Native bee (Hymenoptera: Apiformes) response to ecological restoration in southern Ontario

by

Kylie McLeod

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.
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Abstract

Bee declines have been reported globally and habitat loss and degradation due to urbanization and agricultural intensification are two of the primary drivers. Native bees play a critical role in plant reproduction, and declines in abundance and diversity of bees are expected to impact flowering plant biodiversity and productivity of insect pollinated agricultural crops. Habitat restoration can help mitigate declines by increasing the amount and quality of available bee habitat. However, outside of agroecosystems bees are rarely specified in restoration targets and little is known about how they respond to habitat restoration. My thesis addresses this knowledge gap by: (1) documenting the structure and function of the native bee community at a restored wet meadow to establish a baseline for future monitoring activities, (2) comparing the influence of two restoration approaches on the established bee community, and (3) exploring changes in functional groups and pollination function with time since restoration. I sampled bees at degraded, restored, and (semi)natural habitats at 12 sites in four locations in southern Ontario. I used a combination of structural (abundance, richness, and evenness) and functional (guilds based on social and nesting habits and plant-pollinator interaction networks) characteristics to describe and compare bee communities.

I collected a total of 10,446 bees from 30 genera and six families representing a range of phenologies, social behaviours, and nesting habits. At Dunnville Marsh, a restored wet meadow, I collected 5,010 bee specimens from 27 genera and six families. The bee community at Dunnville Marsh was diverse and well connected within 4-6 years of restoration, emphasizing the importance of wet meadows as native bee habitat. However, wood nesters and cleptoparasites were relatively uncommon suggesting that the community may be less stable compared to older habitats.

Between 2005 and 2008, individual fields at Dunnville Marsh were dug with pits and mounds before planting and seeding or were seeded into weedy ground. Digging pits and mounds did not convey a clear advantage to the establishing bee community, but genus richness was greater in pit and mound sites ($p=0.04$). As well, the restoration approach used influenced the relative representation of guilds within the community. Ground nesters and wood nesters were significantly more abundant in pit and mound treated sites ($p<0.001$), perhaps reflecting the larger amounts of bare ground ($p<0.001$) and the greater potential for sapling survival on mound tops. Stem nesters were more abundant in planted sites ($p<0.001$), and floral richness and abundance did not differ between the two restoration approaches.

Finally, diversity and evenness of guilds based on social and nesting habits increased with age since restoration, indicating that communities in (semi)natural habitats are more functionally diverse than those in restored habitats, but that communities in restored habitats are more functionally diverse than those in degraded habitats. Relative abundance of guilds changed with age since restoration in ways that reflected structural habitat changes associated with succession. Degraded sites had the highest relative abundance of ground nesters, while (semi)natural sites had the highest relative abundance of wood nesters. Plant-pollinator interaction networks did not demonstrate clear trends with respect to age since restoration, but indicated that communities that establish in response to non-targeted restorations can be diverse, robust to extinction, and well connected.

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Chapter 1 Introduction

1.1 Thesis Structure and Objectives

This thesis is structured in the manuscript style, but is prefaced by a literature review (Chapter 1) and a detailed description of the study locations (Chapter 2), and is followed by a brief discussion of the barriers present in pollination-based restoration (Chapter 6). Chapters 3, 4, and 5 use the collective 'we' in reference to all study authors.

In Chapter 3 I surveyed native bees in twelve sites in southern Ontario using pan traps and sweep nets. I used the results of the pan trap collections to compare the influence of pan trap colour on abundance and richness of collections and to identify colour preferences of the five families and the abundant genera. I qualitatively compared collections from pan traps and sweep nets to identify biases in the families and genera collected.

In Chapter 4 I surveyed of native bees at a series of recently restored wet meadows located within Dunnville Marsh, southern Ontario. This allowed me to describe the structure and function of the bee community, to evaluate the status of the restoration so far, and to provide a baseline that can be used to monitor changes to the community. The use of different restoration techniques in the different fields allowed me to compare the bee communities that establish in sites dug with pits and mounds before planting and seeding with communities that establish in sites that are seeded into weeded ground.

In Chapter 5 I surveyed native bees at a series of degraded, restored and (semi)natural sites in the Region of Waterloo, southern Ontario. This allowed me to observe how the relative abundance of functional groups, based on social behaviours and nesting habits, and properties of plant-pollinator visitation networks changed with time since restoration.

In Chapt 6 I identified some of the barriers present in pollination-based restoration research and practice and how they influenced my thesis research.

1.2 Bees as Pollinators

Pollination is the transfer of pollen from anther to stigma. Pollen transfer can occur within a single flower, a single plant, or across plants, and is facilitated by wind, water, gravity, or biotic vectors. Animal mediated pollination accounts for an estimated 90% of flowering plant pollination services worldwide (Friedman and Barrett 2009). Animal pollinators facilitate plant reproduction, increase the recombination of genetic material, and enhance fruit set (Kevan 1999; Kearns et al. 1998;

Faegri and van der Pilj 1971). Animal pollinators include birds, reptiles, and insects; the latter are the primary pollinators in most terrestrial ecosystems (Allen-Wardell et al. 1998). Bees (Hymenoptera: Apiformes) are the most efficient insect pollinators and they possess physical and lifestyle traits that maximize pollen transfer (Thorp 2000; Michener 2000). Tracking pollen transfer by bees can be difficult and time consuming, and flower visitation by known pollinating insects is considered an appropriate proxy for pollination (Alarcon 2010; Vazquez et al. 2005). For the purpose of this thesis, I use floral visitation as a proxy for pollination. Floral visitation is defined as contact by known pollinating insects with a flower's reproductive organs.

Bees are anthophiles and depend on flowers as their primary and often only food source at both mature and larval stages (Michener 2000). This obligate relationship results in multiple flower visits throughout the flight season, providing many opportunities for pollen transfer. Bees are physically distinguished from other Hymenoptera by the presence of branched hairs (Michener 2000). These hairs trap pollen, and electrostatic interactions between the anthers, hairs, and stigma, can enhance pollen attraction and deposition (Vaknin et al. 2007; Thorp 1979). Physical structures such as scopa (hair brushes on the legs or the underside of the metasoma), and corbiculae (fringed plates on the hind legs) are specialized areas for pollen storage that allow for increased pollen transport (Thorp 2000). There are species- or even genera-specific physical structures, often hairs or modified hairs, to help remove pollen from flowers (reviewed in Thorp 2000). Other lifestyle traits that enhance the pollinating abilities of bees relative to other groups include oligolecty (host plant specialization), seasonal synchrony with bloom period, buzz pollination, and daily synchrony with flower openings (Thorp 1979). Because of these adaptations, and their widespread abundance, bees are collectively the most effective overall pollinators of flowering plants and are the focus of this thesis (Allen-Wardell et al. 1998).

1.3 Bees of Canada

Bees (Hymenoptera, superfamily Apoidea) can be distinguished from the sphecoid wasps by branched or plumose hairs, and a broadened hind basitarsus, relative to lower tarsus segments (Michener et al. 1994). Six families of bees, represented by 39 genera have been recorded in Canada east of Manitoba (Packer et al. 2007). The six families – Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Mellitidae – represent a range of social structures, nesting habits, and foraging behaviours (Packer et al. 2007). Bee social structure varies from solitary to eusocial. Social habits are often, but not necessarily, shared by species belonging to the same genera (Michener 2007). *Apis mellifera* (European honeybees) is a well-known eusocial species that lives in colonies with a structured social system of a queen, drones, and sterile workers (Tautz 2008). *A. mellifera* colonies function almost as a single organism with tasks divided among the members of the groups. This organized social structure makes *A. mellifera* an easy to manage species and it is used across the world for crop pollination (Tautz 2008). Feral colonies of *A. mellifera* are rare and are in decline in part due to pest and pathogen spillover from managed colonies (Allen-Wardell et al. 1998). The bumblebees (*Bombus spp.*) are one of the few eusocial bee genera native to Canada, and have been employed by some growers to pollinate greenhouse plants, such as tomatoes (Daly et al. 2012; Goulson 2010; Morandin et al. 2001). In the wild, a single queen emerges in the spring and establishes a colony that can grow to up to 100 members (Goulson 2010). Solitary bees nest alone; however, they may share areas of their nests with other individuals, often sisters (Michener 2000). Because of the range of behaviours, from sharing nests entrances, to sharing nests but not caretaking duties, to sharing some caretaking duties, it can be difficult to classify some species as social or solitary (Michener 2000). Some bee species are parasitic and can classified as either social parasites or cleptoparasites (Michener 2007). Social parasites are less common, but include *Psithyrus*, a parasite of the *Bombus spp*. Social parasites parasitize eusocial hosts and functionally replace the queen, often participating in nest activities (Michener 2007). In contrast, cleptoparasites lay an egg in in a cell of their host's nest and usually leave the nest for the host to feed and raise their young (Michener 2007). Occasionally the cleptoparasite will stay behind and occasionally they will open up a cell and replace a host's egg with their own (Michener 2007). Cleptoparasites are more frequently occurring because their host population, primarily solitary bees, is larger. In all parasitic species, pollen transport adaptations are often reduced (Michener 2007).

Bees exhibit a variety of nesting habits, which are often linked to their social structure. Bumblebees are ground nesters (most underground, some above ground) and the queens must seek out relatively large nest sites in the spring because of the expected growth of her colony over the season (Goulson 2010). A number of solitary bees from the Apidae, Andrenidae, Halictidae, Megachilidae, and Colletidae are also ground nesters (Michener 2000). These bees dig their nests in bare spots of ground with some vegetation, in sandy or silty soil, in southern or western slopes, in the sunshine, and in areas unlikely to flood (Potts et al. 2003; Delaplane and Mayer 2000). Depending on their level of sociality, bees may dig a single nest, or form networks of individual nests with connecting tunnels (Michener 2007). Other bees, including a number of the Megachilidae and the *Ceratina* take advantage of existing holes to use as nest sites. These holes may be in hollow pithy stems (e.g. *Ceratina* and *Hylaeus*), or holes in trees made by other insects (Vickruck et al. 2011; Richards et al. 2011). The *Xylocopa* use their strong jaws to excavate their own tunnels in wood (Keasar 2010).

Bees are anthophiles and, with the exception of most parasitic and cleptoparasitic species, depend on pollen and nectar for food throughout their lifecycle (Michener 2000). This relationship makes them efficient pollinators because adults must make frequent visits to feed themselves and to collect food for their larvae. Bees may be specialist or generalist, and some species have adaptations to facilitate the removal of pollen and/ or nectar from specific host plants (Thorp 2000). Bees with a single host plant (or type of plant) are called oligolectic, while bees with multiple host plants are polylectic. Most plant-pollinator communities are asymmetric, with the majority of the community made up of polylectic species and a few oligolectic species (Winfree 2010; Vazquez et al. 2009; Bascompte et al. 2006; Vazquez and Aizen 2004; Bascompte et al. 2003). This community structure strengthens communities against species loss, but relies on diverse plant and pollinator communities. Bee foraging behaviour varies by species, but most tend to forage during the day, as this is the time that most flowers are open. Some groups, such as the *Bombus spp.*, are more abundant in the early morning, whereas others, such as honeybees, forage later in the day (Thompson and Hunt 1999). A few species forage on night blooms (Carvalho et al. 2012; Warrant 2007); however, no Canadian species have been recorded foraging at night. Bees are most likely to be found foraging on warm sunny days, with no rain, and low wind speeds (Michener 2000). Maximum foraging range can vary from a kilometer for small-bodied solitary bees, up to several kilometers for larger bodied bees (Greenleaf et al. 2007; Gathman and Tscharntke 2002). Foraging distances and patterns can be extremely plastic and are influenced by landscape structure, habitat structure, and the placement of floral rich patches within the habitat (Jha and Kremen 2013; Jauker et al. 2009; Osborne et al. 2008).

The native bees of Canada exhibit a range of social, nesting, and foraging habits. This range of habits is important for the pollination of diverse flowering plant communities in diverse habitat types. The range of habitat requirements needed to fulfill the various social, nesting, and foraging requirements makes bees potentially powerful indicators for assessing ecosystem integrity.

1.4 Pollinator Declines

Over the past few decades, reports of managed pollinator losses have steadily increased and have been reported in most areas of the globe (Neumann and Carreck 2010; Johnson et al. 2009; Allen-Wardell et al. 1998; Steffan-Dewenter et al. 2005; Potts et al. 2010; Winfree 2010). Colony collapse disorder, reduced genetic stock, aggressive exotic species, and pests and diseases are among the primary causes of managed pollinator declines (Allen-Wardell et al. 1998). The European honeybee, *A. mellifera*, is the predominant managed pollinator and is responsible for pollinating an estimated 35% of crops worldwide (Klein et al. 2007). Despite widely expressed fears of declining *A.*

mellifera populations, total stocks of *A. mellifera* have been increasing globally since 1961 (Aizen and Harder 2009). Increases are not globally homogeneous and *A. mellifera* populations in the United States declined between 1961 and 1996 (Aizen and Harder 2009). Localized declines, particularly in a country as large and as agriculturally intensive as the United States are concerning. Even countries with increasing numbers of *A. mellifera* colonies are not necessarily protected from future pollinator deficits. Aizen and Harder (2009) report that the rate of *A. mellifera* population increase is insufficient relative to the growing pollination demand of agricultural crops. Amidst evidence of declining native pollinator populations, Garibaldi et al. (2013) suggest that pollination by *A. mellifera* alone will not be adequate to meet increasing crop pollination needs.

Native bees are likely in global decline; however, in many areas of the world, including North America, there is little historical data available to empirically assess declines (Winfree 2010). In Europe, where there is a greater history of insect record keeping, Biesmeijer et al. (2006) compared pre-1980 bee and hoverfly communities to post-1980 communities in Britain and the Netherlands using a grid system (10km by 10km cells). Biesmeijer et al. (2006) found significant declines in bee richness (number of species) in 52% and 67% of British and Dutch cells, respectively. Species susceptible to decline tended to be diet specialists, long-tongued, and characterized by slower development and lower mobility (Biesmeijer et al. 2006). Species that increased post-1980 tended to be common pre-1980 (Biesmeijer et al. 2006). In North America a recent study, with access to a unique dataset, compared current native bee populations to those recorded over 120 years ago and found that 50% of the original bee species were extirpated (Burkle et al. 2013). Both Burkle et al. (2013) and Biesmeijer et al.'s (2006) also detected associated declines in pollination function and plant community richness, respectively. These findings are troubling because they indicate that the loss of pollinator species can have cascading effects on their associated communities. Certain pollinating groups, such as the *Bombus spp.*, are comparatively well studied and declines, extirpations, and extinctions have been reported for a number of species of this genus (Cameron et al. 2011; Grixti et al. 2009; Williams and Osborne 2009; Colla and Packer 2008; Goulson et al. 2008). In eastern Canada, the only studies that have assessed native bee declines have targeted bumblebees (Colla et al. 2012; Colla and Packer 2008). Colla et al.'s (2012) survey of North American bumblebees using museum specimens assessed one species as critically endangered (*Bombus affinis*), six species as endangered, and four species as vulnerable. Not all species are declining. Species response is variable, and some species, such as *Bombus impatians* a historically common species in Canada, are increasing in both number and range (Colla et al. 2012; Goulson et al. 2008). The extent to which trends in one geographic local are reflected in other areas of the world, and the extent to which trends in *Bombus spp.* are reflected in other groups are uncertain and remain to be tested (Winfree 2010).

Habitat loss and fragmentation are the suspected leading drivers of native bee declines, and where historic records aren't available for comparisons, bee communities have been compared along disturbance gradients to achieve a proxy for community response to landscape changes over time (e.g. Bommarco et al. 2010; Winfree et al. 2009; Kremen et al. 2002). In a meta-analysis of bees' responses to anthropogenic disturbance Winfree et al. (2009) found that wild bee abundance and diversity were significantly negatively affected by disturbance, particularly by habitat loss and fragmentation. Decreasing habitat patch size, as a result of habitat loss and/ or fragmentation, can significantly shift the native bee community (Bommarco et al. 2010), and result in lower species richness (Krauss et al. 2009). Habitat loss and fragmentation are primarily driven by urbanization, suburbanization, and agricultural intensification and are major threats to biodiversity (Hoekstra et al. 2005; Kruess and Tscharntke 1994). Grixti et al. (2009) found that major bumblebee declines in the American Midwest coincided with agricultural intensification. A study of bee response to agricultural intensification in Europe found that solitary bees were even more sensitive than bumblebees (Le Feon et al. 2010). Given this evidence of species loss it is not surprising that agricultural intensification is associated with degradation of pollination services and decreased species richness and abundance (Le Feon et al. 2010; Kremen et al. 2002), while proximity to natural areas is positively related to pollination services (Klein et al. 2012; Garibaldi et al. 2011; Watson et al. 2011; Le Feon et al. 2010; Kremen et al. 2004).

Other drivers of native bee declines are suspected to include climate change, pesticides, pests and pathogens, and introduced species (Potts et al. 2010; Kevan and Imperatriz-Fonseca 2002). It has been speculated that managed and native bees may be the 'canaries in the coal mine', indicator taxa whose recent declines are indicative of broader declines in ecosystem integrity (Kevan and Viana 2003; Kevan 1999). Native bee declines are immediately concerning because of the ecosystem services they provide to (semi)natural and agricultural habitats and the potential cascading effects of the loss of these services to plant communities.

1.5 Ecosystem Services: Valuation of Pollination Services

Ecosystem services are benefits that people directly or indirectly obtain from ecosystems. These benefits can be in the form of provisioning (e.g. agriculture), regulating (e.g. disturbance), supporting (e.g. pollination), and/ or cultural (e.g. aesthetic value of natural areas) services (Liu et al. 2010; Millenium Assessment 2005). Ecosystem services are notoriously difficult to value, but are nonetheless becoming increasingly popular (if controversial) among habitat managers. Because management plans are often driven by lists of pros and cons and associated dollar values, valuing ecosystem services provides a platform for incorporating these services into plans from which they were previously absent. Whether this is the most appropriate way to include these services is controversial. Supporters of ecosystem services valuation argue that valuation is necessary for these services to be even remotely considered in management decisions, and that techniques for valuation are improving with time (e.g. Winfree et al. 2011; Aizen et al. 2009; Allsopp et al. 2008). Others are more critical and caution against relying too heavily on monetary valuation because it will tend to favour conservation strategies only when they align with economic arguments (Kremen et al. 2002). For a service to be valued it needs a recipient, and while in some cases the recipient and value can be defined (e.g. pollination of cash crops), in other cases it is harder to discern (e.g. pollination of natural areas). This dichotomy is reflected in the literature: there are a number of studies assessing the value of crop pollination, but no attempts to value pollination in natural areas. In Ontario, the Ministry of Natural Resources (OMNR) has taken steps towards valuing the services provided by the natural areas of southern Ontario (Troy and Bagstad 2009), but how these services and valuations will be incorporated into management plans remains to be seen.

Pollination is an important ecosystem service that is difficult to value. Native bees are the primary pollinators of flowering plants in most terrestrial ecosystems, and are primary or supplementary pollinators of bee pollinated agricultural crops (Garibaldi et al. 2013; Klein et al. 2007). Efforts aimed at valuing pollination have concentrated on pollination of crop plants. Non-animal pollinated plants such as rice, wheat, and corn provide the bulk of the calories consumed in the world; however, animal pollinated plants make up 87 of the 115 leading global food crops (Klein et al. 2007). Globally, Klein et al. (2007) found that of the leading food crops traded on the world market that are not wind pollinated, self pollinated, or parthenocarpic, pollinators are essential for 13 crops, important for 30, moderately important for 27, slightly important for 21, unimportant for 7, and unknown for 9. Aizen et al. (2009) predicted that the absence of animal pollination would result in a total loss of crop production between 3 and 8%, and identified trends of increasing production of pollinator dependent crops. In terms of dollars, Gallai et al. (2009) estimated that pollinator losses could result in monetary losses of 153 billion Euros with most of the cost attributed to fruit and vegetable crops. This figure does not reflect market responses to losses, nor does it differentiate between the contributions of wild and managed pollinators. More recently, Winfree et al. (2011) presented three valuation methods one of which, the net income method, allows for services to be attributed to different taxa (e.g. native vs. managed pollinators).

No attempts have been made to estimate the value of lost pollination in natural systems due to native pollinator declines. This is because (1) the outcomes of pollination in natural systems are more difficult to quantify and value, and (2) the extent and diversity of natural systems that rely (to some degree) on pollination are too numerous and too vast to effectively determine the impacts of pollinator losses. The value of pollinators in natural areas is often discussed in terms of ecosystem resilience, defined as “the capacity of a system to absorb disturbance and still retain its basic form and function” (Walker and Salt 2006, pg. xiii), as opposed to dollar values (Maler et al. 2008). Reproduction and genetic recombination of flowering plants are important for maintaining resilient and genetically diverse plant communities that can withstand environmental fluctuations in the long term. Native bees are key contributors to resilient plant communities because they are obligately responsible for the reproduction of certain flowering plants, can increase the rate of reproduction of others, and can facilitate the recombination of plant genetic material (Kevan 1999, Kearns et al. 1998; Friedman and Barrett 2009). Diverse plant-pollinator communities are also better at recruiting new (to the community) plant species (and perhaps pollinator species), than are less diverse communities (Fontaine et al. 2006). Diverse plant and pollinator communities tend to have greater capacity to adapt to fluctuations in climate, pests and diseases, and other biotic and abiotic variables (Luck et al. 2003; Winfree and Kremen 2009). For example, Brittain et al. (2013) found that under changing environmental conditions, pollination was greatest in almond orchards with the most diverse pollinator populations. Complementarity between managed and native and/ or among native pollinators allows for flexible responses to changing environments (Winfree and Kremen 2009; Kremen 2005).

Pollination is a valuable ecosystem service, and regardless of whether it is measured by the value of crops produced or by its contribution to ecosystem resilience, the stability of this service relies on diverse plant and pollinator communities. For that reason, efforts within restoration ecology should include restoration of pollinator populations and the wider community that supports them.

1.6 Restoration Ecology

Ecological restoration is “the process of assisting the recovery of an ecosystem that has been damaged, degraded, or destroyed” (SER 2004). One of the central challenges to restoration ecology is defining goals and targets that will guide the assisted recovery of an ecosystem. Originally, the goal of restoration was to restore both the abiotic features and the biotic communities of a degraded site to replicate a historic target state (Harris et al. 2006). As the discipline has evolved over time, so too has the definition of targets. Hildebrand et al. (2005) criticized the feasibility of replicating a historic state and labeled it the ‘myth of the carbon copy’. Replicating a historic state requires the practitioner to have knowledge of the composition and function of a given historic state, and to be able to choose the most appropriate target state from a range of historic states. Identifying the composition and function of a historic target is problematic because written historic records are lacking or incomplete, and many ecosystems lack historic remnants that can be substituted as targets. Even when historic remnants exist, these remnants have often been subject to climatic changes and anthropogenic impacts and no longer resemble the ‘true’ historic state (Jackson and Hobbs 2009; Harris et al. 2006). The problem of identifying appropriate target sites was encountered in this thesis, because there were no (appropriately sized) remnants of natural meadows in the geographic areas where the studied restorations were carried out. If a target *is* identified the practitioner is faced with the challenging task of replicating specific abiotic features in the hopes that these features will attract the specific biotic communities that are desired (Hobbs 2007; Hildebrand et al. 2005; Ehrenfeld 2000). This alone is daunting, but practitioners encounter an impossible task if climatic changes and anthropogenic impacts have altered the landscape such that returning to the historic state is no longer possible (Jackson and Hobbs 2009). Even if returning to a historic state is possible, it may not be practical or desirable (Thorpe and Stanley 2011; Jackson and Hobbs 2009).

Anthropogenic changes to the landscape, including the facilitation of non-native species introductions and human driven climate change, have resulted in hybrid and novel ecosystems. Hybrid ecosystems are ecosystems that combine characteristics of the historic system with novel structural and/ or functional characteristics (Hobbs et al. 2009). Novel ecosystems are ecosystems that have been completely transformed, and no longer resemble the historic system in either structure or function (Hobbs et al. 2009). Differentiating between the two is challenging, but it is generally accepted that novel ecosystems have crossed a threshold and cannot return to their historic state, while hybrid systems could return given a certain amount of effort (Hobbs et al. 2013). In a world where human activities directly or indirectly affect all areas of the globe, historic targets are becoming less realistic and hybrid and novel ecosystems are gaining recognition as legitimate restoration targets (Hobbs et al. 2013).

If hybrid and novel systems are to be the new targets of restoration programs, then relying on structural metrics (e.g. species composition) to assess restoration success becomes problematic because there is no appropriate baseline for determining what *should* be there. Instead, the focus naturally shifts to ecosystem function (e.g. nutrient cycling, pollination). In reality, a combination of structural and functional metrics may be the most holistic way of assessing restoration ‘success’. Ehrenfeld (2000) identified three categories of restoration goals: the species conservation approach, the ecosystem function approach, and the ecosystem services approach. Ecosystem services are differentiated from ecosystem function by the clear (often monetary) value attached to them. Ecosystem function and ecosystem services may overlap, for example pollination is a necessary ecosystem function (necessary for plant reproduction) but it can also be valued as an ecosystem service that enhances fruit production in agricultural fields. Restoring ecosystem function and/ or ecosystem services is usually more flexible than species conservation. For example, restoring pollination can usually be accomplished without fixed species compositions because species with shared ecological function can be interchangeable. Focusing on function over structure may prevent habitat managers from restricting the trajectory to a single path that may become unfavourable over the span of the trajectory (Hildebrand et al. 2005), or from focusing on certain focal species at the expense of all others (Ehrenfeld 2000).

Accepting uncertainty and embracing flexibility are important when establishing restoration goals and when working towards restoration targets (Thorpe and Stanley 2011; Hildebrand et al. 2005; Erenfeld 2000). Just as there is no universally successful restoration technique(s), there is also no single ‘correct’ restoration trajectory, restoration end point, or paradigm. Hildebrand et al. (2005) argue that restorations cannot be expected to follow the same trajectory as secondary succession, nor can the trajectory be accurately predicted, nor can a system be constantly manipulated to align with a desired trajectory without compromising the resiliency of the system. What can be done is to choose flexible but appropriate restoration targets and to early in the process identify the metrics best suited for monitoring those targets (Franklin et al. 2011).

1.7 Restoration Ecology: Pollination

Pollinators play a critical role in most terrestrial ecosystems; however, pollinators are rarely explicitly incorporated into restoration goals and monitoring (Menz et al. 2011). As a result, little is known about how pollinators colonize sites following restoration and whether typical restoration practices attract diverse pollinator populations. This knowledge deficit is of particular concern because of the increasing evidence of declining native bee populations (Colla et al. 2012; Potts et al. 2010; Goulson et al. 2008; Biesjeimer et al. 2006). Ecological restoration has been proposed as a response to reported pollinator declines, and researchers have outlined a conceptual framework for pollination-based restoration programs and called for experimental studies to fill existing knowledge gaps (e.g. Montoya et al. 2012; Menz et al. 2011; Nyoka 2010; Winfree 2010; Dixon 2009). The first step of this framework is to identify restoration goals with respect to pollinators. Goals can range from replicating an exact community to restoring pollination function, and for most ecosystems the desired outcome is likely to fall along this continuum. Restoring pollination function is a more manageable and often sufficient goal for most communities, but exceptions may include communities with a large number of specialists, with rare specialists (plants or pollinators), or endangered pollinators. Apart from defining desired restoration outcomes, several key issues need to be considered as part of a conceptual framework for a pollination-based restoration program: (1) floral resource availability; (2) nest site and nesting materials availability; (3) landscape structure and dispersal barriers; (4) climatic barriers; (5) exotic species; and (6) restoration outcomes.

Most terrestrial restorations focus first, on mitigating heavy site degradation (if present), and second, on establishing plant communities to restore ecosystem structure. In the short term, planting and seeding appropriate mixes of trees and herbaceous plants may be sufficient; however, successful pollination is required for maintaining genetically diverse plant communities over the long term (Friedman and Barrett 2009; Kearns et al. 1998). For those plants that are not self or wind pollinated or parthenocarpic, this requires that suitable animal pollinators are attracted to the site to provide these services. For this to occur pollinators need to have access to adequate floral resources to meet their nutritional needs throughout their lifecycle, either within the restored area or within foraging range. Because restorations are often undertaken in previously inhospitable landscapes, providing these resources within the restored area is generally the most appropriate strategy. Dixon (2009) suggests using a mix of framework and bridge plants. Framework plants are those that provide considerable source of nectar and/ or pollen (Dixon 2009). Framework plants are used as the primary food source for many species, but they are likely to attract pollinators that will service less attractive plants that, in the absence of framework species, would be inadequate attractors to a recently restored area (Menz et al. 2011). Bridging plants are used to provide resources in resource-limited times (Dixon 2009). These plants play an important role in providing year round or long season pollinators with floral resources that would otherwise be absent (Menz et al. 2011). The need for bridging plants will vary by ecosystem and the species present. Some systems may only host short season pollinators and not require bridging plants, while others such as tropical systems may host year round pollinators (Menz et al. 2011). Diverse floral mixtures are important for pollination-based restoration, including a combination of plant species with long, staggered, and overlapping bloom times (Winfree 2009; Dixon 2009). Not surprisingly, a greater abundance and diversity of food sources can support a larger pollinator population and/ or more fecund pollinator individuals (Muller et al. 2006; Williams and Kremen 2007). Another important consideration is the ease of plant restoration. Menz et al. (2011) discuss the need to balance plants that are easy to restore with plants that attract pollinators, and emphasize that these two categories may not always overlap. Because the most attractive plants can be difficult to source or establish (e.g. small propagule source, susceptible to disease) they may not be ideal for rapidly establishing a pollinator community. This suggests that restoration and conservation ecologists need to consider how species can be balanced (proportionally and temporally) to achieve rapid restoration of plants and pollinators that will be viable in the long-term (Menz et al. 2011).

Native bees require quality nest sites, and some species require foraging materials for nest construction (Potts et al. 2003; Delaplane and Mayer 2000). Nest sites can be located underground, at ground level, in stems, in snail shells, in pre-made cavities, and in self-made cavities depending on the species (Michener 2007; Delaplane and Mayer 2000). Species that nest underground or at ground level require patches of bare ground in dry sunny areas (Delaplane and Mayer 2000). Restored sites may be initially advantageous for these species because there may be greater than usual percent bare ground, as plant communities are still establishing. However, it is important to minimize soil disturbance during the restoration process to avoid damaging ground nesting pollinators (Nyoka 2010). Species that nest in cavities often nest in trees or fallen logs, and may require additional help in a newly restored site if there are no nearby natural areas that can meet these needs. Potential nest sites in the form of woody debris, or artificial nests can be added to restored areas to encourage the establishment of cavity nesters (Nyoka 2010; Winfree 2010). Winfree (2010) identifies a need for studies examining the population-level consequences of nest site restoration, and the relative efficacy of restoring different types of nest. A species' breadth of ecological requirements may also determine its ease of restoration. Species with narrow ecological requirements, complex lifecycles, or lifecycles that are slow to recover from local extinction may be more difficult to restore and may have to be specifically targeted (Menz et al. 2011).

Landscape structure and dispersal capacity dictate the ability of pollinators to colonize a newly restored area, and the ability of pollinators within a restored area to meet their ecological requirements. Dixon (2009) uses the term 'ecologically hostile' to refer to spaces where pollinators cannot meet their ecological requirements. In a fragmented landscape ecologically hostile areas between fragments may prevent species with low dispersal capacities from colonizing a restored area (Krewenka et al. 2011; Menz et al. 2011; Dixon 2009). Knowledge about the dispersal and colonization abilities, minimum habitat requirements, and potential dispersal barriers to targeted pollinator groups will help direct restoration planning (Kremen et al. 2004; Kremen et al. 2005; Nyoka 2010; Menz et al. 2011). Providing corridors or 'stepping stones' (natural patches located at distances within dispersal ranges) may an easy way of encouraging native bee colonization in restored areas that are otherwise isolated (Dixon 2009).

Climatic barriers are the barriers associated with planning for changes of historic plant and pollinator phenologies under changing climatic conditions. Dixon (2009) stresses the need for research on how climate change is and will impact pollination services. Under climate change scenarios phenological shifts are expected, and have been observed, in both plants and pollinators

(Dixon 2009; Hegland et al. 2009; Olesen et al. 2008). These phenological shifts may alter the coevolved synchrony among many plants and pollinators and may alter the range of possible interactions (Hegland et al. 2009). However, Forest and Thomson (2011) point out that the coevolution of emergence of many plants and their pollinators arises from shared signals (such as response to rainfall or ground temperature) resulting in similar responses to changing climates. Forest and Thomson (2011) did find that plants are more likely than pollinators to advance their phenology. These relative changes will likely have the most serious impacts for specialized plants and pollinators, and for pollinators who emerge early in the spring or fly late in the fall when flowering resources are rare to begin with. There may also be problems of adequate pollination or provision of food resources if the peak bloom time of a plant no longer coincides with peak populations of its primary pollinator(s). Phenological decoupling alone is not an insurmountable barrier, and a diverse plant community that covers a wide range of bloom times can help avoid the negative effects (hungry bees or un-pollinated flowers) of plant-pollinator asynchrony.

Exotic species are a controversial topic with respect to their role in pollination-based restoration. Despite their negative reputation, many exotic species are deeply entrenched in ‘natural’ ecosystems, and are expected to occur in restored ecosystems (Hobbs et al. 2013; Montoya et al. 2012; Ewel and Putz 2004; Memmott and Waser 2002). In disturbed habitats native bees use, but do not prefer, exotic plant species, indicating that exotic plants are often equally important forage resources as native plants (Williams et al. 2010). In fact, exotic species may have a positive influence if they increase the carrying capacity of the bee population over time (Tepedino et al. 2008). This is consistent with the use of exotic plants to functionally replace extinct or unavailable native species in restored habitats (Evel and Putz 2004). Memmott and Waser (2002) found that exotic plant species integrated into native flower visitation webs, making it likely that the removal of exotic plants will negatively impact the bee community if they are not replaced with native species (Williams et al. 2010). Despite the potential usefulness of exotics and their increasing presence and role in novel ecosystems, there is reason to proceed with caution. Moron et al. (2009) found that the invasion of exotic Goldenrods (*Solidago sp.*) in Polish wet meadows negatively affected all functional groups of native pollinators.

Finally, assessing restoration outcomes is an important component of all restoration projects, and for pollinator-based restoration requires surveying established pollinator communities and assessing pollination function. Monitoring is an often-neglected step in the restoration process due to the cost and the stigma attached to ‘just watching things’ as opposed to ‘actively doing things’. This stigma is misplaced because assessing restoration successes and failures requires, at a minimum, ‘just watching things’ (Block et al. 2001). A number of restoration programs are adopting an adaptive restoration approach, which involves applying the concepts of adaptive management to ecological restoration (e.g. Cummings et al. 2005). Adaptive restoration requires monitoring to inform the ongoing restoration process. Where monitoring is carried out it is often only in the short term (under 10 years), but long term monitoring can unveil results that cannot be detected or that differ significantly from those found in the short term (Herrick et al. 2006). Few studies have assessed pollinator response to restoration, and those that have will be discussed in greater detail below. These studies are limited in scale and scope, and Montoya et al. (2012) emphasize the need for expanding pollination-based restoration research to encompass larger geographic and temporal scales. In practice, pollinators, with the occasional exception of butterflies, are rarely included in post-restoration monitoring (e.g. Woodcock et al. 2012; Waltz and Wallace 2004). This gap is largely due to limited time and financial resources and a lack of technical (insect) knowledge.

The issues presented here, are only the main points of a conceptual framework for pollination-based restoration, and other factors will likely require consideration depending on the specifics of a particular project. Pollination-based restoration is a relatively new field, thought it has been embedded in restoration from the start. Many components of the framework are under-studied (e.g. understanding landscape effects and colonization capacity), and others are unknown (e.g. most appropriate bridge species for North America). Pollination-based restoration has the potential to enhance the ecological, economic, and social success of restoration projects by contributing to the conservation of important ecosystem services providers.

1.8 Restoration Ecology: Pollination in (semi)Natural Ecosystems

Assessing the recovery of pollinator species following ecological restoration is uncommon and has only recently appeared in the published literature (e.g. Williams 2011; Forup et al. 2008; Forup and Memmott 2005). These studies have assessed the recovery of pollinator species (often only bees) by comparing pollinator communities found in restored sites with comparable ‘remnant’ or ‘ancient’ sites (e.g. Williams 2011; Exeler et al. 2009; Forup et al. 2008; Forup and Memmott 2005), or with comparable degraded sites (e.g. Hopwood 2008). While all studies address structural differences in the assemblages (e.g. abundance, diversity, species composition), a few also compare plant-pollinator interaction networks (as introduced in Memmott 1999) to assess the recovery of pollination function (Williams 2011; Forup et al. 2008; Forup and Memmott 2005). These studies provide an important starting point for understanding how pollinator communities establish following restoration. These studies cover a range of habitats including road verges in Kentucky, USA (Hopwood 2008), heath meadows in south England (Forup et al. 2008; Forup and Memmott 2005), riparian forest in California, USA (Williams 2011), and sand dune complexes in northwest Germany (Exeler et al. 2009); however, many habitat types have yet to be studied.

Results of restoration studies show that structural properties of pollinator communities including abundance, richness, and evenness do not differ significantly between restored and target sites (Williams 2011; Forup et al. 2008; Forup and Memmott 2005; Exeler et al. 2009). However, these same properties do differ when comparing restored and degraded sites (Hopwood 2008). Species composition may differ significantly between restored and target and restored and degraded sites; however, species composition is highly variable in time and space and even remnant sites in close geographic proximity have very different compositions (Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008; Forup and Memmott 2005). The function of pollinator communities in restored sites is assessed by comparing properties of their plant-pollinator interaction networks (Memmott 1999) with properties of the networks found in target or degraded sites. The properties of the networks that are compared vary, but they typically involve a combination of structural descriptors – number of upper level species (insects), number of lower level species (plants), and functional descriptors – connectance, linkage density, web asymmetry (see section Network Analysis for a more complete description of these properties). Williams (2011) study of California riparian forests, Forup et al.'s (2008; 2005) studies of English heath meadows, and Devoto et al.'s (2012) study of Scottish pine forests are the first to apply plant-pollinator networks to restoration ecology. Generally, they found that network properties do not differ significantly between restored and target sites and that pollination occurs at similar rates in both restored and target habitats (Williams 2011; Forup et al. 2008; Forup and Memmott 2005). As well, Forup et al. (2008) found that key pollinators were present in restored sites. Despite these similarities between restored and target sites Forup and Memmott (2005) found that restored sites had a lower (not significant) connectance values compared to target sites. While Williams (2011) suggests that pollination function may be less robust due to fewer recorded interactions between pollinators and some native plants.

Overall the initial evidence suggests that pollinators are returning to restored sites and are forming functional communities; however, these studies represent only a handful of restoration projects and are limited in their geographic and temporal scope. These studies are an important starting point, but more experimental studies of this sort are required to gain a better understanding of the processes by which pollinators are restored and of the factors that influence their return. Despite increasing calls for the need for empirical studies of pollinators and pollination function, the number of relevant experimental studies remains limited in the scientific literature.

1.9 Plant-Pollinator Interaction Networks

Ecological network analysis is the practice of constructing ecological models to analyze the structure and the flow of energy or matter through a system (Dame and Christian 2007). Network analysis has been extensively used to study food web ecology; however, in the late 1990's network analysis was re-fitted as a technique to study mutualistic interactions, specifically plant-pollinator interactions (Memmott 1999). Previously pollination biologists tended to focus on one or a few insect species, and a subset of the entire plant community. As a result, there were few studies of pollinator communities or of plant-pollinator interactions at the community scale (Memmott 1999; Mitchell et al. 2009; Burkle and Alarcon 2011). The community context is crucial for addressing ecological questions about community level interactions because most communities are shaped by a diversity of interactions between plants and pollinators that cannot be captured using only a subset of the community (Vazquez et al. 2009; Burkle and Alarcon 2011). Diverse pollinator communities can enhance pollination services and lead to increased ecosystem function, a primary goal of ecological restoration (e.g. Klein et al. 2012; Fontaine et al. 2006). Network analysis is a powerful tool for understanding relationships and for quantifying pollination function. Since its introduction to the study of plant-pollinator mutualisms, network analysis has been used to study structural and functional characteristics of plant-pollinator communities and to answer ecological questions at the community level (e.g. Fontaine et al. 2006; Ives et al. 2007; Bosch et al. 2009; Williams 2011). The following sections will examine the typical structure of plant-pollinator networks and will discuss their limitations.

The Typical Structure of a Plant-Pollinator Network

Plant-pollinator networks are best expressed as a matrix of interactions where individual pollinator species represent columns, plant species represent rows, and the cells of the matrix represent a measure of the interaction between two species. Interactions can be expressed as presence/ absence, as the number of interactions recorded, or as other appropriate measures of interaction frequency or intensity. Two types of plant-pollinator interaction networks - visitation networks and pollen transport networks - are frequently used to address ecological questions. In visitation networks the cells of the matrix represent plant-pollinator interactions measured by presence/ absence or number of interactions. Interactions in visitation networks represent instances were flower visitors (typically insects) were recorded visiting host plants (e.g. *as used in* Forup et al. 2008; Williams 2011). In pollen transport network visitation information is combined with a measure of pollen transport (pollen load). Pollen load is measured by removing, identifying, and quantifying pollen grains found attached to floral visitors (e.g. Alarcon 2009; Bosch et al. 2009). The number of pollen grains of a given plant species found on a given pollinator species makes up the cells of a second matrix. Cells of the two matrices (visitation and pollen load) are then multiplied (strength of interaction x quality of interaction) to produce the pollen transport matrix.

Certain properties of visitation and pollen transport networks are consistent regardless of sampling location, size of network, or species included in the network. Other properties appear to vary with the size of the network, and few with the sampling location (Vazquez et al. 2009). In this thesis plant-pollinator interaction networks will group pollinators by genus and not by species and so certain network properties will not be directly comparable to the species-species networks most commonly found in the literature. In a typical plant-pollinator network the proportion of total potential interspecific interactions that actually occur is quite low (Vazquez et al. 2009; Jordano et al. 2003). Most networks are imbalanced in the number of plant to animal species with up to almost four times as many animal species as plant species (Vazquez et al. 2009). In the case of plant species – pollinator genera, we would expect a more similar balance of group numbers. The distribution of number of links per species tends to be skewed, with a few generalist species and many specialist species (Jordano et al. 2003).

The most commonly reported properties of plant-pollinator interaction networks are connectance and linkage density. Connectance is the number of realized links out of the total number of possible links, and is a measure of how many bee genera are visiting plant species (Jordano 1987). Connectance is expressed as $C = l / ip$. Where l is the number of links, i is the number of insect genera, and p is the number of plant species. Linkage density is the ratio of links per species ($L = l/i+p$). Higher connectance is expected to indicate a more resilient community, because in the case of species loss there are alternate associations to compensate for lost connections. Where l is the number of links, i is the number of insect genera and p is the number of plant species.

Some network properties tend to be consistent regardless of the size of networks, sampling location, and sampling date. Interaction networks tend to be nested (Bascompte et al. 2003; Vazquez and Aizen 2003; Jordano et al. 2003). Nestedness refers to the tendency of species with few connections to interact with a subset of species with many connections (Bascompte et al. 2003). Nestedness also implies that interactions in the pollinator assemblage are highly asymmetric and that the assemblage is organized around a central core of highly connected species (Bascompte et al. 2003). Bascompte et al. (2003) found that nestedness tends to increase with the number of interactions within a community. Network interactions tend to be asymmetric, meaning that specialist species (those with few links) tend to interact with generalist species (those with many links) (Vazquez and Aizen 2004). Interaction frequency, as seen in visitation networks, is often used to approximate interaction strength (Vazquez et al. 2005). Lastly, most networks tend to be modular, with the existence of modules (groups of species) that have many intragroup links, but few intergroup links (Olesen et al. 2007). Simulations of species extinction can be performed on networks to assess their robustness to extinction, it is expected that older and 'healthier' communities will be more robust to random specie extinction (Kaiser-Bunbury et al. 2010).

Limitations of plant-pollinator network analysis

Plant-pollinator interaction networks can provide important ecological information; however, certain limitations should be acknowledged. The overarching limitation is assessing the extent to which the observed network structure represents the 'true' network structure. Vazquez et al. (2009) identify the most influential ecological, evolutionary and historical processes that contribute to the 'true' network structure, including: species phenotypes, historical events, natural demography and dispersal, spatiotemporal distribution, community structure, trait matching, and interaction neutrality. In addition to these influences sampling effects also shape the observed network structure, particularly observation error and observation probability (Vazquez et al. 2009). While observation error can be partly mitigated by collecting samples to confirm species identification, using standardized sampling techniques, and minimizing sampling bias with multiple observers; overcoming observation probability is a greater challenge. Observation probability refers to the situation where the relative abundance of a given species influences the probability of observing an interaction between that species and another (Vazquez et al. 2009). The more rare the species, the less likely it is that an interaction will be observed. Sampling effort (time and intensity) can also affect observed network properties, with rare interactions at risk of being missed if sampling effort is low. Balancing the sampling effort necessary to observe something close to the 'true' network structure, with the time, cost and realities of field sampling is challenge for researchers wanting to create accurate networks. Burkle and Alarcon (2011) remark that it is unsurprising that few researchers are able to provide all networks needed to compare spatial and temporal variations in structure, considering the effort required to create a single network. Hegland et al. (2010) provide suggestions for cost effective and timely community monitoring of plant-pollinator mutualistic networks. These suggestions, while helpful for long-term monitoring programs, are unlikely to result in the best representation of the 'true' network structure.

Interaction networks are temporally variable, suggesting that a network built off of a single season or part of a season, may not accurately reflect the 'true' network structure (Gibson et al. 2011; Vazquez et al. 2009). Some network properties, such as species composition and specific species interactions showed large amounts of yearly variation in a three-year study of network topology (Alarcon et al. 2008). Other network properties including the overall number of links between species, connectance, modularity, number of plant and pollinator species, and nestedness are conserved across years (Dupont et al. 2009; Alarcon et al. 2008). Alarcon et al. (2008) suggested that observed temporal variability in the topology of the interaction network might have been high due to climate variability among years. If single year or season networks are used to answer ecological questions, then it is important to consider and identify the network properties that are likely to remain stable through time and the characters that are likely unique to the sampled year.

Burkle and Alarcon (2011) have also questioned whether single pollination networks are appropriate for describing yearlong systems, or if networks should be divided into biologically meaningful time intervals. This point is worth considering even in systems where pollination is not year-round, but occurs in visibly distinct stages or seasons. Not accounting for different seasons or non-overlapping insect flight times and plant bloom times, could introduce ‘forbidden links’. ‘Forbidden links’ are links in a network that are not ecologically possible and Williams (2011) argues that failure to eliminate these links can distort the appearance of the observed network. To avoid this distortion Williams (2011) removed interactions between plants and pollinators with non-overlapping flight and flowering times. This editing of the interaction network is a more effective means of breaking apart the network into meaningful time scales.

A common criticism of network analysis is that properly defining the system and its boundaries is a challenge. Dame and Christian (2007) show that model outputs for ecological network analysis can be statistically significant; however, they emphasize that their study was conducted in a model system, a salt marsh, which presented a rare opportunity because of its relatively defined boundaries. The boundaries of plant-pollinator mutualistic networks are more difficult to define as pollinators can have ranges that extend outside of the study area, or the study area may be at the edge of their range. Mutualistic interactions are also considered separate from food web interactions, even though many plants and pollinators may be predators or prey to species outside of the plant-pollinator network. Given these constraints, observed plant-pollinator interaction networks should be considered as sub-networks, both of mutualistic interactions at the landscape scale and of all species interactions at a given sampling location.

When Memmott (1999) first introduced the application of network analysis to plant-pollinator mutualisms she discussed two types of networks, visitation and pollen transport. The advantage of pollen transport networks is that they include more information about the quality of plant-pollinator interactions (Memmott 1999; Alarcon 2010), but this information comes at the expense of increased field and lab time. Vazquez et al. (2005) found that interaction frequency (visitation networks) can act as a surrogate for pollination function. However, Vazquez et al. (2005) warn that their results should be interpreted with caution because: (1) data used was restricted to pollen deposition on plants and did not address other important components of successful pollination; (2) the analysis assumed that all visitors have a non-negative effect; (3) the study was limited to the plant perspective (pollination) and results may be different from the animal perspective (nutrition); and (4) the product of interaction frequency and per-interaction effect (used to reflect pollen transfer) may not be a good measure of the total effect. Alarcon (2010) tested the congruence between visitation and pollen-transport networks and found that while the two are congruent, they differ enough that visitation networks should be used as first order approximations. The important difference between the two is that information on which floral visitors carry conspecific pollen is necessary for distinguishing between mutualistic and antagonistic relationships, as well as for assessing the strength of relationships (Alarcon 2011). Because of the additional time required for measuring pollen load, it was not included in the analyses presented in this thesis.

Network analysis can be an insightful and appropriate tool for exploring community level plant-pollinator interactions. Visitation and pollen transport networks can convey information about pollination function that cannot be expressed through measures of species abundance, richness, or evenness.

Chapter 2 Methodology

2.1 Site Descriptions

2.1.1 Dunnville

Dunnville Marsh is located at the southern edge of the Grand River watershed near the shores of Lake Eerie, and near the town of Dunnville in Haldimand County (42˚53.636'N, 079˚35.222'W) (Figure 2-2). Dunnville Marsh is a 396 hectare property owned and managed by the Grand River Conservation Authority (GRCA). Prior to the GRCA acquiring the property, the Canadian Pacific Railway owned the majority and an active railroad runs along the north end of the site. The landscape of marshes and low-lying forest was converted to farmland during European settlement and was used for agriculture up until acquisition by the GRCA. The property has since been restored as a wet meadow and the aim of the restoration is to mimic the conditions in the 'undisturbed' forest and wetland. Previous agricultural activities imposed a unique layout on the site, such that it consists of seven agricultural fields separated by remnant low-lying Carolinian forest. With the exception of a large forested area between Fields one and two, the remaining remnant forest between fields is less than 10m deep. The seven fields have been similarly restored, but some fields have been dug with pits and mounds, while others have been left intact (Table 2-1). Surveys were conducted in Field 1, the natural forest remnant, Field 2, Field 4, Field 5, and Field 7. Sampling all fields was beyond the scope of this project and so Field 3 and Field 6 were excluded from the surveys due to their small size and the potential overlap of foraging ranges with other sampled sites. Pits and mounds were dug in Field 2 and Field 4 in 2005 and in Field 1 in 2006. Field 2 and Field 4 were seeded and planted in 2006, and Field 1 was seeded and planted in 2007 and 2008. Field 5 and Field 7 were planted and seeded in 2008. Herbaceous planting were all done by direct seeding and the following wildflowers were planted: *Verbena hastate* L. (blue vervain), *Rubeckia hirta* L. (brown-eyed susan), *Asclepias tuberosa* L. (butterflyweed), *Scrophularia marilandica* L. (carpenter's square), *Scirpus atrovirens* Willd. (dark green bulrush), *Oenothera biennis* L. (evening primrose), *Penstemon digitalis* Nutt s. Sims (foxglove beardtongue), *Hypericum ascyron* L. (great st. john's wort), *Penstemon hirsutus* L. Willd. (hairy beardtongue), *Ceanothus americanus* L. (new jersey tea), *Lespedeza capitata* Michx. (round-headed bushclover), *Desmodium canadense* L. DC. (showy tick-trefoil), *Asclepias incarnate* L. (swamp milkweed), *Heliopsis helianthoides* L. (sweet ox-eye), and *Pycananthemum virginianum* L. T. Dur. & B.D. Jackson ex B.L. Robins & Fern. (virginia mountain mint). Wildflowers were planted at 1kg/ha in Fields 1, 2, and 4, and at 5.7 kg/ha in Fields 5, 6, and 7. Native grasses were planted in field 1 at 10 kg/ha, and in fields 5, 6, and 7 at 5kg/ha.

Table 2-1 Details of Dunnville Marsh restoration activities

Field Name	Year(s) Planted	Pits and Mounds	Plantings
F1	2007 & 2008	Y (2006)	Herbaceous[1], Tree – direct seeding, tall stock, seedling, and sapling, Invasives control[2]
F2	2006	Y (2005)	Herbaceous, Tree – tall stock and saplings, Invasives control
F4	2006	Y (2005)	Herbaceous, Tree – direct seeding, tall stock, and seedlings, Invasives control
F5	2008	N	Herbaceous, Tree – direct seeding
F7	2008	N	Herbaceous
NAT	N/A	N	N/A

[1] All herbaceous plantings were by direct seeding.

[2] All invasives controls were by broadcast spraying.

2.1.2 Pioneer Tower Natural Area

Pioneer Tower Natural Area is located adjacent to the Grand River in Kitchener, southern Ontario (43˚23.873'N, 080˚24.402'W). Pioneer Tower Natural Area is owned by the GRCA and the site consists of a walking path separated from the Grand River by a degraded area and riparian forest, a natural forest remnant, currently cultivated cornfields, and a restored agricultural field (Figure 2-1). The restored agricultural field was planted with: *Rubeckia hirta* L. (brown-eyed susan), *Desmodium canadense* L. DC. (showy tick trefoil), *Oenothera biennis* L. (evening primrose), *Monarda fistulosa* L. (wild bergamot), *Pycananthemum virginianum* L. T. Dur. &B.D. Jackson ex B.L. Robins & Fern. (virginia mountain mint), *Penstemon digitalis* Nutt s. Sims (foxglove beardtongue), *Verbena hastate* L. (blue vervain), *Asclepias incarnate* L. (swamp milkweed), *Solidago nemoralis* Ait. (grey goldenrod), and *Symphyotrichum leave* L. A. & D. Love (smooth aster). The areas sampled in this survey were the restored agricultural field, the disturbed path verge, and the edge of the remnant forest.

2.1.3 Washington Creek

Washington Creek is located in Oxford County, southern Ontario (Figure 2-1). Washington Creek is 9km long and flows into the Nith River in the Grand River watershed (43˚18.046'N, 080˚33.673'W). The sections of Washington Creek surveyed in this thesis include a restored section and a degraded section. Both sections are located on privately owned properties, and researchers at the University of Guelph carried out the original restoration activities. In 1985 a 1.6km section of

Washington Creek was planted with three varieties of alder (*Alnus incana* subsp. *Rugosa* [Du Roi] R.T. Clausen., *Alnus glutinosa* [L.] Gaertn, and *Alnus rubra* Bong.) and hybrid poplar (*Populus* x *Canadensis* Moench) (Oelbermann et al. 2008). Silver maple (*Acer saccharium* L.) was planted in 1986 and 1990. In 1991 multifloral rosevine (*Rosa multiflora* Thunb.) and red-osier dogwood (*Cornus sericea* L.) were planted in the riparian zone (Oelbermann et al. 2008). The total buffer is 50m deep from the creek (Oelbermann et al. 2008). The rehabilitated area was previously agricultural land use. Currently, the canopy of the restored section of Washington Creek is composed of the originally planted tree species, but the understory is primarily overrun by invasive species including *Alliaria petiolata* M.Bieb. Cavara & Grande (garlic mustard), *Heraculeum mantegazzianum* Sommier & Levier (giant hogweed), and *Hesperis matronalis* L. (dame's rocket). Downstream of the restored site, Washington Creek flows between a rural road (to the North) and agricultural fields (to the South) and is subject to sediment run off and illegal dumping, it has also been channelized in parts. This section of the creek is subject to regular disturbance, and the road verge of this site was mowed twice during the sampling season. Previous studies of the restored section of Washington Creek have assessed the restoration in terms of solar radiation to the creek, streambed sedimentation, organic matter and nutrient fluxes, organic matter transport and retention, bird diversity, and benthic insect and fish diversity (Oelbermann et al. 2008). Assessing pollinator communities provides another metric for evaluating long-term outcomes of this restoration project.

2.1.4 Clair Creek

Clair Creek is located in north Waterloo, southern Ontario (43˚27.537'N, 080˚34.877'W) (Figure 2-1). Clair Creek begins in the Clair Hills and flows into Clair Lake before flowing into Silver Lake in Central Waterloo. The sampled area is located between Clair Creek and a stormwater management pond in the Clair Hills subdivision. This area was restored with the intent of enhancing natural habitat, providing flood storage, and creating a natural feature (Stanley Consulting, 1998). The sampled area is dominated by grasses, and contains a few shrubs, trees, and wildflowers. Details of the restoration are not known.

2.2 Restoration Techniques

2.2.1 Pit and Mound Restoration

Pit and Mound restoration refers to the practice of digging large pits and placing the removed soil in a mound next to the pit. This technique has been used primarily in wetland restoration to mimic the natural process of shallowly rooted trees falling (windfall), where the uprooted roots leave a pit, and the decaying tree creates a mound. Like the natural process, the artificial creation of pits and mounds increases topographic heterogeneity and increases the range of moisture conditions. As in the natural process, water and leaf litter accumulate in the pit bottoms, creating a wet and nutrient rich microenvironment suitable for moisture tolerant plant species and attractive to amphibians. The drier mound tops may not be as nutrient rich as the mounds resulting from decaying trees, but they provide a dry environment for sapling establishment. Sapling loss due to flood related deaths is an expensive reality of many restorations in wet environments, and planting trees on mound tops helps to mitigate these losses.

Pits and mounds are an increasingly common technique in wetland forest restoration (e.g. Ministry of Natural Resources 2012), but because of tight budgets monitoring subsequent changes is absent or infrequent, and publication of the results in the scientific literature is rare. The increased microclimate diversity is expected to increase overall plant diversity, and the few published studies assessing plant establishment on pits and mounds (naturally or artificially created), support this hypothesis (Biederman and Whisenant 2011; Peterson et al. 1990; Ewing 2002; Kooch et al. 2012). In Ontario, pit and mounds have been applied as a restoration technique as part of Ontario Parks' management plan for Clear Creek Forest (MNR 2012). Observational studies of the pits and mounds one and two years after they were dug, suggests that diverse plant communities are establishing and that the pits were effective at accumulating water and attracting amphibians in the spring (Buck 2003).

So far there has been no research addressing the effects of pit and mound restoration on native bee community establishment. As part of this thesis I am interested in whether the creation of pits and mounds influences the establishing native bee communities. Pits and mounds may increase native bee abundance and richness because (1) diverse flowering plant communities are associated with diverse native bee communities (Hopwood 2008; Potts et al. 2003), and (2) increased topographic heterogeneity may result in greater nest site availability due to increased amounts of sloped bare ground leading to more nesting opportunities for ground nesters and greater success of sapling establishment leading to more nesting opportunities for cavity nesters. As an increasingly applied restoration technique, the influence of pits and mounds on biotic communities should be evaluated. In this thesis, native bee communities are the focal biotic community.

Figure 2-1 Map of all study sites, southern Ontario: Clair Creek, Pioneer Tower Natural Area, Washington Creek, and Dunnville Marsh, sampled in 2012. Source, Google Earth, 2013.

Figure 2-2 Map of Dunnville Marsh, Haldimand County, southern Ontario. Fields dug with pits and mounds before planting and seeding are labeled Pit 1, 2, and 3. Fields seeded into weedy ground are labeled Plant 1 and Plant 2. (Semi)natural Carolinian forest is labeled forest remnant. Source, Google Earth, 2013.

Chapter 3 Comparison of sampling techniques and pan trap colour preference in Hymenoptera (Apiformes) in selected southern Ontario sites

Overview

Native bees play a critical role in plant reproduction, and declines in abundance and diversity of bees are expected to impact flowering plant biodiversity and productivity of insect pollinated agricultural crops. In response to reported native bee declines, surveys of bee communities are increasing. Sampling design and biases within and among sampling technique(s) can strongly influence survey outcomes and should be considered when designing experiments and interpreting results. Pan trapping is a frequently used collection method, but trap characteristics influence what is caught. Trap colour is expected to influence the taxa sampled; however, results of North American studies are inconsistent with respect to effectiveness and family preference of different trap colours. In this study we collected 10,602 bees in blue, white, and yellow traps representing 30 genera and six families. Significantly more bees were collected in blue and white compared to yellow ($p<0.001$) traps. All five abundant families demonstrated a significant preference for at least one trap colour. We also compared the composition of pan trap and sweep net collections. Halictidae and Colletidae were relatively more abundant in pan trap compared to sweep net samples, while Apidae were more abundant in sweep net. Our results demonstrate that different coloured traps and different sampling techniques sample different subsets of the community. When sampling overall biodiversity it is best to include a range of trap colours and sampling techniques. If targeting a particular group specific trap colours and the sampling technique that is most effective for that group should be employed.

Introduction

Native bees are essential to the functioning of most terrestrial ecosystems and contribute to the pollination of approximately 90% of flowering plant species (Friedman and Barrett 2009; Kevan 1999). Bees are required for the reproduction of some species of flowering plants, and for others bees enhance fruit set and genetic recombination (Nyak and Davidar 2010; Faegri and van der Pijl 1971). These contributions to plant reproduction are important for maintaining species rich and genetically diverse plant communities, and for maximizing fruit production of insect pollinated crops. Because of this, reported native bee declines are concerning from conservation and agricultural production perspectives. Declines are best documented in Europe where there is a history of monitoring pollinator communities, but there is also evidence of declines throughout North America (Potts et al. 2010; Biesjeimer et al. 2006; Allen-Wardell et al. 1998). To understand the extent and causes of detected declines there has been an increasing number of studies assessing native bee biodiversity and identifying community and taxa traits that may be important for their conservation (e.g. Krewenka et al. 2011; Hannon and Sisk 2009; Winfree 2010; Winfree et al. 2009; Tuell et al. 2008; Kevan 1999). To carry out these studies researchers have adopted a range of sampling techniques including pan traps, trap nests, malaise traps, and sweep netting (Westphal et al. 2008). The relative efficacy of these techniques has been evaluated for various combinations (Westphal et al. 2008; Wilson et al. 2008; Campbell and Hanula 2007; Cane et al. 2000); however, the results of these studies are inconsistent and the most appropriate technique for a given project is likely to vary with the study objectives and the targeted taxa. Sampling design influences the conclusions drawn from a particular study and the comparisons that can be made among studies. There are clear differences in the subset of the insect community sampled using different bee sampling techniques, using variations of these techniques (e.g. pan trap colour), and by applying techniques in different geographic locations. Understanding how a chosen sampling technique influences the study outcomes can have important implications for experimental design and interpreting results. In this study we explore some of the intra- and inter- technique biases associated with two of the most commonly employed sampling techniques, pan trapping and sweep netting.

Pan trapping is widely employed and is the basis for established standardized protocols including the Bee Inventory Plot (BIP) (http://online.sfsu.edu/beeplot/) and the Canadian Pollination Initiative (CANPOLIN) (http://www.uoguelph.ca/canpolin/Sampling/protocols.html). Pan trapping generally involves filling small (15-20cm in diameter) coloured plastic pans with soapy water. Bees will mistake the pan for a flower, land on the water, and drown. Compared to other sampling methods, it is cost and time efficient, requires little technical knowledge, is easy to standardize, and involves minimal collector bias (Droege et al. 2010; Westphal et al. 2008; Campbell and Hanula 2007). Westphal et al. (2008) found that pan traps collected the greatest species richness compared to sampling by observation plots, transect walks, and trap nests; however, depending on site structure and floral abundance this may not always be the case (Munyuli 2013; Wilson et al. 2008; Cane et al. 2000). Like any collection method, pan trapping has a number of biases that should be taken into account. Bees respond to sensory cues from flowers such as size, colour, scent, height and shape (Goulson 2010; Potts et al. 2003; Kevan 1972; Faegri and van der Pijl 1971). Flower colour is a strong attractor and it is therefore unsurprising that many insect groups show fidelity to particular pan trap colours, as they do to particular flower colours (e.g. Campbell and Hanula 2007; Roulston et al. 2007). Colour fidelity can also vary by gender within a given species (Leong and Thorp 1999).

Studies of insect catch by trap colour are relatively common (e.g. Gollan et al. 2011; Wilson et al. 2008; Campbell and Hanula 2007; Romey et al. 2007; Toler et al. 2005; Leong and Thorp 1999). However, the results of North American surveys addressing native bee colour preference are inconsistent. For example, a number of studies found no significant colour preference for combinations of white, blue, red, and yellow pan traps (e.g. Wilson et al. 2008; Roulston et al. 2007; Toler et al. 2005). In contrast, Tuell et al. (2009), Campbell and Hanula (2007), and Romey et al. (2007) did find colour preferences for certain insect taxa, but preferences at the genus or family level were not always consistent across studies. Abrahamczyk et al. (2010) suggest that discrepancies in colour preference among studies are likely caused by differences in the underlying bee community and by differences in habitat type or structure. Understanding the colour preferences of bee groups in a given geographic area can be helpful when designing surveys to best capture a particular insect group (e.g. family). It is also unclear whether colour preference is consistent across taxonomic ranks, such as for genera of a given family. This distinction may also influence experimental design.

Pan trapping is subject to collection biases relative to other collection methods. Because pan traps are competing with flowers for insect visitation, they have been criticized for providing an incomplete picture of the bee community, particularly when blooms are abundant (Wilson et al. 2008; Cane et al. 2000). As well, the perceived attractiveness of pan traps likely varies based on flight patterns, floral visitation patterns, and colour preferences of a given species, leading to preferential catch of certain species over others and a skewed representation of true relative species abundances (Wilson et al. 2008). To mitigate these biases, sweep netting is often used to complement pan trapping (e.g. Williams 2011; Forup et al. 2008; Hopwood 2008). Sweep nets require more technical skill, more active time, and are subject to greater collector bias, but also tend to sample a different subset of the population and thus contribute to a better overall understanding of the ‘true’ bee community (Richards et al. 2011; Westphal et al. 2008; Roulston et al. 2007; Cane et al. 2000). To better understand how the two techniques influence sampling outcomes in our study area of southern Ontario, we compared insect collections from pan trap and sweep net sampling.

We explored intra- and inter- technique biases associated with pan trapping and sweep netting off of flowers by testing the influence of pan trap colour and descriptively comparing the influence of sampling technique on insect collections. Surveys took place in southern Ontario, Canada, in primarily open degraded or recently restored habitats with similar habitat structure. We identified differences by pan trap colour by answering three related questions (1) do bee abundance and genus richness differ between blue, white, and yellow pan traps?; (2) do families demonstrate preference for particular colours?; and (3) is genus preference for the most abundant genera consistent with family preference? To compare pan trap and sweep net collections we focused on three related questions: (1)

does the dominant family differ by collection method?; (2) does the proportional representation of bee genera differ by collection method?; and (3) does the number of exclusive genera differ by collection method?

Methods

Site description

Surveys of bee fauna took place in twelve sites at four locations the Grand River Watershed, in Southern Ontario, Canada (Figure 3-1): (1) Dunnville Marsh, Haldimand County (42˚53.636'N, 079˚35.222'W), (2) Pioneer Tower Natural Area, Region of Waterloo (43˚23.873'N, 080˚24.402'W), (3) Washington Creek, Oxford County (43˚18.046'N, 080˚33.673'W), and (4) Clair Creek, Region of Waterloo (43˚27.537'N, 080˚34.877'W). Pan trapping and sweep netting took place at all four sites; however, sweep net collections from Clair Creek were minimal and were not included in the analysis. At Dunnville Marsh we sampled six areas including one (semi)natural low-lying forest remnant, and five recently restored meadows that were previously used for agriculture. Of the five restored meadows, two had been planted and seeded in 2008, and three had been dug with pits and mounds (two in 2005, one in 2006) before being planted and seeded in 2007. At Pioneer Towers Natural Area we sampled a degraded path edge, a natural forest edge, and a recently restored meadow (previously agricultural land). At Washington Creek we sampled a degraded road edge, and an old restored riparian forest (over 25 years since restoration). At Clair Creek we sampled a restored area between a creek and a storm water management pond. Dunnville Marsh and Washington Creek are located in rural areas where agriculture is the dominant surrounding land use. Pioneer Towers Natural Area and Clair Creek are located in semi-suburban/ suburban areas, respectively, where the surrounding land use is a mixture of single-family dwellings, and remnant natural areas. With the exception of the forest remnant at Dunnville Marsh and the restored forest at Washington Creek, all sites were open and had similar vegetation structure.

Bee and flower sampling

We surveyed bee fauna every ten to fourteen days from May to August 2012, using pan traps and sweep net captures. We sampled each site ten times throughout the study period. Sampling took place on warm (≥14˚C), sunny (<60% cloud cover) days with low wind speeds. At each site we placed 30 pan traps of alternating blue, white, and yellow along a permanent 100m transect. Pan traps were plastic bowls measuring 18cms in diameter and held approximately 6oz of liquid. We filled pan traps ¾ full with a mixture of water and unscented blue Dawn™ dish soap. We spaced pan traps approximately 3m (n = 30) apart and placed them where they would be stable and visible to bees. On sampling days, we laid out pan traps before 09:00 and collected them by 16:00. We passed trap contents through a fine sieve and stored collected specimens in bags filled with 70% ethanol and labeled with the date, site, collection number, time of collection, and pan trap colour.

We conducted sweep net collections in the late morning or early afternoon (11:00-14:00), along two permanent 50m transects. We walked transects at a slow pace for 30 minutes and sweep netted any insect seen in contact with the reproductive parts of a flower (available for pollination). Only insects within one meter of either side of the transect line were netted. Flowers were considered available for pollination if the anthers or stigma appeared fresh. We collected captured insects and recorded the species of plant they were visiting.

Specimen identification and processing

We strored sweep net specimens in a freezer in individual envelopes labeled with their capture information until they could be pinned. Frozen specimens were taken out to defrost for approximately one hour before being pinned and labeled. We stored pan trap specimens in a refrigerator in 70% ethanol until procesing. We washed pan trap specimens with soap and water, rinsed them in 95% ethanol, and dried them before being pinning and labelling. Specimens were identified to genus under a dissecting microscope using Packer et al. (2007).

Data analysis

We examined the relationships among pan trap colour (blue, white, and yellow) and abundance (number of specimens) and richness (number of genera) using total native bee collections from pan traps at the 12 sites. We also examined whether the five collected families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae) demonstrated preference for pan trap colour. Our response variables (abundance and richness) varied by sites. Therefore, we modeled the influence of pan trap colour in a mixed model context. We specified pan trap colour (blue, white, yellow) as a fixed effect and included site as a random effect. Variables were tested for the assumption of normality prior to modeling. We used generalized linear mixed models (GLMM) to test several response variables that were not normally distributed: Andrenidae abundance, Apidae abundance, Colletidae abundance, and Megachilidae abundance. GLMMs allowed us to specify a Poisson error structure (non-normal count data), while still accounting for differences in abundance and richness distributions among the 12 sites. We used linear mixed models (LMM) to test response variables that were normally distributed: overall abundance, richness, and Halictidae abundance. We evaluated model fit of GLMMs and LMMs by visually checking the homoscedasticity and by testing the normality (Shapiro-Wilks) of the model residuals. For models with *p* values of the estimated coefficient below the specified significance level (**α**= 0.05) we performed a Tukey (HSD) *post hoc* test using a Bonferroni correction to determine which colours were significantly different. The Bonferroni correction adjusts the *p* value for multiple comparisons by multiplying the *p* value by the number of comparisons made. All analyses were performed in R (version 2.14.1, 2011). We compared pan trap and sweep net collections descriptively.

Results

Pan Trap Colour Preference

A total of 10,602 bee specimens were caught in pan traps across all sites representing 30 genera and six families. Mellitidae was exluded from analysis because only a single specimen was collected. Of the pan trapped bees 4,682 were caught at Dunnville Marsh, 3,246 at Pioneer Tower, 1,107 at Washington Creek, and 774 at Clair Creek. Significantly more bee specimens were caught in blue (364.6±42.9) and white (308.7±38.0) compared to yellow (208.5±35.7) pan traps (Figure 3-2, Table 3-1: blue-white: z=-2.15, p=0.096; blue-yellow: z=-5.99, p<0.001; white-yellow: z=-3.85, p<0.001). Genus richness was significantly greater in blue (14.08±1.04) and white (12.7±1.0) compared to yellow (10.8±1.0) pan traps (Figure 3-3, Table 3-1: blue-white: z=-1.87, p=0.19; blue-yellow: z=-4.38, p<0.001; white-yellow: z=-2.52, p=0.035).

All families demonstrated a preference for at least one colour (Figure 3-2). Andrenidae were significantly more abundant in yellow (8.8±2.3) compared to white (4.9±1.4) and blue (3.6±0.8) pan traps (Table 3-1: y-w: z=3.54, p=0.001; y-b: z=5.27, p<0.001; w-b: z=2.00, p=0.14). Apidae were significantly more abundant in blue (85.2±17.7) and white (85.2±18.3), compared to yellow pan traps (33.2±5.6) (Table 3-1: b-y: z=-15.96 p<0.001; w-y: z=-15.96, p<0.001). Colletidae were significantly more abundant in yellow (34.9±9.5) compared to white (25.6±6.9) and blue (23.1±8.2) pan traps (Table 3-1: y-w: z=4.14, p<0.001; y-b: z=5.34, p<0.001), but there was no significant difference between white and blue pan traps. Halictidae were significantly more common in blue (230.8±34.8) compared to white (156.5±21.8), and in white compared to yellow (107.1±20.6) pan traps (Table 3-1: b-w: z=-4.40, p<0.001, b-y: z=-7.32, p<0.001; w-y: z=-2.92, p<0.001). Megachilidae were significantly more abundant in blue (11.9±2.2) and white (9.5±2.1) compared to yellow (4.1±0.8) pan traps (Table 3-1: b-w: z=1.80, p=0.24; b-y: z=-6.47, p<0.001; w-y: z=-4.94, p<0.001).

For the most abundant genera (those represented by greater than 60 specimens), pan trap colour preference tended to reflect family pan trap preference (Table 3-3). Notable differences among the Apidae included the *Bombus spp.*, which were significantly more abundant in blue and white compared to yellow pan traps. *Ceratina spp.*, the most abundant genus overall, was significantly more abundant in white compared to blue and in blue compared to yellow pan traps. Among the Halictidae, *Halictus spp.* demonstrated no preference and were equally abundant in blue, white, and yellow pan traps. Among the Megachilidae, *Hoplitis spp.* were significantly more abundant in blue compared to white and white compared to yellow pan traps. *Nomada spp.* were most abundant in yellow traps (total 30 specimens) followed by white (26) then blue (15). The cleptoparasitic Halictidae *Sphecodes spp.* preferred yellow (12.1±5.3) and white (11.9±6.3) over blue (5.6±2.5) pan traps. Another cleptoparasite, *Nomada spp.*, was most abundant in yellow and white traps compared to blue.

Comparison of pan trap and sweep net collection methods

A total of 10,602 bee specimens were caught in pan traps and 597 plant visiting insects were caught in sweep nets across all sites. Pan trap collections were represented by 30 genera and five families; sweep net collections were represented by 15 genera and five families. The five most abundant genera in pan traps were *Lasioglossum spp.* (39%), *Ceratina spp.* (20%), *Auguchlorella spp.* (13%), *Hylaeus spp.* (10%), and *Halictus spp.* (3%). The five most abundant genera in sweep nets were *Ceratina spp.* (24%), *Lasioglossum spp.* (16%), *Melissodes spp.* (15%), *Bombus spp.* (11%), and *Halictus spp.* (7%).

Apidae was the dominant family in sweep net collections while Halictidae dominated pan trap collections (Figure 3-5). Proportionally more Apidae were caught in sweep nets compared to pan traps (57% and 24% of collected specimens). Larger bodied Apidae such as the *Bombus spp.*, *Melissodes spp.*, and *Xylocopa spp.* were caught proportionally more frequently in sweep nets (11%, 15%, and 5% respectively) compared to pan traps (0.6%, 1.6%, and 0.1%). Halictidae and Colletidae were proportionally more abundant in pan trap collections (60% and 10% of collected specimens, respectively), compared to sweep net collections (31% and 5%). The majority of collected Halictidae and Colletidae specimens were small-bodied. *Hylaeus spp.* was the only Colletidae collected in the survey, and small and medium sized *Lasioglossum spp.*, *Augochlorella spp.*, and *Halictus spp.*were the three most abundant Halictidae in pan traps and sweep nets. Andrenidae and Megachilidae were caught in similar abundances using both methods. Andrenidae made up 5% of sweep net collections and 2% of pan trap collections. Megachilidae made up 2% of sweep net collections and 3% of pan trap collections.

Pan traps caught twice as many genera (30) compared to sweep netting (15). Thirteen of the thirty genera caught in pan traps were represented by 10 or fewer specimens (less than 0.1% of total collections). All sweep netted genera were also caught in pan traps, but 15 genera identified in pan traps were not caught in sweep nets. Most of these 15 genera were rare to pan traps and only three were represented by more than ten individuals (*Osmia spp., Peponapis spp.,* and *Nomada spp.*).

Discussion

Understanding differences in collection methods is important for designing and interpreting the results of bee surveys. Our results demonstrate clear differences in bee catch between blue, white, and yellow pan traps and between pan trapping and sweep netting off of flowers. Blue pan traps were the most efficient of the three trap colours employed in our study area. Abundance and genus richness were greatest in blue followed by white and then yellow pan traps. All five families demonstrated a significant preference for at least one colour of pan trap. Pan trap colour preference of abundant genera usually, but not always, reflected family colour preference. Halictidae dominated pan trap collections and Apidae dominated sweep net collections. Pan traps tended to collect more small-bodied specimens, while large bodied specimens were more common in sweep nets. No exclusive genera were caught in sweep nets, but 15 exclusive genera were caught in pan traps.

Comparisons within the pan trap collection method

Blue pan traps were the most efficient at catching the largest number and the most diverse collection of native bees, followed by white and then yellow pan traps (blue>white>yellow). Greater abundances in blue and white compared to yellow traps reflect the colour preferences of the two most abundant families, Apidae and Halictidae. Our results are consistent with a similar study in forests of the southeastern United States (Campbell and Hanula 2007). But contrasts surveys in Australia and Uganda where yellow traps were the most efficient (Gollan et al. 2011; Munyuli 2013), and surveys in logged and un-logged forests of New York State where white traps were the most efficient (Romey et al. 2007). Genus richness trends were similar to abundance trends, significantly more genera were collected in blue and white compared to yellow traps (blue+white>yellow). This is consistent with results of surveys in Uganda (blue>white+yellow) and southeast US (blue>white>yellow) (Munyuli 2013; Campbell and Hanula 2007), but contrasts the results of Australian surveys (yellow>white) (Gollan et al. 2011). In a study of Utah desert habitats, Wilson et al. (2008) found no significant difference in species richness caught in white, yellow, blue, green, pink, and orange traps. The discrepancies among our results and those of previous studies indicates that the relative efficiency of different pan trap colours must vary by geographic location, likely as a result of different underlying species compositions. It is therefore intuitive that the results of our study are most similar to those of Campbell and Hanula (2007) because of the geographic proximity of the study areas leading to a greater likelihood of shared species when compared to Utah, Uganda, or Australia. It also emphasizes the importance of either employing a range of pan trap colours, or if targeting a specific group, of first identifying the most effective colour for that group in the study location. We evaluated the effectiveness of different pan trap colours using structural groups, families and genera. However, colour effectiveness could differ for collections of functional groups, e.g. guilds based on social and nesting habits. Differences are likely to be minimal because specimens of the same genera, and even family tend to share functional traits.

Site features and experimental design can influence the relative attractiveness of pan traps. These include: differences in habitat structure, light quality/intensity, pan trap 'colour', and numbers and colours of blooming flowers. A study of arthropods in tropical forests found that the ratio of Hymenoptera collected in blue compared to yellow pan traps changed with changing canopy cover, while another study found that morphospecies composition of tropical arthropods varied more by habitat type than by collection method (Abrahamczyk et al. 2010; Missa et al. 2009). These results suggest that habitat structure and collection location may play a significant role in determining overall community pan trap colour preference. This could be because differences in habitat structure or site features, such as canopy cover or light intensity, can affect how insects perceive colour and may increase or decrease the attractiveness of a trap (Lunau et al. 1996; Kevan 1972).

Colour preference of the most abundant genera tended to reflect family preference. However, there were a few notable differences. Apidae were equally abundant in blue and white traps (blue+white>yellow), but *Bombus spp.* and *Melissodes spp.* were significantly more abundant in blue compared to white and yellow traps (blue>white+yellow). For *Bombus spp.* the preference for blue and white pan traps was consistent with their preference for similarly coloured flowers. In sweep net samples *Bombus spp.* were caught almost exclusively on white and purple flowers. This is consistent with our understanding that naïve bumblebees are most attracted to wavelengths of 400-420nm (violet) and 510-520nm (cyan) (Gumbert 2000; Lunau et al. 1996). In contrast to the pan trap results, *Melissodes spp.* were caught almost exclusively on the yellow flowers of *Rudebeckia hirta* L. (brown eyed susan). It may be that the frequently recorded interaction was due to *Melissodes spp.*'s mid-summer emergence coinciding with the peak flowering time of brown eyed susan, as opposed to an expression of *Melissodes spp.* colour preference. *Ceratina spp.* (Apidae) was significantly more abundant in white pan traps, which again reflected its preference for pale blooms in sweep net collections. *Ceratina spp.* demonstrated an aversion to yellow traps with less than 2% of the nearly 1,800 specimens caught in yellow traps. *Halictus spp.* (Halictidae) was the only abundant genus (n>60) that did not demonstrate a preference for a particular pan trap colour. Deviations from family preference at the genus level were also observed among some of the more abundant cleptoparasites. *Nomada spp.*'s colour preference, though not significant, aligned with that of their host family, the Andrenidae, as opposed to their own family the Apidae. Similarly the cleptoparasitic Halictidae

Sphecodes spp., mimicked the colour preference of its Andrenidae hosts, preferring yellow and white over blue pan traps. Genera that were not present in one or more colours of trap were caught in very low numbers (n<10 specimens) and there is too little information to distinguish trap colour preference from sampling effects. The only genus represented by more than ten specimens that was not found in all three trap colours was *Xylocopa spp.* (n=15 specimens), which was absent from yellow traps.

Colour preferences for the major bee families were again consistent with the trends identified by Campbell and Hanula (2007). However, like overall abundance and genus richness, family and genus colour preferences are not necessarily consistent across a diversity of studied habitats. For example, in forests of the southeastern United States Halictidae were most abundant in blue pan traps, whereas in New South Wales, Australia Halictidae were significantly more abundant in yellow compared to white pan traps (Gollan et al. 2011; Campbell and Hanula 2007). In our survey Halictidae were significantly more abundant in blue compared to white yellow and in white compared to yellow pan traps. These differences are carried through to the genus level as Gollan et al. (2011) suggest employing yellow traps to target *Lasioglossum spp.*, while our results indicate that blue pan traps would be most effective for this genus. Pan trap colour preference appears consistent at the species level for at least one well-studied species: *Apis mellifera*, who prefers white pan traps across a diversity of geographic locations and habitat types (e.g. Gollan et al. 2011; Tuell et al. 2009).

Similar to previous studies of bee collection methods and pan trap colour preference, our results support the recommendations for employing multiple pan trap colours to best sample native bee community diversity (Munyuli 2013; Gollan et al. 2011; Westphal et al. 2008; Wilson et al. 2008). However, if collections are conducted to target specific taxa then it is most efficient to use pan traps in the preferred colour(s) of that group(s). Because of how much variability there can be between the catch rates of preferred and non-preferred colours, it may be particularly useful to use only the most efficient colour when trying to establish whether a rare species or group is present in a certain area. In open habitats of southern Ontario a combination of blue, white, and yellow traps is best for sampling overall biodiversity. For sampling family groups in southern Ontario, yellow traps would be most efficient for sampling Andrenidae, blue and white for Apidae, yellow for Colletidae, and blue and white for Halictidae and Megachilidae.

Comparison of pan trap and sweep net collection methods

Dominant bee families and genera differed considerably between pan trap and sweep net collection methods. Apidae were proportionally more abundant in sweep net collections while Halictidae dominated pan trap collections. These differences may be partly explained by differences in body sizes, as small bees tend to be over-represented in pan trap captures (Nielsen et al. 2011;

Westphal et al. 2008; Roulston et al. 2007; Cane et al. 2000). Larger bodied genera such as *Bombus spp.*, *Melissodes spp.*, and *Xylocopa spp.* were among the most frequently sweep netted genera and are conspicuous and easy for collectors to spot on flowers, resulting in potential over-representation in sweep nets. These larger bodied genera are also stronger and may be better able to escape from pan traps, resulting in potential under-representation in pan traps. In support of this, captured Halictidae and Colletidae, predominantly small-bodied bees, were proportionally more abundant in pan traps compared to sweep nets (Figure 3-4). Smaller bodied bees are more difficult for collectors to spot on flowers, more likely to evade net capture, and less able to escape once they have landed in a pan trap (Nielsen et al. 2011). Differences between the two methods could also be explained by differences in taxonomic preference for pan traps. Efficiency of pan traps at capturing bees that approach or land in traps has not been tested empirically and so predictions about body size influencing escape ability and taxonomic preferences are speculative or based on previous observations. In a single day survey Roulston et al. (2007) found that sweep netting outperformed (though not significantly) pan trapping for nearly all genera with the exception of two small bodied genera, *Augochlorella spp.* and *Calliopsis spp*. *Bombus spp.* were completely absent from the pan trap collections despite fairly frequent sweep net catches and only a single *A. mellifera* was caught in the pan traps despite being the most abundant netted species.

Some differences between pan trap and sweep net collections from flowers can be attributed to unequal collection effort between the two methods. Sweep net collections of floral visitors requires more active time than pan trapping to obtain equivalent numbers of specimens (Westphal et al. 2008). The large number of pan trap exclusive genera compared to no sweep net exclusive genera may be a result of greater collection effort by pan trap. Those genera of which fewer than ten specimens were caught may not have been detected by sweep net due to lower sampling effort. Three of these genera (*Coelioxys spp.*, *Stelis spp.*, and *Triepeolus spp.*) are cleptoparasites and are more likely to be resting on flowers than to be found in contact with the anthers or stigma. Only three pan trap exclusive genera were represented by more than ten specimens, of these *Nomada spp.* are cleptoparasitic and do not actively collect pollen. The other two, *Osmia spp.* and *Peponapis spp.*, were found in consistently low abundances in pan traps across the entire collection period, so while the overall catch of these genera was higher, they were never very abundant at any one sampling event. Other pan trap exclusive genera were rare to pan traps and tended to be small-bodied genera (e.g. *Augochloropsis spp.*, *Calliopsis spp.*, *Chelostoma spp.*, *Heriades spp.*, and *Pseudopanurgus spp.*).

Differences in the genus composition of collections by the two methods raises the question of which method best represents the true bee community of the surveyed habitats. Westphal et al. (2008) found that in European agricultural landscapes pan traps were the most effective form of population monitoring because they captured a wide range of species and had the advantages of low cost, minimal active time, and negligible collector bias. However, the effectiveness of pan traps appears to vary with the particular biogeography and ecology of sampled areas. Studies in a variety of geographic locales found that pan trapping was less effective than sweep netting. In a single day's sampling in northern Virginia, Roulston et al. (2007) collected 110 specimens representing 15 species from pan traps, compared to 531 specimens representing 29 species from sweep nets. In Uganda Munyuli (2013) captured 314 bee species in pan traps compared to 559 species in sweep nets. In another single day survey in Arizona, Cane et al. (2000) caught fewer specimens, but more species in blue and yellow pan traps compared to sweep netting. One thing to note is that in our study sampling effort was biased in favour of pan traps, whereas in other studies the opposite may be true, but cannot be easily judged. Pan trap sampling by Cane et al. (2000) and Roulston et al. (2007) represent only a single day's worth of collections leaving much room for variation due to weather, light conditions, or species' phenologies.

Pan traps may be more effective in certain studies compared to others because in locations with high densities of floral blooms there may be increased competition between flowers and pan traps with flowers outcompeting pan traps. This has been observed (Wilson et al. 2008), but has yet to be tested empirically (Roulston et al. 2007). Some species may not be interested in the particular combination of colour, scent, size, and shape of the pan traps regardless of whether other flowers are available for pollination. Another explanation for the differences between pan trap and sweep net collections is that pan traps placed on the ground may not be visible or attractive to pollinators foraging above ground levels (Tuell and Isaacs 2009). For example, *A. mellifera* are notoriously rare in pan traps placed on the ground, but are commonly caught in raised traps (Tuell and Isaacs 2009). Ground placement of pan traps may favour the detection of ground nesting bees, but under-sample cavity nesting species (Westphal et al. 2008). In this study pan traps were placed on the ground and were used throughout the study season including time periods with high blooms, potentially biasing the subset of the bee community caught.

Sweep netting is not exempt from biases either, and both collector bias and sampling effort can strongly influence the structure of the detected bee community (Gibson et al. 2011; Hegland et al. 2010; Vazquez et al. 2009; Westphal et al. 2008). Based on the observed differences between pan trapping and sweep netting in our study and between pan trapping and other collection methods reviewed in the literature, a single collection method is unlikely to return a true representation of the bee community (Munyuli 2013; Nielsen et al. 2011; Droege et al. 2010; Cane et al. 2000). In this study, both sampling methods relied on floral attraction, either by using pan traps as a proxy for flowers or by only catching insects touching the reproductive parts of flowers. This focus may under-sample certain groups such as cleptoparasitic species. To avoid this bias, collectors could employ indiscriminate sweep netting, which has the advantages of collecting insects not visiting flowers at the time of sweeping and of returning greater catch per unit of effort, but does not provide information on floral visitation (Richards et al. 2011; Hegland et al. 2010).

The differences in abundance, richness, and relative genus contributions between pan trapping and sweep netting support recommendations from the literature to employ two or more types of collection methods to obtain a more complete survey of the bee community (Munyuli 2013; Vrdoljak and Samways 2011; Missa et al. 2009; Westphal et al. 2008; Wilson et al. 2008; Roulston et al. 2007). This is true regardless of whether the study targets structural (e.g. genus) diversity or functional diversity. Despite its biases, pan trapping will likely continue to be the most widely employed collection technique for biodiversity surveys because it is easy to standardize and to replicate across time and space. Sweep netting appears to be suitable complement to pan trapping (Cane et al. 2000), and sweep netting from flowers has the additional advantage of providing information on floral associations that may be of interest depending on the goals of the project (Hegland et al. 2010; Memmott 2009). When sampling for a particular species, genus, or family that demonstrates a clear colour preference it may be beneficial to only use traps of that colour to maximize capture efficiency.

.

Table 3-1 Total number of bees captured by genus per site and per pan trap colour (B=Blue, W=White, Y=Yellow). Sites codes: Dun F1, F2, F4, F5, and F7 are the restored meadows of fields one, two, four, five, and seven at Dunnville Marsh. Dun Rem is the remnant Carolinian forest of Dunnville Marsh. PTR, PTD, and PTN, are the restored, degraded, and remnant forested areas of Pioneer Tower Natural Area, respectively. WCR and WCD are the restored and degraded areas of Washington Creek. CC is the restored area of Clair Creek.

	Dun F1			**Dun F2**			**Dun F4**			**Dun F5**			**Dun F7**			**Dun Rem**		
Genus	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**
Agapostemon	13	7		8	1					1			1					
Andrena	2	8	9	1	1	3	1	13	5	2	2	3	1	1	3		2	1
Anthidium																		
Anthophora				1		1				1			1					
Apis	10	8		7	6	1	4	4	1	3	1		4	6	1			
Augochlora																		
Augochlorella	79	91	68	70	46	36	116	126	72	33	21	25	76	57	51	2		
Augochloropsis																		
Bombus	1	1	1	9	1	1	3	3		4	1		1					
Calliopsis								1	2									
Ceratina	117	139	54	69	113	23	56	129	32	117	127	29	166	149	64	7	4	3
Chelestoma	1				1													
Coelioxys					1	1												
Halictus	4	5	5	10	13	12	4	8	11	8	2	5	14	9	6		1	
Heriades							1											
Hoplitis	6	3		9	11	2	20	14	4	10	5	4	12	8	2			
Hylaeus	27	24	35	33	35	31	21	35	16	20	19	23	33	15	29		1	
Lasioglossum	85	65	22	174	119	34	123	98	42	242	119	24	92	46	26	13	8	3
Macropis																		
Megachile		5			2		1		1	2	2		3		1			
Melissodes	5		1	16	3		24		1	32	2		28	2				
Nomada					2								2					
Osmia	1			1	8	3	4	4				3						
Peponapis	2									1								
Perdita														2				
Pseudopanurgus																		
Sphecodes			1	1	1	5	1	1	1	1		8		1	1			
Stelis	1				1		1				2	1		1	2			
Triepeolus					1						1							
Xylocopa				6	3		4	1		1								
Total	354	356	196	415	369	153	384	437	188	478	304	125	434	297	186	22	16	7

	PTR			**PTD**			**PTN**			**WCR**			**WCD**			**CC**			**Total**		
Genus	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**	**B**	**W**	**Y**
Agapostemon	9	4	1	1	1		5	5	1	1	3		4	4		1	1		**44**	**26**	**2**
Andrena	8	13	30	9	4	12	2	3	9	4	6	7	4	5	14	4		6	**38**	**58**	**102**
Anthidium	1							1								1	1	3	**2**	**2**	**3**
Anthophora	1											2							**4**	**0**	**3**
Apis	4	4	1	1			4	9		7	3	1	8	6		5	8	2	**57**	**55**	**7**
Augochlora				1			3	2											**4**	**2**	**0**
Augochlorella	18	9	19	8	5		28	27	19	1	4		13	8	12	101	69	54	**545**	**463**	**356**
Augochloropsis							1												**1**	**0**	**0**
Bombus	4		2	2	2		3	4	1	3	1	1	4	2					**34**	**15**	**6**
Calliopsis		2	1					1								1			**1**	**4**	**3**
Ceratina	41	44	24	4	11	9	105	137	56	19	18	7	4	8	6	48	43	27	**753**	**922**	**334**
Chelestoma				1															**2**	**1**	**0**
Coelioxys																			**0**	**1**	**1**
Halictus	21	15	23	17	16	4	19	8	8	7	9	8	10	9	27		3	4	**114**	**98**	**113**
Heriades								2								1			**2**	**2**	**0**
Hoplitis	17	12	2	4	2		10	6	2	1	2		6	3	2	3	2		**98**	**68**	**18**
Hylaeus	16	42	115	10	13	28	12	24	35	1	8	15		5	16	106	115	85	**279**	**336**	**428**
Lasioglossum	326	210	165	343	265	146	168	125	63	52	40	18	344	177	124	50	43	21	**2012**	**1315**	**688**
Macropis																			**0**	**0**	**0**
Megachile	6	3			4		4	6		3			2		2	6	3	4	**27**	**25**	**8**
Melissodes	15	2	3	3			7	1	4	3		13	1						**134**	**10**	**22**
Nomada		6	4	3	8	25		6		10	1	1		1			2		**15**	**26**	**30**
Osmia				2	1	3		1					1	2	2	1			**10**	**16**	**11**
Peponapis	2			2												5			**12**	**0**	**0**
Perdita																			**0**	**2**	**0**
Pseudopanurgus			1			1									1				**0**	**0**	**3**
Sphecodes	6	40	57	22	69	42	25	23	13	5	7	1	5	1	14	1		2	**67**	**143**	**145**
Stelis			1																**2**	**4**	**4**
Triepeolus		1														1			**1**	**3**	**0**
Xylocopa																			**11**	**4**	**0**
Total	495	407	449	433	401	270	396	391	211	117	102	74	406	231	220	335	290	208	4269	3601	2287

Table 3-2 Comparison of mean (SE) overall abundance, genus richness, and Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae abundance in blue, white, and yellow pan traps at Clair Creek, Dunnville Marsh, Pioneer Tower Natural Area, and Washington Creek in 2012. For each variable means followed by the same letter are not significantly different at $p \leq 0.05$ according to the Tukey HSD with Bonferroni correction for multiple comparisons.

	Blue	**White**	**Yellow**	**White - Blue**		**Yellow-Blue**		**White-Yellow**	
				Z	**p**	**Z**	**p**	**Z**	**p**
Abundance	364.6 (42.9)$_{A}$	308.7 (38.0)$_{A}$	208.5 (35.7)$_{B}$	-2.15	0.095	-5.99	<0.001	-3.85	<0.001
Richness	14.1 (1.0)$_{A}$	12.7 (1.0)$_{A}$	10.8 (1.0)$_{B}$	-1.87	0.19	-4.39	<0.001	-2.52	0.035
Andrenidae	3.3 (0.3)$_{A}$	4.9 (1.4)$_{A}$	8.8 (2.3)$_{B}$	2.00	0.14	5.27	<0.001	3.54	0.0012
Apidae	85.2 (17.7)$_{A}$	85.2 (18.3)$_{A}$	33.2 (5.6)$_{B}$	0	1.0	-15.96	<0.001	-15.96	<0.001
Colletidae	23.1 (8.2)$_{A}$	25.6 (6.9)$_{A}$	34.9 (9.5)$_{B}$	1.24	0.64	5.34	<0.001	4.14	<0.001
Halictidae	230.8 (34.8)$_{A}$	156.5 (21.8)$_{B}$	107.1 (20.6)$_{C}$	-4.40	<0.001	-7.32	<0.001	-2.92	0.010
Megachilidae	11.9 (2.2)$_{A}$	9.5 (2.1)$_{B}$	4.1 (0.8)$_{B}$	-1.80	0.21	-6.47	<0.001	-4.94	<0.001

Table 3-3 Comparison of mean (SE) catch of abundant genera in blue, white, and yellow pan traps at Clair Creek, Dunnville Marsh, Pioneer Tower Natural Area, and Washington Creek in 2012. For each genus means followed by the same letter are not significantly different at $p \leq 0.05$ according to the Tukey HSD with Bonferroni correction for multiple comparisons.

Genus	**Blue**	**White**	**Yellow**
Agapostemon	3.67 (1.23)$_{A}$	2.08 (0.70)$_{A}$	0.25 (0.13)$_{B}$
Andrena	3.17 (0.81)$_{A}$	4.83 (1.28)$_{A}$	8.50 (2.26)$_{B}$
Apis	4.75 (0.82)$_{A}$	4.58 (0.90)$_{A}$	0.58 (0.19)$_{B}$
Augochlorella	45.42 (11.76)$_{A}$	38.58 (11.60)$_{B}$	29.58 (7.54)$_{C}$
Bombus	3.17 (0.71)$_{A}$	1.25 (0.37)$_{B}$	0.50 (0.19)$_{B}$
Ceratina	62.75 (15.33)$_{A}$	77.67 (17.49)$_{B}$	27.75 (5.95)$_{C}$
Halictus	9.50 (2.04)$_{A}$	8.17 (1.40)$_{A}$	9.42 (2.31)$_{A}$
Hoplitis	8.17 (1.77)$_{A}$	5.33 (1.42)$_{B}$	1.83 (0.39)$_{C}$
Hylaeus	23.25 (8.26)$_{A}$	28.00 (8.72)$_{A}$	35.67 (9.33)$_{B}$
Lasioglossum	167.67 (34.62)$_{A}$	109.58 (22.18)$_{B}$	57.33 (16.02)$_{C}$
Melissodes	11.17 (3.33)$_{A}$	0.83 (0.32)$_{B}$	1.75 (1.01)$_{B}$
Sphecodes	5.58 (2.50)$_{A}$	11.92 (6.30)$_{B}$	12.08 (5.31)$_{B}$

Figure 3-1 Map of all study sites, southern Ontario: Clair Creek, Pioneer Tower Natural Area, Washington Creek, and Dunnville Marsh, sampled in 2012. Source, Google Earth, 2013.

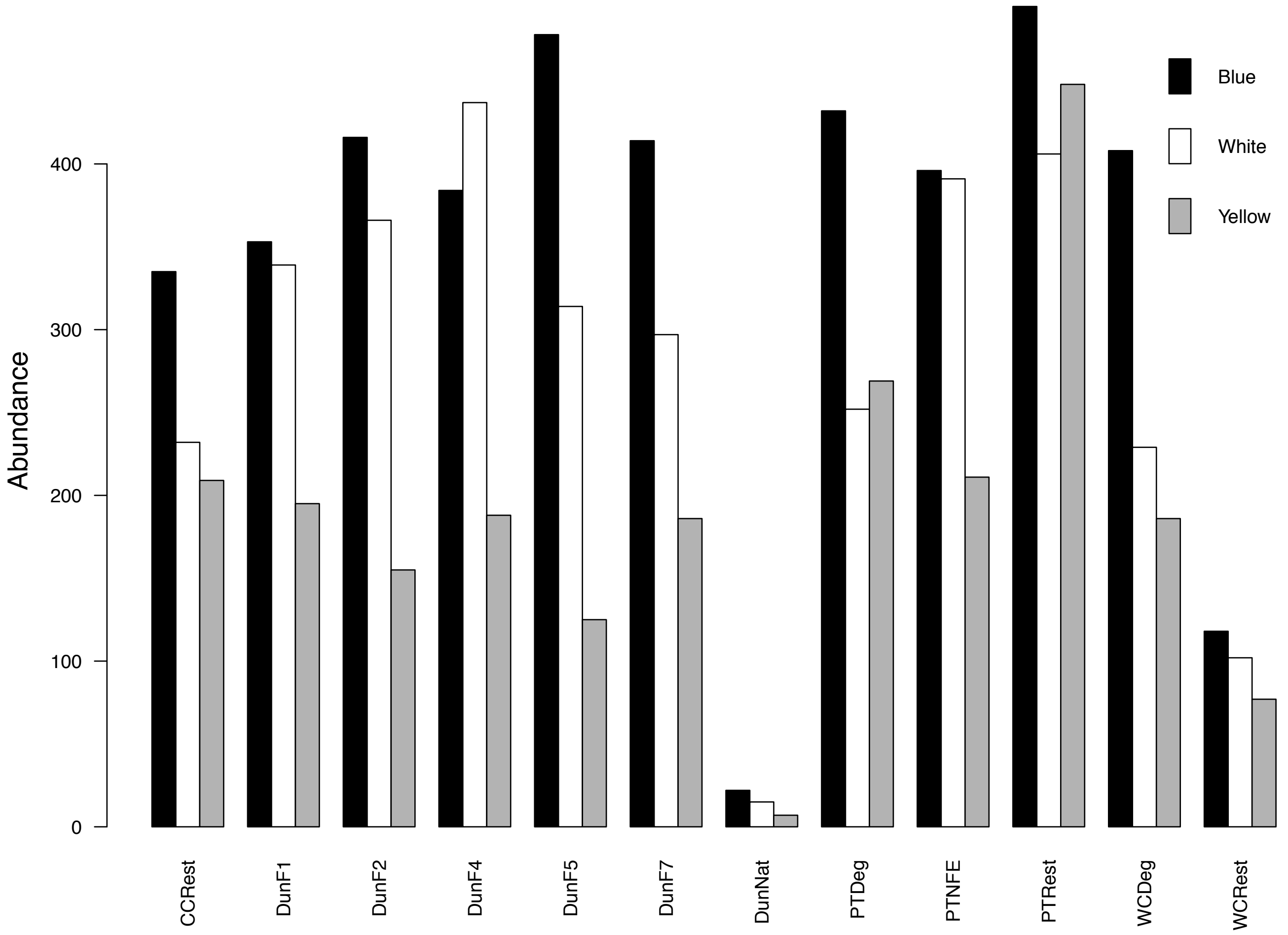

Figure 3-2 Bee abundance collected in blue, white, and yellow pan traps at Clair Creek, Dunnville, Pioneer Tower Natural Area, and Washington Creek sampled in southern Ontario, 2012.

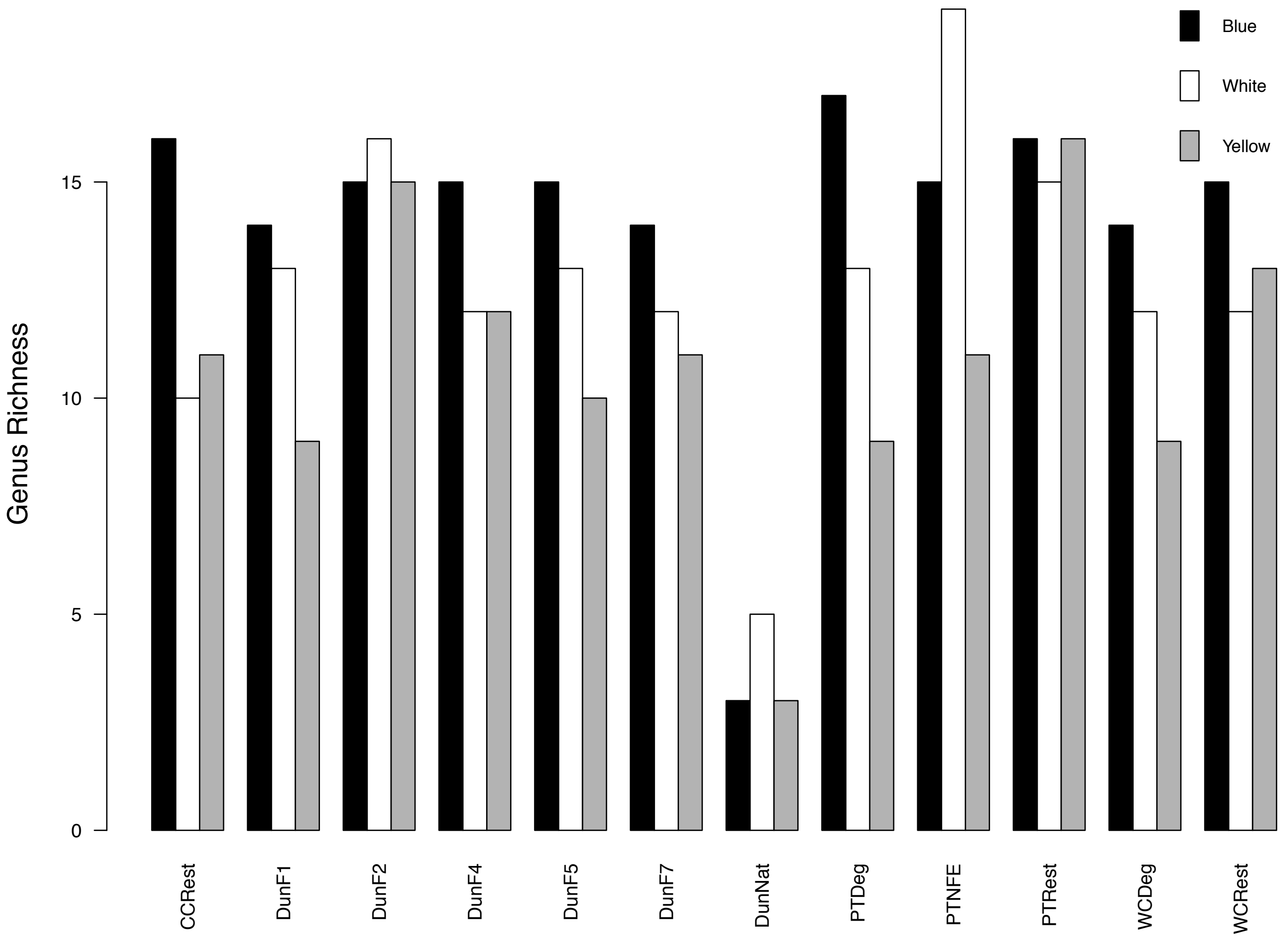

Figure 3-3 Bee genus richness collected in blue, white, and yellow pan traps at Clair Creek, Dunnville, Pioneer Tower Natural Area, and Washington Creek sampled in southern Ontario, 2012.

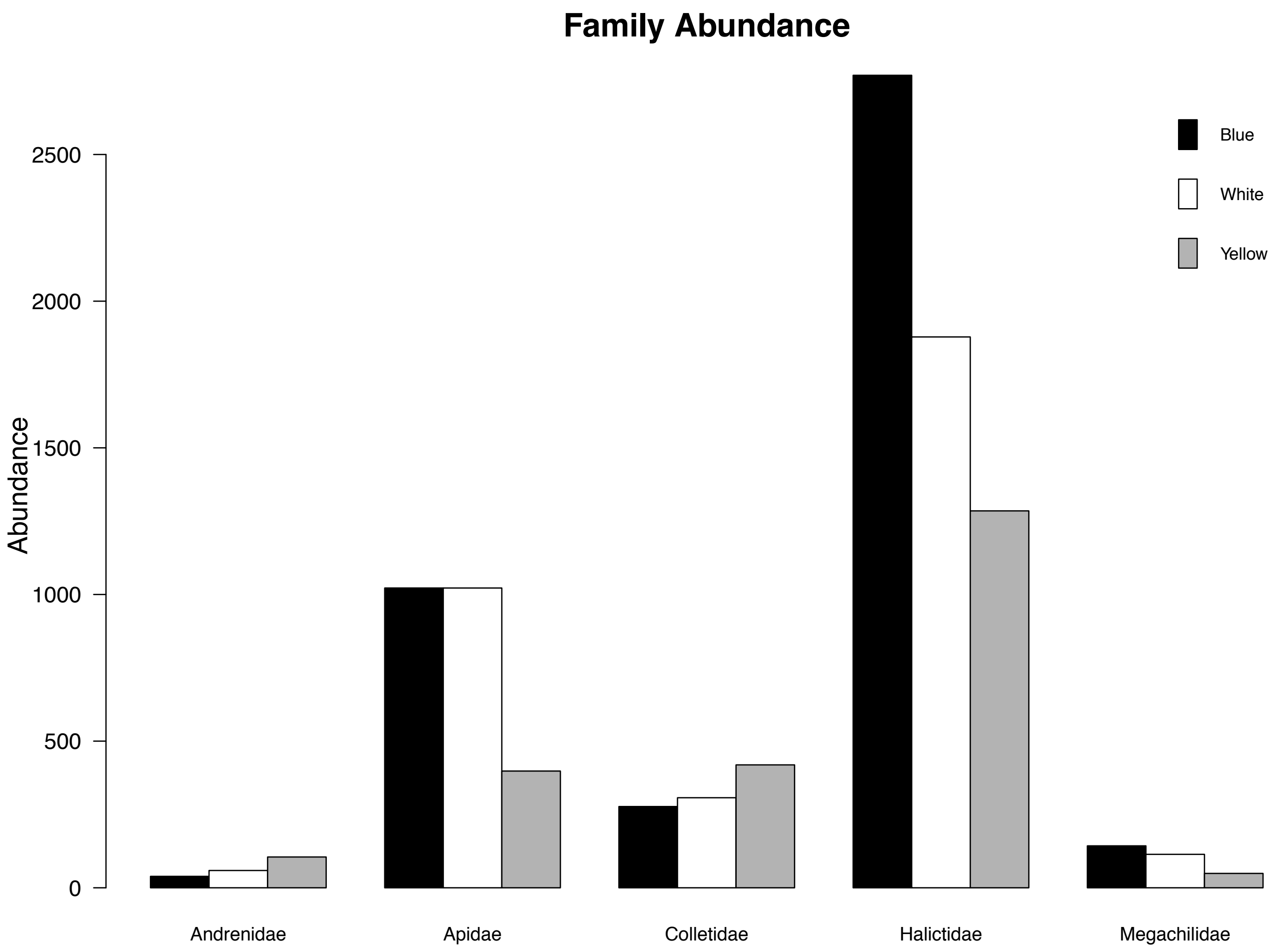

Figure 3-4 Total pan trap catches by pan trap colour for the five families: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae collected from Clair Creek, Washington Creek, Dunnville Marsh, and Pioneer Tower Natural Area in southern Ontario, 2012

Figure 3-5 Relative abundance of bees caught in sweep net and pan trap collections at Clair Creek, Dunnville Marsh, Pioneer Tower Natural Area, and Washington Creek in southern Ontario, 2012.

Chapter 4 Wet meadow restoration in southern Ontario: An evaluation of native bee (Hymenoptera: Apiformes) diversity and the influence of pit and mound restoration on establishing bee communities

Overview

Native bees are important pollinators of flowering plants in most terrestrial ecosystems and play a key role in the long-term functioning and resilience of restored ecosystems. However, little is known about how bees establish following restoration and the influence of different restoration techniques on establishing communities. We surveyed bee and floral communities in a series of restored wet meadows in southern Ontario's Carolinian life zone to describe the native bee community and to compare the communities that established in sites restored using two restoration approaches. We collected 5,010 bees representing 27 genera and six families. The bee community at the restored marsh was diverse, well connected and included a range of phenologies, social behaviours, and nesting habits. However, cleptoparasites and wood nesters were present at lower relative abundances compared to surveys of older sites in the region. We compared the bee communities in sites dug with pits and mounds before planting and sites seeded into weedy ground. Neither pit and mound nor planted only sites conveyed a clear advantage to bee communities, but communities were influenced by restoration technique. Bare ground, ground nesters, and wood nesters were more abundant in pit and mound sites ($p<0.001$ all comparisons), and stem nesters were more abundant at planted sites ($p<0.001$). Richness was greater at pit and mound sites ($p=0.04$), but abundance and evenness were not. Regardless of restoration technique, diverse bee communities established in the meadows soon after restoration, emphasizing the importance of wet medows as habitat for native bees.

Introduction

Native bees are the primary pollinators of flowering plants in most terrestrial ecosystems (Friedman and Barrett 2009; Kevan 1999), and the services they provide are necessary for maintaining diverse flowering plant communities (Kearns et al. 1998). In the past decade there has been increasing evidence of declines in native bee abundance and diversity in both Europe and North America. Because of their role in plant reproduction, bee declines are expected to strongly impact flowering plant communities and may lead to the loss of associated flowering plant species. In Europe, Biesmeijer et al. (2006) compared pre- and post-1980 bee and hoverfly communities in Britain and the Netherlands and detected extensive declines in bee richness, and bee pollinated plant diversity. In North America, historical records of pollinator communities are rare, making it difficult to identify and quantify short and long-term changes (Winfree 2010). However, there is localized evidence for declining species richness and pollination function (e.g. Burkle et al. 2013). For better-studied groups, such as the bumblebees (*Bombus spp.*), there is evidence of declines across North America, including southern Ontario (Colla et al. 2012; Goulson 2010; Williams and Osborne 2009). Recent bee conservation research has focused on agro-ecosystems because of the economically valuable contribution of pollinators to crop production (Klein et al. 2012; Samnegard et al. 2011; Isaacs and Kirk 2010; Klein et al. 2007; Julier and Roulston 2009; Winfree et al. 2008). However, native bees also play a critical role in (semi)natural ecosystems where they contribute to plant reproduction, enhance fruit size and seed set, and facilitate genetic recombination (Nyak and Davidar 2010; Kevan 1999; Faegri and van der Pijl 1971).

Habitat loss and degradation due to urbanization, suburbanization, and agricultural intensification are the primary drivers of pollinator declines with pests and disease, climate change, and pesticides playing supporting roles (Potts et al. 2010; Kremen et al. 2002). Pre-European settlement, forests and forested wetlands dominated southern Ontario; however, other ecosystems favoured by bees, including meadows and prairies, also occurred (Riley and Mohr 1994). Estimates of historic forest cover often fail to account for slash and burn agriculture by first nations groups and disturbance events (e.g. drought), which contributed to a dynamic landscape that likely consisted of a matrix of meadow, wetland, and forested habitat capable of supporting diverse bee communities. Early agricultural activities may have benefitted native bee communities by opening up forest habitat to a greater variety of bee pollinated meadow and crop plant species. However, the transition to industrialized agriculture and the growth of urban centers and accompanying infrastructure has degraded the integrity of remaining forested and non forested ecosystems (Riley and Mohr 1994). Changes to the landscape associated with industrial agriculture, urbanization, and suburbinization tend to reduce food and nest site availability, either by direct elimination or by introducing dispersal barriers (Krewenka et al. 2011; Menz et al. 2011; Jauker et al. 2009; Winfree et al. 2007). While some bee species can thrive in degraded habitats (Ahrne et al. 2009; Winfree et al. 2007), most are negatively impacted by these changes.

Ecological restoration is a way to potentially mitigate native bee losses by increasing the amount and quality of available natural habitat (Menz et al. 2011; Winfree 2010; Dixon 2009). The response of native bees to habitat restoration has been relatively well explored in the context of agro-ecosystems (e.g. Samnegard et al. 2011; Hannon and Sisk 2009; Pywell et al. 2005). However, our understanding of how geographic location, habitat type, restoration approach, and temporal scale influence establishing bee communities in (semi)natural ecosystems is incomplete and based on only a few recent studies (Montoya et al. 2012; Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008). Most restoration projects focus on structural elements of ecosystems, such as establishing key plant species, in the hopes that non-targeted species, including pollinators, will colonize over time as conditions become favourable (Hildebrand et al. 2005; Palmer et al 1997). For pollinators, this approach assumes there are source populations within appropriate dispersal distances and unimpeded by landscape barriers (Krewenka et al. 2011; Kohler et al. 2008). This assumption may not hold true in heavily modified landscapes, and few studies have actually tested this assumption by surveying pollinator communities and pollination function in restored (semi)natural ecosystems (*but see* Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008; and Forup and Memmott 2005).

Consistent with restoring structural site properties, evaluating restoration outcomes has historically relied on structural community characteristics, such as species composition, abundance, and richness (Memmott 2009; Ruiz-Jaen and Aide 2005). However, using only structural characteristics can be problematic because it assumes that there is a known target for a restored community (Memmott 2009). Restoration tends to create partially historic (hybrid) or novel ecosystems that do not resemble historic systems, making it difficult to identify appropriate reference sites (Hobbs et al. 2009). When reference sites do exist, they too have likely been subjected to anthropogenic impacts and no longer resemble their historic state. This absence of appropriate structural targets for restorations generally, and restored pollinator communities specifically, has initiated a shift towards emphasizing ecosystem function as an alternate metric for assessing restoration outcomes (e.g. Sheffield et al. 2013; Montoya et al. 2012; Williams 2011; Memmott 2009; Forup et al. 2008). In this study we evaluate ecosystem function using the abundance of functional groups (guilds) based on nesting habits and social behaviour, and pollination function based on plant visitation by pollinating insects. We use these metrics to evaluate restoration outcomes at Dunnville Marsh, a series of restored wet meadows in southern Ontario.

Little is known about how restoration approaches and management influence establishing bee communities (*but see* Cusser and Goodell 2013; Devoto et al. 2012; Tarrant et al. 2012). One restoration technique, pit and mound, is often applied in wetland and wet meadow restoration. The pit and mound technique involves digging holes (approximately 2m in diameter) and using the removed material to create adjacent mounds. The purpose of this technique is to imitate the action of trees uprooting (creating pits) and rotting (creating mounds), increasing topographic heterogeneity. It is expected that the increased heterogeneity will allow for the colonization of species with different habitat requirements, in particular amphibians, reptiles, and herbaceous plants are expected to directly benefit from the creation of wet pit bottoms and dry mound tops (Falk et al. 2006). Despite the increasing popularity of pit and mound restoration, its impact on restored plant and wildlife communities has been rarely studied and there is limited empirical evidence to support its predicted advantages.

Native bees are not directly targeted by the creation of pits and mounds, but changes to site topography and the expected changes to plant communities may indirectly benefit bees by increasing floral and nesting resources. Pit and mound restoration is expected to increase herbaceous plant abundance and richness by increasing the range of available microhabitats, though empirical evidence is sparse (*but see* Ewing 2002). Bees (except cleptoparasitic species) are obligate florivores and flowering plant abundance and richness are positively associated with pollinator abundance and richness (Hopwood 2008; Kohler et al. 2008; Potts et al. 2005). Therefore, if pit and mound restoration enhances flowering plant diversity, we would expect cascading benefits to the bee community. The creation of pits and mounds also may increase the availability of nest sites for ground and cavity nesting bees. Ground nesting bees prefer to nest in sunny, sloped bare ground, which is more abundant in areas dug with pits and mounds. In wet meadows, dry mound tops can serve as refuges for establishing woody plant species that may otherwise be lost to flood events. In restored habitats, this may lead to quicker establishment of woody plant species and an increased availability of nest sites for cavity nesters. The impact of pit and mound restoration on target and non-target communities has received minimal attention in the literature (*but see* Ewing 2002; Dhillion 1999), and no study has investigated the influence of pits and mounds on native bee communities.

The first objective of our survey was to describe the structure and function of the bee community at Dunnville Marsh to evaluate the status of the restoration so far and to provide a baseline that can be used to monitor ongoing changes in the bee community. We described the bee community in terms of diversity, phenology, and social and nesting habits. We assessed pollination function of the meadow using plant visitation by pollinating insects as a proxy for pollination. The second objective of this study was to determine whether restoration approach influenced the established bee communities. We asked four related questions: (1) how do abundance, richness, and evenness differ between pit and mound and planted sites?; (2) how do site characteristics including floral richness and abundance and nest site availability differ between pit and mound and planted sites?; (3) how does the abundance of functional groups based on social and nesting habits differ between pit and mound and planted sites?; and (4) how do properties of plant-pollinator visitation networks including connectance, nestedness, and robustness to extinction differ between pit and mound and planted sites?

These two objectives provide important insight into the structure and function of the pollinator communities of the restored wet meadows at Dunnville Marsh. The first provides baseline information that is currently lacking for Carolinian wet meadows, and that will enable future community monitoring. The second provides a preliminary assessment of the influence of pit and mound restoration on the structure and function of pollinator communities. Both objectives provide additional insight into how functional metrics can be applied to evaluate restoration status.

Methods

Site Description

We conducted surveys at Dunnville Marsh, a 400-hectare property of mixed marsh, restored wet meadow, and low-lying forest located in Canada's Carolinian life zone. Dunnville Marsh is located on Grand River near the town of Dunnville in Haldimand County, southern Ontario. In Canada, the Carolinian life zone is found only in the extreme southwestern corner of Ontario, but hosts a diverse range of habitats and species (Line et al. 2000). The high diversity of this life zone is due to the unique climate and the mingling of southern species at the northernmost point of their range with northern species and species endemic to the Great Lakes (Kanter et al. 2004). Many of the ecosystem types and species found in the Carolinian life zone are rare in Canada due to the limited geographic extent of the life zone and the widespread conversion of forests and grasslands to agricultural land during European settlement (Allen et al. 1990; Reid and Symmes 1997; Line et al. 2000). Because of the high conservation value of the life zone, there is significant motivation to acquire sensitive habitats for restoration.

In 1993 the Nature Conservancy of Canada acquired 343 ha of the current Dunnville Marsh property from the Canadian Pacific Railway, and passed ownership on to the Grand River Conservation Authority (GRCA). In 2008 Ducks unlimited helped the GRCA acquire an additional 53 hectares. Prior to European settlement the study area was a mix of marsh and low-lying forest. Following settlement most of the land was converted to farmland. Before restoration, Dunnville Marsh consisted of seven adjacent agricultural fields separated by remnants of Carolinian forest. We surveyed bee communities in five restored fields and one forest remnant. We named surveyed fields (from west to east) Pit 1, Pit 2, Pit 3, Plant 1, and Plant 2, based on their treatment status of pit and mound (Pit) or planted (Plant) (Figure 4-1). Restoration activities were conducted between 2005 and 2008 began with the digging of pits and mounds in Pit 2 and Pit 3 in 2005, and in Pit 1 in 2006. Pits and mounds were approximately two meters in diameter, and covered most but not the entire field where they were dug. Tree and herbaceous planting and seeding took place in 2006 for Pit 2 and Pit 3, and in 2007 for Pit 1. Plant 1 and Plant 2 were seeded into weedy undisturbed ground in 2008. No restoration activities occurred in the remnant forest.

Bee Sampling

We sampled bees within the sites every 10 to 14 days from May through August 2012, using pan traps and sweep netting from flowers (Roulston et al. 2007; Campbell and Hanula 2007). All six sites were sampled within three days of each other, with three sites sampled per day. We sampled each site ten times over the study period. Sampling took place on sunny (<60% cloud cover), warm (>14˚C) days with low wind speeds.

In each field we established one permanent 100m pan trap transect across the width of the field beginning at a randomly predetermined point along the fields' length. We placed ten each of alternating yellow, blue, and white pan traps (n=30) along the transect line at 3m intervals. We avoided placing the pan traps under shrubs, tall grass, or on the slopes of pits and mounds. Pan traps were approximately 18cm in diameter, held 6oz of liquid and were filled ¾ full with a mixture of waster and unscented blue Dawn™ dish soap. Upon collection, we passed the contents of the traps through a fine sieve and stored specimens in labeled bags with 70% ethanol. We set out pan traps for a total of seven hours beginning at approximately 09:00 and ending at 16:00.

For sweep net surveys, we established two permanent 50m transects in each field. We placed transects across the width of the field starting at randomly predetermined coordinates (length, width). We walked each sweep net transect once between 11:00 and 14:00. We sweep netted any insect actively visiting a flower within 1 meter of either side of the transect line. Active visitation was defined as the insect being in contact with the anther or stigma of the visited flower.

Flower and nest site sampling

We assessed floral abundance at each site using 20 1x1m quadrats. Ten quadrats were evenly spaced along each of the sweep net transects and were placed on alternating sides of the transect line. In each quadrat we identified and counted the number of flowers available for pollination. For species with very small and numerous flowers (e.g. Asteraceae, *Daucus carota* L.) we counted the number of inflorescences. We identified flowering plants using field guides (Newcomb 1977). Flowers available for pollination were defined as those with unwilted petals and visible (fresh) anthers or stigmas. The percent of bare ground was estimated within the quadrats to obtain an estimate of nest site availability for ground nesting species (Potts et al. 2005).

Identification of specimens and sorting into guilds

We refrigerated and stored all insects collected from pan traps in 70% ethanol until processing. We identified specimens to genus under a dissecting microscope using Packer et al. (2007) and sorted specimens into guilds based on social (social vs. solitary) and nesting habits (ground vs. cavity). We determined guilds based on eastern bee Canadian literature that had sorted into guilds or identified social and nesting habits (e.g. Richards et al. 2011; Grixti and Packer 2006). For those genera not previously sorted, we based our decisions on relevant literature (e.g. Michener 2000; Hurd et al. 1974).

Genera were sorted into six guilds as follows: Guild A - solitary ground nesters, Guild B – social ground nesters, Guild C – cavity nesters, Guild D – *Bombus spp.* Latreille, Guild E – parasites, and Guild F – *Apis mellifera* Linnaeus. Genera belonging to each guild are presented in Table 4-1. We also formed groups based on nesting habits for all but the parasitic genera. For ground nesters we combined Guilds A and B. We split Guild C into stem nesters (*Ceratina spp.* and *Hylaeus spp.*) and wood nesters (all other Guild C genera).

Analysis: Comparison of the bee community in pit and mound and planted treatments

To compare the two restoration approaches we compared surveys from Pit 2 and Pit 3 (pit and mound treatment) to surveys from Plant 1 and Plant 2 (planted treatment). Pit 1 was left out of the comparisons because of differences in the restoration timeline compared to the other pit and mound fields

We compared overall abundance, richness, evenness, and abundance of each of the six guilds between pit and mound and planted sites. All comparisons were based on pan trap data. For all comparisons we examined boxplots of the response variable of interest by site to check that data were similarly distributed in each of the four fields. This was done so that we could exclude 'site' as a model variable. We tested for correlation of sampling events through time using the autocorrelation function (R package nlme). Because no correlation was detected, sampling events were treated independently for all comparisons.

All variables were examined for assumptions of normality prior to analysis using the Shapiro Wilks test. We used appropriate pair-wise comparisons, general linear model or generalized linear model, to compare variables of interest between the two comparisons. General linear models assume a normal error distribution, while generalized linear models allow for response variables with other than normal distributions. For all generalized linear models we specified a Poisson distribution (non-normal count data). We evaluated model fit by testing the normality (Shapiro Wilks) of the model residuals. Abundance was as the total number of bees collected at a site on a day of sampling. Genus richness was the total number of genera recorded at a site on a day of sampling. Shannon's evenness was a measure of how close in numbers each genus in a habitat is. Evenness was calculated for each sampling event at each site using the equation H/H_{max}. Where H is the Shannon diversity index and H_{max} is the maximum value (ln[genus richness]). Evenness was included because pit and mound and planted sites may exhibit similar genus richness, but different genus evenness, which would indicate differences in community composition between the two treatment types.

We compared abundance of each of the six guilds, abundance of the three nesting habit groups, floral richness and floral abundance, between the two restoration approaches using generalized linear models (GLM). This allowed us to specify a Poisson distribution (non-normal count data). We tested the correlation between nest site abundance for ground nesters and sampling event using Pearson's correlation coefficient. Because nest site availability was correlated with time, we compared availability between sites in a mixed model context. We speficied restoration treatment as the fixed effect, sampling event as a random effect, and a Poisson error structure All analyses were carried out in R (version 2.14.1 2011) using the lme4 package (version 0.999375-42, 2011).

Plant-pollinator interaction networks

We constructed a plant-pollinator visitation matrix for Dunnville Marsh using records of floral visitation taken from the combined sweep net collections of all sampled restored sites. The matrix contained the total number of visits observed for each insect-flower interaction. Floral visitation does not account for pollen transfer and is therefore not a precise measure of pollination success, but it is a good first-order approximation (Alarcon 2010; Vazquez et al. 2005). Plant-pollinator interaction networks were visualized using the bipartite package (version 1.17, 2011) in R (2.14.1). We calculated the following network properties: the number of higher and lower order groups, network connectance, linkage density, Shannon's diversity, weighted nestedness, and robustness of higher and lower order groups to extermination.

Connectance is the number of realized links out of the total number of possible links, and is a measure of how many bee genera are visiting plant species (Jordano 1987). Linkage density is the ratio of links per species ($L = l/i+p$). Where l is the number of links, i is the number of insect genera and p is the number of plant species. Weighted nestedness is the tendency of highly connected groups to interact with less connected groups and is weighted by interaction frequency (Galeano et al. 2009). Weighted nestedness approaches zero when the nestedness pattern of the matrix is close to that of equivalent random matrices, and approaches one when the nestedness pattern of the matrix is close to the maximum nested matrix. Robustness is an expression of the ability of a network to withstand species loss and is calculated as the area below the extinction curve (Burgos et al. 2007). The extinction curve for a given group (e.g., pollinators) is based on what would happen to that group if a fraction of the other group (e.g., plants) were removed. An R=1 corresponds to a curve that decreases mildly until a point where almost all species are eliminated. An R=0 corresponds to a curve that decreases abruptly as soon as species are eliminated.

To determine whether the function of the pollinator community differed between pit and mound and planted sites we used sweep net collections to construct plant-pollinator visitation networks for each of Pit 2, Pit 3, Plant 1, and Plant 2. We compared the properties of these networks descriptively.

Results

Bee diversity

We collected 5,010 bee specimens of 27 genera from pan and net samples at Dunnville Marsh (Table 4-2). Specimens represented all six bee families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Mellitidae) present in North America (Packer et al. 2007). Of these specimens 4,735 were collected in pan traps and 275 were collected in sweep nets. Wasps and flies were included in sweep net samples if they met the collection criteria; as a result the total number of sweep netted specimens was 333. In pan traps, Apidae had the highest genus richness (10 genera), and comprised 35% of specimens. Halictidae was represented by seven genera, and was most abundant family overall (52% of specimens) (Figure 4-2). Colletidae had the lowest genus richness (only *Hylaeus spp.*), but made up 8% of the overall abundance. The least common families were Andrenidae (1%), Megachilidae (3%), and Mellitidae (single specimen).

The ten most common genera caught in pan traps in order of abundance, and excluding *Apis mellifera,* were *Ceratina spp. (*29.7%), *Lasioglossum spp*. (28.2%), *Augochlorella aurata* (20.4%), *Hylaeus spp*. (8.4%), *Melissodes spp*. (2.4%), *Halictus spp*. (2.5%), *Hoplitis spp*. (2.3%), *Andrena spp.* (1.2%), *Bombus spp*. (0.6%), and *Osmia spp*. (0.5%), with the three most frequently collected genera making up nearly 80% of the specimens.

In sweep nets, Apidea made up the majority of the captured specimens (57%), which represented 5 genera (Figure 4-3). Halictidae was represented by 6 genera and comprised 31% of the captured specimens. Of the Andrenidae, only *Andrena spp.* were captured in sweep nets (5%). Of the Megachilidae only *Hoplitis spp*. and *Megachile spp*. were sweep netted and comprised 2% of the captured specimens. *Hylaeus spp*. was the only Colletidae captured in both sweep net and pan trap collections and made up 5% of the sweep net collections.

Social ground nesters (Guild B) and solitary cavity nesters (Guild C) were the most abundant guilds at Dunnville Marsh, with 2,485 and 1,977 specimens, respectively. Solitary ground nesters (Guild A) were less common, 177 specimens, and collections were dominated by *Andrena spp.* and *Melissodes spp*. *Bombus spp*. and *Apis mellifera* (Guilds D and F) were found in relatively low numbers overall (25 and 38 specimens) compared to the proportion caught in sweep nets. parasites (Guild E) were also uncommon (39 specimens), compared to other guilds.

Bee phenology

During 2012 we observed four abundance peaks in the native bee community (Figure 4-4). The first two peaks occurred in the spring at sampling events one and three, the second in mid-summer over sampling events five and six, and the final peak occurred in late summer over events 9 and 10. The five bee families displayed distinct phenologies, with some common trends (Figure 4-4). Andrenidae were most abundant in the spring with 67% of the specimens caught at event 1 and a second smaller peak at the 3rd event. Apidae were most abundant at events 1 (20%) and 3 (21%), with two smaller peaks at events 5 (11%) and 9 (14%). Colletidae were most abundant at the end of the season (21% caught on event 10), with a slightly smaller peak at the 3rd event (18%). Halictidae, the most abundant family, was most abundant at the 1st event (24%) followed by events 3 (15%), 5 (12%), and 6 (14%). Megachilidae were most abundant at event 3 (23%), followed by events 5 and 6 (10% and 14%). The entire bee community had a distinctly low abundance in mid summer at sampling event 7. Apidae, Colletidae, and Andrenidae phenologies were consistent with this overall trend. Halictidae and Megachilidae were neither abundant nor at an obvious minimum at this time (Figure 4-5, 4-6). Phenologies of the most abundant genera were similar to those of their respective families (Figure 4-5, 4-6).

Plant-pollinator interaction network

The plant-pollinator interaction network for Dunnville Marsh was composed of 15 higher trophic genera (pollinators), and 30 lower trophic species (plants) (Table 4-4). The generality (mean number of plants per pollinator) of the network was 6.52 and the vulnerability (mean number of pollinators per plant) was 4.06. Network connectance was 0.23, linkage density was 5.29, and weighted nestedness was 0.45. Robustness of plants to extermination was 0.78 and the robustness of pollinators to extermination was 0.62. Shannon diversity of the network was 3.98 and the interaction evenness was 0.86.

Floral resources and nest site availability

Specimens were sweep netted from 30 species of flowering plants, and 36 species of bee-pollinated flowering plants were recorded in vegetation surveys. Plants that are known to be bee-pollinated but on which no bees were caught tended to be uncommon in the vegetation surveys. Many of the surveyed plant species were planted in the fields of Dunnville Marsh as part of the seed mixes used in the restoration program. In addition to plants introduced as part of the restoration, we encountered a number of species exotic to southern Ontario. Pit 1 was particularly susceptible to the establishment of *Lythrum salicaria* L. (purple loosestrife) and *Dipsacus fullonum* L. (teasel).

Based on sweep net captures, most surveyed plants and pollinators appeared to be generalists, though a few genera demonstrated an affinity for particular plant species. *Rudbeckia hirta* L. (brown eyed susan) had the highest number of recorded interactions (67), and was especially attractive to *Melissodes spp*. (49 interactions). Other attractive plants included *Penstemon digitalis* Nuttal (white beard tongue), *Leucanthemum vulgare* Lam. (oxeye daisy), and purple loosestrife. Others species appeared to be important early (e.g. *Barbarea vulgaris* R. Brown, *Taraxacum officinale* F.H. Wigg) or late (e.g. *Solidago canadensis* L.) season forage resources. Some species were more likely to be visited by a specific genus of pollinator. For example, nine of the fourteen recorded visits to *Cirsium vulgare* (Savi) Tenore (bull thistle) plants were made by *Bombus spp*. Many plant species (n = 17) had less than five recorded visits. Available ground nesting sites, estimated based on the percentage of bare ground per floral quadrat decreased over the course of the survey period (r=-0.58, Figure 4-9).

Comparison of bee communities and resources between pit and mound and planted sites

Pan trap samples in pit and mound and planted sites yielded a total of 3,862 specimens, from five families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), representing 24 genera. Of these specimens 2,015 were caught in pit and mound sites and 1,847 were caught in planted sites. When all observations were included in the analysis, overall bee abundance was significantly greater in pit and mound compared to planted sites (z=-2.70, p=0.0069). However, model fit, determined by checking the normality of model residuals, was poor. Plots of model residuals suggested that analysis was influenced by a small number of extreme outliers. We used boxplots of overall abundance by site to determine a cut off for outliers (n>150 specimens per sampling event). This resulted in the largest observation being dropped from each site. We removed outliers from the dataset and compared overall abundance using a GLM with a Poisson error distribution. With these observations removed, there was no longer a significant difference between the two treatments (z=-1.77, p=0.076), though there was still a trend towards greater abundance in pit and mound compared to planted sites (Table 4-3). The results indicated that a few extreme outliers were responsible for most of the detected difference in abundance between pit and mound and planted sites. Genus richness was not normally distributed (W=0.94, p=0.034), but had equal variances (F=1.71, df=19, p=0.25). Because the distribution was near normal and variances were equal, genus richness of the two treatments was compared using a t-test. Genus richness was significantly greater in pit and mound compared to planted sites (z=-2.16, p=0.037), and we confirmed model fit by checking the normality of the residuals (Shapiro Wilks). Evenness was normally distributed (W=0.96, p=0.24), and did not differ significantly between pit and mound and planted sites, though there was a trend towards greater evenness in pit and mound sites (z=-1.51, p=0.14).

Solitary ground nesters (Guild A) did not differ significantly between the two restoration approaches. Social ground nesters (Guild B) were significantly more abundant in pit and mound compared to planted sites (*z*=-5.91*, p*<0.001); however, the model fit, evaluated by checking the normality of model residuals, was poor due to a small number of outliers. We identified outliers using boxplots of Guild B abundance by site and removed observations greater than 100 specimens. With outliers removed, Guild B abundance was still significantly greater in pit and mound sites (*z*=-3.54*, p*<0.001). Cavity nesters (Guild C) were significantly more abundant in planted compared to pit and mound sites (*z*=4.08*, p*<0.001). There was no significant difference in the abundance of *Bombus spp*. (Guild D), cleptoparasites (Guild E), and *Apis mellifera* (Guild F) between the two restoration approaches.

Ground nesters were significantly more abundant in pit and mound compared to planted sites (Table 4-3). Ground nester abundance was first compared using all observations (*z*=-5.55*, p*<0.001), but model fit, evaluated by checking the normality of model residuals, was poor due to a small number of outliers. We identified outliers using boxplots of ground nester abundance by site and removed observations greater than 100 specimens. Ground nesters were significantly more abundant in pit and mound compared to planted sites (*z*=-2.72*, p*=0.0066). Wood nesters were significantly more abundant in pit and mound (total 102 specimens) compared to planted (total 55 specimens) sites (*z*=-3.69*, p*<0.001). Stem nesters were significantly more abundant in planted sites compared to pit and mound sites (*z*=5.55*, p*<0.001).

Floral richness and floral abundance did not differ significantly between pit and mound and planted sites (Table 4-3). Nest site availability was greater in pit and mound compared to planted sites when the top three outliers (n>30% bare ground) were removed (*z*=-5.22*, p*=0.001).

We removed outliers from a number of the analyses because of the disproportionate influence they had on the results. However, it is important that they aren't completely disregarded. The outliers in our study are biologically relevant and reflect peaks in the phenologies of the most abundant or most frequently caught species (e.g. *Auguchlorella spp., Lasioglossum spp., Ceratina spp.*). For overall, Guild B, and ground nester abundance there was no trend as to whether the largest of the outliers were found in pit and mound or planted sites. For stem nesters, the observations of greatest abundance were less extreme, but the top two were in planted sites.

Comparison of plant-pollinator visitation networks in restored pit and mound and planted sites

Network properties of plant-pollinator interaction networks did not demonstrate any clear trends with respect to restoration treatment (Table 4-4). Instead, networks for three of the sites were similarly complex, both visually and with respect to network properties, while that of Plant 1 was less so. Connectance, the proportion of realized links, was similar in Pit 2 (0.24) and Pit 3 (0.26). Plant 1 and Plant 2 had the highest and lowest connectance values, 0.27 and 0.18, respectively. Weighted nestedness, Shannon Diversity, and robustness to pollinator extermination were highest in Pit 3 followed by Plant 2, Pit 2, and Plant 1 (Table 4-4). Robustness to plant extermination was highest in Pit 3 followed by Plant 2, Plant 1, and Pit 2 (Table 4-4).

Discussion

Dunnville Marsh bee community 2012

Bee diversity

For native bees to colonize a restored habitat floral and nesting resources must be available within foraging range and source populations within dispersal distance (Roulston and Goodell 2011; Kohler et al. 2008; Potts et al. 2005; Gathmann and Tscharntke 2002). Dunnville Marsh met these three criteria for 27 genera with a range of floral preferences, social behaviours, and nesting habits. The genus richness of native bees found at Dunnville Marsh is similar or greater than that of other studies with similar sampling effort conducted in southern Ontario in the Niagra region (29 genera, Richards et al. 2011), Huron County (21, Taylor 2007) City of Waterloo (23, Horn 2010), Peel County (27, Grixti and Packer 2006), and Norfolk County (20, Taylor 2007). Like most bee communities, the community at Dunnville Marsh was composed of a few very abundant genera and many uncommon genera.

We identified specimens to genus and sorted them into functional groups because we were primarily interested in whether functional roles within the community were filled. Identifying to species is useful for cataloguing species diversity, but species composition is not necessarily the most useful metric for comparing the structure of bee communities. Rutgers-Kelly (2005) found that genus richness was correlated with species richness, making it a suitable proxy when taxonomic expertise for species identification is not readily available. As well, there is a large amount of yearly species turnover in bee communities (Alarcon et al. 2008), and species composition can vary greatly even among sites that are geographically close and structurally similar (e.g. Williams 2011; Forup et al. 2008). These fluctuating species compositions make it difficult to detect the true community structure, to distinguish resident species from transient species, and to compare communities across time and space (Burkle and Alarcon 2011; Vazquez et al. 2009; Alarcon et al. 2008). Because the restoration of Dunnville Marsh did not target any particular species, we felt it appropriate to use a mix of genus richness and functional groups instead of species composition to compare and describe the native bee communities.

The abundance of guilds present at Dunnville Marsh appears to relate to the availability of nesting habitat. Social ground nesters (Guild B) were abundant, likely because their preferred nesting habitat, dry, sloped, bare ground is common in early restoration stages. Cavity nesters (Guild C) were also abundant, but *Ceratina spp.* and *Hylaeus spp.*, two genera that are known to nest in pithy stems, dominated the collections (Vickruck et al. 2011). In southern Ontario, *Ceratina spp.* are common and have been frequently recorded nesting in the stems of three common pithy-stemmed plants present at Dunnville Marsh: raspberry (*Rubus spp*.), teasel (*Dipsacus fullonum*), and staghorn sumac (*Rhus typhina*) (Vickruck et al. 2011). Wood nesters were notably scarce in all surveyed fields, and may be limited by the amount of appropriate nest sites. Grixti and Packer (2006) found that wood-nesting bees made up only 6% of the total abundance in an early succession field compared to 22% in the same unmanaged field 34 years later. The authors attributed this change to an increase in available nest sites as woody plant species established in later years.

Cleptoparasitic bees may be a suitable indicator taxa for overall bee community health because their success is dependent on the presence of a diverse community of lower order bees, they play a stabilizing role in communities, and they are easy to identify (Sheffield et al. 2013). The relative abundance of cleptoprasites at Dunnville Marsh was lower than that found in abandoned apple orchards and old fields in Nova Scotia (Sheffield et al. 2013), and an abandoned southern Ontario field (Grixti and Packer 2006), but higher than in naturalized rock quarries in the Niagra region (Richards et al. 2011). In contrast, the number of cleptoparasitic genera found in our study was similar to that of all three studies (Sheffield et al. 2013; Richards et al. 2011; Grixti and Packer 2006).

The presence of a diverse assembly of native bees representing a range of life histories indicates that the restoration has been at least preliminarily successful at attracting a rich native bee community. However, the low relative abundance of cleptoparasites and wood nesters suggests that the bee community is less functionally diverse and perhaps less resilient compared to communities found in similar older habitats.

Bee phenology

In 2012 we observed two early season peaks in bee abundance, one mid season peak, and one late season peak. Early peaks occurred in the middle of May (1st peak) and early June (2nd peak). The smaller mid season peak occurred near the end of July/ early August (3rd peak). The late season peak occurred in mid-end of August (4th peak). The phenology patterns of both families and genera are consistent with other southern Ontario bee assemblages (Cordero 2011; Richards et al. 2011; Rutgers-Kelly 2005). *Ceratina spp.*, *Augochlorella spp.*, and *Lasioglossum spp.* dominated the first peak. The large numbers of these three genera represent adult females emerging from overwintering. Emerging overwintered female *Andrena spp.* were most abundant at the first sampling event in mid-May and were uncommon thereafter. Unusual early spring weather patterns in 2012 may have resulted in under-sampling of early emerging bee genera. Temperatures warmed to a maximum 26˚C in mid-March, but dropped to consistently below zero minimum temperatures throughout late March and April (Environment Canada 2013). This resulted in premature bloom and death of many early flowering species, including the widespread loss of apple crops throughout southern Ontario. By mid-May, temperatures were consistently above 20˚C, and sampling began. During this early spring period of fluctuating temperatures, early season emergers may have been killed off or gone unsampled.

The second peak is likely an extension of the first peak and was dominated by large numbers of *Ceratina spp.* and *Lasioglossum spp.*. This is consistent with the time period during which Vickruck et al. (2011) caught the greatest number of emerging *Ceratina spp.* females in a study in the Niagra region. Also abundant were the bivoltine *Hylaeus spp.* and univoltine *Hoplitis spp.* that overwinter as larvae and emerge as adults (Michener 2000).

The third peak was dominated by the worker generation of the eusocial ground nesters, *Augochlorella spp.* and *Lasioglossum spp.* (Packer et al. 1988). Three genera that peaked at this time were either previously absent or present in very small numbers were: *Melissodes spp.* (Apidae), *Halictus spp.* (Halictidae), and *Agapostemon spp.* (Halictidae). The solitary ground nester and common southern Ontario species, *Halictus ligatus,* awake between late April and early May, but do not leave their burrows until late May to early June (Packer 1986). This pattern of emergence is consistent across a number of *Halictus* species (Dunn 1998), and indicates that the observed *Halictus spp.* peak was likely the emergence of overwintering females. This is supported by low male abundance. We also observed a second, smaller peak for *Hoplitis spp.* and *Hylaeus spp*.

The final peak occurred in mid-August and was primarily composed of Apidae and Colletidae. The predominantly univoltine genus, *Ceratina spp.* demonstrated a small peak, which is consistent with Vickruck et al.'s (2011) observation of a small second brood emerging around this time. The peaks in bivoltine genera *Hylaeus spp.*, *Halictus spp.*, and *Bombus spp.* were likely due to the emergence of a second generation.

Of particular interest is the lack of bees at event 7 in mid-July. This trend was observed in all families, for nearly all of the most abundant genera, and is consistent with previous studies of native bee phenology in the Niagra region (Cordero 2011; Richards et al. 2011; Rutgers-Kelly 2005). The exceptions to this trend were *Apis mellifera*, a managed species whose presence depends on the presence of nearby hives, and *Augochlorella spp.* and *Lasioglossum spp.*, abundant genera that were present in relatively low numbers at this time but did not exhibit an obvious minimum. This time of low abundance in the bee community appears to represent the break between the first and second broods of at least three bivoltine genera *Hylaeus spp., Halictus spp.*, and *Bombus spp.*, and of the typically univoltine *Ceratina spp.* (Vickruck et al. 2011). Despite clear similarities in the overall phenology trends, there are differences in exact timing of family and genus peaks between our study and that of Cordero (2011), Richards et al. (2011), and Rutgers-Kelly (2005). This is to be expected as bee phenology is strongly influenced by temperature and floral resources (Roulston and Goodell 2011; Goulson 2010).

The restoration of Plant-Pollinator Interactions

The plant-pollinator interaction network of the restored Dunnville Marsh (Figure 4-7, Table 4-4) indicates that pollination function was restored. Interaction networks are typically based on plant species interactions with insect species, but more general groupings have been used (e.g. Geslin et al. 2013; Power and Stout 2011). We present a plant species - pollinator genera network, which prevents us from making direct comparisons with species-species networks, but which serves as an example of a more general classification. Interestingly, values of quantitative properties (e.g. connectance, linkage density) of our species-genera network are similar to values of restored habitat species-species networks (e.g. Williams 2011; Forup et al. 2008).

The Dunnville Marsh plant-pollinator interaction network illustrates the use of exotic plant species as forage resources by native bee species. Purple loosestrife, an aggressive invasive plant was frequently visited by *Bombus spp.*, as were teasel and bull thistle. Other exotic species including queen ann's lace, swamp milkweed, and fleabanes were also visited by native bee species. Exotic plant species can provide nesting resources, including sites and materials. For example, teasel is a known nest site for the abundant *Ceratina spp.* (Richards et al. 2011; Vickruck et al. 2011; Cheesman 1998). The implication of the integration of exotic plants into the plant-pollinator community at Dunnville Marsh is that if invasive plant species are ever targeted for removal the resources they provide to the pollinator community need to be replaced.

The importance of meadow habitat for native bees

Land use surrounding Dunnville Marsh is predominantly intensive agricultural and residential, with fragments of remnant Carolinian forest. Carolinian forest was once abundant in southern Ontario, but is now rare due to the widespread conversion of forests and prairies to agricultural land following European settlement (Kanter et al. 2004). The goal of the GRCA with respect to Dunnville Marsh is to restore the acquired land to resemble remnant Carolinian forest. It is therefore important to recognize the critical role of meadow habitat in providing nest sites and forage resources for native bees. Native bees were almost completely absent from the remnant forest surveyed in this study. This is not unexpected as increased forest cover is associated with decreased bee abundance and species richness (Romey et al. 2007; Winfree et al. 2007). If bees are foraging in canopied forests, it is likely to be in the spring when there is the greatest availability of blooms (Heinrich 1976). With the exception of *Geranium maculatum* L. (wild germanium) and *Podophyllum peltatum* L. (mayapple) whose spring bloom times corresponded with the greatest bee abundance (n=14 specimens), flowering plants were absent from the understory of the forest remnant at Dunnville Marsh. Because the ground was wet for much of the summer and heavily shaded, the forest remnant lacked appropriate nest sites for ground nesters, but the mature trees did provide abundant potential nest sites for cavity nesters. The forage and nesting resources available in the wet meadows of Dunnville Marsh including: abundant and diverse floral blooms, sunny, dry bare ground, and pithy stemmed plants, complement those found in the forest remnant.

Meadows are often considered a transition stage in the restoration trajectory, and as a result are often overlooked as key habitat. However, our results emphasize the importance of maintaining meadows beyond early restoration stages to support native bee communities and to complement forest habitat. Together, meadow and forested habitats can meet the floral and nesting needs of a more diverse bee community than either habitat type could support individually.

Did the pit and mound restoration technique make a difference?

Pit and mound restored sites demonstrated the potential to enhance pollinator diversity but not pollination function, and to target different functional groups, compared to seeding into undisturbed weedy ground. Native bee genus richness was significantly greater in pit and mound compared to planted sites, but evenness and abundance did not differ significantly between approaches. Richness has been associated with stability of pollinator communities (e.g. Brittain et al.

2013; Winfree and Kremen 2009), and greater richness in pit and mound sites could indicate a more robust community.

Floral richness and abundance are often associated with bee richness and abundance (Roulston and Goodell 2011; Potts et al. 2003; Kearns et al. 1998); however, floral resources were not significantly greater in pit and mound compared to planted sites. Ground nesting species prefer to nest in dry, sunny, sloped bare ground, and the proportion of bare ground is commonly used as a proxy for nest site availability (Hopwood 2008; Potts et al. 2005). Our results indicated that percent bare ground and ground nesting bee abundance were significantly greater in pit and mound compared to planted sites. Increased amounts of bare ground in pit and mound sites is caused by the initial disturbance of creating pits and mounds and the slower establishment of plant species on the slopes of pits and mounds. Digging pits and mounds also increases the amount of sloped ground, which is favoured by ground nesting bees (Potts et al. 2005). Thus, there is preliminary evidence that the pit and mound treatment at Dunnville Marsh increases the available habitat for ground nesting species and enhances the overall abundance of ground nesting genera.

Stem nesters *Ceratina spp.* and *Hylaeus spp.*, are known to nest in pithy stems, and were more abundant in planted compared to pit and mound sites, while wood nesters were more abundant in pit and mound sites. We did not survey potential nest sites for stem and wood nesters so we can only speculate that their preferred nest sites were more widely available in the treatments in which they were respectively most abundant, or that other variables not measured in this study influenced their occurrence. Habitat for wood nesters may be more abundant in pit and mound sites if the dry mound tops promote the establishment of woody plant species compared to level ground. In wet meadows, saplings at level ground can be washed out or waterlogged by flood events. A 2009 winter flood event at Dunnville Marsh submerged all but the mound tops and may have killed off saplings that established on level ground. Nest site limitation is difficult to isolate and test empirically (Roulston and Goodell 2011); however, it is believed that wood nesters are nest site limited in early successional stages (Grixti and Packer 2006). Cleptoparasitic bees were similarly abundant and diverse in both restoration treatments, suggesting that though functional groups may differ between the two approaches, the communities may be similarly robust (Sheffield et al. 2013b).

Comparisons of plant-pollinator interaction networks for the four fields indicated that for Dunnville Marsh the dynamics of a site are likely more important than the restoration approach. Connectance values and the number of higher and lower order species were similar for both pit and mound sites (Pit 2 and Pit 3), but planted sites had the highest (0.27) and lowest (0.18) connectance values. The highest connectance value was surprisingly found in Plant 1, the network with the lowest plant and pollinator richness. Smaller numbers of network participants (low richness) generally results in higher network connectivity simply because there are fewer possible links (Vazquez et al. 2005). Of the four networks, that of Pit 3 appears the most complex based on measured network properties, it has the highest diversity (Shannon's Diversity), it is the most nested, and it has the greatest robustness to both plant and pollinator extinction. Based on the same properties the three remaining fields can be ranked from most to least complex as Plant 2, Pit 2, and Plant 1.

Conclusion

We provide evidence that a diverse bee community has established 4-5 years following initial restoration activities. Low rates of wood nesters and cleptoparasites indicate that this community may not be as functionally diverse and ultimately as robust as similar older communities; however, plant-pollinator interaction networks suggest that the plant and pollinator communitiy was relatively well connected. By assessing the current state of the Dunnville Marsh restoration and describing the bee community at a previously unstudied site and habitat type we established a baseline for monitoring changes to pollinator functional groups andplant-pollinator interactions over the restoration trajectory.

Comparisons of pit and mound and planted restoration approaches, demonstrated that structural changes to a site can influence the establishing bee community. Neither approach was obviously advantageous, but different nesting habits were favoured in the two treatments and genus richness was significantly greater at pit and mound sites potentially indicating a more robust community. This study is a first attempt at identifying the effects of pit and mound restoration on establishing bee communities. While it is limited in its scope, both geographically and in terms of replicates, our results suggest that the questions are worth addressing at a larger geographic scale and over a longer timescale. Despite its growing use as a restoration tool there are very few published studies of the effects of pit and mound restoration on establishing plant and animal communities (*but see* Kooch et al. 2012; Ewing 2002; Peterson et al. 1990). Understanding how changing site topography influences community assembly and succession can help inform the decision making process with respect to what techniques are applied for a given restoration project.

Table 4-1 Complete list of genera sorted into guilds based on social (social vs. solitary) and nesting (ground vs. cavity vs. parasitic) habits.

Guild	**Genera**
A Solitary ground nesters	*Agapostemon* Roberts and Brooks, *Andrena* Fabricius, *Melissodes* Latreille, *Perdita* Smith, *Pseudopanurgus* Cockerell
B Social ground nesters	*Augochlorella* Sandhouse, *Halictus* Latreille, *Lasioglossum* Curtis, *Peponapis* Robertson
C Cavity nesters	*Anthidium* Fabricius, *Anthophora* Latreille, *Augochlora* Smith, *Ceratina* Latreille, *Chelostoma* Latreille, *Heriades* Spinola, *Hoplitis* Klug, *Hylaeus* Fabricius, *Megachile* Latreille, and *Osmia* Panzer, *Xylocopa* Latreille
D Bumblebees	*Bombus* Latreille
E Parasites	*Coelioxys* Latreille, *Nomada* Scopoli, *Sphecodes* Latreille, *Stelis* Panzer, *Triepeolus* Latreille
F Honeybees	*Apis mellifera* Linnaeus

Table 4-2 Complete list of genera caught at Dunnville Marsh from pan traps and sweep netting from flowers. Acronyms for plant names are noted at the bottom of the table.

Family and Genus	Social habit	Nesting habit	Pans	Flowers	Total	Flower associations
Andrenidae						
Andrena	Solitary	Ground	58		58	
Calliopsis	Solitary	Ground	3		3	
Perdita	Solitary	Ground	2		2	
Andrenidae TOTAL			63	0	63	
Apidea						
Anthophora	Solitary	Stems	4		4	
Apis	Eusocial	Cavities	56	12	68	OI,RH,LS,PV,RA
Bombus	Eusocial	Ground	30	24	54	PD,LS,DF,PV,EP,CV,SC,EG
Ceratina	Solitary	Stems	1407	90	1497	BV,FV,TO,OI,EH,TH,PS,RQ,LV,PD,ES,GT,RH,CS,LS,PV,EP,CV,EG
Melissodes	Solitary	Ground	114	59	173	RH,CV,SC,HH,PD
Nomada	Parasitic		4		4	
Peponapis	Social	Ground	3		3	
Triepeolus	Parasitic		2		2	
Xylocopa	Social	Wood	15	19	34	PD,RH,LS,AS,PV,EP,LI
Apidae TOTAL			1635	204	1839	
Colletidae						
Hylaeus	Solitary	Stems/ cavities	397	15	412	BV,RQ,LV,PD,ES,PR,PV
Halictidae						
Agapostemon	Communal	Ground	31	2	33	CV,HH
Augochlora	Solitary	Wood		2	2	RA,PD
Augochlorella	Eusocial	Ground	969	17	986	BV,FV,RQ,PD,GA,ES,RH,PV

Family and Genus	Social habit	Nesting habit	Pans	Flowers	Total	Flower associations
Halictus	Eusocial/ (solitary)	Ground	117	7	124	EH,LV,ES,RH,HP,PV
Sphecodes	Parasitic		22		22	
Halictidae TOTAL			2474	49	2523	
Megachilidae						
Chelostoma	Solitary	Cavities	2		2	
Coelioxys	Parasitic		2		2	
Heriades	Solitary	Cavities	1		1	
Hoplitis	Solitary	Cavities	110	2	112	PD
Megachile	Solitary	Cavities	17	5	22	RH,EP,CV,SC
Osmia	Solitary	Cavities	24		24	
Stelis	Parasitic		9		9	
Megachilidae TOTAL			165	7	172	
Mellitidae						
Macropis			1		1	
Grand TOTAL			4735	275	5010	

Flower abbreviations: AS - Asclepias syriaca, BV - Barbarea vulgaris, CS – *Convolvulus sepium*, CV – *Cirsium vulgare*, DC – *Dauscus carota*, DF – *Dipsacus fullonum*, EG – *Euthamia graminifolia*, EH – *Erigero philadelphicus*, EP – *Eupatorium perfoliatum*, ES – *Erigeron strigosus*, FV – *Fragaria vesca*, GA – *Geum aleppicum*, GT – *Galium trifidum*, HH – *Heliopsis helianthoides*, HP – *Hypericum perforatum*, LI – *Lobelia siphilitica*, LS – *Lythrum salicaria*, LV – *Leucathemum vulgare*, OI – *Orithogalum umbellatum*, PD – Penstemon digitalis, PR – *Potentilla recta*, PS – *Potentilla simplex*, PV – *Pycanthemum virginianum*, RA – *Rubus allegheniensis*, RH – Rudebeckia hirta, RQ – *Rananculus aquatilis*, SC – *Solidago Canadensis*, SM – *Stellaria media*, TH – *Trifolium hybridum*, TO – *Taraxacum officinale*

Table 4-3 Comparison of bee and plant community response variables in pit and mound compared to planted sites at Dunnville Marsh, southern Ontario. Reported as mean counts (standard error). Bee community measures are calculated from pan trap collections. Nest site availability is expressed as mean (SE) percentage of bare ground. Guilds represent the following combinations of social and nesting behaviour: Guild A – solitary ground nesters, Guild B – social ground nesters, Guild C – cavity nesters, Guild D – *Bombus*, Guild E – cleptoparasites, and Guild F – *Apis mellifera.* Letters indicate results of GLM analyses. The p value of significant results are in bold.

	Treatment			
	Pit and Mound	**Plant**	**Z**	**p**
Bee abundance	100.8 (17.0)$_A$	93.6 (13.8)$_B$	-2.70	**0.0069**
Bee abundance w/o outliers	80.7 (7.5)$_A$	76.8 (8.3)$_A$	-1.77	0.076
Bee genus richness	9.2 (0.4)$_A$	8.2 (0.3)$_B$	-2.16	**0.037**
Bee evenness	0.7(0.01)$_A$	0.7(0.03)$_A$	-1.51	0.14
Social and nesting guilds				
Guild A	3.6 (1.1)$_A$	3.9 (1.7)$_A$	0.57	0.57
Guild B	56.2 (12.7)$_A$	43.0 (7.5)$_B$	-5.91	**<0.001**
Guild B w/o outliers	41.7 (5.4)$_A$	34.4 (4.9)$_B$	-3.54	**<0.001**
Guild C	34.8 (4.9)$_A$	42.8 (7.4)$_B$	4.08	**<0.001**
Guild D	0.8 (0.3)$_A$	0.5 (0.2)$_A$	-0.99	0.32
Guild E	0.8 (0.3)$_A$	1.0 (0.3)$_A$	0.67	0.51
Guild F	1.2 (0.3)$_A$	0.8 (0.3)$_A$	-1.29	0.20
Nesting habit				
Ground nesters	59.7 (13.6)$_A$	46.9 (8.2)$_B$	-5.55	**<0.001**
Ground nesters w/o outliers	44.3 (5.9)$_A$	38.4 (6.3)$_B$	-2.72	**0.0066**
Stem nesters	29.7 (4.5)$_A$	40.1 (7.2)$_B$	5.55	**<0.001**
Wood nesters	5.1 (0.8)$_A$	2.8 (0.5)$_B$	-3.69	**<0.001**
Site characteristics				
Floral abundance	232.7 (39.8)$_A$	218.4 (59.2)$_A$	10.53	**<0.001**
Floral richness	5.8 (0.3)$_A$	5.0 (0.50)$_A$	-1.16	0.25
Nest site availability	13.4 (2.4)$_A$	7.2 (1.7)$_B$	-6.04	**<0.001**

Table 4-4 Qualitative and quantitative network properties of overall, pit and mound (Pit 2 and Pit 3), and planted (Plant 1 and Plant 2) plant-pollinator visitation networks based off of sweep net collections taken at Dunnville Marsh, southern Ontario.

Site/Property	**Overall**	**Pit 2**	**Pit 3**	**Plant 1**	**Plant 2**
# Pollinators	15	11	13	7	13
# Plants	30	14	13	8	15
Generality	6.52	3.09	4.42	2.20	3.00
Vulnerability	4.06	3.25	4.18	1.94	2.74
Connectance	0.23	0.24	0.26	0.27	0.18
Weighted nestedness	0.45	0.34	0.52	0.17	0.40
Shannon Diversity	3.98	3.09	3.54	2.09	3.19
Robustness lower exterminated	0.77	0.46	0.65	0.52	0.64
Robustness higher exterminated	0.62	0.59	0.64	0.50	0.59

Figure 4-1 Map of Dunnville Marsh, southern Ontario. The Dunnville Marsh property is owned and managed by the Grand River Conservation Authority. Pit and mound treated sites are Pit 1, Pit 2, and Pit 3. Planted sites are Plant 1 and Plant 2. (Semi)natural Carolinian forest is Forest Remnant. Source, Google Earth, 2013.

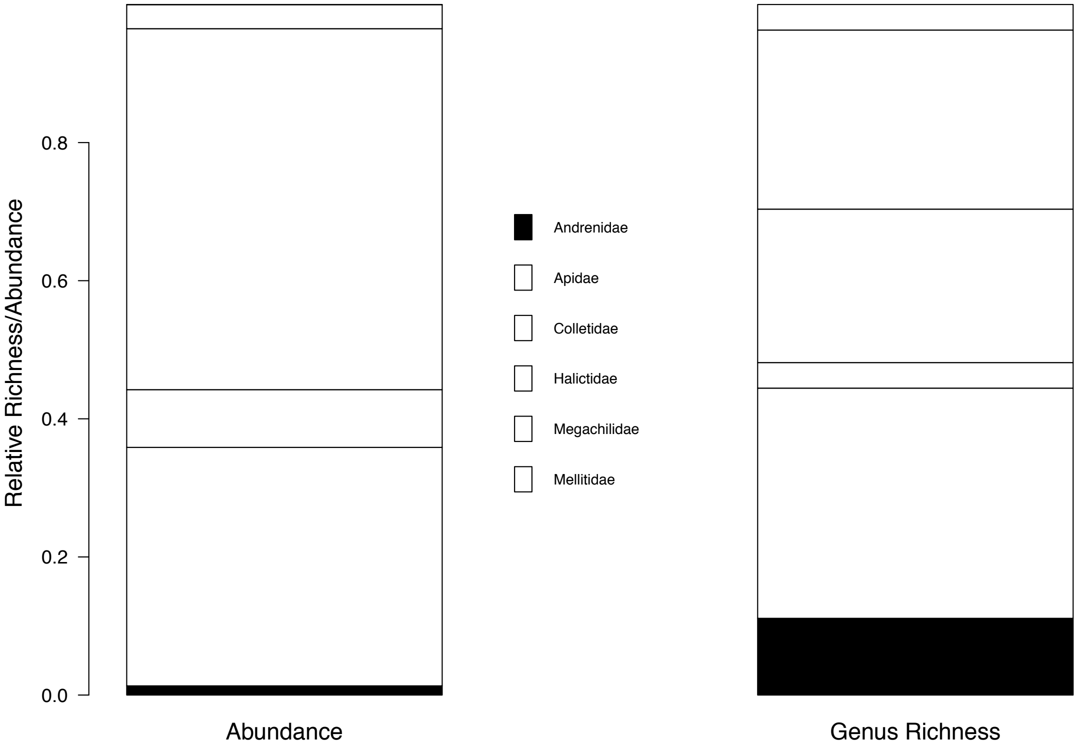

Figure 4-2 The relative abundance and genus richness of bee families collected in pan traps from five restored and one remnant site at Dunnville Marsh, southern Ontario in 2012. The distribution among families is different for abundance and genus richness.

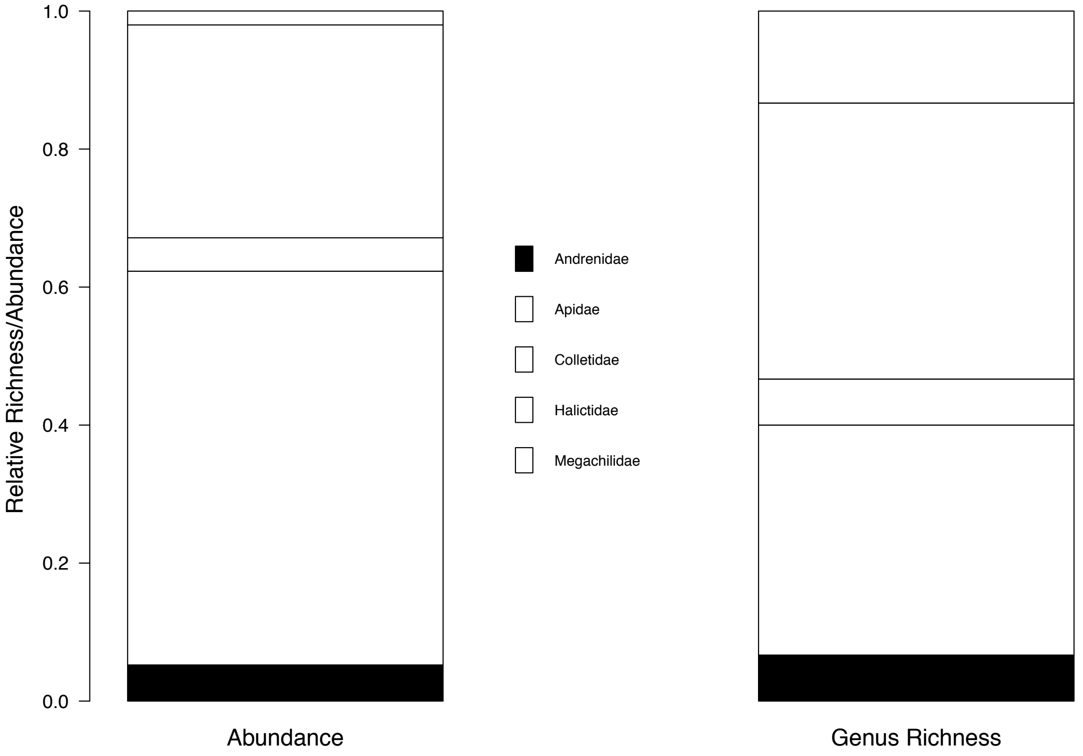

Figure 4-3 The relative abundance and genus richness of bee families collected in sweep nets from five restored and one remnant site at Dunnville Marsh, southern Ontario in 2012. The distribution among families is different for abundance and genus richness.

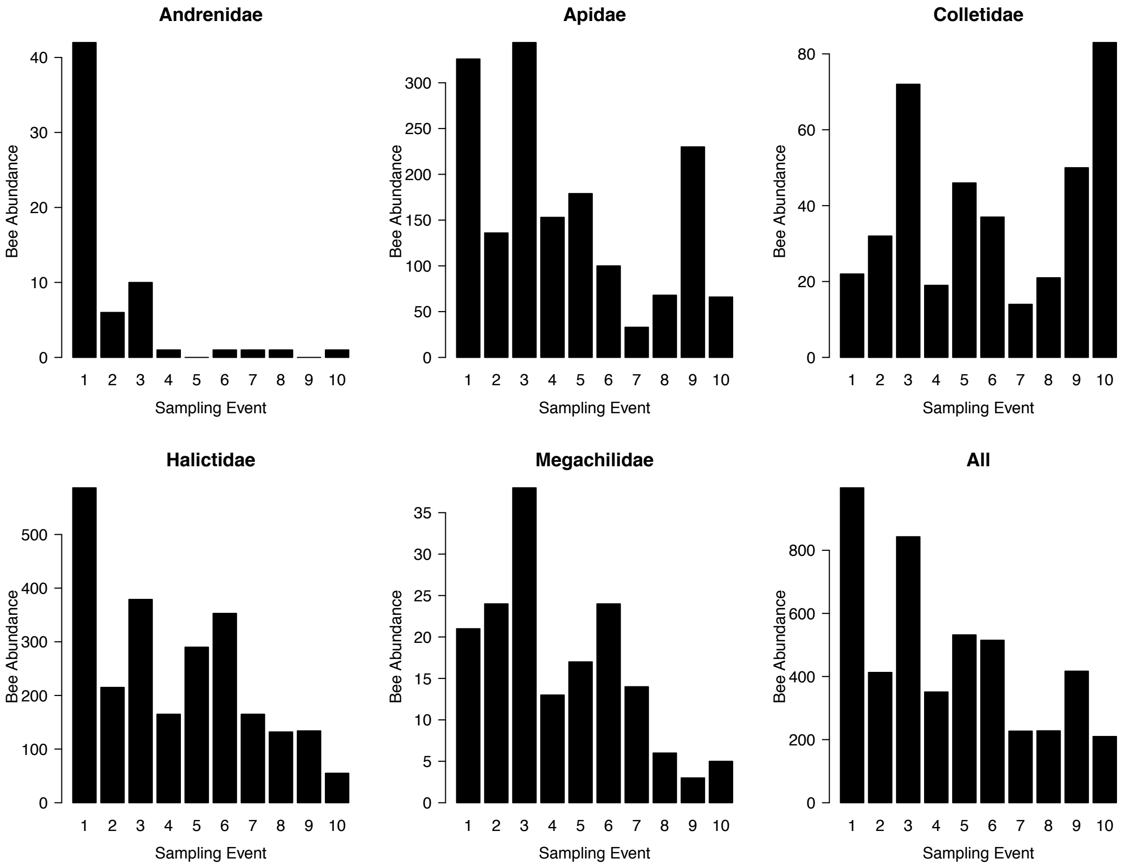

Figure 4-4 Phenologies of the five families caught at Dunnville Marsh, southern Ontario in 2012: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae.

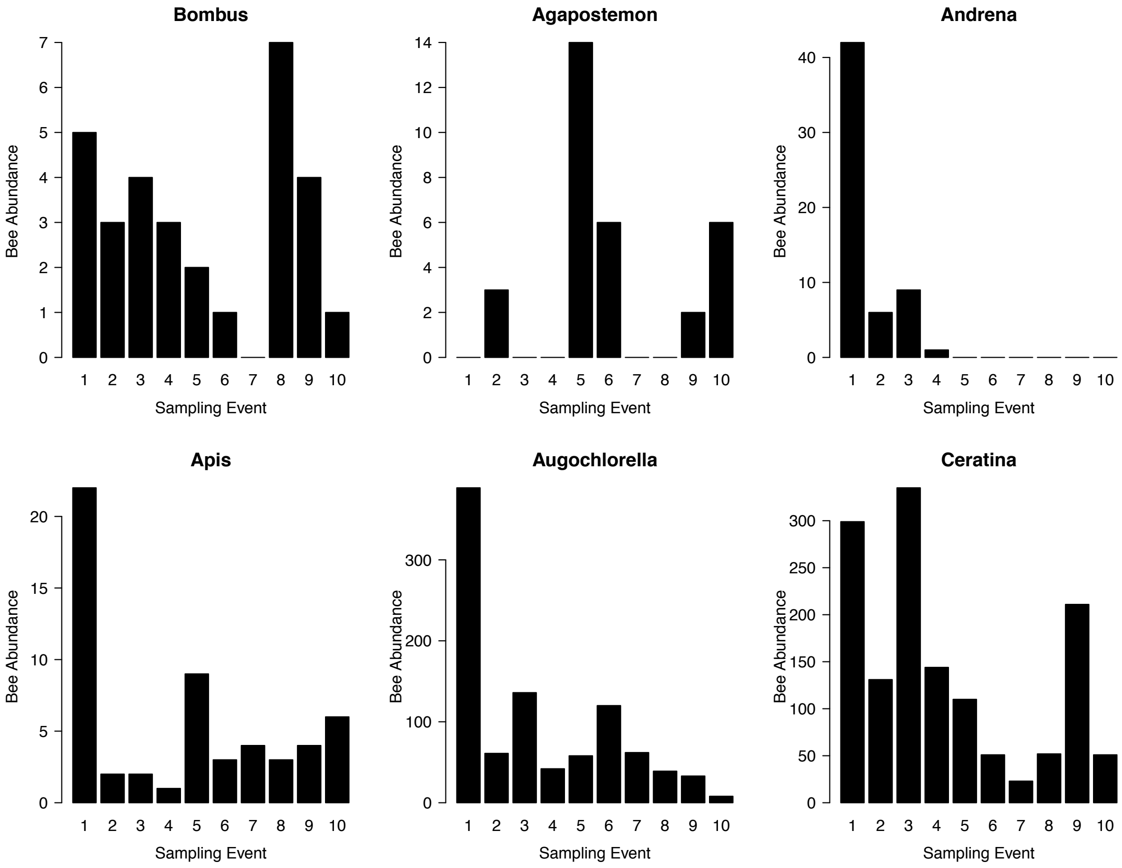

Figure 4-5 Phenologies of six abundant genera caught at Dunnville Marsh, southern Ontario in 2012: *Bombus spp., Agapostemon spp., Andrena spp., Apis sp., Augochlorella spp.,* and *Ceratina spp.*

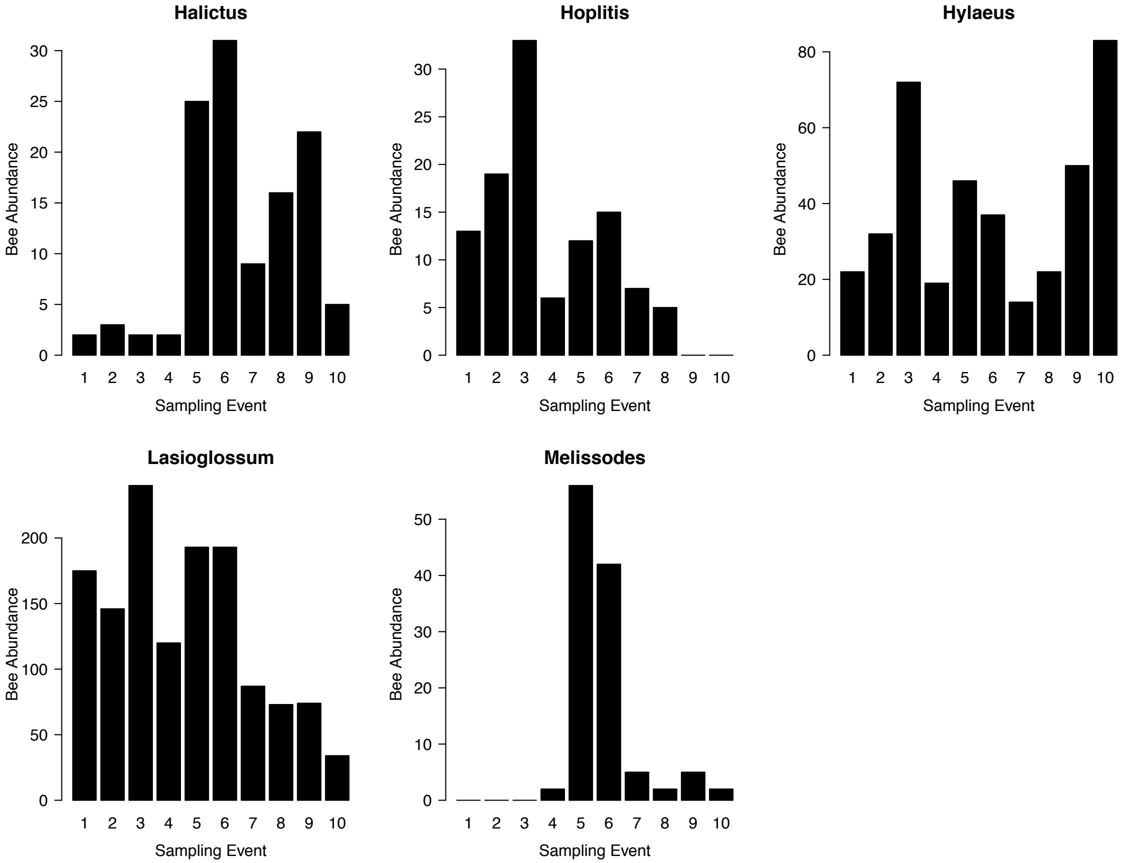

Figure 4-6 Phenologies of five abundant genera caught at Dunnville Marsh, southern Ontario in 2012: *Halictus spp., Hoplitis spp., Hylaeus spp., Lasioglossum spp.,* and *Melissodes spp*.

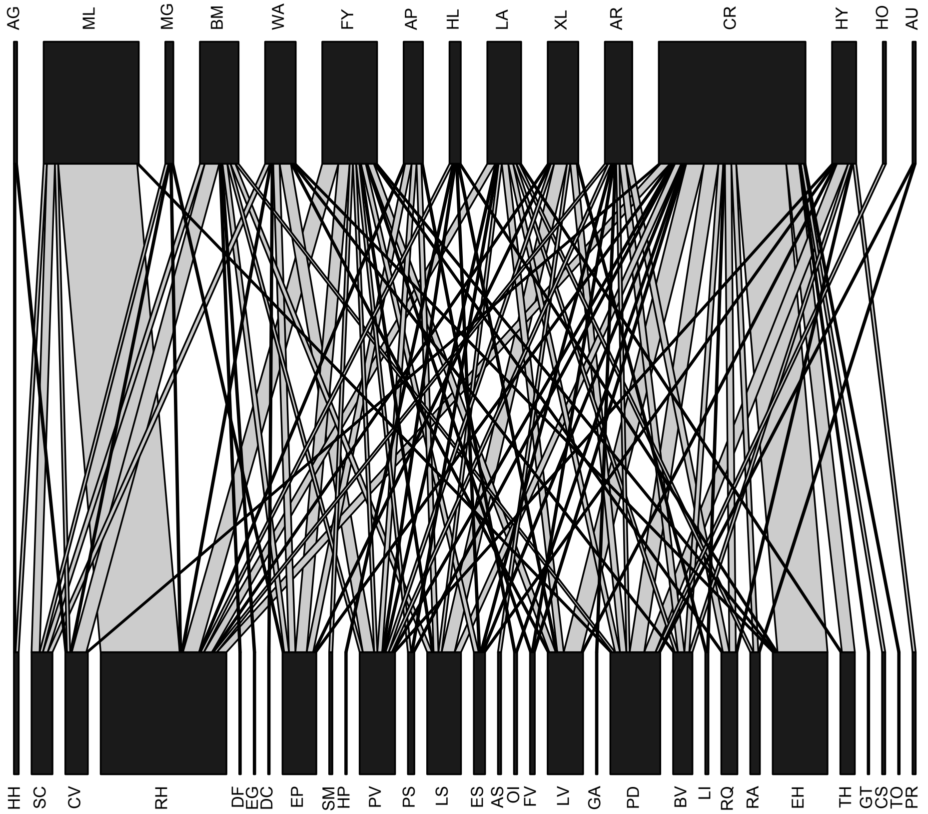

Figure 4-7 Plant-pollinator visitation network based on 2012 sweep net collections at Dunnville Marsh, southern Ontario. Pollinator genera are represented in the top row, plant species are represented in the bottom row. Pollinator acronyms (left to right): AG – *Agapostemon*, ML – *Melissodes*, MG - *Megachile*, BM - *Bombus*, WA - wasp, FY - fly, AP - *Apis*, HL - *Halictus*, LA - *Lasioglossum*, XL - *Xylocopa*, AR - *Andrena*, CR - *Ceratina*, HY - *Hylaeus*, HO - *Hoplitis*, AU – *Augochlorella*. Plant acronyms are listed below Table 4-2.

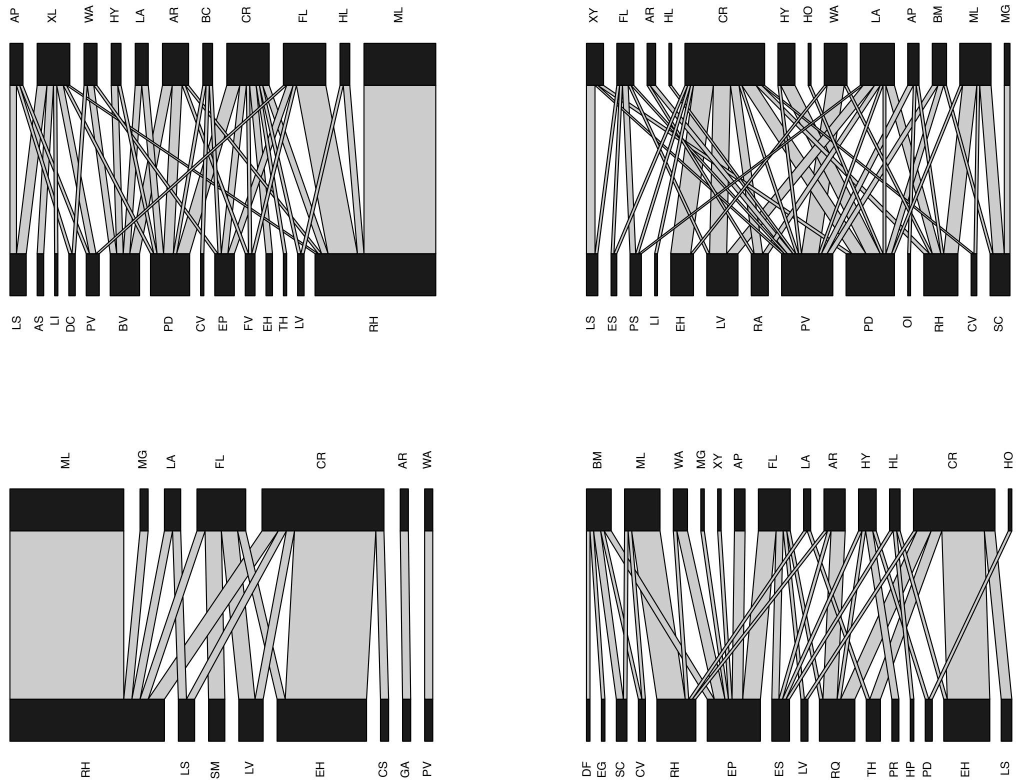

Figure 4-8 Plant-pollinator visitation networks for fields (clockwise from top left): Pit 2, Pit 3, Plant 2, and Plant 1 based on 2012 sweep net collections at Dunnville Marsh, southern Ontario. Pollinator genera are represented in the top row, plant species are represented in the bottom row. Pollinator acronyms: AG – *Agapostemon*, ML – *Melissodes*, MG - *Megachile*, BM - *Bombus*, WA - wasp, FY - fly, AP - *Apis*, HL - *Halictus*, LA - *Lasioglossum*, XL - *Xylocopa*, AR - *Andrena*, CR - *Ceratina*, HY - *Hylaeus*, HO - *Hoplitis*, AU – *Augochlorella*. Plant acronyms are listed below Table 4-2.

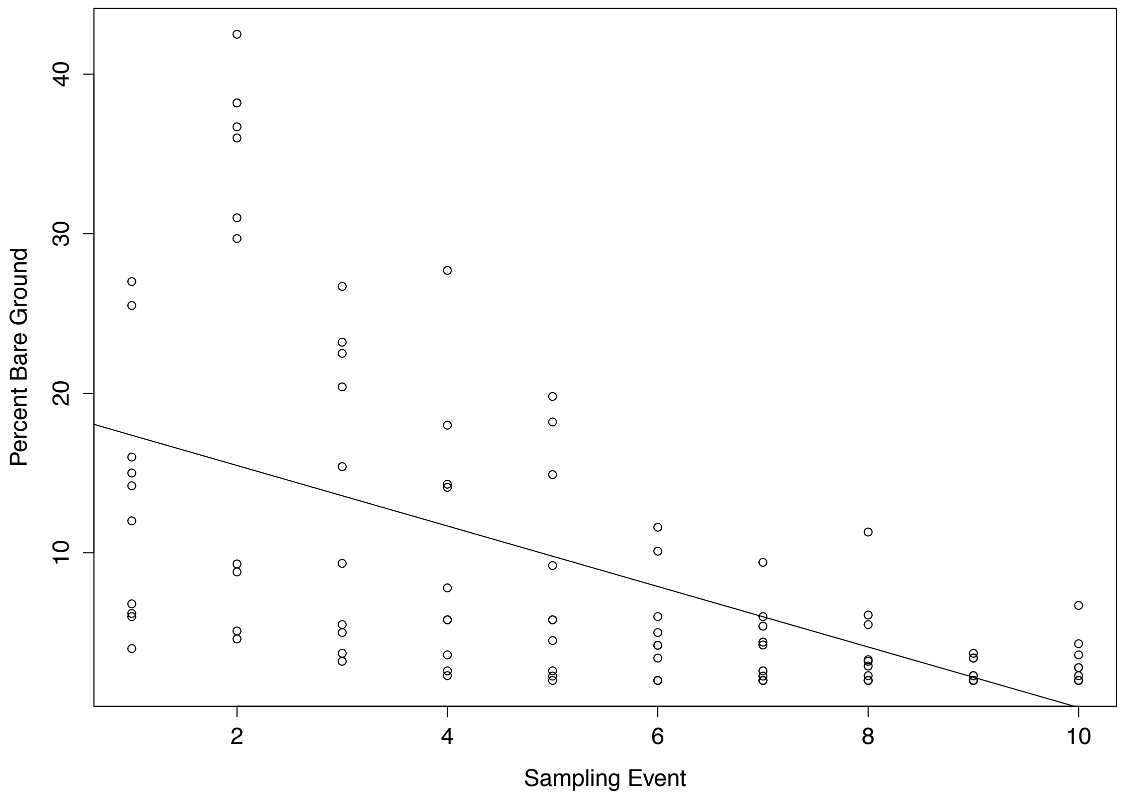

Figure 4-9 Nest site availability expressed as percent of bare ground for five restored fields at Dunnville Marsh, southern Ontario. Sampling events took place at approximately two-week intervals between May and August 2012. Correlation coefficient: r=-0.58.

Chapter 5 The restoration of pollinator functional groups and plant-pollinator interactions in selected southern Ontario sites

Overview

Establishing a functioning ecosystem is the primary goal of ecological restoration; however, restoration activities tend to focus on restoring structural site properties with the expectation that groups and processes critical to ecosystem function will establish over time. Native bees are critical to ecosystem function but are rarely included in restoration plans and their response to restoration is poorly understood. Native bee declines have been reported globally and understanding how bees respond to habitat restoration in (semi)natural areas can help inform future restoration and management plans. We explored how functional properties of pollinator communities differed between degraded, restored, and (semi)natural habitats in southern Ontario to determine whether restoration activities enhanced pollinator community function relative to degraded habitats, and to identify gaps in community function between restored and (semi)natural habitats. We evaluated community function using guilds based on ecological traits and plant-pollinator visitation networks. Functional group diversity and evenness were greatest in (semi)natural sites, followed by restored, then degraded. Functional diversity is often linked to community stability and sites with higher functional diversity may be more resilient to disturbance and environmental change. The relative abundance of guilds reflected structural changes associated with succession. Ground nesters were relatively more abundant in degraded sites, which were characterized by bare ground and weedy vegetation. Wood nesters were relatively more abundant in (semi)natural sites, which were characterized by mature trees and shrubby understories. Interaction networks did not demonstrate clear trends with respect to site status, but did indicate that restored communities can be diverse, robust to extinction, and well connected.

Introduction

Ecological restoration is “the process of assisting the recovery of an ecosystem that has been damaged, degraded, or destroyed” (SER 2004), and has the ultimate goal of re-establishing a self-sustaining system that supports many of the functional and structural properties of a predegraded state. Ecological restoration and its associated academic discipline, restoration ecology, have largely focused on the botanical sciences (Young 2000). Plants are the cornerstone of most restoration projects because they provide a structural foundation that is relatively inexpensive and easy to establish and monitor. However, the recovery of plant communities does not ensure successful habitat restoration and this limited focus may neglect other important ecosystem components (Herrick et al. 2006).

Restoring wildlife is often addressed with an 'if we build it they will come' approach (Williams 2011; Memmott 2009; Herrick et al. 2006; Block et al. 2001; Golet et al. 2008). With the exception of some focal groups and keystone species, wildlife are rarely purposefully introduced and post-restoration monitoring tends to only follow a few taxa (Golet et al. 2008; Woodcock et al. 2012; Waltz and Covington 2004). However, many non-targeted taxa are essential to the long-term functioning of restored habitats. Native bees are the primary pollinators in many terrestrial ecosystems, and the services they provide are critical for creating and maintaining flowering plant diversity (Potts et al. 2003; Kevan 1999; Kearns et al. 1998). The contributions of native bees are particularly important for flowering plants in restored sites, where the establishing plant communities often have a narrow genetic base and can benefit from bee-mediated genetic recombination (Menz et al. 2011; Dixon 2009). While diverse bee communities are critical for establishing resilient plant communities, the opposite is also true (Potts et al. 2003; Kearns et al. 1998). Habitat loss and degradation due to agricultural industrialization, urbanization, and suburbanization are the leading causes of native bee declines (Potts et al. 2010; Winfree 2010; Biesmeijer et al. 2006; Kremen et al. 2002; Allen-Wardell et al. 1998). Ecological restoration can help mitigate declines by increasing the amount, quality, and connectivity of appropriate habitat (Menz et al. 2011; Winfree 2010). Researchers have called for incorporating pollinators into restoration planning and for studying how pollinators respond to restoration activities (Montoya et al. 2012; Menz et al. 2011; Nyoka et al. 2010; Dixon 2009). However, to date only a few studies have looked at the response of native bees to habitat restoration outside of agroecosystems (Devoto et al. 2012; Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008; Forup and Memmott 2005).

Restoration ecology and pollination biology are necessarily linked by the functional role of pollinators. Already, researchers have capitalized on pollination function to assess pollinator response to habitat restoration by using plant-pollinator interaction networks (Williams 2011; Forup et al. 2008; Forup and Memmott 2005). These networks provide a snapshot of community interactions and are useful for comparing and evaluating the functional success of habitat restoration when community composition differs widely among sampled habitats (Williams 2011;

Vazquez et al. 2009). Functional groups based on life-history traits can also be used to evaluate restoration outcomes. Bees with different life history traits tend to be responsible for pollinating different plant groups and the absence of certain bee functional groups is likely to have a stronger impact on the flowering plant community compared to the absence of a single species (Munyuli 2012). Like plant-pollinator interaction networks, functional group diversity shifts the focus away from restoring a specific community structure and composition and towards restoring ecosystem function (Cadotte et al. 2011).

Diversity is associated with community stability (Ives and Carpenter 2007) and functional diversity often considered the most important component of diversity (Tilman et al. 1997). Functional group diversity can increase bee-pollinated crop productivity (Hoehn et al. 2008), and buffer pollination services from disturbance and environmental change (Brittain et al. 2013). The absence of certain functional groups can also indicate gaps in habitat requirements or disturbance events that could be missed if focusing on species diversity alone. Bees with different social habits, social vs. solitary, and nesting habits, ground, stem, or wood, have divergent responses to disturbance, and likely to habitat restoration (Williams et al. 2010). Cleptoparasitic bees are morphologically and ecologically divergent from other bee groups and their response to disturbance and restoration is expected to be distinct. Because cleptoparasitic bee species depend on large host populations, they are expected to respond to disturbance ahead of lower order species, and have been used to evaluate the overall health of bee communities (Sheffield et al. 2013).

We explored native bee response to non-targeted restoration in unmanaged habitats using community data collected from degraded, restored, and (semi)natural sites in the Region of Waterloo, southern Ontario. We asked how functional properties of pollinator communities changed with site status to determine whether restoration activities enhanced pollinator community function relative to degraded habitats, and to identify gaps in community function between restored and (semi)natural habitats. We evaluated community function using guilds based on ecological traits and plant-pollinator visitation networks. We expected that functional group diversity and evenness would be greater in (semi)natural habitats compared to degraded habitats, and that interaction networks in (semi)natural habitats would be more diverse, connected, and robust to extinction compared to networks in degraded habitats. We expected that functional group diversity and network properties in restored habitats would be intermediate to those in degraded and (semi)natural habitats.

Methods

Site Description:

We sampled three locations in the Grand River Watershed: (1) Pioneer Tower Natural Area, Kitchener, Region of Waterloo (43˚23.873'N, 080˚24.402'W), (2) Washington Creek, Oxford County (43˚18.046'N, 080˚33.673'W), and (3) Clair Creek, Waterloo, Region of Waterloo (43˚27.537'N, 080˚34.877'W). At Pioneer Tower we sampled three areas: (1) a degraded trail edge between a walking trail and the Grand River, (2) a (semi)natural forest remnant edge habitat, and (3) a recently restored meadow. Disturbed bare ground, weedy plant species, and *Solidago sp.* (goldenrod) characterized the degraded site. Exotic and native wildflowers, shrubs, and nearby mature trees providing partial canopy cover characterized the (semi)natural forest edge. Bare ground, wildflower species, and old stems (e.g. *Monarda fistulosa* L. and *Rudbecki hirta* L.) characterized the restored site. Washington Creek we sampled two areas: (1) a degraded road margin, and (2) a restored riparian forest. Periodically mowed grasses, native and exotic wildflowers, and a few shrubby species characterized the degraded road margin. Researchers from the University of Guelph restored a section of Washington Creek (previously a degraded agricultural field margin) between 1986 and 1991 by planting a mix of native tree species. Now, mature maples and dogwoods make up the canopy and a mix of wildflowers and invasive exotic species (e.g. *Alliaria petiolata* (M.Bieb.) Cavara & Grande and *Heracleum mantegazzianum* Sommier & Levier) dominate the understory. Clair Creek is located within a suburban development in north Waterloo. This section of Clair Creek sampled was restored as part of a development plan for the subdivision. Grasses, exotic and native wildflowers (e.g. *Dipsacus fullonum* L.), and a few mature trees characterized this site.

The sites are classified as follows: degraded – Pioneer Tower degraded and Washington Creek degraded, low restoration effort – Clair Creek, high restoration effort – Pioneer Tower restored, old restoration – Washington Creek restored, and (semi)natural – Pioneer Tower (semi)natural.

Bee and flowering plant surveys

We surveyed bee fauna every ten to fourteen days from May to August 2012, using pan traps and sweep net captures. We sampled each site ten times throughout the study period and sampling took place on warm (≥14˚C), sunny (<60% cloud cover), days, with low wind speeds. All site at a location were sampled on the same day. At each site we established a 100m permanent transect for pan trapping. On each sampling day we laid out 30 pan traps of alternating blue, white, and yellow separated by 3m along the transect line. Pan traps were small bowls approximately 18cm in diameter and we filled them ¾ full with a mixture of water and blue Dawn™ dish soap. We took care to make sure pan traps would be visible to bees by avoiding thick vegetation. Pan traps were put out at 09:00 and collected at 16:00. Insects collected from different coloured pan traps were collected separately and stored in bags filled with 70% ethanol.

At each site we established two 50m permanent transects for sweep netting. On each sampling day one collector spent 30 minutes walking each transect in the late morning or early afternoon (11:00-14:00). We sweep netted all insects that came in contact with the anthers or stigmas of flowers available for pollination, along the transect line and up to 1m on either side of the line. We considered flowers to be available for pollination if the anthers or stigma looked fresh. Newcomb's (1977) was used for flowering plant identification.

We surveyed floral richness and abundance and nest site availability along the two 50m sweep net transects. We surveyed ten 1m by 1m quadrats along each transect for a total of 20 quadrats for each site and each sampling event. Within each quadrat we recorded the species of flowering plants that were in bloom and the total number of flowers or inflorescences (e.g. *Asteracea* L.*,* *Solidago spp.* L., and *Daucus carota* L.) of each species. Percent bare ground was recorded as a proxy for available nest sites for ground nesting bee species (*as per* Potts et al. 2005).

Bee identification and guild classification

We washed, dried, pinned, and labeled all insects collected in pan traps. We stored insects collected in sweep nets in a freezer until they could be pinned and labeled. We identified specimens to genus under a dissecting microscope using Packer et al. (2007). We sorted specimens into guilds based on previous studies in eastern Canada (Sheffield et al. 2013; Richards et al. 2011; Grixti and Packer 2006) or based on relevant literature (e.g. Michener 2000). Genera were sorted into six guilds as follows: Guild A - solitary ground nesters, Guild B - social ground nesters, Guild C - cavity nesters, Guild D - *Bombus* Latreille, Guild E - parasites, and Guild F - *Apis mellifera* Linnaeus. Genera belonging to each guild can be found in Table 5-1. We also sorted non-parasitic genera by only nesting habit. Ground nesters included Guild A, Guild B, and *Bombus spp.* stem nesters included *Ceratina spp.* and *Hylaeus spp.* (from Guild C), and wood nesters included all other Guild C genera. Guild F was excluded because we assumed that all *A. mellifera* nested in managed hives.

Guilds were reported by their percent contributions to the overall bee community. Shannon's diversity and Shannon's evenness were calculated using guilds in the place of species. Shannon's diversity is a diversity index that accounts for the abundance and evenness of guilds present. Shannon's evenness, a measure of how close in numbers each group in a habitat is, was calculated as H/H_{max} where H is the Shannon diversity index and H_{max} is its maximum value (ln[number of guilds]).

Plant-pollinator interaction network analysis

We constructed plant-pollinator interaction matrices for each site with the exception of Clair Creek. We excluded Clair Creek because we caught fewer than ten specimens visiting flowers over all sampling events. We included flies and wasps meeting the floral visitation criteria in the matrices, but they were not sorted into more specific taxonomic groups. Matrices contained the total number of interactions between plants and pollinators for all sampling events combined. Matrices were visualized as plant-pollinator visitation networks using the bipartite package (Dormann et al. 2009) in *R* (R Development Core team 2011). We calculated qualitative and quantitative network properties using the bipartite package. Qualitative network properties included the number of plant and pollinator taxa. Quantitative network properties included: connectance, linkage density, Shannon's diversity, and robustness of higher and lower order groups to extinction.

Connectance is the number of realized links out of the total number of possible links, and is a measure of how many bee genera are visiting plant species (Jordano 1987). Linkage density is the ratio of links per species ($L = l/i+p$). Where 'l' is the number of links, 'i' is the number of insect genera and 'p' is the number of plant species. Shannon's diversity is an indexed measure of network diversity. Robustness is an expression of the ability of a network to withstand species loss and is calculated as the area below the extinction curve (Burgos et al. 2007). The extinction curve for a given group (e.g., plants) is based on what would happen to that group if a fraction of the other group (pollinators) were removed. An 'R=1' corresponds to a curve that decreases mildly until a point where almost all species are eliminated. An 'R=0' corresponds to a curve that decreases abruptly as soon as species are eliminated. Therefore higher values of 'R' are associated with a more robust community.

Results

We collected 5,436 specimens from five families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), representing 30 genera in pan trap collections (Table 5-2). By study area we caught 832 bee specimens at Clair Creek, 1,104 from Pioneer Tower degraded, 998 from Pioneer Tower (semi)natural forest edge, 1,351 from Pioneer Tower restored, 855 from Washington Creek degraded, and 297 from Washington Creek old restored.

Geographic location appeared to have a stronger influence on overall abundance than did treatment type. The three sites with the highest overall abundances were the three sites at Pioneer Tower Natural Area. Average genus richness was highest in the restored meadow of Pioneer Tower (mean number of genera ± SE, 10.8±0.6), followed by Pioneer Tower (semi)natural (9.5±0.7), Pioneer Tower and Washington Creek degraded (7.8±0.8 and 7.8±1.0, respectively), Clair Creek (7.4±0.6), and was lowest in Washington Creek old restored (6.5±1.0). Evenness was lowest in the two degraded sites (0.43 and 0.40, Pioneer Tower and Washington Creek respectively), followed by Clair Creek and Pioneer Tower restored (0.58 and 0.58, respectively), and Pioneer Tower (semi)natural (0.62), and Washington Creek restored (0.78).

Diversity and evenness of functional groups were greatest in Pioneer Tower (semi)natural and Washington Creek old restored, followed by Pioneer Tower restored and Clair Creek, and Pioneer Tower degraded and Washington Creek degraded (Table 5-3).

Descriptive analysis of the relative representation of bee functional groups

The native bee community at Pioneer Tower degraded and Washington Creek degraded shared a number of similar features (Figure 5-1, Table 5-2). At both sites Guild A made up less than 3% of the total collection, Guild C less than 10%, and Guild D less than 1%. Of Guild C, both stem and wood nesters were notably scarce (Figure 5-2). In contrast, Guild B was abundant and represented 73.2% and 85.9% of collections at Pioneer Tower degraded and Washington Creek degraded. Guild E was uncommon at Washington Creek, but surprisingly high at Pioneer Tower degraded. Compared to all surveyed sites, Pioneer Tower degraded had the highest number and relative frequency of parasitic specimens (15.31%).

The distribution of relative frequencies by guild was similar in the two older sites, Pioneer Tower (semi)natural and Washington Creek restored (Figure 5-2, Table 5-2). Guild B was present at lower frequencies compared to degraded and recently restored sites and represented 48.7% and 47.2% of collections at Pioneer Tower and Washington Creek. Washington Creek had the highest relative frequency of Guild A (10.8%), and wood nesting specimens (4.5%). Guild E was relatively common in both sites, representing 6.7% and 8.4% of collections at Pioneer Tower and Washington Creek.

The relative representation of guilds at Clair Creek was distinct from all other sites (Figure 5-2, Table 5-2). Guilds A and B were present in low relative frequencies. In contrast, Guild C made up 54.0% of collected specimens. Stem nesting *Hylaeus spp.* dominated cavity nester collections, and wood nesters made up only 3% of the total collections. No *Bombus spp.* were caught in pan traps at Clair Creek. The relative abundance of Guilds A, B, C, D, and E at Pioneer Tower restored fell between the values recorded for degraded and older sites (Figure 5-2, Table 5-2).

Feral *A. mellifera* colonies are rare and the occurrence of Guild F is primarily due to the presence of managed hives in the vicinity of a sampled site. *A. mellifera* are not native, but they do contribute to the pollination of native (and exotic) plants. *A. mellifera* made up < 5% of the sampled community at any site.

Plant-pollinator interaction networks

We caught 265 flower-visiting insects across all surveyed sites in sweep net collections. Collected specimens represented 15 bee genera of five families, 'flies', and 'wasps'. Networks were similar with respect to topology and structure (Figure 5-3, Table 5-4). Networks had an average of 11.4 (±1.0) pollinator genera and 11.8 (±1.2) plant species. Pioneer Tower restored had the largest number of both plant (16) and pollinator (13) groups. The least rich network was Washington Creek degraded with 9 plant and 8 pollinator groups.

Connectance was similar across all sites. Linkage density was greatest at Pioneer Tower degraded (4.34) and Pioneer Tower restored (3.17) and similar at the remaining three sites. Shannon's diversity was greatest at Pioneer Tower restored (3.35), Pioneer Tower degraded (3.21), and Pioneer Tower (semi)natural (2.96).

Robustness of the insect community to extinction was highest in Pioneer Tower degraded (0.62), Pioneer Tower restored (0.59), Washington Creek old restored (0.58), Pioneer Tower (semi)natural (0.56), and lowest in Washington Creek degraded (0.51). Robustness of the plant community to extinction was highest in Pioneer Tower restored (0.63), Washington Creek old restored (0.57), Pioneer Tower (semi)natural (0.55), Pioneer Tower degraded (0.46), and lowest in Washington Creek degraded (0.44).

Discussion

How did the relative representation of bee functional groups differ between degraded, restored, and (semi)natural sites?

Diversity and evenness of functional groups increased with age since restoration, and the relative representation of functional groups reflected structural site changes associated with succession. Differences in the relative representation of functional groups among degraded, restored, and (semi)natural sites were likely influenced by nest site availability at different successional stages. Washington Creek and Pioneer Tower degraded had abundant bare ground, but few woody trees or pithy stemmed plants, providing nesting opportunities for ground nesters but limited sites for stem and wood nesters. Pioneer Tower restored had a mix of bare ground, pithy stemmed plants, and few woody plants, providing nest sites for ground and stem nesters but few opportunities for wood nesters. Washington Creek old restored and Pioneer Tower (semi)natural had a canopy of mature trees, a shrubby understory, and little dry, sunny, bare ground, providing few nesting opportunities for ground nesters and many options for stem and cavity nesters. These changes are consistent with Grixti and Packer's (2006) sampling of a southern Ontario field site 34 years after it was first surveyed. Between the first sampling period in 1968/1969 and the second sampling period in 2002/2003, the field underwent structural changes associated with succession and the abundance of wood nesters increased from 6% to 22% (Grixti and Packer 2006). These results suggest that wood nesters in degraded and recently restored habitats may be limited by nest site availability (Roulston and Goodell 2011). Though it is difficult to empirically determine if nest site availability influences the structure of the bee community, bee groups with different nesting habits are known to have divergent responses to fragmented habitat size (Neame et al. 2013), disturbance (Williams et al. 2010), and local site conditions (Potts et al. 2005), demonstrating that nesting resources play an important role in structuring bee communities (Roulston and Goodell 2011; Potts et al. 2005). We did not observe any consistent trends in social habits among degraded, restored, and (semi)natural sites, though social ground nesters were more abundant in degraded sites and solitary ground nesters were most abundant at Washington Creek restored.

Cleptoparasitic bees may be a good indicator taxa because they rely on large host populations and are therefore expected to be more sensitive to habitat changes compared to their hosts (Sheffield et al. 2013). Cleptoparasites tend to be most abundant in older, low disturbance habitats compared to intensively managed or degraded habitats (Sheffield et al. 2013). In our study, more parasitic specimens were collected in Pioneer Tower restored, Pioneer Tower (semi)natural, and Washington Creek old restored) compared to Washington Creek degraded and Clair Creek. However, the highest relative abundance of cleptoparasites was found at Pioneer Tower degraded and was nearly two times greater than that of the next most abundant site. The higher than expected occurrence of cleptoparasites at Pioneer Tower degraded could be attributed to sampling effects, transient individuals, or other biotic or abiotic site or surrounding habitat features that were not measured in this study.

The detected shifts in the contribution of guilds based nesting habits represent shifts in the functional diversity and evenness of the bee communities. At Pioneer Tower and Washington Creek degraded, ground nesters represented over 70% of the captured specimens, more than 20% above the relative abundance of ground nesters we found in older sites. This strongly influenced the functional diversity and evenness of the bee community (Shannon's diversity and evenness indices based on the six guilds). Washington Creek old restored and Pioneer Tower (semi)natural were the most functionally diverse and even compared to all other sites (Table 5-3). Diversity is generally associated with community stability (Ives and Carpenter 2007), and functional diversity has been suggested as the most important component of diversity (Hulot et al. 2000; Tilman et al. 1997). Increased diversity of pollinator functional groups is associated with increased productivity in agricultural settings (e.g. Hoehn et al. 2008), while the loss of functional groups is associated with a decline in ecosystem resilience (O'Gorman et al. 2011). Because different bee functional groups have different impacts on pollination services to wild and managed plant species, understanding changes to these groups can help focus management strategies. For example, knowing that wood nesters are uncommon in early restoration stages, ecosystem managers could include woody debris, posts, or commercial cavity nests in restoration plans to provide nesting opportunities and potentially enhance cavity nester abundance in early years (Nyoka 2010; Winfree 2010). Increasing functional diversity of the bee community in early restoration stages could have cascading effects on the plant community, including the recruitment of a more diverse plant community (Fontaine et al. 2006).

Increased functional diversity can also act as a buffer against disturbance. Functional groups based on nesting habits are known to respond differently to disturbance. For example, above ground nesters are more negatively affected by intensive agriculture and isolation from natural areas compared to below ground nesters, whereas below ground nesters are more susceptible to tilling (Williams et al. 2010). Therefore, a more diverse community could have a better chance of withstanding disturbance or environmental change (e.g. Brittain et al. 2013). In our case study (semi)natural habitats were the most functionally diverse despite not having the highest genus richness. Functional diversity and the relative representation of indicator taxa (e.g. cleptoparasites) can be useful for evaluating restoration 'success' when species composition of bee communities is variable across time and space (Montoya et al. 2012; Cadotte et al. 2011).

How do plant-pollinator interaction networks differ among degraded, restored, and (semi)natural sites?

Plant-pollinator interaction networks in degraded, restored, and (semi)natural sites did not demonstrate any clear trends. However, Pioneer Tower restored had the most plant and pollinator groups, the highest diversity, and high robustness to extermination of both plants and pollinators. This demonstrates that pollination function can be restored in response to non-targeted restoration. It is not surprising that we did not find any clear trends between restored and (semi)natural habitats, since no significant differences have been detected in previous comparisons of restored and remnant interaction networks (e.g. Williams 2011; Forup et al. 2008; Forup and Memmott 2005).

Washington Creek degraded had the least plant species and pollinator genera, the lowest diversity, and was the least robust to simulated plant and pollinator extinction events. Surprisingly, the Pioneer Tower degraded interaction network was well connected, diverse, and relatively robust to higher and lower order extinction. Under-sampling of plant-pollinator interactions may partly explain why the networks of the two older sites (Pioneer Tower (semi)natural and Washington Creek old restored) were less diverse, less robust to extinction, and had fewer plant and pollinator groups compared to Pioneer Tower restored and Pioneer Tower degraded. Both sites possessed partial or full canopies that limited understory growth. Fewer understory plants does not necessarily imply a less robust plant and pollinator community, but it does mean that there were fewer flowering plants to sample from when conducting sweep net surveys, and as a result lower interaction frequencies.

The complex plant-pollinator interaction network of Pioneer Tower restored compared to the lack of a network at Clair Creek suggests that restoration effort can influence the established bee community. Despite structural similarities in the vegetation at the two sites, the observed richness of floral resources differed considerably and strongly influenced sweep net collections. *Lotus corniculatus* L. (birdsfoot trefoil) was abundant at Clair Creek, but other flowering plant species were uncommon. In contrast, the flowering plant community at Pioneer Tower restored was represented by a mix of native and exotic species with a wide range of floral shapes and colours, and bloom times that ranged from early spring through fall. The lack of sweep net collections along with the absence of *Bombus spp.* at Clair Creek, suggest that restoration effort, particularly with respect to plantings, can influence the established bee community.

Conclusions

How native bees respond to habitat restoration is poorly understood; however, our case study demonstrates that within a few years, restoration activities can enhance diversity and evenness of functional groups based on ecological traits relative to degraded sites, but not to the levels found in older restored and (semi)natural sites., As well, changes in the relative representation of functional groups reflected changes in habitat structure associated with succession. Our findings contribute to the academic discussion of pollinator response to restoration and provide feedback for the involved ecosystem managers (e.g. the Grand River Conservation Authority). First, relative guild representation and plant-pollinator interaction networks at Pioneer Tower restored provided positive feedback to ecosystem managers that non-targeted restoration activities can increase the diversity and evenness of functional groups, genus richness, and potentially the connectance and robustness of the plant-pollinator community relative to comparable degraded habitats. Second, differences between sweep net collections at Pioneer Tower restored and Clair Creek and the resulting plant-pollinator visitation networks emphasized the importance of providing adequate forage resources as part of restoration activities. Third, differences in the representation of nesting behaviours among habitat types identified areas where ecosystem managers could focus restoration activities. For example, providing nesting habitat for stem and wood nesters in early restoration stages may encourage the establishment of wood nesters. Finally, the surveys of native bee communities serve as an important baseline for future monitoring activities.

Table 5-1 Complete list of genera sorted into guilds based on social (social vs. solitary) and nesting (ground vs. cavity vs. parasitic) habits.

Guild	**Genera**
A Solitary ground nesters	*Agapostemon* Roberts and Brooks, *Andrena* Fabricius, *Melissodes* Latreille, *Perdita* Smith, *Pseudopanurgus* Cockerell
B Social ground nesters	*Augochlorella* Sandhouse, *Halictus* Latreille, *Lasioglossum* Curtis, *Peponapis* Robertson
C Cavity nesters	*Anthidium* Fabricius, *Anthophora* Latreille, *Augochlora* Smith, *Ceratina* Latreille, *Chelostoma* Latreille, *Heriades* Spinola, *Hoplitis* Klug, *Hylaeus* Fabricius, *Megachile* Latreille, and *Osmia* Panzer, *Xylocopa* Latreille
D Bumblebees	*Bombus* Latreille
E Parasites	*Coelioxys* Latreille, *Nomada* Scopoli, *Sphecodes* Latreille, *Stelis* Panzer, *Triepeolus* Latreille
F Honeybees	*Apis mellifera* Linnaeus

Table 5-2 Complete list of genera caught at Clair Creek, Pioneer Tower Natural Area, and Washington Creek from pan traps and sweep netting from flowers. Acronyms for plant names are below table. Site abbreviations: CC- Clair Creek, PTD – Pioneer Tower degraded, PTN – Pioneer Tower (semi)natural, PTR – Pioneer Tower restored, WCD – Washington Creek degraded, and WCR – Washington Creek restored.

Family and Genus	Social habit	Nesting habit	Pans						Sweep Nets						Tot	Floral Associations
			CC	PTD	PTR	PTN	WCD	WCR	CC	PTD	PTR	PTN	WCD	WCR		
Andrenidae																
Andrena	Solitary	Ground	10	25	51	14	23	17		1	10	3	5	7	166	TH, RA, HM, AO, SC, TP, TO
Calliopsis	Solitary	Ground	1		3	1									5	
Pseudopanurgus	Solitary	Ground		1	1		1								3	
Apidae																
Anthophora	Social	Stem			1			2							3	
Apis	Eusocial	Cavities	15	1	9	13	14	11		2	1				66	TO, PV
Bombus	Eusocial	Ground		4	6	8	6	5	4	5	15	4		2	59	RH, RA, TO, GH, SC, TP, MF, LC
Ceratina	Social	Stems	118	24	109	298	18	44		2	10	7	2	6	638	RH, CV, CA, EH, EA, CN, EM, HP, RQ, GC, PD
Melissodes	Social	Ground		3	20	12	1	15		1	9	4		1	66	SC, CN, EG, EM
Nomada	Parasitic		2	32	10	6	1	12							63	
Peponapis	Social	Ground	5	2	2		2								11	
Triepeolus	Parasitic		1		1										2	
Xylocopa											1	1		1	3	TC, HM, PD
Colletidae																
Hylaeus	Solitary	Stems/ cavities	306	51	173	71	21	24	1	1	4	1	1	1	655	TH, EH, CS, SC, DC, GC, VU
Halictidae																

Agapostemon	Commu.	Ground	2	2	14	11	8	4		1	5				47	RA, TO, ES, IC
Augochlora	Solitary	Wood			1	5				1		4			11	SC, ES, GC
Augochlorella	Eusocial	Ground	223	13	46	74	33	5	1	1		1			397	CA, AM
Augochloropsis						1									1	
Halictus	Eusocial/ (solitary)	Ground	7	37	59	35	46	24		8	11	2	3	2	234	TH, RH, AM, OL, EA, TO, AO, ES, CN, DC, TP, LC
Lasioglossum	Eusocial	Ground	114	754	701	356	645	110		33	9	2	4	8	2736	RH, EV, AM, EH, HM, TO, ER, AO, SC, ES, CN, DC, GS, EM, HP,VU, MF, LP
Sphecodes	Parasitic		3	133	103	61	20	13		3	1	1			338	TO, ES, DC, GC
Megachilidae																
Anthidium			5		1	1									7	
Chelostoma	Solitary	Cavities		1											1	
Heriades	Solitary	Cavities	1			2									3	
Hoplitis	Solitary	Cavities	5	6	31	18	11	3			2				76	MF
Megachile	Solitary	Cavities	13	4	9	10	4	3			1				44	TH
Osmia	Solitary	Cavities	1	6		1	1	5							14	
Stelis	Parasitic				1										1	

Flower abbreviations: AM – *Arctium minus,* AO – *Alliaria officinalis,* AS - Asclepias syriaca, CA – *Cirsium arvense,* CN – *Carduus nutans,* CS – *Convolvulus sepium*, CV – *Cirsium vulgare*, DC – *Dauscus carota*, EA – *Erigeron annuus,* EG – *Euthamia graminifolia*, EH – *Erigero philadelphicus*, EM – *Eupatorium maculatum,* EP – *Eupatorium perfoliatum*, ER – *Epilobium strictum,* ES – *Erigeron strigosus*, EV – *Echium vulgare*, GA – *Geum aleppicum*, GC – *Geum canadense*, GH – *Glechoma hederacea*, GS – *Galium asprellum,* HH – *Heliopsis helianthoides*, HM – *Hesperis matronalis,* HP – *Hypericum perforatum*, IC – *Impatiens capensis,* LC – *Lotus corniculatus,* LI – *Lobelia siphilitica*, , LP – *Lysimachia punctate,* LV – *Leucathemum vulgare*, MF – *Monarda fistulosa,* OL – *Oenothera laciniata,* PD – *Penstemon digitalis*, PV – *Pycanthemum virginianum*, RA – *Rubus allegheniensis*, RH – *Rudebeckia hirta*, RQ – *Rananculus aquatilis*, SC – *Solidago Canadensis*, TC – *Teucrium canadense*, TH – *Trifolium hybridum*, TO – *Taraxacum officinale,* TP – *Trifolium pretense,* TY – *Thalictrum* polygamum, VU – *Verbena urticifolia*.

Table 5-3 Percent representation of Guilds A, B, C, D, E, F, and stem, wood, and ground nesting habits. Site abbreviations: CC- Clair Creek, PTD – Pioneer Tower degraded, PTN – Pioneer Tower (semi)natural, PTR – Pioneer Tower restored, WCD – Washington Creek degraded, and WCR – Washington Creek (semi)natural.

Site/Guild	**A**	**B**	**C**	**D**	**E**	**F**	**Stem**	**Wood**	**Ground**
CC	1.3	42.2	54.0	0.0	0.7	1.8	51.0	3.0	43.5
PTD	2.7	73.2	8.3	0.4	15.3	0.1	6.8	1.5	75.9
PTN	3.2	47.8	40.2	0.8	6.7	1.3	37.0	3.2	51.0
PTR	5.6	60.9	24.0	0.4	8.5	0.7	20.9	3.1	66.4
WCD	2.9	85.9	6.4	0.7	2.5	1.6	4.6	1.9	88.8
WCR	10.8	48.2	27.3	1.7	8.4	3.7	22.9	4.4	58.9
Mean	4.4	59.7	26.7	0.7	7.0	1.5	23.8	2.9	64.1
SE	1.4	7.0	7.5	0.2	2.1	0.5	7.3	0.4	6.8

Table 5-4 Functional group evenness and diversity, overall genus richness, and overall abundance at Clair Creek, Pioneer Tower Natural Area, and Washington Creek in 2012. Functional groups are Guilds A, B, C, D, E, and F. Diversity is Shannon's H Diversity and evenness is Shannon's Evenness. Site abbreviations: CC- Clair Creek, PTD – Pioneer Tower degraded, PTN – Pioneer Tower (semi)natural, PTR – Pioneer Tower restored, WCD – Washington Creek degraded, and WCR – Washington Creek (semi)natural.

Site/ Metric	**WCD**	**PTD**	**CC**	**PTR**	**PTN**	**WCR**
Evenness	0.52	0.60	0.70	0.72	0.75	0.80
Diversity	1.58	1.32	1.53	1.58	1.66	1.77
Genus Richness	15	15	16	19	15	15
Overall Abundance	855	1104	832	1352	998	297

Table 5-5 Plant-pollinator interaction network properties for sites at Washington Creek and Pioneer Tower Natural Area in 2012. Site abbreviations: CC- Clair Creek, PTD – Pioneer Tower degraded, PTN – Pioneer Tower (semi)natural, PTR – Pioneer Tower restored, WCD – Washington Creek degraded, and WCR – Washington Creek (semi)natural.

Site/Descriptor	WCD	PTD	PTR	WCR	PTN
# Pollinators	8	13	13	10	13
# Plants	9	12	16	11	11
Generality	2.18	5.47	3.25	2.40	1.98
Vulnerability	2.44	3.22	3.10	2.10	2.76
Connectance	0.24	0.21	0.18	0.20	0.15
Linkage density	2.61	4.34	3.17	2.25	2.38
Shannon Diversity	2.65	3.21	3.35	2.81	2.96
Robustness lower exterminated	0.44	0.46	0.63	0.57	0.55
Robustness higher exterminated	0.51	0.62	0.59	0.58	0.56

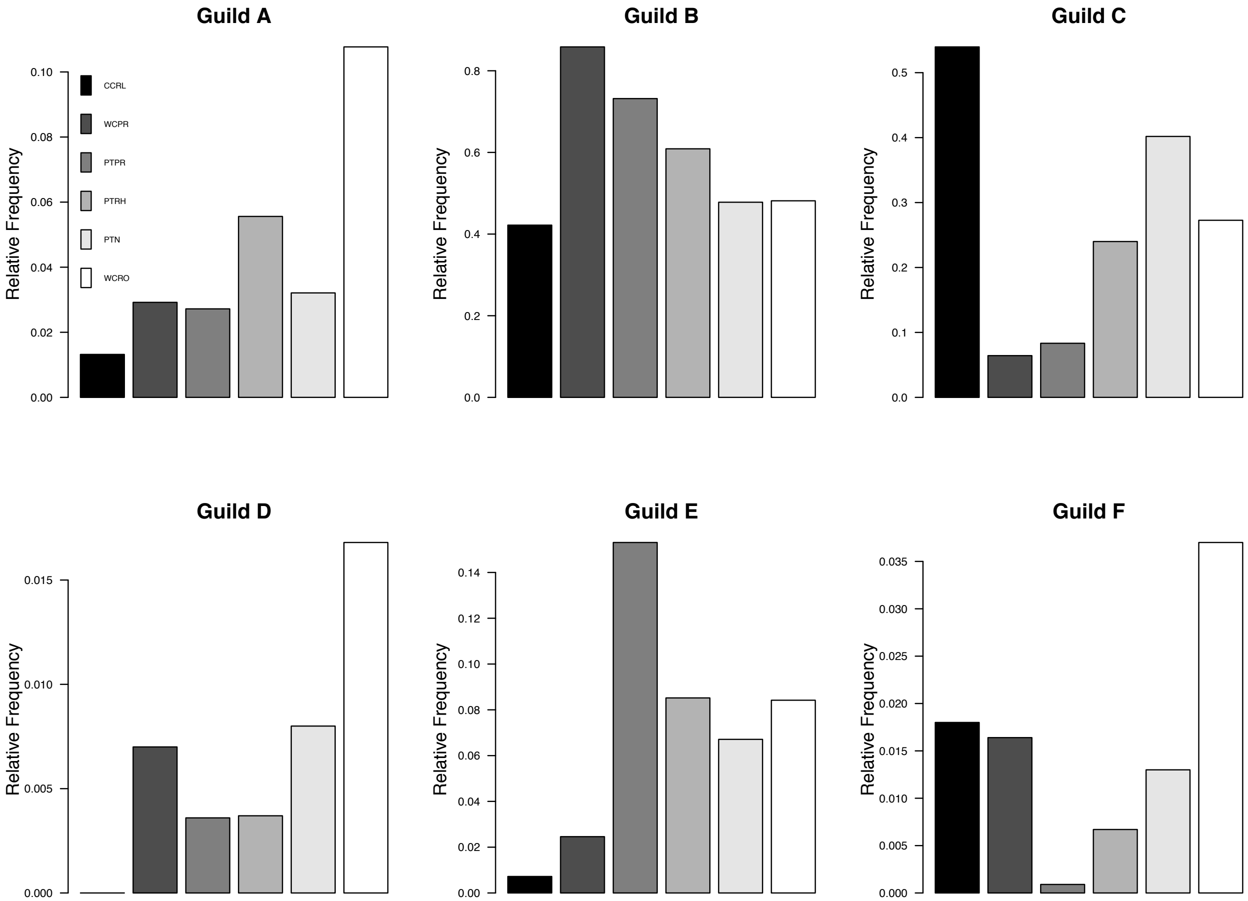

Figure 5-1 Relative abundance of guilds (in order on graph) at Clair Creek, Washington Creek degraded, Pioneer Tower degraded, Pioneer Tower restored, Pioneer Tower (semi)natural, and Washington Creek old restored in 2012. Guild A – solitary ground nesters, Guild B – eusocial ground nesters, Guild C – cavity nesters, Guild D – *Bombus sp.*, Guild E – cleptoparasites, and Guild F – *Apis mellifera*. CC- Clair Creek, PTDEG – Pioneer Tower degraded, PTN – Pioneer Tower (semi)natural, PTREST – Pioneer Tower restored, WCDEG – Washington Creek degraded, and WCREST – Washington Creek (semi)natural.

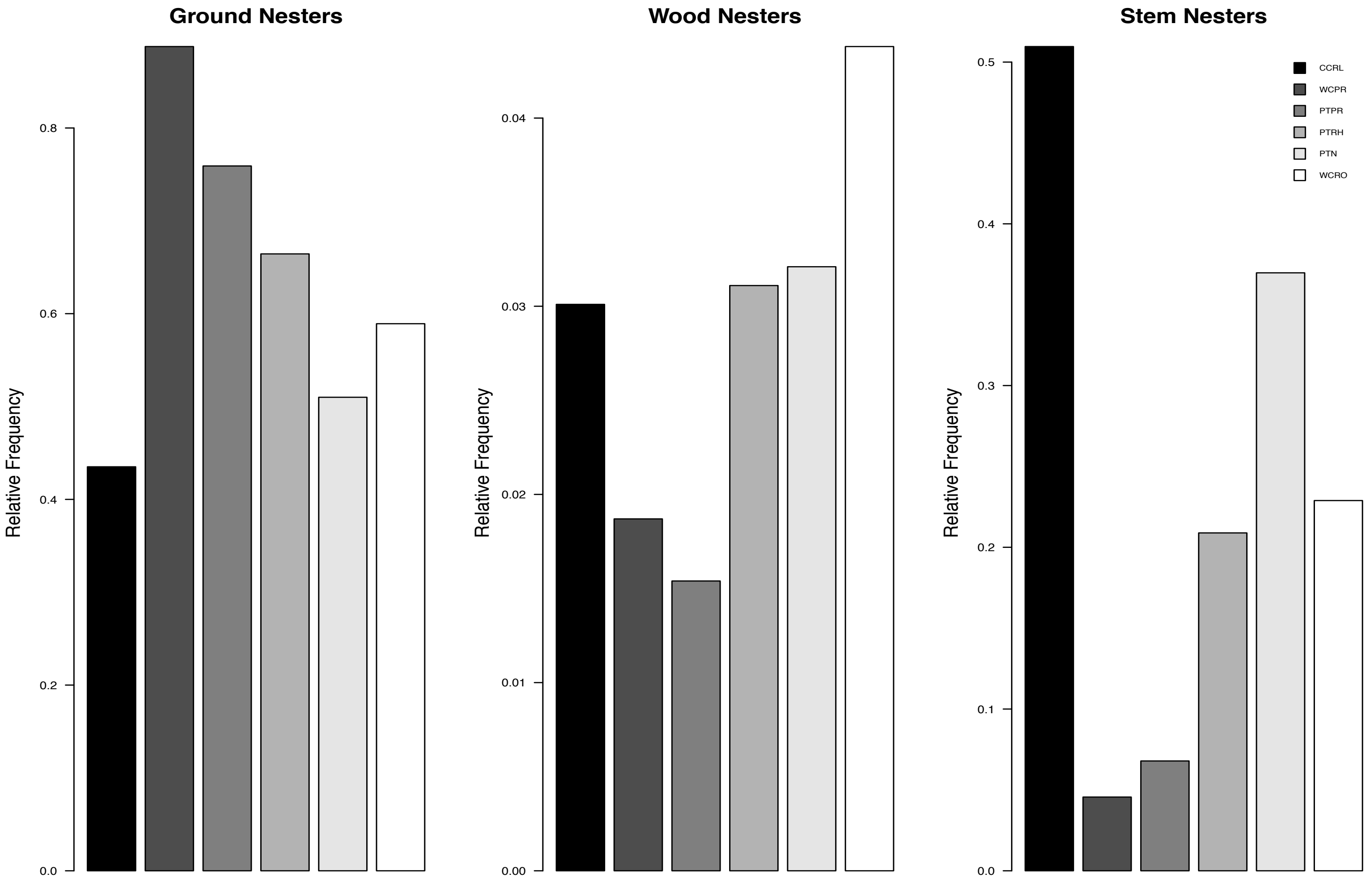

Figure 5-2 Relative abundance of nesting habit – stem, wood, and ground - at (in order appearing on charts) Clair Creek, Washington Creek degraded, Pioneer Tower degraded, Pioneer Tower restored, Pioneer Tower (semi)natural, and Washington Creek old restored in 2012.

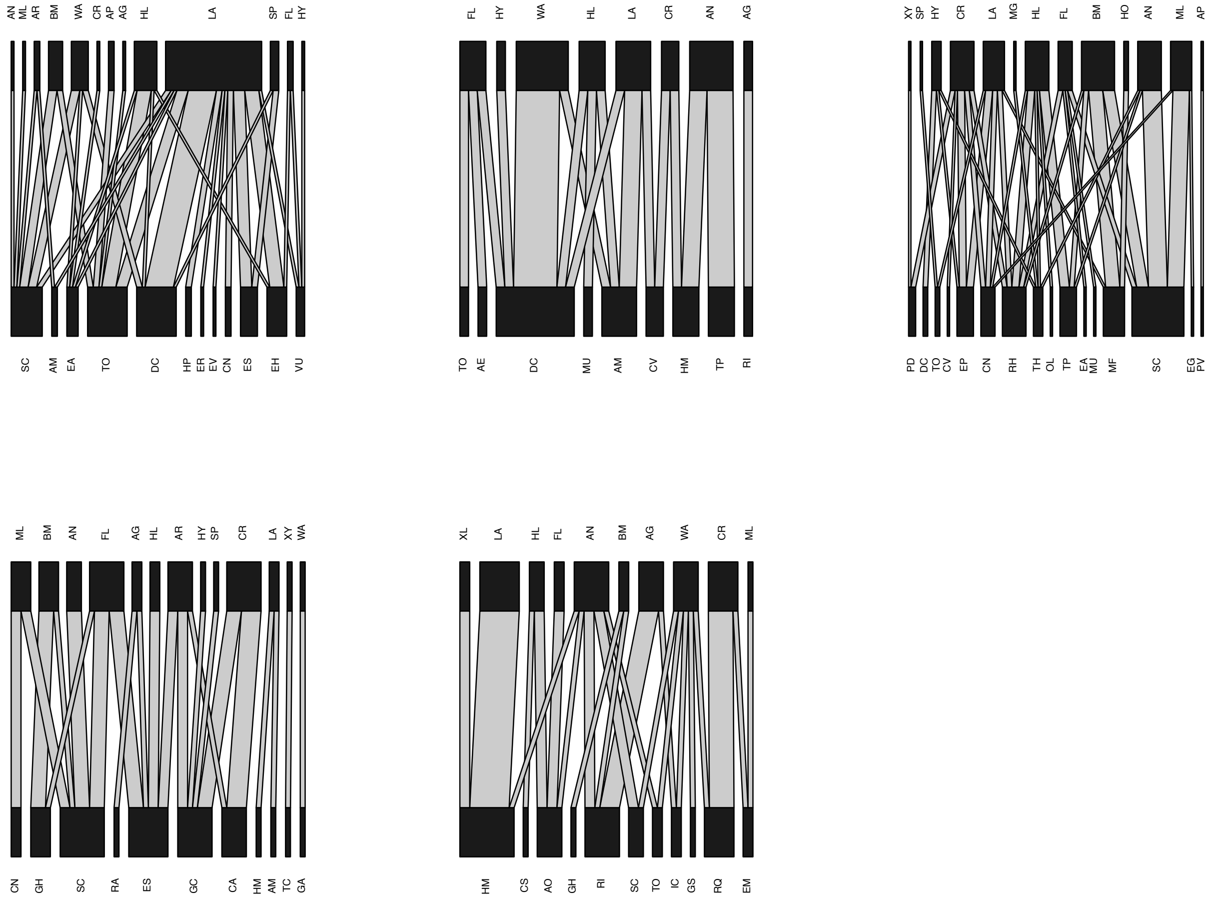

Figure 5-3 Plant-pollinator visitation networks for Pioneer Tower and Washington Creek in 2012. Clockwise from top left: Pioneer Tower degraded, Washington Creek degraded, Pioneer Tower restored, Washington Creek old restored, and Pioneer Tower (semi)natural. Insect abbreviations: AG – *Agapostemon*, AN – *Andrena*, AP - *Apis*, AR - *Augochlorella* , AU – *Augochlora*, BM - *Bombus*, CR - *Ceratina*, HL - *Halictus*, HO - *Hoplitis*, HY – *Hylaeus*, LA - *Lasioglossum*, MG - *Megachile*, ML – *Melissodes*, XL – *Xylocopa,* FY - fly, WA - wasp. Plant abbreviations are listed below Table 5-1.

Chapter 6 Bridging the gap between research and practice in pollination-based restoration

In this thesis I addressed three main objectives to gain a better understanding of native bee response to ecological restoration: I (1) documented the structure and function of the native bee community at a restored wet meadow to establish a baseline for future monitoring activities, (2) compared the influence of two restoration approaches on the established bee community, and (3) explored changes in functional groups and pollination function with time since restoration. These objectives fit within the repeated requests for incorporating pollinators into restoration planning and for studying how pollinators respond to habitat restoration (Montoya et al. 2012; Menz et al. 2011; Nyoka et al. 2010; Dixon 2009). To date, despite the increasing interest in restoration ecology and pollination biology, only a few studies have investigated the response of native bees to habitat restoration outside of agroecosystems and none of these studies have taken place in Canadian ecosystems (Devoto et al. 2012; Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008; Forup and Memmott 2005). The lack of pollination-based restoration studies can be partly attributed to the novelty of the integration of disciplines, but also to a few fundamental disconnects between the two disciplines. Here I review three areas where pollination-based restoration research and communication could be strengthened and how they influenced my thesis research.

First, ecological restoration tends to lack replicates. Due to the unique combination of abiotic and biotic features present in a given habitat it is rare for any two (or more) sites to be restored in exactly the same manner. A lack of replicates contradicts our ingrained understanding of a scientifically rigorous experiment, particularly when statistical tools are not applicable (*see* Michener 1997). This bias is present in empirical studies of pollination-based restoration, where only studies with replicated experimental designs have been published (Williams 2011; Exeler et al. 2009; Forup et al. 2008; Hopwood 2008; Forup and Memmott 2005). These studies represent only a small fraction of the contributions needed to make substantial knowledge advancement, and identifying and publishing alternative approaches may widen our knowledge base. Replicates were not widely available for the sites I worked with. Dunnville Marsh provided a unique opportunity where restoration approaches were replicated, albeit minimally. In Chapter 4 I used a combination of true (fields) and time-for-space (sampling event) replicates to compare two restoration approaches at Dunnville Marsh. In Chapter 5 I presented a case study without statistically comparable replicates that allowed me to identify and describe trends in the functional composition of the pollinator community with respect to age since restoration.

Second, the ‘success’ of ecological restoration is often determined by comparing one or multiple attributes of restored sites to those found in reference sites. However, appropriate reference sites are increasingly rare due to habitat loss, degradation, and fragmentation. Anthropogenic impacts, such as exotic species introductions and climate change, influence all of Earth directly or indirectly resulting in novel and hybrid ecosystems (Hobbs et al. 2013; Hobbs et al. 2009). These drivers cause ecosystem shifts that are irreversible in the case of novel systems and potentially reversible for hybrid system (Hobbs et al. 2009). This means that when assessing restoration ‘success’ there may no longer be a single reference site with comparable structural or functional properties, and the conditions for ‘success’ may have to be re-evaluated (Thorpe and Stanley 2011; Jackson and Hobbs 2009). In Chapter 4 I surveyed a series of restored wet meadows at Dunnville Marsh. When evaluating the ‘success’ of the entire restoration project, there was no appropriate reference site for comparison. Instead, I compared primarily functional properties of the bee community to previously studied southern Ontario communities. In Chapter 5 I used both degraded and (semi)natural reference sites; however, these were not replicated and comparisons were limited to functional properties of the bee community.

Third, pollination-based restoration knowledge transfer between researchers and ecosystem managers is poor (Young et al. 2005). This can be alleviated by communicating research findings in a publicly accessible manner and by identifying specific outcomes of scientific studies that can be applied by ecosystem managers to target pollinators in restoration plans or monitoring. For example, Hopwood (2008) recommends planting native plant species along highway verges to increase native bee abundance and diversity, based on the author’s study of degraded and restored road verges. Poor communication between researchers and managers can also impact the research process. For researchers, it may be difficult to find or access appropriate habitats to address a particular hypothesis, or it may be difficult to find sufficient replicates. For ecosystem managers, conducting pollinator surveys can be time and resource consuming and access to training for technical skills such as collection methods and insect identification may be unavailable. Montoya et al. (2012) suggest increasing the number of partnerships between researchers and ecosystem managers to overcome these obstacles. A large proportion of my surveys took place on property owned and managed by the Grand River Conservation Authority (GRCA). This partnership provided me access to sites with known restoration histories, and in return provided the GRCA with information about the plant and pollinator community that they do not have the resources to collect. Pollinator surveys can also be made more accessible to ecosystem managers by focusing on functional groups and pollination function. This eliminates the time consuming step of species identification, but returns the information most pertinent to ecosystem managers - how is the system is functioning?

These disconnects serve as an entry point into the discussion of what makes a valuable scientific study. In the field of restoration, information worth sharing is often un-replicated and lacking appropriate reference sites, and yet replicated and referenced studies dominate the published pollination-based restoration literature. Acknowledging alternate approaches to evaluating data will enhance the resources available for knowledge advancement. Identifying tangible applications from basic research will help translate knowledge advancement into restoration and conservation strategies. Michener (1997) stated it well in saying “Unless the results of even the most informal of evaluations are made public, we won’t be able to benefit from the gained knowledge in the future”.

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