by *Bombus impatiens*, but 15 plant species were outside of our reference collection.

Plant taxa	2014		2015		Total	Percent
	Conventional	Organic	Conventional	Organic		
<i>Achillea millefolium</i> L.	0	0	116	351	467	4.25
Amaranthaceae	0	0	2	11	13	0.12
<i>Anagallis arvensis</i> L.	103	0	0	0	103	0.94
Asteraceae	4	0	183	176	363	3.31
<i>Astragalus agrestis</i> Douglas ex G. Don	0	0	3	1	4	0.04
Brassicaceae	0	0	0	37	37	0.34
<i>Brassica napus</i> L.	28	0	0	0	28	0.26
<i>Carthamus tinctorius</i> L.	46	87	55	217	405	3.69
<i>Caryopteris clandonensis</i> hort. ex Rehder	109	0	0	0	109	0.99
<i>Cirsium arvense</i> (L.) Scop.	0	0	13	37	50	0.46
<i>Cirsium</i> sp.	130	55	0	0	185	1.69
<i>Cirsium vulgare</i> (Savi) Ten.	229	93	36	32	390	3.55
<i>Consolida ajacis</i> (L.) Schur	0	1	0	0	1	0.01
<i>Convolvulus arvensis</i> L.	21	15	0	0	36	0.33
Corylaceae	154	35	3	23	215	1.96
<i>Dasiphora fruticosa</i> (L.) Rydb.	0	6	0	3	9	0.08
Fabaceae	4	0	0	12	16	0.15
<i>Fagopyrum esculentum</i> Moench	0	0	74	320	394	3.59
<i>Oenothera suffrutescens</i> (Ser.) W.L. Wagner & Hoch	2	0	2	0	4	0.04
<i>Gentianella</i> sp.	7	0	0	0	7	0.06
<i>Grindelia squarrosa</i> (Pursh) Dunal	0	0	0	3	3	0.03
<i>Helianthus annuus</i> L.	9	2	149	180	340	3.10
<i>Heterotheca villosa</i> (Pursh) Shinnars	1	2	101	394	498	4.54
<i>Lactuca tatarica</i> (L.) C.A. Mey. var. <i>pulchella</i> (Pursh) Breitung	83	7	0	0	90	0.82

Table B2 continued

Plant taxa	2014		2015		Total	Percent
	Conventional	Organic	Conventional	Organic		
<i>Liatris punctata</i> Hook.	0	0	1	8	9	0.08
<i>Lonicera</i> sp.	0	0	87	331	418	3.81
<i>Medicago sativa</i> L.	343	924	1225	1870	4362	39.73
<i>Melilotus officinalis</i> (L.) Lam.	99	41	40	81	261	2.38
<i>Parnassia palustris</i> L.	0	61	0	0	61	0.56
<i>Pisum sativum</i> L.	2	0	7	7	16	0.15
Poaceae	0	0	26	17	43	0.39
<i>Polygonum convolvulus</i> L.	0	0	0	12	12	0.11
<i>Portulaca</i> sp.	0	0	0	15	15	0.14
<i>Prunella</i> sp.	8	3	73	2	86	0.78
Rosaceae	0	0	16	30	46	0.42
<i>Salsola kali</i> L.	1	8	0	15	24	0.22
<i>Solidago mollis</i> Bartlett	0	0	264	100	364	3.32
<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	0	0	166	226	392	3.57
<i>Taraxacum officinale</i> F.H. Wigg.	0	0	0	48	48	0.44
<i>Thlaspi arvense</i> L.	0	0	0	46	46	0.42
<i>Tragopogon dubius</i> Scop.	0	0	358	79	437	3.98
<i>Vaccaria hispanica</i> (Mill.) Rauschert	0	0	0	3	3	0.03
<i>Verbena</i> sp.	0	0	3	0	3	0.03
<i>Machaeranthera pinnatifida</i> (Hook.) Shinners	1	9	0	0	10	0.09
<i>Zea mays</i> L.	0	0	258	297	555	5.06
Total	1384	1349	3261	4984	10978	100

Source for verification of scientific names and authorities: <http://plants.usda.gov/>



Figure C1. A bee hive placed on a platform of PVC pipes tightly tied together and firmly anchored in the ground in a spring wheat field at Big Sandy, MT

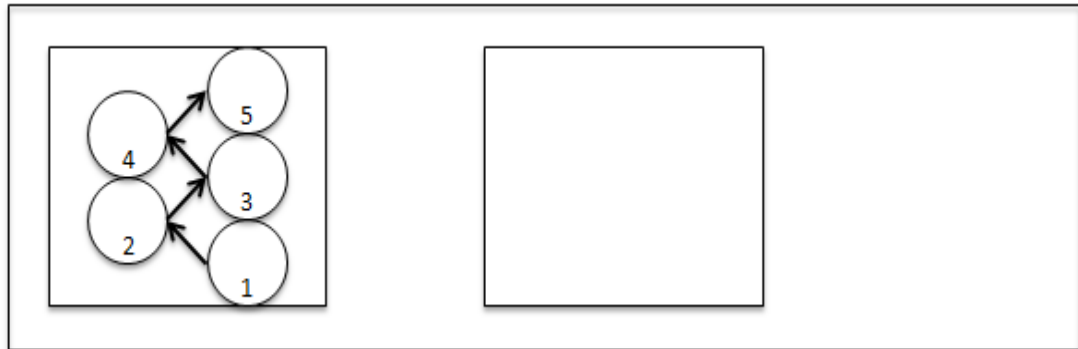


Figure C2. Schematic diagram of a pollen slide showing a “W” - shaped sub-sampling technique. All five sub-samples were pooled to make a single sample per bee/slide. Pollen was collected off of bumble bee colonies.