Habitat Use in Undisturbed Forest and the Effect of Variable Retention Harvesting on Pollinator Assemblages (Apoidea, Syrphidae) in the Boreal Forest of Alberta

by

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Abstract

While pollination in agricultural areas has been well studied, pollinators in forests have received much less attention, particularly in the boreal forest. Bees, especially native bees, and hoverflies are the two most important groups of pollinators providing crucial ecological and economical services worldwide. However, many pollinator populations are in decline, and their conservation depends on an understanding of how they are distributed in undisturbed forest and how they respond to disturbances. Variable retention harvesting is a form of logging that aims to better emulate natural disturbance, e.g., stand replacing wildfire. The objectives of this thesis were: 1) to establish what species of bees and hoverflies are present in the boreal forest of northwest Alberta, 2) to describe how bees and hoverflies are distributed within undisturbed forest stands, and 3) to determine the effect of variable retention harvesting on bees and hoverflies in deciduous and coniferous forest cover. This was accomplished by sampling bees and hoverflies by net and pan trap in 2012 and 2013 at the Ecosystem Management Emulating Natural Disturbance (EMEND) study site. Pollinators were studied in uncut control compartments in four forest types: deciduous-dominated (DDOM), deciduous-dominated with spruce understory (DDOMU), mixedwood (MIXED), and coniferous dominated (CDOM). Additional sampling was conducted in clearcut, 20% retention, and 50% retention compartments in the DDOM and CDOM forest cover types and along roadsides in forested and agricultural areas within the EMEND landscape. I identified 57 species of bees and 64 species of hoverflies at EMEND. There was no significant difference in their abundance among the four forest cover types within uncut forest. Species richness was also similar among DDOM, DDOMU and MIXED compartments. However, CDOM compartments had a higher bee and hoverfly species richness as well as more species exclusive to a cover type. Bees did not differ significantly in abundance between forest and agricultural roadsides, but species richness was higher for agricultural roadsides. They were more abundant and diverse along forest roadsides than forest compartments. Hoverflies also did not differ in abundance between forest and agricultural roadsides but species richness was higher for forest roadsides. They were more abundant along forest roads than in forest compartments but species richness was higher in forest compartments than along forest roadsides. Within previously harvested compartments, post-harvest retention had no overall significant effect on the abundance of bees or hoverflies. Nevertheless, I observed that bee abundance increased with decreasing harvest retention in CDOM compartments, hoverfly abundance increased with increasing retention in DDOM compartments, and hoverfly response differed between subfamilies in CDOM compartments. Bee species diversity generally decreased as harvesting retention increased. However, hoverfly species diversity was highest in compartments with 50% retention. Forest cover type significantly affected bee abundance within harvested compartments with more bees caught in CDOM than in DDOM compartments. Canopy cover, shrub cover, and flower abundance all significantly explained variation in bee abundance, with canopy cover and shrub cover included in the best supported linear model and canopy cover and flower abundance significant in an RDA analysis. Canopy and shrub cover were both significantly related to hoverfly abundance, however, only canopy cover was included in the best supported linear model. Abundance of particular plant families had no significant effect on total bee or hoverfly abundance. In contrast, flower colour was important, with white and purple flowers having a significant positive effect and pink flowers having a significant negative effect on total bee abundance. White flowers, in contrast, had a significant positive effect on total hoverfly abundance. Several species of bees and hoverflies were identified as indicators, including *Bombus rufocintus* (agricultural roads), *B. terricola* (all roadsides), and *Megachile relativa* (low retention CDOM compartments). While *B. terricola* is in decline in parts of its range, it was the fourth most abundant species at EMEND. Additionally, I recorded 56 flowering plant species, including one previously unrecorded at EMEND (*Lycopus uniflorus*). Flower abundance and diversity did not significantly differ among treatments, though abundance decreased with increasing harvest intensity. Canopy and shrub cover were lower in CDOM than DDOM compartments and increased with retention in CDOM. Forest management wishing to minimize impacts on pollinators should take forest cover type into account and aim to increase retention to benefit groups such as Megachilidae and Eristalinae.

Preface

This thesis is an original work by Jared Amos. The overall study design was determined by the Ecosystem Management Emulating Natural Disturbance (EMEND) project and the details of my study design were established by Jared Amos, John Spence, and David Langor. Specimens and data were gathered by Jared Amos, Owen Clarke, and Kyle Winters. Insect preparation and identification, analyses, the writing of the text, and creation of graphs and tables was completed by Jared Amos. Particular help with identifications, statistics, and edits are outlined in the Acknowledgements.

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List of Abbreviations

DDOM= Deciduous-Dominated

DDOMU= Deciduous-Dominated with Spruce Understory

CDOM= Coniferous-Dominated

Clear= Clearcut

Cont= Control

EMEND= Ecosystem Management Emulating Natural Disturbance

IFD= Ideal Free Distribution

ISA= Indicator Species Analysis

LT= Long-Tongued

MIXED= Mixedwood

PSP= Permanent Sample Plot

perANOVA= Permutational Analysis of Variance

RDA= Redundancy Analysis

ST= Short-Tongued

VIF= Variance Infalation Factor

20%= 20% Retention

50%= 50% Retention

Chapter 1: Introduction

A variety of animals serve as pollinators, providing a crucial ecosystem service. While bees are the most important group of such pollinators and receive much attention, pollination is also provided by an assortment of other animals, ranging from insects (e.g., flies, butterflies, moths, beetles, wasps, and others) to birds (e.g., hummingbirds) and mammals (e.g., bats and primates) (Allen-Wardell et al. 1998). There is evidence of humans propagating honey bees (*Apis* spp.) for honey and bees wax from at least 3000 BCE and the importance of bees as pollinators has been understood since at least the 18th century (Crane 2004). In addition to honey, bees provide bees wax, royal jelly, propolis, and venom (Michener 2007, Cherniak 2010, Kluser et al. 2010), all with a multitude of medical uses (Cherniak 2010). Above all, pollinators provide essential pollination for crops. This service was valued at over €150 billion globally in 2005 (Gallai et al. 2005). Collectively, animals pollinate 78% of all flowering plant species in temperate regions, and 87.5% of all flowering plant species worldwide (Ollerton et al. 2011). Bees alone pollinate 64% of the world's crops (Kluser et al. 2010). Additionally, pollination increases seed set and reduces inbreeding in plants (Kearns and Inouye 1997, Greenleaf and Kremen 2006, Michener 2007).

Native bees play an important, yet often overlooked, role in pollination. Many native bee species are more efficient pollinators than honey bees by foraging for longer hours, visiting flowers at a more frequent rate, foraging in colder temperatures, and by leaving more pollen available to flowers on their bodies (Winfree et al. 2007, Abrohl 2011). Many crop species are pollinated by native bees in addition to honey bees, and, therefore, native bees also provide a form of insurance against the loss of honey bees (Greenleaf and Kremen 2006, Winfree et al. 2007, Abrohl 2011). Furthermore, some native bee species (e.g., *Megachile rotundata*) generally forage in fields in which they nest and are consequently not much affected by pesticide applications in adjacent fields (Abrohl 2011). Remarkably, the presence of native bee species may increase the pollination efficiency of honey bees by altering their movement patterns (Brittain et al. 2013).

While native bees are essential pollinators, flies are also important contributors to pollination. Hoverflies are likely the second most important group of pollinators after bees (Larson et al. 2001). They comprise three subfamilies, each with different feeding strategies as larvae. Larvae of Eristalinae are phytophagous, mycophagous, and saprophagous, those of Syphinae are predaceous, mostly on homopterans, and larvae of the Microdontinae are scavengers or predators within ant nests (Vockeroth and Thompson 1987, Sommaggio 1999). As hoverflies with different feeding strategies have different habitat requirements, and are easy to find in a variety of habitats, they can be used as indicator species in studies of disturbance (Sommaggio 1999). In addition, the larvae of Syrphinae may play a significant role in the pest control of homopterans (Vockeroth and Thompson 1987, Sommaggio 1999).

Alarmingly, many pollinator populations are in decline. Honey bees, for example, have been declining for decades (Kearns and Inouye 1997, Allen-Wardell et al. 1998, Kluser et al. 2010, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Smith et al. 2013, Goulson and Nicholls 2016) with declines increasing precipitously starting in 2006 (vanEngelsdorp and Meixner 2010, Smith et al. 2013, Goulson and Nicholls 2016). Many of these losses have been described under the term 'colony collapse disorder', in which severe annual loss in numbers occurs without any sign of dead bees or clear explanation for the cause, although brood and a queen remain in the hive (Williams et al. 2010, Smith et al. 2013). The mite *Varroa destructor* and associated pathogens have caused serious decreases in the number of honey bee colonies in many regions (Allen-Wardell et al. 1998, National Resource Council [NRC] 2007, Kluser et al. 2010, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Williams et al. 2010, Smith et al. 2013, Goulson and Nicholls 2016). Additional losses have been attributed to improper pesticide use (e.g., neonicitonoids, miticides) (Allen-Wardell et al. 1998, NRC 2007, Kluser et al. 2010, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Smith et al. 2013, Goulson and Nicholls 2016), habitat degradation (Kluser et al. 2010 vanEngelsdorp and Meixner 2010), weather and climate change (Allen-Wardell et al. 1998, Kluser et al. 2010, vanEngelsdorp and Meixner 2010), pollution (Kluser et al.

2010), agricultural practices (e.g., monocultures, transgenic crops) (Brodschneider and Crailsheim 2010, vanEngelsdorp and Meixner 2010, Goulson and Nicholls 2016), changes to beekeeping practices (e.g., transportation of colonies, diet, splitting colonies) (Kluser et al. 2010). Furthermore, many of these factors may act synergistically to cause honey bee declines (Potts et al. 2010, Williams et al. 2010, Smith et al. 2013).

Population declines, however, are not exclusive to honey bees as many native bee species populations are also in decline. For example, many species of *Bombus*, a group that is relatively well studied, are declining (NRC 2007, Colla and Packer 2008, Evans et al. 2008, Goulson et al. 2008, Grixti et al. 2009, Williams and Osborne 2009, Potts et al. 2010, Cameron et al. 2011, Meeus et al. 2011, Colla et al. 2012, Szabo et al. 2012, Goulson and Nicholls 2016), with members of the subgenus *Bombus sensu stricto* particularly at risk (Colla and Packer 2008, Evans et al. 2008, Williams and Osborne 2009, Cameron et al. 2011). The major factor in these declines was believed to be pathogen spillover from managed bumble bees in greenhouses previously reared in Europe (Evans et al. 2008, Goulson et al. 2008, Otterstatter and Thomson 2008, Williams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Szabo et al. 2012, COSEWIC 2015, Goulson and Nicholls 2016). However, a recent analysis on the origins of *Nosema* casts doubt on claims that a new strain of *Nosema* was introduced from Europe (Cameron et al. 2016). Other suggested causes of decline in *Bombus* populations include pesticide use, habitat loss, introduced pollinator species, and climate change (Evans et al. 2008, Goulson et al. 2008, Williams and Osborne 2009, COSEWIC 2015, Goulson and Nicholls 2016).

Despite the alarming observations, the status of the majority of bee species is unknown in both Canada (Sheffield et al. 2014) and worldwide (NRC 2007, Goulson and Nicholls 2016). Nonetheless, among studied species, many are either in decline or have limited ranges (Magnacca 2007, NRC 2007) with some species now considered threatened (Red List of Bees). Troublingly, little is also known about the global population status of pollinating flies such as hoverflies (Allen-Wardell et al. 1998, Kearns 2001, NRC 2007), though they appear to be increasing in some regions and declining in others (NRC 2007, Potts et al. 2010).

Pollinators are crucial to the function of the boreal forest (Kevan et al. 1993), as bees and hoverflies pollinate many understory plants (Michener 2007). These understory species contribute the majority of plant species diversity in the boreal forest (La Roi 1967) and, in turn, provide food and shelter for wildlife, help with water retention and preventing erosion, and contribute shade for seedlings of sun-intolerant trees, and are thereby involved in natural succession (Kevan et al. 1993, Michener 2007).

Pollinator assemblages are affected by the disturbance regime in the boreal forest. Fires, insect outbreaks, and windstorms are common disturbances (Shorohova et al. 2011, Brandt et al. 2013, Gauthier et al. 2015) and in western Canada, many aspects of forest structure and succession are driven by stand-replacing fires on the landscape (Rowe and Scotter 1973, Shorohova et al. 2011, Brandt et al. 2013). Pollinators also respond to anthropogenic disturbances such as logging (Fye 1972, Sueyoshi et al. 2003, Cartar 2005, Makino 2006, Nol et al. 2006, Deans et al. 2007, Nielsen and Totland 2007, Romey et al. 2007, Pengelly and Cartar 2010, Schleuning et al. 2011, Proctor et al. 2012) and the construction of roads (Fye 1972, Jackson et al. 2014).

Objectives

My thesis will examine bee and hoverfly assemblages at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site in northern Alberta in order to address three primary objectives. The first is to establish what species of bees and hoverflies are present in the boreal forest of northwestern Alberta (Chapter 3). Bumble bees were previously examined in deciduous forest cover at EMEND (Cartar 2005, Pengelly and Cartar 2010) but other recent studies on bees in northern Alberta have been focused in agricultural landscapes (e.g., Morandin and Winston 2006). Bee specimens have been collected in the boreal forest (Global Biodiversity Information Facility 2016), however, there has been no reliable inventory of boreal bee species in Alberta. Although a key with range maps exists for all Nearctic hoverflies (Miranda et al. 2013), it does not include information about which species are found in the boreal forest.

The second objective of the thesis is to describe how bees and hoverflies are distributed within the EMEND landscape by examining the assemblages in unharvested ‘control’ forest compartments at EMEND (Chapter 3) and along roadsides adjacent to forest and agricultural areas (Chapter 2). This understanding is critical for determining whether forest harvest causes significant changes in pollinator communities.

The third objective of the thesis is to determine the effect of variable retention harvesting on assemblages of bees and hoverflies in deciduous and coniferous forest cover types (Chapter 2). This provides a wider perspective than previous studies on bees at EMEND; Cartar (2005) and Pengelly and Cartar (2010) only examined bees in deciduous forest cover.

Chapter 2: Pollinator (Apoidea, Syrphidae) habitat use and responses to retention harvest in northwest Alberta.

Abstract:

The effects of forest harvest on boreal pollinators have received limited attention, particularly, the impacts of variable retention harvesting. I sampled bee and hoverfly assemblages at the Ecosystem Management Emulating Natural Disturbance (EMEND) study site in northwestern Alberta during 2013 using net capture and pan traps. Pollinators were studied in clearcut, 20% retention, 50% retention, and uncut (control) compartments in deciduous dominated (DDOM) and coniferous dominated (CDOM) forest cover, as well as along forested and agricultural roadsides within the EMEND landscape. Bees were generally more abundant along forest roadsides than agricultural roadsides, although their assemblages were more diverse along agricultural roadsides. They were also more abundant and diverse along forest roadsides than in forest compartments. Hoverflies were both more abundant and diverse along forested roadsides than agricultural roadsides and were generally more abundant along forest roadsides than in forest compartments. However, hoverflies were more diverse within forest compartments than along roadsides. Within compartments harvested 14 years previously, amount of post-harvest retention had no overall significant effect on the abundance of bees or hoverflies. However, the following trends were observed: 1) the abundance of bees increased as harvest retention decreased in CDOM compartments, 2) hoverfly abundance increased with increasing retention in DDOM compartments, except for that of Syrphinae which decreased, and 3) hoverfly responses in CDOM compartments varied among subfamilies. Bee species diversity generally decreased as harvesting retention increased. However, hoverfly species diversity was highest in compartments with 50% retention. Forest cover type significantly affected bee abundance with more bees caught in CDOM than in DDOM compartments. Canopy cover, shrub cover, and flower abundance all significantly explained variation in bee abundance, with canopy cover and shrub cover included in the best supported linear model and canopy cover and flower abundance significant in an RDA analysis. Canopy and shrub cover were both significantly related to hoverfly abundance, however, only canopy cover was included in the best supported linear model. Abundance of particular plant families had no significant effect on total bee or hoverfly abundance. In contrast, flower colour was important, with white and purple flowers having a significant positive effect and pink flowers having a significant negative effect on total bee abundance. White flowers also had a significant positive effect on total hoverfly abundance. Several species of bees and hoverflies were identified as indicators, including *Bombus rufocintus* (agricultural roads), *B. terricola* (all roadsides), and *Megachile relativa* (low retention CDOM compartments).

Introduction:

Bees and hoverflies comprise >17000 (Michener 2007) and c. 6000 species (Vockeroth and Thompson 1987), respectively, worldwide, and are the two most important groups of insect pollinators (Larson et al. 2001). More than 75% of flowering plant species require pollinators to set seed (Ollerton et al. 2011), and thus pollination is central to community function. While the benefits of pollinators in agriculture are well known, bees and hoverflies are also integral to the ecological function of the boreal forest (Kevan et al. 1993). Although most tree species are wind pollinated, bees and hoverflies pollinate many species of understory plants (Michener 2007). These species make up the majority of plant species in the boreal forest (La Roi 1967) and, in turn, provide many essential ecosystem services (Kevan et al. 1993, Michener 2007).

Pollinator community structure is strongly influenced by forest structure. For example, as forest cover increases, bee abundance decreases (Winfree et al. 2007a). Disturbances, including fires, insect outbreaks, and windstorms, are common in the boreal forest (Shorohova et al. 2011, Brandt et al. 2013, Gauthier et al. 2015) and in western Canada, forest structure reflects succession after stand-replacing fires on the landscape (Rowe and Scotter 1973, Shorohova et al. 2011, Brandt et al. 2013)**.** Effects of fire on pollinators have been well studied. Immediately following a fire, the abundance and species richness of bees and hoverflies increase (Potts et al. 2003, Moretti et al. 2004, Moretti et al. 2006) but subsequently decrease with time since the last fire (Moretti et al. 2006, Moretti et al. 2009) until reaching pre-fire levels (Moretti et al. 2006). The magnitude of these changes depends on the climatic region (Moretti et al. 2009), the number of fires in a given area (Moretti et al. 2006), and the life-history traits of the pollinators in question (Moretti et al. 2009, Williams et al. 2010), and thus some studies have found no significant effect or even a negative effect of fire on bee abundance (Winfree et al. 2009, Williams et al. 2010).

While fire-pollinator interactions are relatively well studied, potential effects of logging on populations of pollinators have received considerably less attention. Limited work on harvested systems have found that bees are more abundant (Fye 1972, Cartar 2005, Nol et al. 2006, Nielsen and Totland 2007, Romey et al. 2007, Pengelly and Cartar 2010, Schleuning et al. 2011) and diverse (Fye 1972, Makino 2006, Nol et al. 2006, Romey et al. 2007, Pengelly and Cartar 2010) in recently logged areas. Likewise, the same appears to apply to hoverflies with regards to both abundance (Sueyoshi et al. 2003, Nol et al. 2006, Deans et al. 2007, Nielsen and Totland 2007) and diversity (Sueyoshi et al. 2003, Makino et al. 2006, Nol et al. 2006, Deans et al. 2007, Proctor et al. 2012). In addition, Rubene et al. (2015) observed a positive relationship between clearcut size and number of bee species observed. Like post-fire responses, abundance of pollinators appears to decrease with increasing time since harvest (Sueyoshi et al. 2003, Makino et al. 2006, Nol et al. 2006), in some cases dropping below the abundance of unlogged sites for several years (Sueyoshi et al. 2003). However, logging does not always significantly affect pollinator abundance (Winfree et al. 2009) or species diversity (Cartar 2005, Schleuning et al. 2011, Proctor et al. 2012).

In recent decades, logging practices have moved away from clear-cutting and forest managers increasingly seek to integrate production of commercial timber with maintaining ecological processes, structural complexity and biological diversity (Franklin et al. 1997, Rosenvald and Lõhmus 2007, Van Damme et al. 2014). Many modern approaches to forestry attempt to emulate natural disturbance patterns, leaving increased heterogeneity (Bergeron and Harvey 1997, Van Damme et al. 2014) and structural complexity (Franklin et al. 1997, Van Damme et al. 2014) on forested landscapes. Variable retention harvesting, for example, retains biological legacies such as species, snags and logs, creates more structurally complex stands, and enhances landscape connectivity (Franklin et al. 1997, Rosenvald and Lõhmus 2007).

Although many studies have shown positive effects of green-tree retention on several groups of animals (reviewed in Rosenvald and Lõhmus 2007), information on the effects of variable retention harvesting on pollinator assemblages is limited. As expected, the abundance of bees generally increases as the amount of retention decreases, and similar trends have been observed for the species diversity of bees (Romey et al. 2007, Pengelly and Cartar 2010). Although hoverflies are generally more abundant and diverse in harvested stands, Deans et al. (2007) suggests their abundance and species diversity is highest in stands with moderate levels of retention. However, despite increased pollination with decreasing harvest retention, Schleuning et al. (2011) found no effect of logging at any intensity on overall species diversity of pollinators.

In this study I have examined the effects of variable retention harvesting on boreal bee and hoverfly assemblages in northern Alberta fourteen years post-harvest. I hypothesized that bee and hoverfly abundance and species richness would be highest in stands that had been harvested with higher intensity. As forestry also requires creation of roads, I compared pollinator assemblages along forested and agricultural roadsides with forest landscapes. Additionally, the study also aimed to illuminate the extent to which local environmental factors (canopy cover, shrub cover and flower abundance and diversity) explain variation in bee and hoverfly abundance.

Methods:

Study Site

Field work was conducted in the boreal mixedwood forest on the Ecosystem Management Emulating Natural Disturbance (EMEND) landscape located approximately 90km northwest of Peace River, Alberta, Canada. The EMEND experiment encompasses four forest cover types: 1) deciduous dominated (DDOM), in which over 70% of the trees in the canopy are deciduous, 2) deciduous dominated with a spruce understory (DDOMU), in which over 70% of the trees in the canopy are deciduous over an understory of white spruce, 3) mixedwood (MIXED), in which the canopy is composed of 40-60% spruce and aspen, and 4) coniferous dominated (CDOM), in which over 70% of the trees in the canopy are coniferous. Clearcuts and four retention harvest prescriptions were applied to 10ha compartments of each cover type during the winter of 1998/1999. Retention harvests were achieved by cutting machine corridors through each compartment and then removing trees from the retention strips to reach the desired level of retention: 10%, 20%, 50%, and 75% retention. Unharvested compartments were left as controls in each block of replication. Each treatment was replicated three times in each forest cover type (see Work et al. 2010 for details about EMEND and harvest prescriptions). Each compartment contains a baseline running through the compartment in addition to 3-6 permanent sample plots (PSP) used for core research.

Pollinator Sampling

Pollinators were sampled at EMEND during the summer of 2013 between 31 May and 15 August, 14 years after experimentally prescribed harvests were applied to initiate the experiment. We used both net capture and pan traps as these methods sample complementary assemblages of pollinators (Grundel et al. 2011). We sampled clearcut, 20% retention, 50% retention, and unharvested control compartments from stands originally characterized as DDOM and CDOM at the time of harvest. Despite significant deciduous growth in coniferous stands in the 14 years following harvest, stands will be referred to here with respect to their state at time of harvest, *i.e.*, as simply DDOM and CDOM. Because pollinators seemed to be more abundant along roadsides than in the forest, we also sampled three forested roadsides within the EMEND site (at km 230 and km 234 along Haul Road P2-200 and c. km 62 on Canfor Road (the access road on the southern edge of 868)) and three roadsides in the agricultural area adjacent to the forest of the EMEND landscape (Township Road 874 at Range Road (RR) 251, RR 253, and RR 260).

All net sampling was conducted between 9 AM and 5 PM by two people who independently sampled different flower patches encountered during the same time period adjacent to the baselines of the same EMEND compartments or on either side of the road. Flower patches were identified as aggregations of plants in flower, regardless of the number of species or flower abundance. The patch was sampled over a five minute period by netting all pollinators that visited the flowers in a half-circle with a radius of 1.5m of a constant position at the patch edge (corresponding to the length of the handle of the net, Figure 2.1a). We sampled each compartment for an hour regardless of how many flower patches were sampled and whether the compartment boundary was reached (min=2, max=12, mean=9.09±0.19). We killed all captured pollinators using ethyl acetate and placed them in glassine envelopes to be pinned within a few days for subsequent identification. We sampled most sites three times over the season. However, we also net sampled six sites (compartments 850, 853, 852, 898, km 62, RR 260) a fourth time earlier in the season and one roadside (km 230) only twice because it had been mowed just prior to the third sampling period and no flowers were present.

Pan traps were constructed using 4oz Solo© translucent polystyrene soufflé portion cups painted white (Tremclad® semi-gloss white high-performance rust-enamel), yellow (Rona© fluorescent yellow), or blue (Devflex^{TM} HP semi-gloss high performance waterborne acrylic from Dulux 42076 150000). Pan traps were set out in lines consisting of thirty traps placed in ten groups of three traps (one of each colour) with each group separated by a 3m interval (Figure 2.1b). Pan traps in forest compartments were placed in lines adjacent to the two EMEND permanent sample plots (PSPs) closest to the centre of the compartment to minimize potential edge effects. Each line was placed c. 5m south of the west end of the PSP and oriented directly to the east. All traps were a minimum of 10m from the nearest compartment edge for PSPs close to boundaries (i.e., 940 P4). At roadside sites, we placed a similarly constructed line of pan traps on each side of the road. Each trap was set out two-thirds full of propylene glycol to serve as a killing agent and preservative, and specimens were retrieved after one week and stored in ethanol. New glycol was added as needed to counter dilution by rainfall. Subsequently in the laboratory, we washed and dried bees (Droege 2015) and rinsed hoverflies in ethyl acetate prior to pinning to facilitate their identification. We sampled all forest sites four times and roadsides three times using pan traps.

A number of environmental variables of potential relevance to pollinators were also measured during net capture periods. The species identity and abundance of each flowering plant in blossom was recorded at each flower patch. Individual plants with multiple flowers were counted as one plant with the exception of *Linnaea borealis* where each stalk was counted as a flower. In addition to floral data, we recorded the canopy cover and shrub cover at flower patches. We estimated canopy cover using a concave spherical densitometer by counting the number of intersection points that show canopy and dividing this number by the total number of intersection points. Canopy cover was not measured at roadside points as there was little overstory at these sites. We visually estimated shrub cover within the flower patch by comparing the amount of area covered by shrubs to Figure 16.1.1 of Beckingham and Archibald (1996) (Figure 2.2).

Analysis

The taxon names used in this study follow Michener (2007) for bees, Miranda et al. (2013) for hoverflies and the USDA plant database (USDA, NRCS 2015) for flowers. I identified pollinators to species with the exception of those in *Colletes*, *Mellisodes*, *Protandrena*, *Platycheirus*, *Pipiza*, and *Heringia* which were identified to genus and bees in the genus *Lasioglossum* which were identified to subgenus. Two specimens of *Megachile* could not be identified due to missing metasomal sterna (S6) and were not included in analysis.

Analysis was performed using R (version 3.1.1) using α=0.05 to define significance throughout. The abundance of netted pollinators was standardized among sites by dividing their respective abundances by the number of times each site was sampled. Catches from pan traps at each site were standardized by dividing the abundance by the number of days that traps were left out at each site. In analyses using environmental variables, I used the compartment-level means for: percent canopy cover per flower patch, percent shrub cover per flower patch, flower abundance per flower patch, and number of species of plants flowering.

In addition to analyzing the entire assemblages of bees (Apoidea) and hoverflies (Syrphidae) in relation to my questions, I examined the assemblages of Eristalinae and Syrphinae separately due to differences in larval life history.

I used non-parametric tests to analyze the data because it could not be considered normally distributed. Data representing pollinator catches in forest compartments were tested to ensure homogeneity of variance using the function betadisper prior to performing a perANOVA (permutational analysis of variance) and all groups met the assumption except where indicated in the tables.

I first used a Wilcoxon signed rank test (R function wilcox.test) to test for significant differences in non-standardized abundance of pollinators caught by net capture and pan trap. In view of the fact that abundances were significantly different for bees, I analyzed pollinators caught by net and pan trap separately in all subsequent tests to avoid confounding results due to different methods.

Subsequently, I used a Mann-Whitney test to determine if there were significant differences in abundance between agricultural roads and forested roads and between forest roadsides and forest compartments (including harvest treatments and controls).

To analyze differences in abundance between harvest treatments and cover types, I performed perANOVA tests using adonis. After applying Hellinger distances to abundance data (Legendre and Gallagher 2001), I created constrained ordinations using a redundancy analysis (RDA) to explore variation in pollinator assemblages among harvest treatments and between the two forest cover types. Standardized pollinator abundance was contrained by harvest treatment and forest cover type using the rda function in the Vegan package and the adjusted R^2 value for each model was obtained using the function RsquareAdj, also from the Vegan package. I added ellipses representing 0.95 confidence limits using standard errors around harvest treatment groups using the function ordiellipse in the Vegan package. Eigenvalues and the percent of explained variation they accounted for were obtained using the summary function to examine the importance of constrained components for RDA 1 and RDA 2.

Total species richness of bees and hoverflies was compared between cover types and between harvest treatments within each cover type by combining data from both net capture and pan trap samples. Additionally, species richness at equal sample coverage (sample completeness) was compared between treatments for each sampling method following Chao et al. (2014) using iNEXT and ggiNEXT in the iNEXT package in R with Hill number set to q=0 (representing species richness). Hill numbers support easy comparison of different measures of species diversity (Chao et al. 2014). Raw abundance data were used for this analysis since calculations require integers.

In order to determine which environmental variables best explained pollinator abundance, I analyzed the effect of canopy cover, shrub cover, flower abundance, and flowering plant species diversity on the abundance of pollinators caught by net using three different approaches. Firstly, I created univariate linear models (using the function lm) of the effect of each factor on the total number of pollinators caught by net in the sample and examined adjusted R^2 values so as to determine the relationship between each environmental factor and pollinator abundance. Secondly, I created univariate linear models including all environmental variables and selected variables using selection in both directions choosing to include the variables that resulted in the lowest AIC value. Since canopy cover was low and unmeasured at roadsides, these sites were excluded from linear models of the relationship between abundance and canopy cover as well as models including all variables. Thirdly, I used constrained RDA ordinations (function rda, package Vegan) to analyze how the environmental variables (canopy cover, shrub cover, flower abundance, and flowering plant species diversity), the abundance of flowers within each plant family, and the abundance of flowers of each colour influenced assemblages of bees and hoverflies, following the same procedures as described above for harvest treatments and forest cover type. I used compartment-level means per flower patch for canopy cover, shrub cover, and flower abundance, and the total number of flowering plant species for each compartment to characterize flowering plant species diversity. I arbitrarily set the canopy cover of the roadsides equal to 50 to include these sites in the RDA analysis. This conservative estimate was chosen to minimize bias toward selection of canopy cover as the true value for this variable is lower at all roadside sites. For all RDAs with environmental variables, I used a variance inflation factor (function vif.cca) to remove all factors that were collinear and excluded all terms with a value greater than ten. This was followed by forward selection based on R^2 values using the function ordiR2step to select which terms to include in the model (Blanchet et al. 2008). R^2 values and eigenvalues and the percent data explained by them were obtained for each model following the methods described above for the RDAs contrained by harvest treatment and forest cover. I calculated interset correlations for RDA 1 and RDA 2 for each factor to determine the most important factors along each axis using the fuction intersetcor from the Vegan package. Interset correlations were considered significant above a critical (absolute) value of 0.361 ($p \leq 0.05$, d.f.=28). Following tests on flower abundance from each plant family and colour, univariate linear models were used to determine whether significant factors had a positive or negative effect on pollinator abundance.

I also tested for significant differences in the environmental variables among harvest treatments and forest cover types using an analysis of variance (ANOVA) followed by linear post-hoc contrasts if significant differences were found. Shrub cover and flower abundance did not meet the assumption of normality and perANOVA tests were used to test significance and Mann-Whitney tests (wilcox.test) were used for post-hoc tests.

To determine if the abundance of any pollinator species was strongly associated with particular harvest treatments, forest cover type, or type of roadside, I performed indicator species analysis (ISA) using the multipatt function from the indicspecies package in R which provides site specificity (A) and site fidelity (B). Species were only considered to be formal indicator species if the p-value for a species was less than 0.05.

Results

I caught 771 bees representing at least 54 species (Table A.1). This total is comprised of mostly long-tongued bees (92.3% of the bees caught) with the genus *Bombus* representing over half of all bee caught (50.1% of total bees caught). Additionally, I caught 369 individual hoverflies representing at least 47 species (Table A.2). Each subfamily made up roughly half of the hoverfly captures (Eristalinae: 48.5% of total hoverflies caught, Syrphinae: 51.5% of total hoverflies caught). The three most abundant genera of hoverflies were *Xylota* spp. (22.8% of total hoverflies caught), *Temnostoma* spp. (15.2% of total hoverflies caught), and *Syrphus* spp. (11.4% of total hoverflies caught).

I caught significantly more bees using pan traps (521 specimens) than by net capture (252 specimens) (Table 2.1). More species of bees were also caught in pan traps than by net capture (50 vs. 28 species) (Table A.1). Furthermore, 26 species of bees were caught exclusively in pan traps, but only 4 species of bees were caught exclusively by netting.

While total catches were more similar between sampling methods for hoverflies, I caught more total hoverflies and Syrphinae by net capture, and more Eristalinae by pan trap, though differences were not statistically siginificant (Table 2.1). However, the difference was striking for the eristaline *Xylota* spp. (4 individuals by net vs. 80 in pan traps) and syrphine *Syrphus* spp. (39 by net vs. 2 in pan traps) (Table A.2). Comparable numbers of species of hoverflies were caught by netting (33 species) and pan traps (32 species); however, representation of species by subfamily differed between the two methods (Table A.2). More species of Eristalinae were caught in pan traps than by netting (13 by net vs. 19 in pan traps) while the opposite was found for the Syrphinae (20 by net vs. 13 in pan traps). These differences appear to reflect real differences in relative capture efficiency of the two methods between these subfamilies as 15 species of hoverflies were caught exclusively by netting, including 10 species of Syrphinae, while 14 species of hoverflies were caught exclusively by pan traps, including 11 species of Eristalinae (Table A.2).

Overall, pan traps provided a more complete characterization of species composition for these groups of pollinators; however, it is important to note that net capture contributed the sole records of c. 18.8% of the species, each of which were uncommon species caught fewer than 5 times in the study.

Comparison of Pollinators along Roadsides and in Forested Areas

More bees were caught by net along agricultural roadsides than forest roadsides but this difference was not significant (Table 2.2). Conversely, more bees were caught by pan trap along forest roadsides than agricultural roads, but again this difference was not significant (Table 2.2).

Although more total bees were caught along forest roadsides, more bee species were caught along agricultural roadsides (38 species) than forest roadsides (33 species). Pan traps completely characterized bee assemblages along forest roadsides while the two sampling methods yielded distinct species assemblages along agricultural roadsides. Additionally, agricultural roadsides returned more unique species with 23 species that were not caught along forest roadsides (23 vs. 17), 13 of which were not sampled in any forest compartment. Both introduced bee species present in this study (*A. mellifera* and *Megachile rotundata*) were caught along agricultural roadsides. Of the species caught along forest roadsides, 17 were not caught along agricultural roadsides, and 6 of these were not sampled in any forest compartment but were confined to forest roadsides.

Bee abundance was significantly higher along forest roadsides than in forest compartments for both sampling methods (Table 2.2). Bee species richness was also somewhat higher along forest roadsides (33 species) than in forest compartments (29 species). Twelve of the species caught along forest roadsides were not caught in forest compartments while only 8 forest species were not caught along forest roadsides.

Although differences were not statistically significant, slightly more hoverflies were caught along forest roadsides than agricultural roadsides by both netting and pan traps (Table 2.2). While 19 individuals of *Xylota* spp. were caught by pan trap along roadsides, none were caught by net along roadsides of any type, underscoring the point that accuracy of faunal comparisons depends on the sampling methods employed.

Hoverfly richness showed a similar pattern, with more species caught along forest roadsides (26 species) than along agricultural roadsides (8 species). There were 24 species caught only along forest roadsides, including 8 not caught in any forest compartment, and 4 species caught exclusively along agricultural roadsides, with only a single species that was not also caught in any forest compartment.

Similar to bees, hoverflies were more abundant along forest roadsides than in forest compartments (Table 2.2). This was true for all samples of hoverflies, except Syrphinae caught by pan trap, but the differences were statistically significant only for net captures of total hoverflies and Syrphinae. However, more species of hoverflies were caught in forest compartments (37 species) than along forest roadsides (26 species). Twenty species caught in forest compartments were not caught along forest roadsides, while only 9 of the species caught along forest roadsides were absent from forest compartments.

Effects of Harvest and Cover Type

Bee assemblages were similar across harvest treatments but differed among cover types and there was a significant harvest treatment by cover type interaction (Table A.3, Figures 2.3a). In the ordination there was some separation of bee assemblages between DDOM and CDOM compartments (Table A.3, Figure 2.3a). The RDA ordination arranged bee assemblages from CDOM compartments along the x-axis in a gradient of increasing harvesting intensity ranging from control to clearcut compartments while there was no such clear pattern for the DDOM compartments (Figures 2.3a).

Bee abundance, by either netting or pan traps, did not differ with the amount of retention left after harvest 14 years earlier, but did differ between the two cover types (Figure 2.4, Table A.4). Bee abundances were greater in compartments that were CDOM at harvest than in those that were DDOM (Figure 2.4), significantly so for net capture abundance ($F_{(1,16)}$=13.6, p=0.003). Although there was no significant effect of harvest treatment, nor a harvest treatment by cover type interaction, data from both sampling methods suggest trends of increased abundance for bees in CDOM compartments with lower retention (Figure 2.4). The abundance of *Bombus* spp. caught by net in DDOM was higher in the 20% retention than in clearcut or 50% while abundance of *Bombus* sp. In CDOM compartments was highest in the clearcut treatment declining with increasing retention level (Figure B.1, not tested statistically).

Assemblages of hoverflies showed no significant differences in species composition between harvest treatments or forest cover types, but there was a significant cover type by harvest interaction for net captures (Table A.3). This was due to the assemblage of Syrphinae caught by net, for which there was a difference beteen DDOM and CDOM compartments, especially among control compartments, as shown in the RDA ordination (Figures 2.3b). In the RDA ordination, assemblages of Syrphinae caught by net in low retention CDOM compartments differed along the x-axis from those caught in high retention compartments (Figure 2.3b). Additionally, assemblages of Syrphinae caught by net in DDOM clearcut compartments differed from assemblages in other DDOM treatments and controls (Figure 2.3b).

As seen for bees, amount of retention had no significant effect on the abundance of most groups of hoverflies caught by either netting or pan traps and there were no harvest treatment by cover type interactions (Figure 2.4, Table A.4). More hoverflies were generally caught in CDOM than in DDOM compartments for all groups of hoverflies (Figure 2.4) and this difference was significant for Eristalinae caught by pan trap (Table A.4; $F_{(1,16)}$=6.95, p=0.017). In DDOM compartments, there was a weak trend of increased hoverfly abundance in retention and control blocks as compared to clearcuts based on net captures. There were no clear trends for CDOM compartments. There were more Syrphinae caught by net in low than high retention CDOM compartments (Figure 2.4g) but the opposite was true for Syrphinae caught by pan trap (Figure 2.4h).

Response of bee species diversity followed different patterns in the two forest cover types. Raw species richness, using the combined number of species caught by both sampling methods, was higher in CDOM compartments than in DDOM compartments, and total bee species richness decreased as harvest retention increased in CDOM (Figure 2.5a). Compared at equal sample coverage, species richness based on net captures was lowest in CDOM control compartments (Figures 2.5b-c) but this was not not evident for pan trap data. In contrast, raw species richness in DDOM compartments was highest in 50% retention compartments (Figure 2.5a), and this pattern held when species richness was compared at equal sample coverage for pan trap data, although not significantly for netted samples (Figures 2.5b-c). Few species were exclusively caught in control compartments within each cover type (2 species in DDOM, 1 in CDOM) and the 2 species caught exclusively in DDOM control compartments were also caught in harvested CDOM compartments. Conversely, 8 species found in CDOM compartments were exclusive to compartments that had been clear-cut.

Hoverfly raw species richness increased with increasing harvest retention to a maximum in 50% retention compartments but dropped in control compartments for both forest cover types (Figure 2.5d). However, species richness did not differ significantly among treatments at equal sample coverage, although more species were caught by pan traps in 50% retention compartments than control and clearcut DDOM compartments (Figure 2.5b-c). Unlike for bees, more species of hoverflies were exclusively found in control compartments than clearcut compartments within CDOM compartments (5 vs. 2 species).

In conclusion, variation in harvest prescriptions did not significantly affect pollinator abundance or diversity at equal sample coverage, though assemblages within CDOM compartments suggested a response along the gradient of harvest intensity. Forest cover type, however, was significantly related to bee abundance, and although trends in pollinator response to harvesting were not significant, they seemed to differ between DDOM and CDOM compartments. Bee abundance in harvested compartments did not differ from that in controls in DDOM but diversity was highest in 50% retention compartments. In contrast, bee abundance and diversity in CDOM was highest in low retention compartments. Hoverfly abundance tended to decrease with increasing harvesting intensity in DDOM compartments while, in CDOM, their abundance did not differ between harvested compartments and controls, although raw hoverfly species richness was highest in 50% retention compartments of both cover types.

Pollinator Responses to Environmental Variables

Measures of environmental variables differed between forest compartments and roadsides, and I explored whether these differences explained differences in pollinator abundance using net capture data. I used univariate linear models and multivariate RDA models in attempts to explain variation in the abundance and assemblages, respectively, of bees and hoverflies caught by net, using data on canopy cover, shrub cover, flower abundance, and flowering plant species diversity recorded at both forest compartments and roadsides during net capture.

Canopy Cover

Mean percent canopy cover ranged from 32.8% in one of the CDOM clearcut compartments to 96.3% in one of the DDOM clearcuts. Overall, DDOM compartments had more canopy cover than CDOM compartments (Figure B.2a, Table A.5). There was a more-or-less continuous gradient of increasing cover from clearcut CDOM compartments to clearcut DDOM compartments with control compartments falling near the middle of the gradient (Figures B.1a).

Canopy cover significantly explained 19.6% (in Syrphinae) to 55.6% (in Apoidea) of the variation in pollinator abundance (Figure 2.6a,e,i,m). Bee abundance significantly decreased with increasing percent canopy cover. The total abundance of hoverflies, as well as the abundance of Syrphinae was also significantly negatively related to canopy cover. The relationship with canopy cover was not significant for abundance of Eristalinae.

Shrub Cover

Mean percent shrub cover per compartment ranged from 0.579% along one of the forest roadsides to 33.9% in one of the 20% retention DDOM compartments. Overall, there was significantly more shrub cover in DDOM and DDOM compartments than along roadsides ($U=72$, $p \leq 0.001$), and more shrub cover in DDOM than CDOM compartmnets, though not significantly so (Figure B.2b, Table A.6). Furthermore, there was a non-significant trend of decreasing shrub cover with increasing harvest retention in DDOM compartments and the opposite in CDOM compartments (Figure B.2b).

Amount of shrub cover significantly explained 67.8% of the variation in total bee abundance (Figure 2.6b). Bee abundance decreased as the mean percent shrub cover per compartment increased. Shrub cover had a similar significant effect on the total abundance of hoverflies and, more specifically, the abundance of Syrphinae (Figure 2.6f,n). However, the variation explained by the amount of shrub cover for hoverflies was relatively weak ranging from 13.2% in Syrphinae to 13.9% in total hoverfly abundance. Shrub cover did not significantly predict abundances of Eristalinae.

Flower Abundance and Diversity

I recorded 15894 flowers from at least 57 understory plant species at flower patches visited during net sampling (Table A.7). Mean flower abundance per patch ranged from 2.85 flowers/patch in one of the DDOM clearcut compartments to 92.9 flowers/patch along one of the agricultural roadsides. Flowers were more abundant along both forest and agricultural roadsides than in forest compartments and more abundant along agricultural roadsides than forest roadsides, though differences were not significant after a Bonferroni correction (Figure B.2c, Table A.6). The number of species in flower per compartment ranged from 6 species in one of the 50% retention DDOM compartments to 19 species in one of the 50% retention CDOM compartments, but this number was not consistently affected by harvest treatment or forest cover type (Table A.5).

Bee abundance increased significantly with flower abundance with flower abundance explaining 61.0 % of the variation in bee abundance (Figure 2.6c). However, the number of plant species in flower recorded in a compartment did not significantly predict bee abundance (Figure 2.6d). Likewise, neither flower abundance nor flowering plant species diversity significantly predicted the abundance of any group of hoverflies (Figure 2.6g,h,k,l,o,p).

Models using all Variables

I included all 4 environmental variables in linear models to explain bee abundance and evaluated model fits using AIC (Table 2.3). Canopy cover, shrub cover, and flower abundance were all selected in the best model for bee abundance and canopy cover and shrub cover were significant. The model was significant in explaining 68.0% of the variation in bee abundance.

I constructed an RDA to further explore the effects of these same variables on the multivariate assemblage of bees. Canopy cover and flower abundance were significant as explanatory variables for the overall assemblage of bees (Table 2.4). However, overall the RDA ordination with the highest adjusted R^2 value included all variables. Canopy cover was significantly positively correlated with RDA 2 (interset correlation= 0.593), shrub cover was significantly negatively correlated with RDA 1 (interset correlation= -0.525), and flower abundance was significantly positively correlated with RDA 1 (interset correlation= 0.765) (Figure 2.7). The structure of assemblages of bees in harvested CDOM compartments were negatively associated with canopy cover and positively associated with flowering plant species diversity. Furthermore, assemblages of bees in agricultural roadsides were positively associated with flower abundance and were negatively associated with the amount of shrub cover.

However, assemblages of bees within forest compartments did not separate along a gradient of flower adundance.

Canopy cover alone provided the best linear model significantly explaining the total abundance of hoverflies, as well as the best model for Syrphinae (Table 2.3). These models explained 19.6% to 20.9% of the variation in hoverfly abundance in these groups. However, no model including these environmental variables was significant for Eristalinae. Additionally, none of the multivariate RDAs of assemblage constrained by environmental variables were significant for any group of hoverflies (Table 2.4).

Flowering Plant Family

Since flower abundance significantly predicted bee abundance, I explored relationships between the abundance of each plant family and pollinator assemblages. Fabaceae was the most abundant family of wildflowers, accounting for 53.9% of flowers recorded and reflecting the high abundance of *Melilotus officinalis* and *Trifolium* spp. along roadsides. The Cornaceae and Asteraceae accounted for 14.0% and 8.24% of the flowers recorded, respectively, while 16 additional families accounted for the remaining 23.4% of plant records. Asteraceae was the most diverse family encountered at flower patches with 11 species observed in my study. Data about the Asteraceae, Caryophyllaceae, Cornaceae, Fabaceae, Orchidaceae, and Scrophulariaceae were removed from the final analysis due to multicollinearity (i.e., a variance inflation factor greater than 10) with the other included families.

The assemblage of bees was not predicted by the abundance of any flowering plant family (Table A.8). Furthermore, the overall RDA model was not significant and the amount of variation explained by this model was negligible.

The assemblages of Syrphidae and Eristalinae were also not predicted by the abundance of any flowering plant family. However, an RDA constrained by flowering plant familes was significant for

Syrphinae (Table A.8), showing that their abundance was significantly and negatively affected by the abundance of Boraginaceae ($F_{(1,16)}$=2.26, p=0.017), Ericaceae ($F_{(1,16)}$=2.06, p=0.015), and Rubiaceae ($F_{(1,16)}$=1.91, p=0.034). In the ordination, the abundance of Boraginaceae was significantly negatively correlated with RDA 1 (interset correlation= -0.445) and significantly positively correlated with RDA 2 (interset correlation= 0.370), the abundance of Onagraceae was significantly positively correlated with RDA2 (interset correlation= 0.422), the abundance of Pyrolaceae was significantly positively correlated with RDA 1 (interset correlation= 0.374), and the abundance of Rubiaceae was significantly negatively correlated with RDA 2 (interset correlation= -0.405)(Figure 2.8). The ordination demonstrates, specifically, that assemblages of Syrphinae in high retention DDOM compartments were negatively associated with Boraginaceae and Ericaceae and positively associated with Pyrolaceaeare primarily in DDOM compartments while the negative association with Rubiceae is in low retention CDOM compartments. Likewise, the abundance of Onagraceae was positively associated with assemblages of Syrphinae in clearcut and 20% retention CDOM compartments and negatively associated with assemblages along roadsides. Agricultural roadsides were positively associated with Rubiaceae. The amount of variation in abundance explained by an RDA constrained by plant families was 14.3% and negligible for overall hoverfly assemblages and Eristalinae.

Flower Colour

I also grouped flowers by flower colour (Table A.7). Of the total number of flowers recorded, 9018 were white (56.7% of total), 3974 were yellow (25.0% of total), 1567 were pink (9.86% of total), 1184 were purple (7.45% of total), 98 were blue (0.613% of total), and 52 were green (0.327% of total).

An RDA of bee assemblages constrained by flower colour significantly explained 12.5% of variation in local bee assemblages (Table A.9). Overall bee abundance increased with the abundance of white (Apoidea: $F_{(1,23)}$=2.53, p=0.012) and purple flowers (Apoidea: $F_{(1,23)}$=2.79, p=0.008) and decreased with increasing abundance of pink flowers (Apoidea: $F_{(1,23)}$=2.33, p=0.025). The abundance of white flowers was significantly negatively correlated with RDA 1 (interset correlation= -0.457) and significantly positively correlated with RDA 2 (interset correlation= 0.480), the abundance of yellow flowers was significantly negatively correlated with RDA 1 (interset correlation= -0.485) and significantly postiviely correlated with RDA 2 (interset correlation= 0.481), the abundance of pink flowers was significantly positively correlated with RDA 1 (interset correlation= 0.558), and the abundance of blue flowers was significantly negatively correlated with RDA 2 (interset correlation= -0.423)(Figure 2.9a). Assemblages of bees caught along agricultural roadsides were positively associated with the abundance of yellow and white flowers, reflecting the abundance of *Melilotus* spp. and *Trifolium* spp. along agricultural roadsides. On the other hand, assemblages caught along forest roadsides were positively associated with the abundance of purple flowers and negatively associated with the abundance of blue flowers. Additionally, assemblages of bees caught in harvested CDOM compartments were positively associated with the abundance of pink flowers while assemblages caught in CDOM control compartments were positively associated with the abundance of blue flowers.

RDAs constrained by flower colour also significantly explained up to 10.6% of the variation in assemblages of hoverflies (Table A.9). Overall hoverfly abundance and the abundance of both Eristalinae and Syrphinae were positively associated with the abundance of white flowers (Syrphidae: $F_{(1,23)}$=2.13, p=0.006, Eristaliane: $F_{(1,23)}$=2.22, p=0.042, Syrphinae: $F_{(1,23)}$=2.51, p=0.007). The abundance of Syrphinae was also negatively associated with the abundance of blue flowers ($F_{(1,23)}$=2.49, p=0.016). In the ordination for assemblages of Syrphinae, the abundance of white and yellow flowers were significantly positively correlated with RDA 2 (white: interset correlation= 0.710, yellow: interset correlation= 0.447), the abundance of pink flowers was significantly negatively correlated with RDA 2 (interset correlation= -0.601), and the abundance of blue flowers was significantly positively correlated with RDA 1 (interset correlation= 0.488)(Figure 2.9b). Specifically, along agricultural roadsides, assemblages of Syrphinae were positively associated with white and yellow flowers, again reflecting high abundances of *Melilotus* spp. and *Trifolium* spp. recorded at these sites. Assemblages of Syrphinae in CDOM compartments were positively associated with the abundance of blue flowers. The abundance of blue flowers is represented almost entirely by *Mertensia paniculata*. This relationship is clearest for assemblages of Syrphinae in DDOM control compartments where there are few *M. paniculata* and assemblages are negatively correlated with the abundance of blue flowers. Assemblages of Syrphinae caught in low retention CDOM compartments were positively correlated with the abundance of pink flowers.

Indicator Species

Several species of bees were identified as indicator species for harvest treatments and roadsides (Table 2.5). Six indicators were identified using the data from netting, and seven species, including three also identified among those caught by net, were identified from pan trap data. For those caught by net, *A. mellifera*, *Bombus rufocinctus*, and *Bombus ternarius* significantly indicated agricultural roadsides; *B. terricola* was an indicator for all roadsides; *Megachile relativa* indicated harvested CDOM compartments. Furthermore, *Bombus vagans* was an indicator species for the combination of harvested CDOM stands (clearcut and retention levels of 20%, 50%), unharvested DDOM stands, and roadsides. For pan trap data, *Andrena algida*, *Andrena frigida*, and *B. rufocinctus* indicated agricultural roadsides, while *Megachile gemula* and *B. terricola* indicated forest roadsides. Two species indicated combinations of habitats. *Hoplitis albifrons* indicated both clearcut CDOM compartments and forest roads; and *M. relativa* indicated the combination of harvested CDOM compartments (clearcut, 20%, and 50% CDOM compartments) and forest roadsides.

Three species of hoverflies were identified as indicators of harvest treatments and roadsides using data from net capture (Table 2.5). *Melangyna umbellatarum* indicated forest roads. *Epistrophe* *grossulariae* indicated the wide-ranging combination of clearcut and 20% retention CDOM compartments, 20% and 50% DDOM compartments, and forest roadsides. Finally, *Syrphus ribesii* indicated the combination of clearcut and 20% CDOM stands, 20%, 50%, and control DDOM stands, and forest roadsides. No significant indicator species were identified among hoverflies caught by pan trap.

Several flowering plant species were also identified as indicators of harvest treatments and roadsides (Table A.10).

Discussion

Comparison of Pollinators along Roadsides and in Forested Areas

The impact of building roads to facilitate harvest of forested areas has been often overlooked in studies about the effects of harvesting on pollinator assemblages. Bees and hoverflies were more abundant along forest roadsides in my study than in either unharvested controls or post-harvest compartments 14 years after experimentally prescribed logging. As found in this work, previous studies have also shown that bees were more abundant along roadsides than in nearby interior forest areas (Fye 1972, Jackson et al. 2014), including previously harvested forests (Fye 1972). Pollinator abundance apparently remains high for several years after roads are built (Fye 1972, Jackson et al. 2014), but falls as roads become unused (Fye 1972) and the surrounding harvested forest matures (Jackson et al. 2014). Pollinator abundance likely increases because reduced canopy cover allows more light penetration and, thus, development of increased floral resources (Fye 1972, Jackson et al. 2014). However, some groups of pollinators were more abundant in forest compartments at EMEND (Megachilidae, *Xylota* spp., *Temnostoma* spp., *Syrphus* spp.) (Table A.11) and some species were caught exclusively in forested areas. Additionally, while building roads can increase pollinator assemblages, which is likely a positive effect, we observed several invasive plant species (e.g. *Melilotus* spp.) along roadsides and the recovery of understory plant communities can be slow (e.g. >80 years following logging) (Duffy and Meier 1992, Wyatt and Silman 2010).

Pollinators were more abundant along forested than agricultural roadsides, a finding that demonstrates the importance of forested areas for pollinator populations and assemblages. In general, as agriculture intensity increases on landscapes, bee abundance (Williams et al. 2010) and diversity (Hendrickx et al. 2007) declines, despite the critical need of pollination for agricultural production. However, increasing the amount of forest cover or decreasing the distance to forest cover in agricultural areas may increase pollinator abundance (Bergman et al. 2004, Morandin and Winston 2006, Öckinger and Smith 2007) and species richness (Bergman 2004, Ricketts 2004, Kim et al. 2006, Hendrickx et al. 2007, Öckinger and Smith 2007). Thus, maintaining some forested areas locally leads to increased pollination services for agricultural crops (Kremen et al. 2004, Ricketts 2004, Greenleaf and Kremen 2006, Morandin and Winston 2006) and seems to increase honey yield (Sande et al. 2009). Increasing forested area may increase the number of native bee species in an agricultural area, and this in turn can provide many additional benefits. Native bees provide insurance against declining numbers of honey bee colonies (Greenleaf and Kremen 2006, Winfree et al. 2007b), are more efficient pollinators than honey bees in many cases (Winfree et al. 2007b, Abrohl 2011), and their presence can increase the pollination efficiency of honey bees by altering their behaviour (Brittain et al. 2013).

Effects of Harvest and Cover Type

There has been little work on the bees of the boreal forest in northern Alberta, and previous studies at EMEND have been limited to the distribution of bumble bees (*Bombus* spp.) within deciduous dominated compartments (DDOM and DDOMU) based on data from net capture only (Cartar 2005, Pengelly and Cartar 2010, Table A.12). Thus, it is not surprising that the present study doubled the number of *Bombus* species recorded at EMEND from 7 to 14 species, while also adding at least 41 additional bee species to the geo-referenced faunal list. We netted only 3 species of *Bombus* in DDOM compartments, one of which was previously unreported, but use of pan traps in DDOM compartments added an additional 3 species to those caught by net, including another unreported species. An additional 2 species were caught in CDOM compartments. These findings underscore the importance of using multiple sampling methods to characterize faunal communities and of the mixedwood landscape for supporting bee diversity. The most significant increase in *Bombus* species came from the inclusion of roadsides in the sampling program. All *Bombus* species were caught along roadsides, including 5 previously unreported species. Interestingly, *B. sylvicola* was not caught in this study though it was recorded in both previous studies. *B. sylvicola* inhabits open grassy areas (Williams et al. 2014) and the aspen regrowth may have eliminated suitable habitat. Since bumble bees were identified without being captured in those studies, however, confirmation of species identity is not possible and several similar species of *Bombus* (e.g., *B. melanopygus* or *B. rufocinctus*) also exist in the area.

While none of the differences between harvest treatments were statistically significant, they suggest insight about post-harvest changes in bee distributions. Immediately following harvest, foraging bumble bees were most abundant in control stands but by the end of that summer, they were most abundant in 50-75% retention compartments (Cartar 2005). Eight to nine years after harvest, foraging bumble bees were most abundant in compartments that had been clearcut (Pengelly and Cartar 2010). Thus, bee activity appeared to increase in recently harvested areas (Fye 1972, Nol et al. 2006, Nielsen and Totland 2007, Romey et al. 2007). In the present study, conducted fourteen years after harvest, bumble bees caught by net were most abundant in 20% retention compartments of both cover types (Figure B.1), suggesting a decline in abundance in the years following clear-cutting as observed by other authors (Makino et al. 2006, Nol et al. 2006). This pattern is further supported by higher net capture rates for all bees in 50% retention compartments compared to clearcut compartments in my study (Figure 2.4a).

The rate of changes in bee abundance after harvest appears to differ between the two original cover types. While abundance was highest in 50% retention compartments in DDOM compartments, bee abundance in CDOM compartments was highest in 20% retention for net capture and clearcuts for pan traps. This difference is associated with a slower regeneration rate of canopy in CDOM than in DDOM stands evidenced by the fact that canopy cover was consistently higher in DDOM compartments than CDOM compartments (Figure B.2a). An open canopy allows more light to reach the forest floor and promotes higher flower abundance (Kumar et al. 2017). Given these differences and the significant effect of forest cover type on bee abundance, forest cover likely affects pollinator assemblages more than the exact amount of harvest retention.

No increase in the number of *Bombus* species was observed in DDOM compartments compared to previous bee studies at EMEND (Cartar 2005, Pengelly and Cartar 2010). Although Schleuning et al. (2011) and Proctor et al. (2012) observe similar stability, species richness of bees increased following harvest in several other studies (Fye 1972, Nol et al. 2006, Nielsen and Totland 2007, Romey et al. 2007, Pengelly and Cartar 2010). However, data about bee diversity were not recorded for other genera before or immediately following harvesting and it is therefore not possible to examine trends in overall bee species diversity over the same period.

Hoverflies have not been studied previously at EMEND, so we may draw no direct inferences about how populations have changed over time in response to variation in harvest prescriptions. Although not statistically significant, more hoverflies were caught in harvested compartments than in control compartments, suggesting that harvest leads to local increases in at least some populations, as observed elsewhere in the boreal forest (Deans et al. 2007, Nielsen and Totland 2007) and other forest biomes (Sueyoshi et al. 2003, Nol et al. 2006). However, the weak trend observed for hoverfly abundance to increase with harvest retention level, with the exception of Syrphinae caught by net in CDOM compartments, supports previous findings that hoverflies are more abundant in harvested areas with high retention than in clearcut forest (Deans et al. 2007). Thus, compartments harvested with high levels of retention may offer more suitable habitat for hoverflies than sites harvested to lower levels of retention.

In contrast to the findings of Nol et al. (2006) for temperate deciduous forests, harvests at EMEND seem to have affected the two main subfamilies of hoverflies differently. The Eristalinae, including *Xylota* spp. and *Temnostoma* spp., were most abundant in compartments harvested to 50% retention, while the Syrphinae, including *Syrphus* spp., were most abundant in more intensively harvested compartments (i.e., clearcuts and 20% retention). This likely reflects differences in larval feeding strategies: larvae of Eristalinae are saprophagous and phytophagous while larvae of Syrphinae are predaceous (Vockeroth and Thompson 1987, Sommaggio 1999). Boreal saprophagous species are most abundant and diverse at intermediate and high levels of retention while predaceous species are most abundant and diverse in clearcut stands with vigorous young growth supporting homopteran populations (Deans et al. 2007, Nielsen and Totland 2007). High retention compartments likely provide more decaying material for saprophagous larvae. On the other hand, the high shrub cover found in low retention compartments (Figure B.2) may provide a food source for homopterans and, in turn, support higher numbers of predaceous syrphid larvae (Nol et al. 2006, Nielsen and Totland 2007).

Pollinator Response to Environmental Variables

Among the environmental variables that I studied, a negative relationship with amount of canopy cover was most important for explaining variation in pollinator abundance among compartments. This relationship was included in all linear models and was significant in explaining variation in overall abundance of bees, overall abundance of hoverflies, and the abundance of Syrphinae. This is consistent with observations that local abundance and diversity of both bees (Winfree et al. 2007a) and hoverflies

(Kula 1997) decreases as forest land cover increases, although Taki et al. (2007) found the opposite when sampling was done before leaf-out. The difference in canopy cover was larger between forest cover types than within each forest cover type (Figure B.2). Generally, flower abundance increases with decreasing canopy cover (Kumar et al. 2017). Although this trend is not observed within each forest cover type, CDOM compartments had lower canopy cover and higher flower abundance than DDOM compartments. Sites with high levels of canopy cover (and hence fewer flowers) should attract few pollinators and these results reinforce the conclusion that forest cover type more strongly affects pollinator abundance than does amount of harvest retention. In addition to affecting flower abundance, canopy cover may also influence site micro-climate (e.g., temperature, humidity) as well as the ability of pollinators to find floral resources (Kreyer et al. 2004) which may affect the distribution of pollinators.

Amount of shrub cover was negatively related to abundance of bees, but as for canopy cover this seems to reflect mainly cover type effects. Shrub cover was inversely related to flower abundance across all forest cover types (including roadsides). This relationship is not seen within each cover type. Shrub stems may provide nesting sites for many groups of cavity nesting bees such as species of Megachilidae and *Hylaeus* (Michener 2010, Sheffield et al. 2014). However, many species are capable of foraging over distances larger than the 10ha compartment size (St. Amand et al. 2000, Gathmann and Tscharntke 2002, Zurbuchen et al. 2010) and foraging preferences may be poorly correlated to nesting sites. A negative relationship with shrub cover was also significant in explaining variation in overall abundance for hoverflies and the Syrphinae. While shrub cover may support homopteran populations used by larvae of Syrphinae, my data reflects only foraging preferences of adult hoverflies.

Although flower abundance had a significant positive relationship with abundance of bees and was significant in the multivariate RDA model, it was not significant in the linear model. Additionally, flower abundance was not significant in explaining the abundance of any group of hoverflies, corroborating the results of previous work (Hegland and Boeke 2006, Nielsen and Totland 2007). It is possible that habitat characteristics associated with the life history of larval syrphids are more important than floral resources for adults in determining the distribution of syrphids (Hegland and Boeke 2006). Nonetheless, the generally low correlation observed at EMEND between flower and pollinator abundance is surprising given the close relationship between other pollinators and flowering plants (Cartar 2005, Hegland and Boeke 2006, Nielsen and Totland 2007, Pengelly and Cartar 2010, Roulston and Goodell 2010), and the suggestion that increased flower abundance is the reason for increased pollinator abundance in recently logged sites (Makino et al. 2006, Nol et al. 2006).

The diversity of flowering plants had no significant relationship with any pollinator group and explained very little variance in abundance, consistent with findings of Hegland and Boeke (2006). Because some pollinators that are specialist or oligolectic foragers are associated exclusively with specific plant species or genera, high local diversity of flowering plants may accommodate the needs of many pollinator species simultaneously (Hegland and Boeke 2006). However, most species of bees and hoverflies are generalists (Heinrich 1979, Waser et al. 1996, Larson et al. 2001, Michener 2007), and all but 5 species of bees present in this study are generalist foragers (Sheffield et al. 2014) for which obtaining a high value nectar reward efficiently is most important (Heinrich 1979, Hegland and Boeke 2006). Likewise, the low correlation between pollinator abundance and the abundance of particular plant families likely reflects the generalist nature of the species found at EMEND.

Preference for a specific flower colour is likely explained by a high abundance from particular species at flower patches where bees were sampled rather than a genuine preference to forage on that colour. Four of the five most abundant species of plant that were flowering were white which may explain why the abundance of white flowers was significant for so many pollinator groups. On the other hand, green flowers were much less abundant and had no significant effect on pollinator abundance.

Indicator Species, Bumble Bee Declines, and B. terricola

While several pollinator species were identified as significant indicators, none exclusively indicated unharvested forest, perhaps reflecting in part the large foraging ranges of many pollinator species. Conversely, however, many species were identified as indicators of disturbed forest and roadsides. The honeybee, *A. mellifera*, which is a managed agricultural species, specifically indicated agricultural roadsides and *B. terricola*, a species of conservation concern, was an indicator for both agricultural and forest roadsides. No hoverfly species indicated agricultural roadsides, emphasizing their preferences for forested areas in this study.

Although bumble bees (*Bombus* spp.) were the most abundant and diverse group of pollinators sampled in this study, worrisome declines have been observed for bumble bees in recent years (Colla and Packer 2008, Evans et al. 2008, Goulson et al. 2008, Grixti et al. 2009, Williams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Colla et al. 2012, Szabo et al. 2012), particularly those in the subgenus *Bombus* sensu stricto (Colla and Packer 2008, Evans et al. 2008, Williams and Osborne 2009, Cameron et al. 2011). These declines have been attributed to pathogen spillover from managed bumble bees in greenhouses, pesticides, habitat loss, introduced species, and climate change (Evans et al. 2008, Goulson et al. 2008, Otterstatter and Thomson 2008, Williams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Szabo et al. 2012, COSEWIC 2015). One species in this subgenus, *B. terricola*, was the sixth most abundant bee species in this study and the fourth most abundant species of *Bombus*. Significant declines have been reported for *B. terricola*, especially in eastern North America (Colla and Packer 2008, Evans et al. 2008, Goulson et al. 2008, Wiiliams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Colla et al. 2012, Szabo et al. 2012, COSEWIC 2015). However, similar declines have not been observed in Alberta (COSEWIC 2015). *B. terricola* was positively affected by disturbance in the study (Figure B.1) and was an indicator of roadsides. Comparisons between the habitats in which *B.*

terricola is found in Alberta and regions experiencing rapid declines may offer insight into factors contributing to population declines.

Future Considerations and Implications for Management

The strength of my analysis was somewhat limited by low sample sizes, given time and manpower available for this work, and I am left with many questions unanswered. Additionally, temperature and humidity might be recorded at sites in future work to provide information about how bees and hoverflies select microclimates within compartments for foraging. Evaluating pollinators in larger stands would test the generality of my results under more realistic harvesting scenarios. In future studies, comparisons of harvested and burned sites of similar age would allow us to explore how recovery differs between the two forms of disturbance in the boreal forest, and provide insights into how to best emulate fire effects on pollinators through harvesting.

Road management will likely affect pollinator assemblages in forested areas. Mowing and spraying ditches along roads leads to an abundance of flowering plants as a food source to pollinators and the resulting increases in abundance of pollinators can provide pollination services to nearby forested and agricultural areas. However, this may come at the cost of increasing the abundance and facilitating the spread of invasive species.

Undisturbed forests have fewer bee species than other regions, with bees preferring habitat with fewer trees (Michener 2007). Logging causes a local increase in abundance of pollinators which benefits the increased flower and shrub cover in these areas. However, some groups, Eristaline hoverflies in particular, decrease in abundance with increasing harvest intensity. Variable retention harvesting can be applied as a tool to minimize negative effects of harvesting on pollinators. Most groups of pollinators were more abundant in compartments with some retention compared to clearcutting. Clearcutting in DDOM forests results in lower bee and hoverfly abundances 14 years post-harvest than undisturbed forest. This can be mitigated by leaving 20-50% retention in this cover type. Harvesting in CDOM forests further reduce negative impacts on pollinators as increases in abundance are sustained over a longer time period and generally remain high relative to undisturbed forest. Nonetheless, some regions with high retention (50-75%) are required in both forest cover types to maintain habitat for Eristaline hoverflies. Forest management plans that include both high and low retention blocks would produce a heterogeneous landscape with available habitat for all pollinator groups.

Tables

Table 2.1: Comparison of the abundance of bees and hoverflies caught between net capture and pan traps summed across all sample sites (harvest treatments, controls, and roadsides). Significant differences in abundance between net capture and pan traps were tested using a Wilcoxon signed rank test. Results are considered significant below a p-value of 0.05.

	Net Capture Abundance	Pan Trap Abundance	V value	P value
Apoidea	**252**	**521**	**73**	**0.003**
Syrphidae	197	172	232.5	0.508
Eristalinae	72	107	117.5	0.359
Syrphinae	124	64	272.5	0.113

Table 2.2: Comparison of the abundance of bees and hoverflies caught between forest and agricultural roadsides using two-sample t-tests and between forest roadsides and forest compartments using Mann-Whitney tests. I used mean abundance/sampling period/site for net capture data and mean abundance/day/site for pan trap data with total raw abundance included in parentheses. Results were considered significant below a p-value of 0.05. [a] Data did not meet assumption of normality, value represents U value from a Mann-Whitney test.

	Forest Road vs. Agricultural Road (Net)				Forest Road vs. Agricultural Road (Pan)			
	Forest Road	Ag. Road	t value	P value	Forest Road	Ag. Road	t value	P value
Apoidea	6.44 (59)	9.75 (95)	1.58	0.188	3.44 (217)	2.24 (127)	-1.38	0.239
Syrphidae	6.86 (61)	1.28 (13)	0[a]	0.100	0.492 (31)	0.0317 (2)	1[a]	0.184
Eristalinae	0.972 (9)	0.667 (6)	-0.405	0.706	0.413 (26)	0 (0)	1.5[a]	0.197
Syrphinae	5.89 (52)	3.2 (7)	0[a]	0.100	0.0794 (5)	0.0317 (2)	3	0.643
	Forest Road vs. Forest (Net)				Forest Road vs. Forest (Pan)			
	Forest Road	Forest	U value	P value	Forest Road	Forest	U value	P value
Apoidea	**6.44 (59)**	**1.33 (98)**	**0**	**0.005**	**3.44 (217)**	**0.260 (175)**	**0**	**0.006**
Syrphidae	**6.86 (61)**	**1.68 (123)**	**6**	**0.022**	0.492 (31)	0.207 (139)	22.5	0.315
Eristalinae	0.972 (9)	0.785 (57)	23.5	0.351	0.413 (26)	0.120 (81)	19.5	0.205
Syrphinae	**5.89 (52)**	**0.899 (66)**	**1**	**0.007**	0.0794 (5)	0.0865 (58)	37.5	0.938

Table 2.3: Linear models of the effect of environmental variables on standardized pollinator abundance showing only the models resulting in the lowest AIC. Environmental variables with no T or p-values are not included. Roadsides were not included in the model due to missing canopy cover values. Results with a p-value less than 0.05 are shown in bold.

	Intercept		Canopy Cover		Shrub Cover		Flower Abundance		Flower Diversity		Overall Model		
	T value	P value	T value	P value	T value	P value	T value	P value	T value	P value	F value	P value	Adj. R^2
Apoidea	**7.70**	**≤0.001**	**-5.31**	**≤0.001**	**-3.06**	**0.006**	-1.40	0.178			**17.3**	**≤0.001**	**0.680**
Syrphidae	**4.26**	**≤0.001**	**-2.66**	**0.014**							**7.08**	**0.014**	**0.209**
Eristalinae	**2.70**	**0.013**	-0.94	0.358	-1.25	0.227					1.79	0.191	0.0642
Syrphinae	**3.92**	**≤0.001**	**-2.57**	**0.017**							**6.62**	**0.017**	**0.196**

Table 2.4: Redundancy analysis showing the effect of percent canopy cover (C), percent shrub cover (S), mean flower abundance per patch (FA), and the number of species flowering recorded in the compartment (FD) on assemblages (A) of bees and hoverflies caught by net. Canopy cover was not recorded at roadsides so a conservative value of 50% was used to ensure that roadsides were included in the models. Variables with a variance inflation factor over 10 were removed prior to analysis and the best model was selected using adjusted R^2 values with the function ordiR2step. Results with a p-value less than 0.05 are shown in bold. Eigenvalues are included for the first two axes (RDA 1 and 2) and the corresponding proportion of variation explained by each axis. Interset correlations are also provided for RDA 1 and RDA 2 of each factor with values above the critical value for Pearson's r for d.f.= 28 (0.361) shown in bold.

	Model		Eigenvalues		Canopy Cover				Shrub Cover			
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2
Apoidea	**1.68**	**0.024**	0.0492 (43.5%)	0.0402 (35.6%)	**2.40**	**0.023**	-0.277	**0.593**	1.52	0.138	**-0.525**	0.268
Syrphidae	0.976	0.530	0.0475 (48.5%)	0.0234 (23.8%)	0.893	0.577	-0.249	**-0.457**	1.50	0.105	**-0.714**	-0.288
Eristalinae	1.03	0.414	0.0496 (60.6%)	0.0185 (22.6%)	1.05	0.361	-0.214	**-0.369**	1.89	0.080	**-0.517**	-0.162
Syrphinae	1.03	0.430	0.0443 (48.9%)	0.0222 (24.4%)	0.921	0.508	-0.0520	**-0.559**	1.58	0.113	**0.451**	**-0.532**

	Flower Abundance				Flower Diversity				R^2 Model
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	Adj. R^2
Apoidea	**1.91**	**0.050**	**0.765**	-0.113	0.893	0.518	-0.154	-0.223	0.0858
Syrphidae	0.938	0.505	**0.787**	0.002	0.577	0.911	-0.0332	-0.214	-0.00327
Eristalinae	0.936	0.470	**0.532**	-0.0419	0.232	0.989	-0.122	0.00358	0.00366
Syrphinae	1.07	0.377	**-0.587**	0.293	0.530	0.898	-0.0985	-0.213	0.00344

Table 2.5: Indicator species analysis for pollinators caught by net capture and pan trap showing the specificity and the fidelity of the species to the given group. Only species with a p-value less than 0.05 are included in the table. No significant indicator species were identified for hoverflies caught by pan trap.

Bees- Net Capture					
Group	**Species**	**Specificity**	**Fidelity**	**Sqrt(IndVal)**	**P Value**
Agricultural Roads	*Apis mellifera*	1.00	1.00	1.00	0.006
	Bombus rufocinctus	1.00	1.00	1.00	0.006
	Bombus ternarius	1.00	1.00	1.00	0.006
Roadsides	*Bombus terricola*	0.896	0.833	0.864	0.010
CDOM Clearcut, 20%, and 50%	*Megachile relativa*	0.868	0.778	0.821	0.012
CDOM Clearcut, 20% and 50%, DDOM Control, and Roadsides	*Bombus vagans*	0.980	0.889	0.933	0.004
Bees- Pan Trap					
Group	**Species**	**Specificity**	**Fidelity**	**Sqrt(IndVal)**	**P Value**
Agricultural Roads	*Andrena frigida*	1.00	1.00	1.00	0.005
	Bombus rufocinctus	0.966	1.00	0.983	0.005
	Andrena algida	0.907	1.00	0.952	0.005
Forest Roads	*Megachile gemula*	1.00	1.00	1.00	0.004
	Bombus terricola	0.887	1.00	0.942	0.004
CDOM Clearcut and Forest Roads	*Hoplitis albifrons*	1.00	0.833	0.913	0.003
CDOM Clearcut, 20%, 50% and Forest Roads	*Megachile relativa*	0.912	0.750	0.827	0.039
Hoverflies- Net Capture					
Group	**Species**	**Specificity**	**Fidelity**	**Sqrt(IndVal)**	**P Value**
Forest Roads	*Melangyna umbellatarum*	0.890	1.00	0.944	0.009
CDOM Clearcut and 20%, DDOM 20% and 50%, and Forest Road	*Epistrophe grossulariae*	0.954	0.733	0.836	0.030
CDOM Clearcut and 20%, DDOM 20%, 50% and Control, and Forest Roads	*Syrphus ribesii*	0.977	0.778	0.872	0.019

Figures

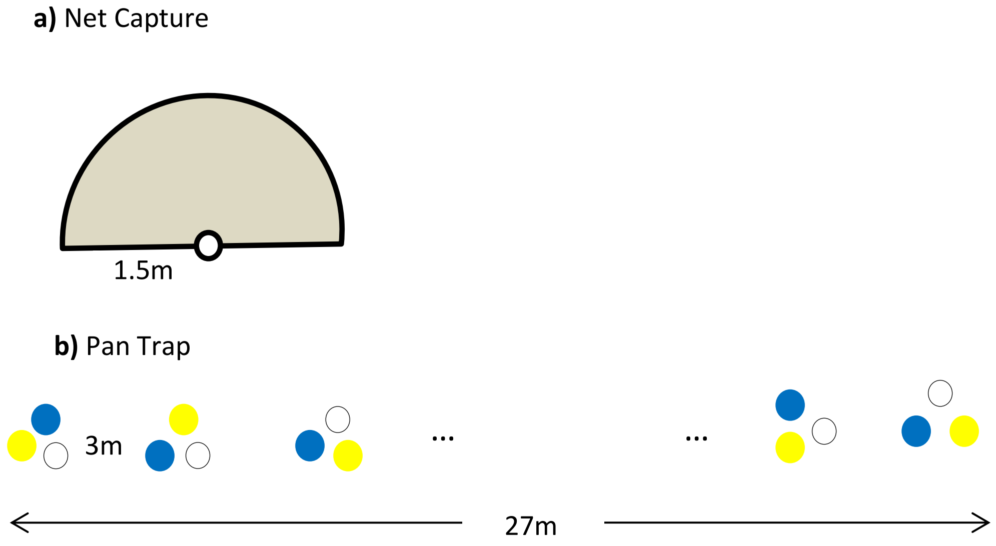

Figure 2.1: Diagram of a) flower patch during net capture with a field technician standing at the centre of a half circle of radius 1.5m and b) set-up of 30 pan traps (4oz painted cups) at 3m intervals for a total length of 27m. Flower patches were identified as aggregations of plants in flower, regardless of the number of species or flower abundance and the radius corresponded to the length of the handle of the net. Pan traps were set out in lines running directly east adjacent to EMEND PSPs.

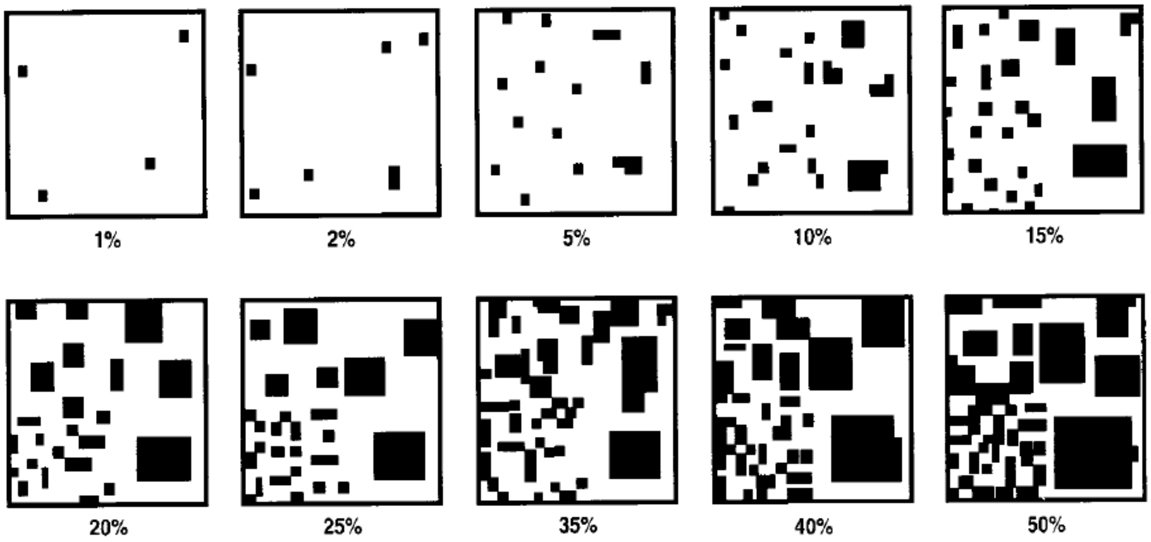

Figure 2.2: Shrub cover estimation guide taken from Beckingham and Archibald 1996 (Fig 16.1.1). Reproduced with the permission of Natural Resources Canada, Canadian Forest Service, 2019.

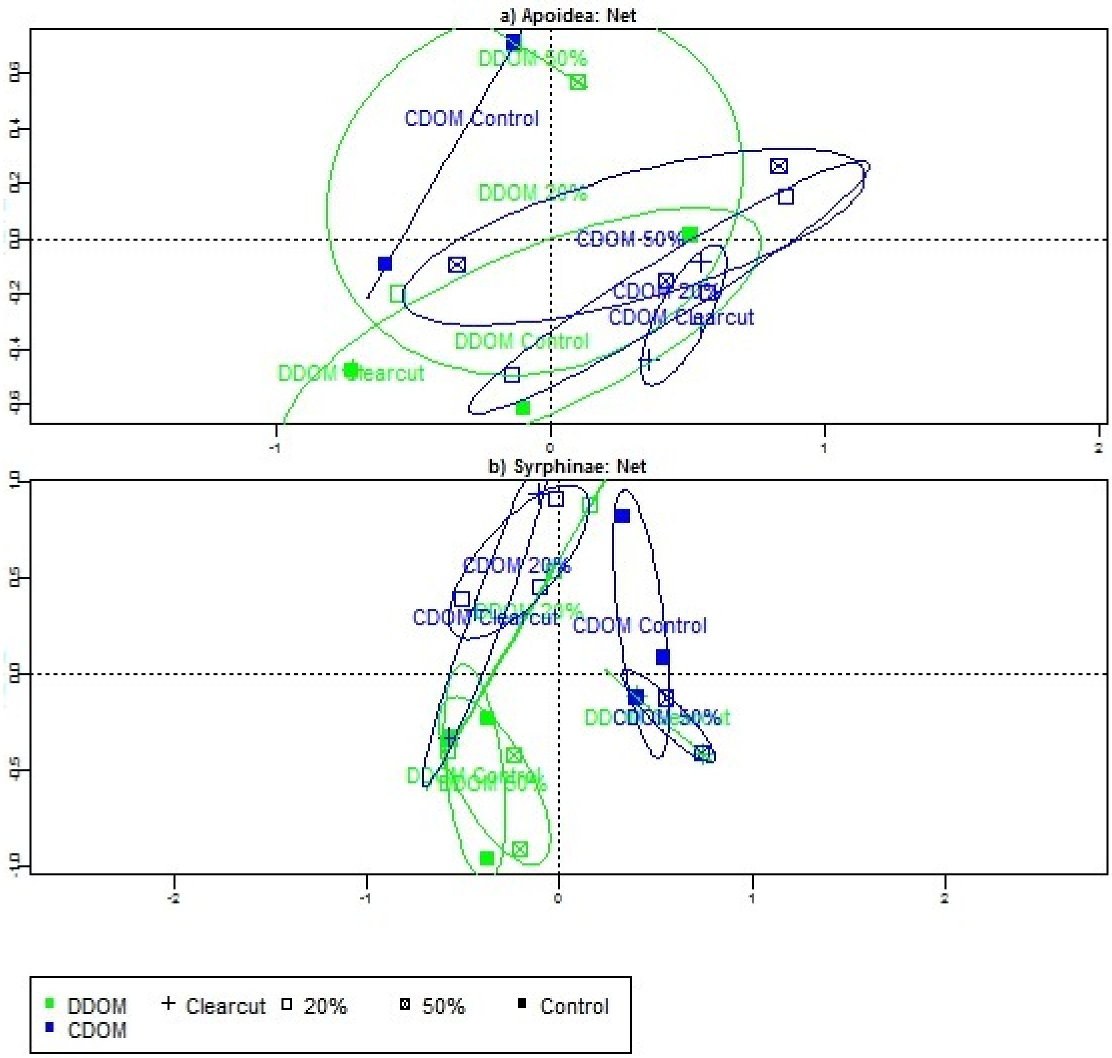

Figure 2.3: Ordination of a constrained redundancy analysis (RDA) of the composition of (a) all bees ($F_{(7,16)}$=1.67, p=0.033, R^2=0.170), and (b) Syrphinae ($F_{(7,16)}$=1.77, p=0.006, R^2=0.191) caught by net constrained by harvest treatment and forest cover type. Ellipses show 0.95 conifidence limits around harvesting treatment groups using standard errors. A Hellinger transformation was applied to pollinator abundance prior to analysis. Only ordinations with a significant overall model (p≤0.05) are shown (Table A.3).

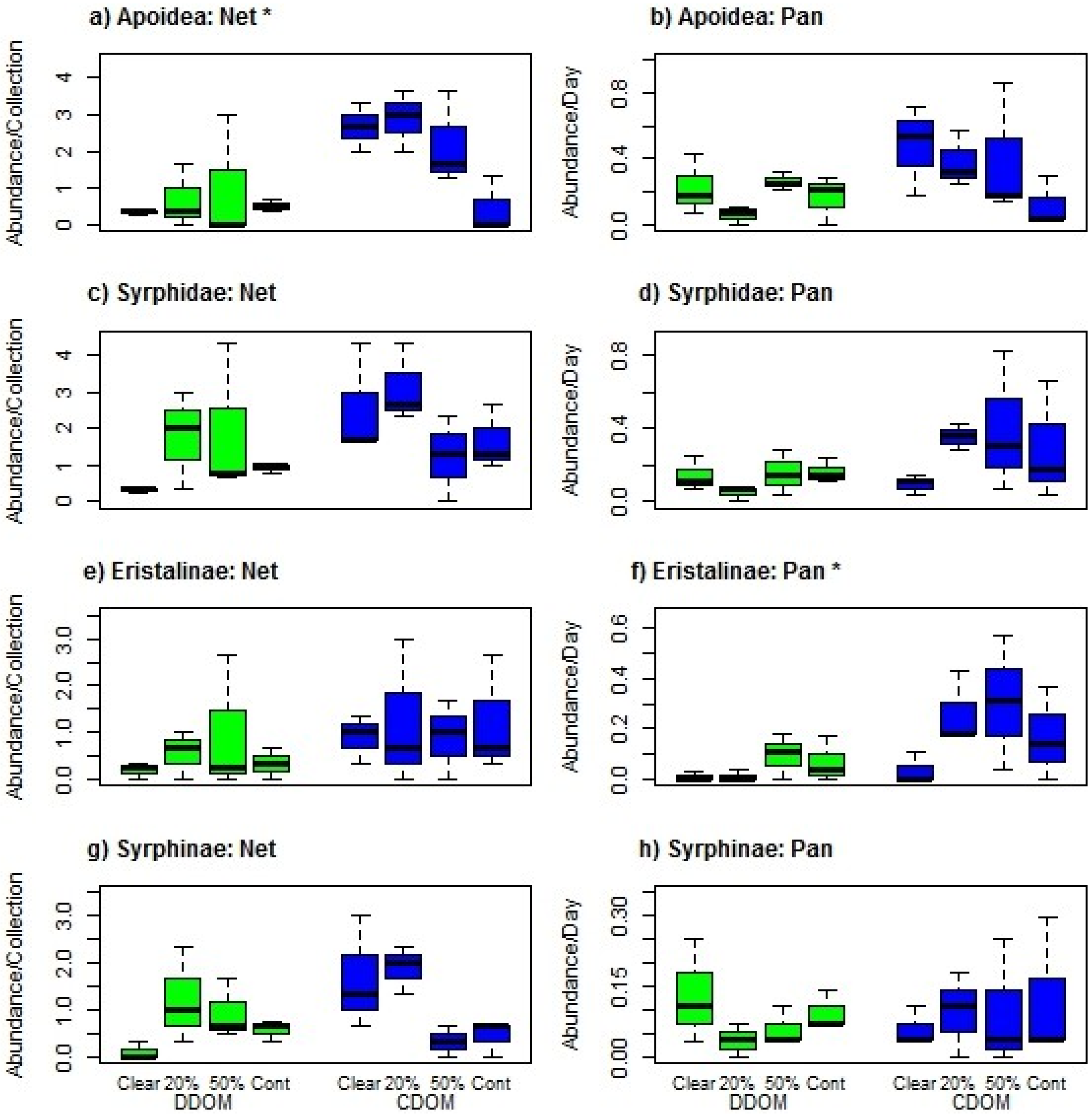

Figure 2.4: Boxplot of abundance of all bees (a-b), all hoverflies (c-d), Eristalinae (e-f), and Syrphinae (g-h) caught by net (abundance/collection) and by pan trap (abundance/day) in each harvest treatment. The central horizontal line is the median, the upper and lower edge of the boxes represent 1st and 3rd quartiles, respectively, and the whiskers represent data extremes. Significant differences in cover type ($p \leq 0.05$) are denoted by *****. (Clear= clearcut, 20%= 20% retention, 50%= 50% retention, Cont= control, DDOM= deciduous-dominated, CDOM= coniferous-dominated)

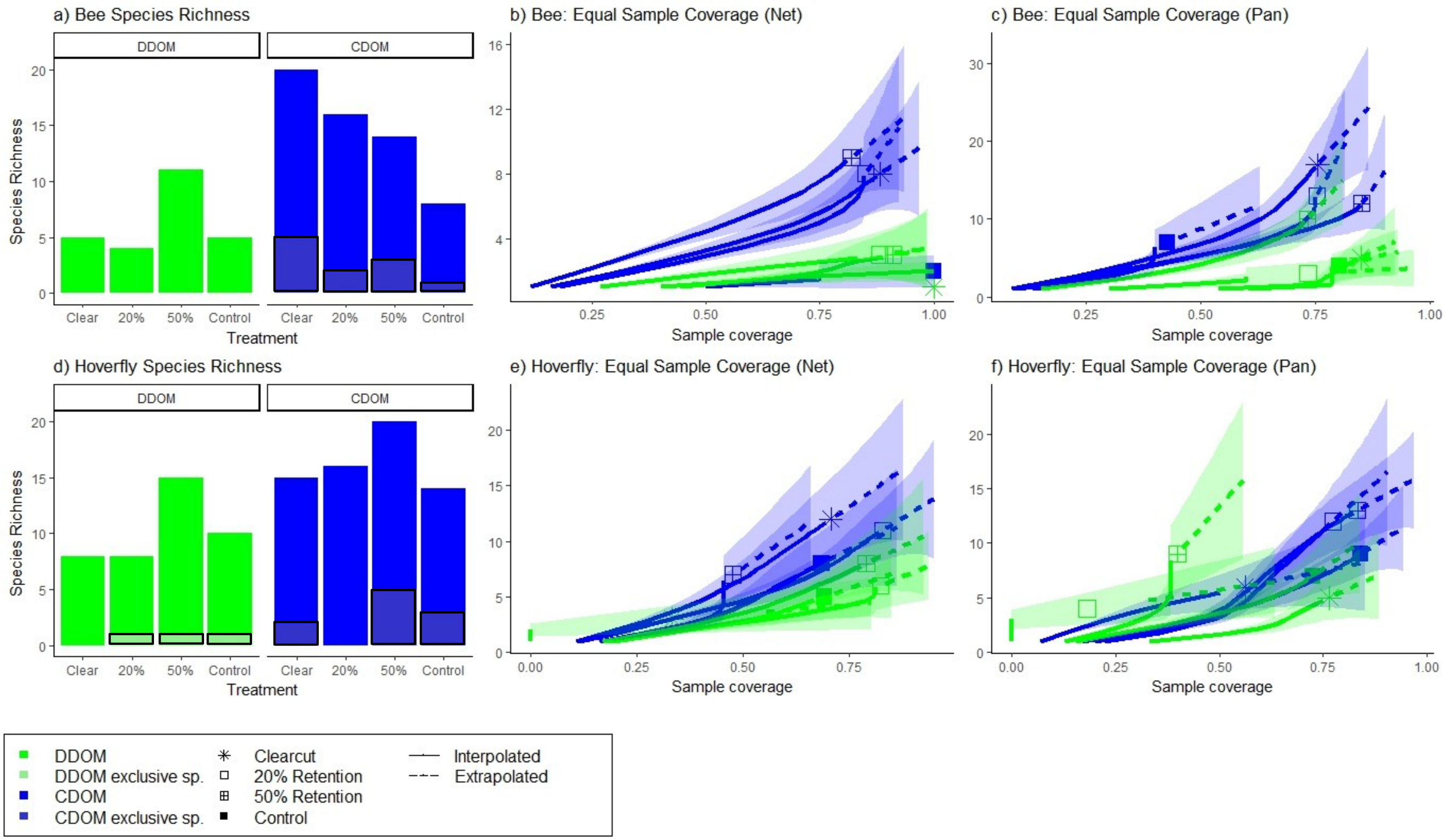

Figure 2.5: Species diversity of bees and hoverflies in each treatment represented by both raw species richness using the combined number of species observed by net capture and pan traps and including the number of species exclusive to each treatment (a,d) and coverage-based rarefaction curves of species richness (q=0) for pollinators caught by net capture (b,e) and pan traps (c,f) with 95% confidence intervals.

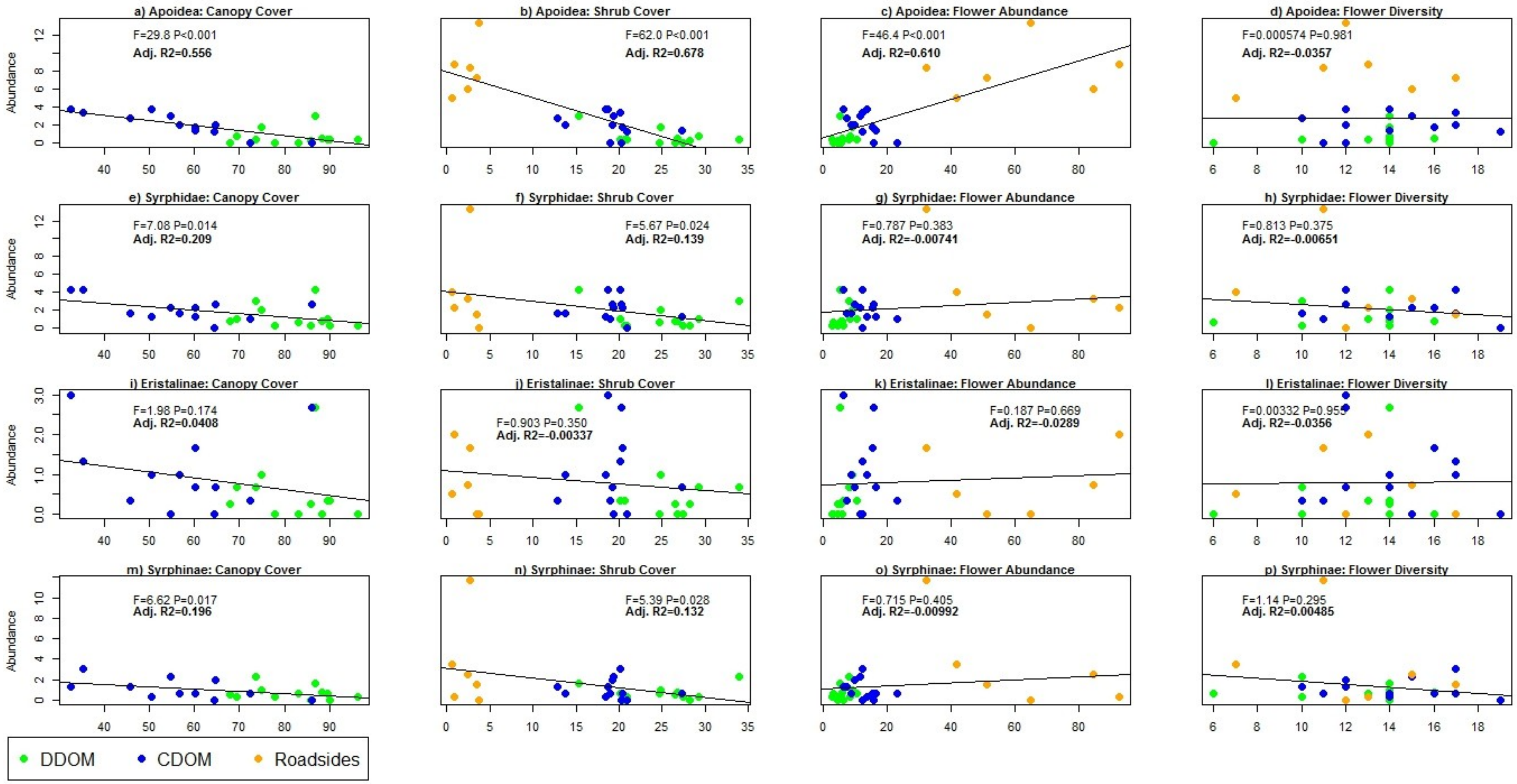

Figure 2.6: Linear regressions of the effect of mean percent canopy cover per flower patch (a, e, i), mean percent shrub cover per patch (b, f, j), mean flower abundance per patch (c, g, k), and flowering plant species diversity per compartment (d, h, l) for the sum of total abundance for Apoidea (a-d), Asyrphidae (e-g),Eristalinae (i-l) , and Syrphinae (m-p) using net capture data. Roadsides were not included in the regressions for canopy cover as it was not recorded. The equations of the trend lines are a) y=5.222-0.056x, b) y=7.897-0.288x, c) y=0.567+0.107x, d) y=2.753-0.005x, e) y=4.276-0.037x, f) y=4.517-0.110x, g) y=1.817+0.017x, h) y=4.083-0.145x, i) y=1.801-0.015x, j) y=1.091-0.017x, k) y=0.733+0.003x, l) y=0.748+0.003x, m) y=2.475-0.023x, n) y=3.065-0.094x, o) y=1.085+0.014x, p) y=3.334-0.149x

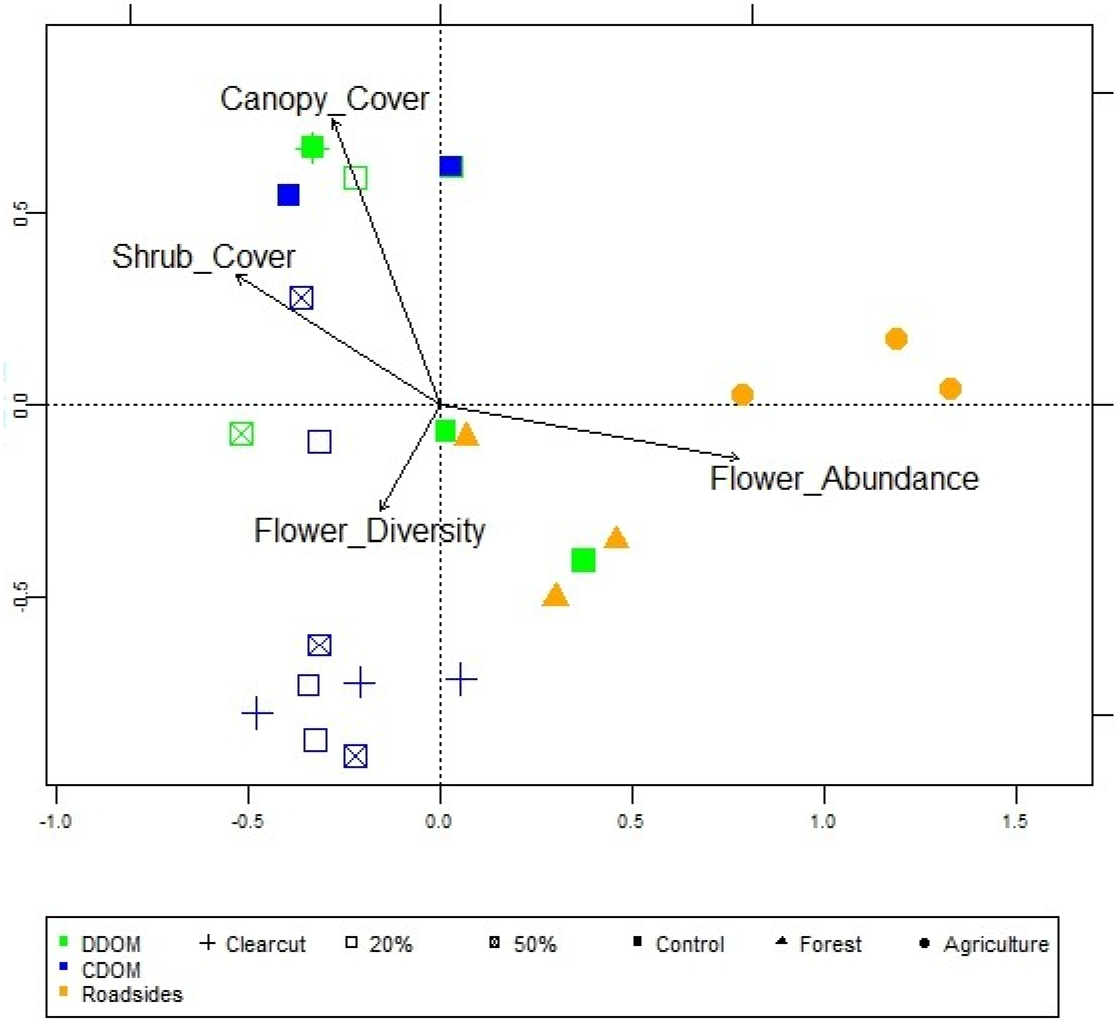

Figure 2.7: Ordination of a constrained redundancy analysis (RDA) of the composition of all bees (Apoidea) ($F_{(4,25)}$=1.68, p=0.024, R^2=0.0858) constrained by the mean percent canopy cover per flower patch, mean percent shrub cover per flower patch, mean flower abundance per flower patch, and number of species flowering per compartment. Canopy cover was not recorded at roadsides so a value of 50% was used in the analysis. A Hellinger transformation was applied to bee abundance prior to analysis. Only ordinations with a significant model (p≤0.05) are shown (Table 2.4).

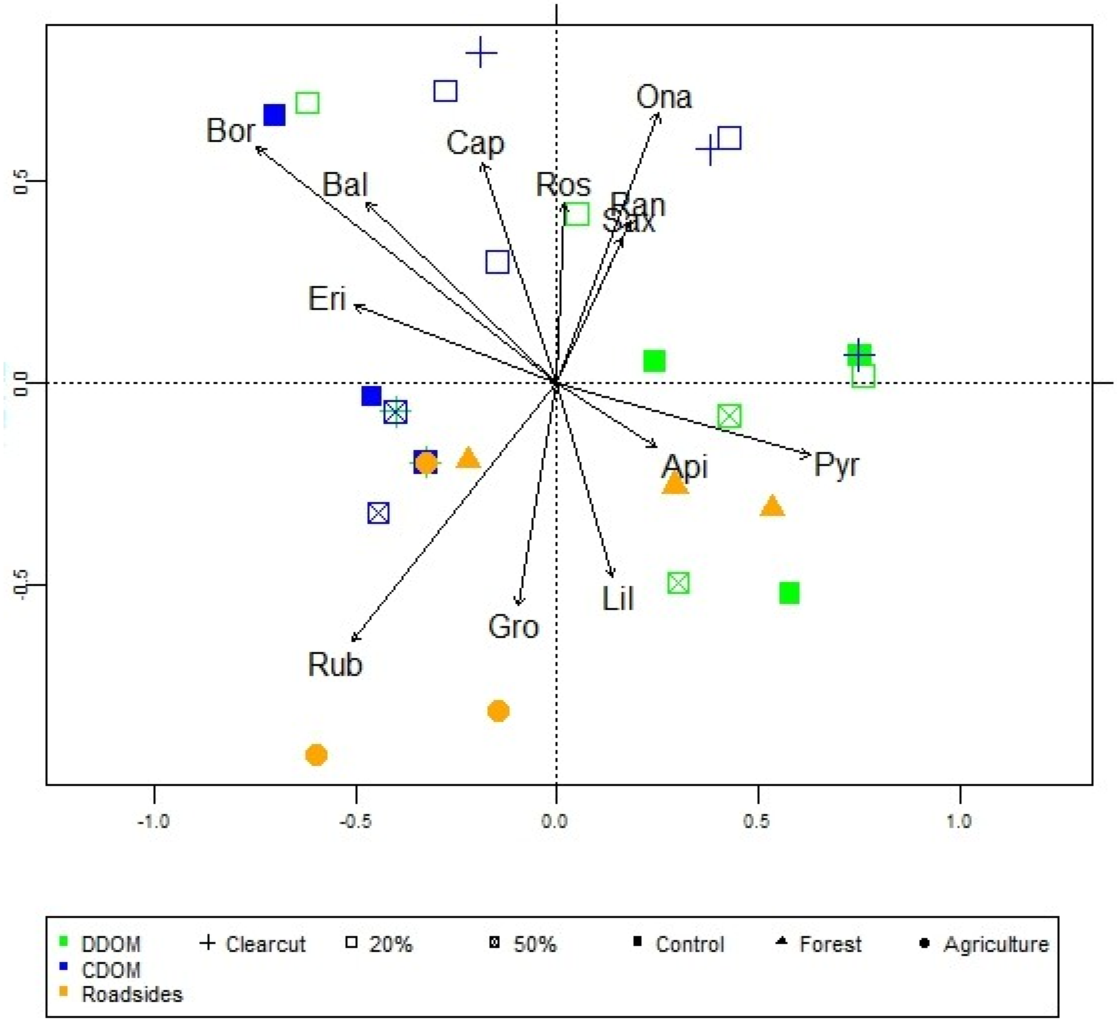

Figure 2.8: Ordination of a constrained redundancy analysis (RDA) of the composition of Syrphinae constrained by the mean abundance of flowers of each family of flowering plants per flower patch ($F_{(13,16)}$=1.37, p=0.023, R^2=0.143). Families with a variance inflation factor over 10 were removed prior to analysis. A Hellinger transformation was applied to hoverfly abundance prior to analysis. Ordinations for other bee and hoverfly groups were not significant (p>0.05)(Table A.8). (Api.= Apiaceae, Bal.= Balsaminaceae, Bor.= Boraginaceae, Cap.= Caprifoliaceae, Eri.= Ericaceae, Gro.= Grossulariaceae, Lil.= Liliaceae, Ona.= Onagraceae, Pyr.= Pyrolaceae, Ran.= Ranunculaceae, Ros.= Rosaceae, Rub.= Rubiaceae, Sax.= Saxifragaceae).

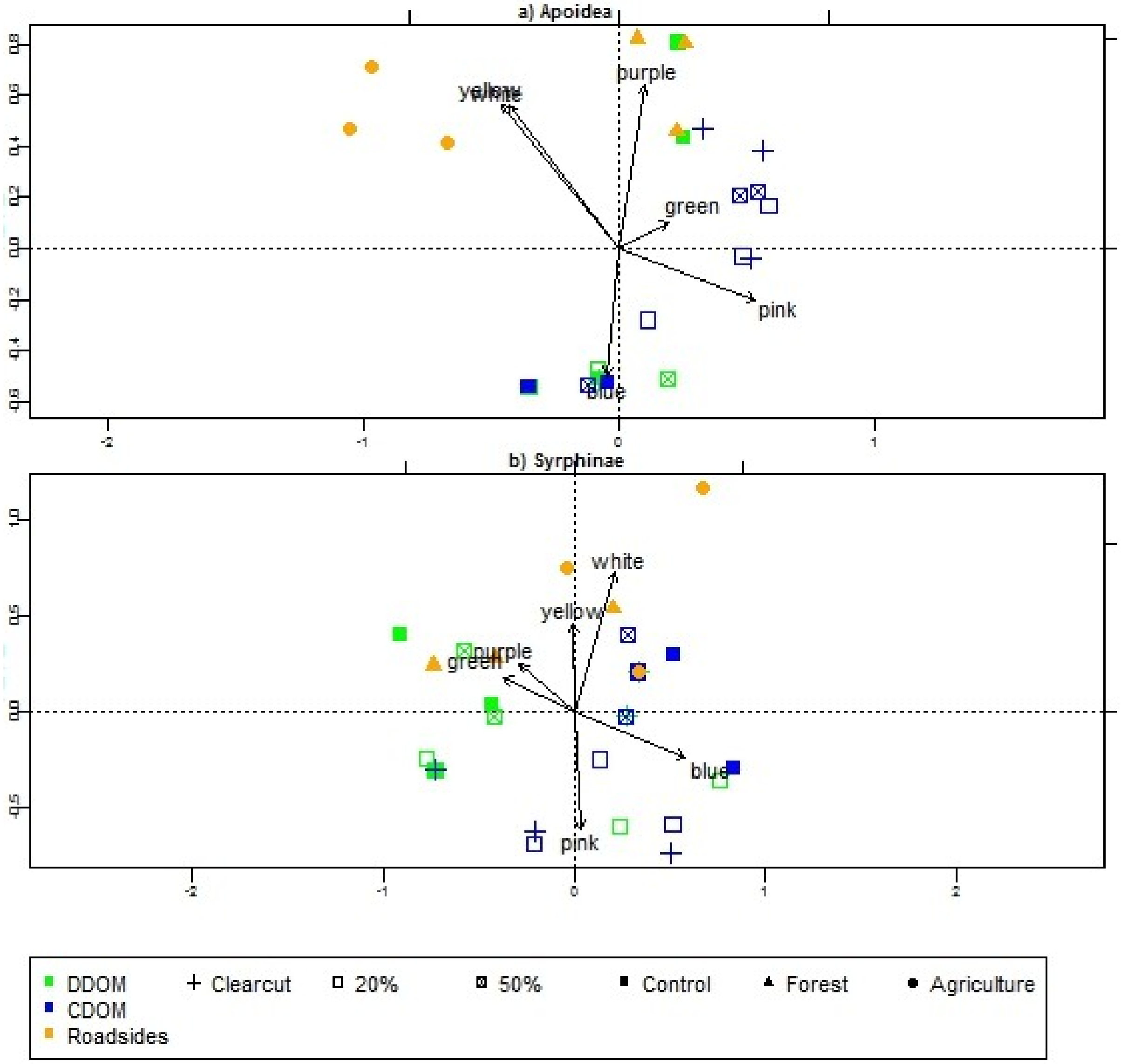

Figure 2.9: Ordination of a constrained redundancy analysis (RDA) of the composition of (a) bees ($F_{(6,23)}$=1.690, p=0.006, R^2=0.125) and (b) Syrphinae ($F_{(6,23)}$=1.575, p=0.009, R^2=0.106) constrained by the mean abundance of flowers of each colour per flower patch. A Hellinger transformation was applied to pollinator abundance prior to analysis. Only ordinations with a significant model ($p \leq 0.05$) are shown (Table A.9).

Chapter 3: General Discussion

Boreal forest species survey

The first objective of my thesis was to identify which species of bees and hoverflies are present in the boreal forest of Alberta. I identified 57 species of bees (Table A.13). Previously, seven species of bumble bees had been identified at EMEND in DDOM and DDOMU compartments (Cartar 2005, Pengelly and Cartar 2010, Table A.12). I increased the number of known bumble bees in the area to 15 in addition to adding another 42 species of bees. The increase in bumble bee species is due to the use of pan traps in addition to netting and the inclusion of CDOM compartments. Interestingly, *B. sylvicola* was recorded in EMEND in 1998/1999 (Cartar 2005) and 2007/2008 (Pengelly and Cartar 2010) but was not recorded in the present study. *B. sylvicola* inhabits open grassy areas (Williams et al. 2014) and the aspen regrowth may have eliminated suitable habitat or a similar species of *Bombus* (e.g., *B. melanopygus* or *B. rufocinctus*) may have been misidentified as *B. sylvicola* in the previous studies. I also identified 64 species of hoverflies (Table A.14). A recent key to Nearctic hoverflies (Miranda et al. 2013) provides range maps but does not include information about which species are found in the boreal forest. None of these species were exclusive to agricultural roadsides and, therefore, this total is a good representation of boreal forest hoverfly diversity. However, many species likely remain undetected and the extrapolated species richness is approximately 75 species each of bees and hoverflies (Figure 3.1).

Furthermore, I recorded 56 species of flowering plants (Table A.15). Flowering plants have been recorded at EMEND during previous pollinator studies (Cartar 2005, Pengelly and Cartar 2010) and many other studies (e.g., Macdonald and Fenniak 2006, Craig and Macdonald 2009, Chavez and Macdonald 2010b, Pengelly and Cartar 2011, Echiverri 2016). However, seven species were not recorded in the previously listed studies nor recorded by EMEND core research (Table A.16). While four of these species were only seen along roadsides, three species (*Astragalus agrestis*, *Melilotus alba*, *Melilotus officinalis*) were found along forest roadsides and could also potentially be found in adjacent forest compartments (*Caragana arborescens* was seen only along agricultural roadsides). Another two species (*Erigeron glabellus* and *Viburnum opulus*) are similar to species previously identified at EMEND and could have been misidentified in this study. However, I added one species (*Lycopus uniflorus*) to the list of understory plant species at EMEND. Flowering plant diversity and abundance gathered in the present study may also contribute to studies on changes in understory plant assemblages following harvesting.

Distribution of pollinators in undisturbed forest

The second objective of the study was to describe how bees and hoverflies are distributed within undisturbed stands at EMEND by examining the abundance and species richness of pollinators in control compartments. There was no statistically significant differences in abundance among the four forest cover types from two years of sampling (Appendix C). . Even prior to harvest, bumble bee abundance did not significantly differ between undisturbed forest transects in different forest cover types (Cartar 2005). Additionally, bee and hoverfly species richness was highest in CDOM compartments and similar among the other three forest cover types, and more species were exclusive to CDOM compartments than other forest cover types (Appendix C). Although logging would therefore affect more species in CDOM forest than other forest cover types, pollinators re-distribute themselves across the landscape to match resources following logging (Cartar 2005). However, logging may have a greater impact on species found exclusively in one forest cover type. This would be the case for many hoverfly species as more hoverflies were found exclusively in undisturbed forest than bees.

Although pollinators were distributed evenly across undisturbed compartments, this was not the case over across the entire forest landscape. Pollinators were more abundant and diverse in harvested compartments and along forest roadsides (576 bees representing 38 species, 353 hoverflies representing 49 species) than control compartments (178 bees representing 17 species, 279 hoverflies representing 41 species), despite sampling control compartments in two years. Additionally, this study only examined forested compartments and did not take into account other pollinator habitat within the boreal forest such as forest margins, regions of natural disturbance, fields, meadows, and bogs (Heinrich 1979, Michener 2008). Undisturbed forests harbor fewer bee species than other regions, especially moving further north, and bees prefer habitat with fewer trees such as disturbed areas (Michener 2008). The larger variation in environmental variables (canopy cover, shrub cover, flower abundance) among habitats may result in greater differences in abundance and species diversity than among forest cover types and including these sites allows for a more complete characterization of pollinator diversity within the boreal landscape.

Effect of variable retention harvesting on pollinators

The third objective of the study was to determine the effect of variable retention harvesting on assemblages of bees and hoverflies in deciduous and coniferous forest cover (discussed in detail in Chapter 2). In general, the amount of retention prescribed 14 years previously had no significant effect on the abundance of bees or hoverflies. However, there were some suggestive trends observed. Bee abundance generally decreased with increasing retention in CDOM compartments. Overall hoverfly abundance generally increased in DDOM compartments with increasing retention. However, the response to harvesting differed between subfamilies: the abundance of Eristalinae, including *Xylota* spp. and *Temnotoma* spp., increased with increasing retention to a maximum in 50% retention compartments while the abundance of Syrphinae, including *Syrphus* spp., decreased with increasing retention. These differences likely arise from different larval feeding strategies between the two subfamilies.

Fewer studies have been done on the long-term effects of harvesting on pollinator assemblages. As a project expected to run for one complete stand rotation (80-100years), EMEND offers the unique opportunity to study temporal changes in a single location without space-for-time substitution as is done in other studies (e.g., Makino et al. 2006, Nol et al. 2006, Nielsen and Totland 2007). Studies using a space-for-time substitution do not provide enough detail to determine the mechanisms of change, an undertaking better accomplished by long-term studies (Pickett 1989). In deciduous stands, bumble bees were most abundant in 50-75% retention compartments by the end of the summer following harvest (Cartar 2005), in clearcut compartments 8-9 years following harvest (Pengelly and Cartar 2010), and in 20% retention compartments in the current study (Figure B.1). The shift away from clearcut compartments and the higher abundance of bumble bees in 50% retention compartments than clearcut compartments suggest a decline in the years following harvest as the forest regrows as observed by other authors (Makino et al. 2006, Nol et al. 2006) and may be correlated to the dense canopy cover in DDOM clearcuts (Figure B.2a). Although bumble bee species richness did not increase significantly when comparing DDOM compartments to previous studies (Chapter 2), there was an increase from 6 species in 1998/1999 (Cartar 2005) to 9 species when DDOMU compartments are included as was done in previous studies at EMEND. Similarly, many other studies have found increased species richness following harvest in several other studies (Fye 1972, Nol et al. 2006, Nielsen and Totland 2007, Romey et al. 2007, Pengelly and Cartar 2010). However, one species, *B. sylvicola*, was recorded previously at EMEND but was not identified in the current study.

Forest cover type was more significant in explaining pollinator abundance than was amount of retention. Cover type may be important because some species, especially hoverflies, are exclusive to certain forest cover types. Additionally, environmental variables had greater variation between DDOM and CDOM cover types than among different harvesting treatments within the same forest cover type. These differences are explained by the rapid regeneration of *Populus tremuloides* in harvested DDOM compartments such that canopy cover in clearcut compartments is higher than control compartments while there has been little recovery in the canopy of harvested CDOM compartments (Figure B.2a).

Likewise, Macdonald and Fenniak (2006) found that understory plant cover and diversity differed between deciduous and coniferous forest cover types but harvesting did not have a significant effect on understory plant cover in deciduous compartments.

Harvesting necessitates the creation of access roads, which further impacts pollinator assemblages (Chapter 2). Bee and hoverfly abundance was higher along forest roadsides than harvest and control compartments, a difference that will likely persist for many years (Fye 1972, Jackson et al. 2014). While increased pollinator abundance along roadsides can be beneficial to adjacent forests and crops, some groups were negatively affected by roadsides (Megachilidae, *Xylota* spp., *Temnostoma* spp., *Syrphus* spp.) (Table A.11) and invasive plant species (e.g. *Melilotus* spp.) were observed along roadsides.

A high abundance of pollinators is important in providing pollination to understory plants, but it is also of interest to consider how pollinators are distributed relative to floral resources. Bumble bees in unharvested forest matched resources according to an ideal free distribution (IFD) prior to harvest (Cartar 2005). However, following harvest, bumble bees in clearcuts and unharvested compartments undermatch floral resources, i.e. there are too many or too few bees relative to floral resources, leading to inefficient foraging (Cartar 2005, Pengelly and Cartar 2010). Bumble bees were optimally distributed relative to floral resources in compartments with retention: they were in an IFD in 50-75% compartments in the summer following harvest (Cartar 2005) and eight to nine years after harvest, bumble bees were in an IFD in all harvest treatments (including clearcuts) with regards to flower abundance but only 10-20% retention compartments when nectar production rates are considered (Pengelly and Cartar 2010). These results are interesting as they demonstrate that logging can negatively impact nearby unharvested forest (Cartar 2005, Pengelly and Cartar 2010) with effects that persist for at least nine years (Pengelly and Cartar 2010).

The findings of this study show the effect of logging on pollinator foraging preferences rather than on pollinator populations because the foraging ranges of pollinators are much larger than the size of compartments at EMEND. Bumble bees are capable of foraging several kilometers in search of resources (Heinrich 1979, Abrohl 2011, Ogilvie and Forrest 2017), especially in areas with low resource availability (Ogilvie and Forrest 2017). Similarly, many solitary bees are capable of foraging several hundred metres, and some over one kilometer (St. Amand et al. 2000, Gathmann and Tscharntke 2002, Zurbuchen et al. 2010, Rader et al. 2011), and many hoverfly species are also able to forage at least several hundred meters (Rader et al. 2011). The pollinators in control compartments at EMEND are therefore affected by harvest treatments since foraging insects are capable of visiting flowers from surrounding compartments. Larger harvest and control compartments would be required to eliminate any edge effect from the surrounding landscape. Presumably, larger compartments would also better simulate realistic harvest scenarios. Surprisingly however, Pengelly and Cartar (2010) found no significant edge effect on bumble bee distributions at EMEND.

Effect of harvesting on environmental variables

Harvesting creates many changes in environmental variables. Canopy and shrub cover had similar responses to harvest. While harvesting leads to an immediate reduction in canopy and shrub cover relative to unharvested controls (Macdonald and Fenniak 2006), these variables did not recover at a similar rate in each forest cover type. Fourteen years after harvest, canopy cover and shrub cover were significantly higher in DDOM than CDOM compartments (Figure B.2a-b), as is generally the case in both harvested (Macdonald and Fenniak 2006) and unharvested (Macdonald and Fenniak 2006, Chavez and Macdonald 2010a (shrub cover only)) stands. The recovery of these variables was influenced by the amount of retention and their response differed within each cover type. Canopy and shrub cover in DDOM harvest treatments were now similar to levels in unharvested controls, although canopy cover in clearcut compartments was now higher due to aspen regeneration. In CDOM compartments, canopy and shrub cover increased with harvest retention and the differences between treatments were still higher than in DDOM compartments. Interestingly, amount of canopy cover formed a more-or-less continuous gradient of increasing canopy cover from clearcut CDOM compartments to clearcut DDOM compartments with control compartments falling in the middle (Figure B.2a).

Canopy cover and shrub cover affect the local abundance of flowering understory plants. Generally, understory plant cover increases with decreasing shrub (Chavez and Macdonald 2010b) and canopy cover (Kumar et al. 2017) and, consequently, should increase following logging. Despite higher flower species richness in harvested CDOM compartments, flower abundance and diversity did not differ significantly between treatments fourteen years post-harvest (Figure B.2c-d). Furthermore, mean flower abundance was lower in harvested compartments than unharvested controls and decreased with increasing harvesting intensity for both forest cover types. This is consistent with findings of decreased herb cover 1-2 years following harvest at EMEND and no effect on diversity (Macdonald and Fenniak 2006). The effects of logging on understory plant communities have been well studied but with mixed results. Several studies have found an increase in understory herb cover or richness (North et al. 1996, Beese and Bryant 1999, Fredericksen et al. 1999, Battles et al. 2001, Lilles et al. 2018), with an increase in herb cover inversely proportional to the amount of remaining retention (Beese and Bryant 1999, Battles et al. 2001, Lilles et al. 2018) and either an increase (North et al. 1996, Beese and Bryant 1999) or decrease (Fredericksen et al. 1999, Battles et al. 2001, Lilles et al. 2018) in diversity with increasing retention. Many studies have found no significant effect (Reader and Bricker 1992, Fredericksen et al. 1999, Nagaike et al. 1999, Deal 2001, Gilliam 2002), and yet others a decrease following harvest (Duffy and Meier 1992). Interestingly, the majority of studies listed above finding an increase following harvest were in coniferous stands while the majority of findings of no effect were in deciduous stands. This is consistent with the greater variation in flower diversity among treatments in CDOM compartments in my study. Deciduous harvest treatments may also be more similar to each other due in part to the greater amount of light transmission through the canopy compared to coniferous stands resulting in more herbaceous growth in spite of increased canopy cover (Constabel and Lieffers 1996, Messier et al. 1998).

These changes to environmental variables affect local assemblages of pollinators. Canopy cover, shrub cover, and, to a lesser degree, flower abundance significantly affected bee abundance while only canopy cover was included in models explaining the abundance of hoverflies (Chapter 2). The importance of canopy and shrub cover and the lack of influence of flower abundance and diversity are understandable given the significant effect of harvesting on canopy and shrub cover and the non-significant effect on flower abundance and diversity and for reasons discussed in detail in Chapter 2.

Pollinator declines and indicator species

Pollinator declines have garnered much attention in recent years. *Bombus terricola*, the third most abundant *Bombus* species and fourth most abundant bee species in the study (Table A.13), has experienced significant declines in portions of its range, especially in eastern North America (Colla and Packer 2008, Evans et al. 2008, Goulson et al. 2008, Wiiliams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Colla et al. 2012, Szabo et al. 2012, Williams et al. 2014, COSEWIC 2015, Jacobson et al. 2018). These declines have been less dramatic in other regions (Colla et al. 2012) and have not been observed in Alberta (COSEWIC 2015). Many sources have attributed the declines to pathogen spillover from managed bumble bees in greenhouses (Evans et al. 2008, Goulson et al. 2008, Otterstatter and Thomson 2008, Williams and Osborne 2009, Cameron et al. 2011, Meeus et al. 2011, Szabo et al. 2012, COSEWIC 2015). There are fewer commercial greenhouses in Alberta when compared to British Columbia, Ontario, and Quebec (COSEWIC 2015) which may explain why *B. terricola* is stable within the province. Comparisons between the habitats in which *B. terricola* is found in Alberta and regions experiencing rapid declines may offer additional insight into factors contributing to population declines. Further sampling of *B. terricola* nest sites may also reveal the status of *B. bohemicus* (formerly *B. ashtoni*), a social parasite of *B. terricola*. *B. bohemicus* appears to be rapidly declining throughout its range (Colla and Packer 2008, Goulson et al. 2008, Colla et al. 2012, Bartomeus et al. 2013, COSEWIC 2014, Williams et al. 2014, Hatfield et al. 2016, Jacobson et al. 2018). Recently, it has been largely absent through most of its range (COSEWIC 2014, Williams et al. 2014, Hatfield et al. 2016), including Alberta where only a few individuals have been observed in recent years (COSEWIC 2014). The decline in abundance and reduction in range is likely correlated to declines in its host species, *B. terricola*, *Bombus affinis*, and *Bombus occidentalis* (COSEWIC 2014, Hatfield et al. 2016).

B. terricola was an indicator of roadsides, and forest roadsides specifically by pan trap (Table 2.5). Many other species of bees and hoverflies were also identified as indicator species. Ecological indicators of disturbance should be easy to sample and store, be abundant, be taxonomically well known and easy to identify, have a well-known biology, be important to the environment, and be found in a variety of habitats (McGeoch 1998, Hodkinson and Jackson 2005). Hoverflies are good candidates as indicator species since larvae with different feeding strategies have different habitat requirements, they are easy to find, and they are fairly easy to identify (Sommaggio 1999, Maleque et al. 2009) and have been used in that capacity in several studies (e.g., Haslett 1997, Straw et al. 2017). Three species of hoverflies with predaceous larvae were selected as indicators of disturbance using net capture data: *Melangyna umbellatarum*, *Epistrophe grossularia*, and *Syrphus ribesii* (Table 2.5). *Syrphus ribesii* was the third most abundant species in the study (Table A.14) and could be used in future studies to indicate disturbed areas. However, no species indicated undisturbed forest and no species were selected as indicators using pan trap data. Future studies using hoverflies as indicators of disturbance should include traps in the canopy for a more complete characterization of the hoverfly community because more species and individuals are caught above ground level (Straw et al. 2017).

Management Implications

Pollinators were generally more abundant along forest roadsides than agricultural roadsides, and some species were more abundant or exclusively caught within forest compartments (Chapter 2). Therefore, increasing forested areas within the agricultural landscape may increase the diversity and abundance of native bees (discussed in Chapter 2) that, in addition to providing increased pollination services, provide many benefits over using honey bees alone (discussed in Chapter 1).

Road management will likely also affect pollinator assemblages. Mowing and spraying ditches along roads has led to a high abundance of flowering plants and a correspondingly high abundance of bees (Figure 2.6). However, managing for this type of habitat may come at the cost of increasing the abundance and facilitating the spread of invasive species. Several costs and benefits must be considered in determining the frequency in which to mow roadsides. While infrequent mowing reduces the visibility of animals along roadsides and potentially increase traffic incidents, mowing too frequently would remove floral resources for bees. The resulting increase in abundance of bees can provide pollination services to many nearby forested and agricultural areas.

The effects of logging are less clear. Overall pollinator abundance increases with increasing harvest intensity, especially *Bombus* spp. and Syrphinae. On the other hand, pollinator species that require stems for nesting, e.g., Megachilidae, or saprophageous species requiring decaying matter, e.g., Eristalinae, are more abundant in compartments with some harvest retention and clearcutting would have a negative impact on their populations. A harvest prescription with low retention would therefore result in the maximum pollinator abundance and species richness while maximizing timber production. Bee and hoverfly abundance was generally highest in 20% retention. However, retention levels between 2% and 20% were not included and should be included in future studies to determine if current levels of 1-15% retention used in Alberta are sufficient (Gustafsson et al. 2012). The choice of cover type to harvest has a larger impact on pollinator assemblages due to differences in regeneration and pollinator species that are exclusive to each cover type.

Figures

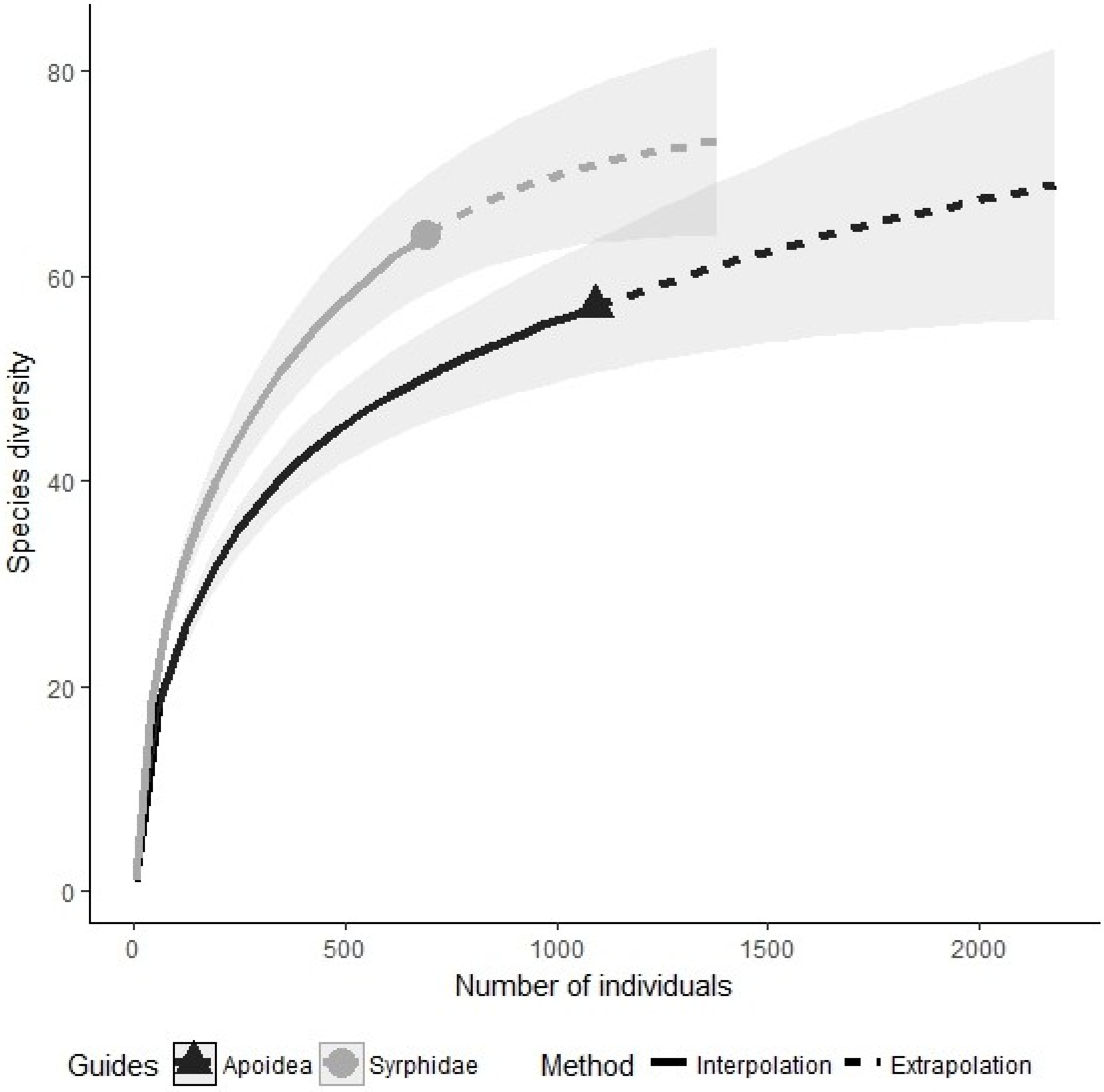

Figure 3.1: Sample-size-based rarefaction of species richness (q=0) for all bees and hoverflies caught at EMEND in 2012 and 2013 with 95% confidence intervals.

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Appendix A: Supplementary Tables

Table A.1: Abundance of each species of bee caught by net and by pan trap prior to standardization (Chapter 2). Melittidae was identified to the family level, *Colletes* and *Protandrena* were identified to genus, and *Lasioglossum* was identified to subgenus. Two specimens of *Megachile* (*) could not be identified to species and were not included in the total abundance or analyses. Taxon names to genus level follow Michener (2007).

Family	Genus	Species	Abundance Caught by Net Capture	Abundance Caught by Pan Trap	Total Abundance
Colletidae	*Colletes*	*Colletes sp.*	0	1	1
	Hylaeus	*H. annulatus*	0	5	5
		H. modestus	0	4	4
Andrenidae	*Andrena*	*A. algida*	0	9	9
		A. canadensis	0	1	1
		A. frigida	0	3	3
		A. nigrihirta	0	4	4
		A. nivalis	1	1	2
		A. thaspii	0	5	5
	Protandrena	*Protandrena sp.*	2	4	6
Halictidae	*Halictus*	*H. rubicundus*	1	0	1
		H. confusus	0	2	2
	Lasioglossum	*L. (Dialictus)* spp.	2	3	5
		L. (Evylaeus) spp.	1	2	3
		L. (Lasioglossum) spp.	0	6	6
Melittidae			0	2	2
Megachilidae	*Hoplitus*	*H. albifrons*	0	8	8
		H. producta	0	5	5
	Osmia	*O. bucephala*	0	15	15
		O. simillima	1	18	19
	Anthidium	*A. clypeodentatum*	0	2	2
	Stelis	*S. foederalis*	0	1	1
		S. nitida	0	1	1
		S. subemarginata	0	1	1
	Ceolioxys	*C. funeraria*	2	2	4
		C. porterae	1	2	3
		C. sodalis	0	1	1
	Megachile	*M. brevis*	0	1	1
		M. circumcincta	0	8	8
		M. frigida	6	5	11
		M. gemula	1	4	5
		M. inermis	11	53	64

		M. lapponica	0	1	1
		M. melanophaea	0	6	6
		M. pugnata	0	1	1
		M. relativa	21	58	79
		M. rotundata	0	7	7
		*M. relativa/lapponica**	0	2	2
Apidae	*Eucera*	*E. frater*	0	1	1
	Anthophora	*A. bomboides*	1	2	3
		A. terminalis	4	31	35
	Bombus	*B. bifarus*	1	0	1
		B. borealis	3	0	3
		B. fervidus	1	2	3
		B. flavidus	1	4	5
		B. flavifrons	49	92	141
		B. frigidus	4	2	6
		B. mixtus	3	10	13
		B. nevadensis	2	0	2
		B. perplexus	1	1	2
		B. rufocinctus	22	40	62
		B. ternarius	5	2	7
		B. terricola	21	25	46
		B. vagans	50	45	95
	Apis	*A. mellifera*	34	10	44
Total			**252**	**519**	**771**

Table A.2: Abundance of each species of hoverfly (Syrphidae) caught by net and pan trap prior to standardization (Chapter 2). *Lejops*, *Heringia*, *Pipiza*, and *Platycheirus* were only identified to genus. Taxon names follow Miranda et al. (2013).

Subfamily	Genus	Species	Abundance Caught by Net Capture	Abundance Caught by Pan Trap	Total Abundance
Eristalinae	*Blera*	*B. nigra*	0	1	1
	Brachyopa	*B. notata*	0	2	2
	Chalcosyrphus	*C. nemorum*	0	2	2
	Cheilosia	*C. sialia*	0	2	2
	Eristalis	*E. compactus*	0	1	1
		E. interrupta	4	0	4
		E. rupium	3	1	4
	Helophilus	*H. fasciatus*	0	1	1
		H. hybridus	3	0	3
		H. intentus	1	0	1
		H. obscurus	10	3	13
	Lejops	*L. (Anasimyia) sp.*	0	1	1
	Sericomyia	*S. chalcopyga*	1	0	1
		S. lata	1	0	1
	Temnostoma	*T. alternans*	4	1	5
		T. balyras/obscurus	4	6	10
		T. excentrica	36	5	41
	Volucella	*V. facialis*	1	1	2
	Xylota	*X. annulifera*	1	4	5
		X. confusa	0	3	3
		X. flavitibia	0	1	1
		X. naknek	0	6	6
		X. quadrimaculata	0	1	1
		X. subfasciata	3	65	68
	Total Eristalinae		**72**	**107**	**179**
Syrphinae	*Baccha*	*B. elongata*	0	3	3
	Chrysotoxum	*C. derivatum*	5	4	9
	Dasysyrphus	*D. venustus*	1	1	2
	Doros	*D. aequalis*	1	0	1
	Epistrophe	*E. grossularia*	22	3	25
	Eupeodes	*E. americanus*	0	1	1
		E. curtus	1	0	1
	Heringia	*Heringia* spp.	0	7	7
	Lapposyrphus	*L. lapponicus*	3	1	4
	Melangyna	*M. labiatarum/subfasciata*	1	0	1
		M. umbellatarum	18	1	19
	Melanostoma	*M. mellinum*	2	9	11

	Meliscaeva	*M. cinctella*	2	0	2
	Paragus	*P. haemorrhous*	1	0	1
	Parasyrphus	*P. genualis*	2	0	2
		P. new sp. Thompsoni	1	0	1
	Pipiza	*Pipiza* spp.	2	5	7
	Platycheirus	*Platycheirus* spp.	12	25	37
	Scaeva	*S. pyrastri*	3	0	3
	Sphaerophoria	*S. philanthus*	9	2	11
	Syrphus	*S. ribesii*	34	3	37
		S. torvus	1	0	1
		S. vitripennis	4	0	4
	Total Syrphinae		**125**	**65**	**190**
Total			**197**	**172**	**369**

Table A.3: Redundancy Analysis showing the effect of harvest treatment (T) and forest cover type (C) on assemblages (A) of bees and hoverflies caught by net capture and pan trap. Results are considered significant below a p-value of 0.05 and are shown in bold. The best model was selected using adjusted R^2 values with the function ordiR2step. Eigenvalues are included for the first two axes (RDA 1 and 2) along with the corresponding proportion of explained variation that is due to each axis.

Net Capture											
	Model		Treatment		Cover		T x C		R^2 model	Eigenvalues	
	F value	P value	F value	P value	F value	P value	F value	P value	Adj. R^2	RDA 1	RDA 2
Apoidea	**1.67**	**0.033**	1.31	0.204	**2.29**	**0.044**	**1.84**	**0.047**	0.170	0.0934 (43.6%)	0.0668 (31.2%)
Syrphidae	1.26	0.087	0.970	0.531	1.39	0.152	**1.50**	**0.047**	0.0723	0.106 (41.5%)	0.0578 (22.5%)
Eristalinae	1.01	0.460	0.821	0.681	1.38	0.182	1.06	0.401	0.00138	0.0650 (37.9%)	0.0476 (27.7%)
Syrphinae	**1.77**	**0.006**	1.33	0.136	1.60	0.096	**2.28**	**0.004**	0.191	0.137 (49.3%)	0.0634 (22.8%)
Pan Trap											
	Model		Treatment		Cover		T x C		R^2 model	Eigenvalues	
	F value	P value	F value	P value	F value	P value	F value	P value	Adj. R^2	RDA 1	RDA 2
Apoidea	1.08	0.323	1.07	0.368	**2.03**	**0.022**	0.776	0.832	0.0238	0.0568 (31.0%)	0.0509 (27.7%)
Syrphidae	1.10	0.292	1.42	0.096	0.83	0.601	0.858	0.657	0.0282	0.0766 (35.4%)	0.0467 (21.6%)
Eristalinae	1.05	0.391	1.20	0.269	0.796	0.542	0.980	0.456	0.0148	0.0596 (45.1%)	0.0379 (28.6%)
Syrphinae	0.943	0.601	1.38	0.123	0.428	0.930	0.673	0.893	-0.0178	0.0693 (37.6%)	0.0465 (25.5%)

Table A.4: Permutational Analysis of Variance (perANOVA) results showing the effect of harvest treatment (T) and forest cover type (C) on the abundance (A) of bees and hoverflies caught by net capture and pan trap. Results are considered significant below a p-value of 0.05 and are shown in bold.

Net Capture						
	Treatment		Cover		T x C	
	F value	P value	F value	P value	F value	P value
Apoidea	2.29	0.120	**13.6**	**0.003**	2.08	0.145
Syrphidae	1.09	0.372	3.34	0.080	1.54	0.245
Eristalinae	0.192	0.897	1.85	0.194	0.289	0.842
Syrphinae	2.97	0.067	1.87	0.203	3.12	0.056
Pan Trap						
	Treatment		Cover		T x C	
	F value	P value	F value	P value	F value	P value
Apoidea	1.24	0.329	3.67	0.081	0.870	0.484
Syrphidae	0.723	0.579	4.13	0.057	0.996	0.430
Eristalinae	1.73	0.188	**6.95**	**0.017**	0.856	0.479
Syrphinae	0.256	0.865	0.120	0.737	0.595	0.628

Table A.5: Analysis of Variance results showing the effect of harvest treatment (T) and forest cover type (C) on canopy cover, shrub cover, flower abundance, and species richness of flowering plants. Roadsides were not included in the analysis of canopy cover. [a]Did not meet the assumption of normality so a perANOVA test was used. Post-hoc contrasts given in Table A.6.

	Treatment		Cover		T x C	
	F Value	P Value	F Value	P Value	F Value	P Value
Canopy Cover	2.05	0.141	**35.0**	**≤0.001**	3.04	0.054
Shrub Cover[a]	**27.8**	**≤0.001**	**13.6**	**≤0.001**	1.35	0.264
Flower Abundance[a]	**21.1**	**≤0.001**	2.03	0.170	0.165	0.919
Flower Diversity	0.493	0.776	1.25	0.273	1.52	0.236

Table A.6: Post-hoc contrasts using Mann-Whitney tests to compare shrub cover and flower abundance between harvesting treatments (including roadsides) and forest cover types (shrub cover only) (see also Table A.5). Comparisons were not mutually orthogonal so a Bonferroni adjustment was applied. Results with a p-value less than 0.0028 (shrub cover) or 0.0033 (flower abundance) are considered significant and shown in bold. (0= clearcut, 20= 20% retention, 50= 50% retention, 100= control, For= forest roadsides, Ag.= agricultural roadside, DDOM= deciduous-dominated, CDOM= coniferous-dominated, Road= roadsides).

	0 vs. 20		0 vs. 50		0 vs. 100		0 vs. For.		0 vs. Ag.		20 vs. 50		20 vs. 100		20 vs. For.	
	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value
Shrub Cover	14	0.589	14	0.589	13	0.485	18	0.024	18	0.024	23	0.485	16	0.818	18	0.024
Flower Abundance	13	0.485	14	0.589	7	0.093	0	0.024	0	0.024	9	0.180	0	0.024	0	0.024

	20 vs. Ag.		50 vs. 100		50 vs. For.		50 vs. Ag.		100 vs. For.		100 vs. Ag.		For. vs. Ag.	
	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value	U value	P value
Shrub Cover	18	0.024	12	0.394	18	0.024	18	0.024	18	0.024	18	0.024	2	0.400
Flower Abundance	0	0.024	9	0.180	0	0.024	0	0.024	0	0.024	0	0.024	2	0.400

	DDOM vs. CDOM		DDOM vs. Road		CDOM vs. Road	
	U value	P value	U value	P value	U value	P value
Shrub Cover	121	0.004	**72**	**≤0.001**	**72**	**≤0.001**

Table A.7: Species of flowers recorded at flower patches during net capture (Chapter 2) along with the flower colour and abundance prior to standardizing by the number of flower patches. Taxon names follow the USDA Natural Resource Conservation Service plant database (USDA, NRCS 2015).

Family	Species	Colour	Abundance
Liliaceae	*Maianthemum canadense*	White	187
	Maianthemum stellatum	White	43
Orchidaceae	*Corallorhiza maculata*	Pink	47
	Goodyera repens	White	81
	Platanthera spp.	Green	12
Caryophyllaceae	*Stellaria longifolia*	White	4
	Stellaria sp.	White	1
Ranunculaceae	*Delphinium glaucum*	Purple	252
	Ranunculus macounii	Yellow	6
Saxifragaceae	*Mitella nuda*	Green	4
	Parnassia palustris	White	10
Grossulariaceae	*Rhibes oxyacanthoides*	White	10
Rosaceae	*Fragaria* spp.	White	138
	Geum aleppicum	Yellow	12
	Potentilla norvegica	Yellow	7
	Rosa acicularis	Pink	479
	Rubus idaeus	White	60
Fabaceae	*Astragalus agrestis*	Purple	138
	Astragalus americanus	White	20
	Caragana arborescens	Yellow	18
	Lathyrus ochroleucus	White	151
	Melilotus alba	White	579
	Melilotus officinalis	Yellow	3209
	Trifolium spp.	White	3968
	Vicia americana	Purple	481
Balsaminaceae	*Impatiens noli-tangere*	Yellow	20
Onagraceae	*Chamerion angustifolium*	Pink	266
Apiaceae	*Heracleum maximum*	White	152
Cornaceae	*Cornus canadensis*	White	2231
Pyrolaceae	*Moneses uniflora*	White	40
	Orthilia secunda	Green	36
	Pyrola asarifolia	Pink	221
Ericaceae	*Ledum groenlandicum*	White	13
Polemoniaceae	*Polemonium acutiflorum*	Blue	1
Boraginaceae	*Mertensia paniculata*	Blue	97
Scrophulariaceae	*Rhinanthus minor*	Yellow	210
Rubiaceae	*Galium boreale*	White	563
	Galium triflorum	White	3

Caprifoliaceae	*Linnaea borealis*	Pink	554
	Viburnum edule	White	194
	Viburnum opulus	White	1
Asteraceae	*Achillea millefolium*	White	494
	Achillea sirbirica	White	11
	Arnica sp.	Yellow	2
	Cirseum arvense	Purple	82
	Erigeron glabellus	Purple	14
	Eurybia sp.	Purple	217
	Packera paupercula	Yellow	4
	Solidago canadensis	Yellow	373
	Taraxacum officinale	Yellow	73
	Composite sp. 1	Yellow	36
	Composite sp. 2	Yellow	4
	Unknown White Flower	White	50
	Unknown White Branched Flower	White	14
	Unknown sp. 1		1
	Unknown sp. 2		1
	Unknown sp. 3		1
Total			**15 894**

Table A.8: Redundancy Analysis showing the effect of the abundance of each family of flower on assemblages of bees and hoverflies caught by net. Families with a variance inflation factor over 10 were removed prior to analysis and the best model was selected using adjusted R^2 values with the function ordiR2step. In all cases, the best model included all families shown below. Results with a p-value less than 0.05 are shown in bold. Eigenvalues are included for the first two axes (RDA 1 and 2) along with the corresponding proportion of explained variation that is due to each axis. Interset correlations are also provided for RDA 1 and RDA 2 with each factor with values above the critical value for Pearson's r for d.f.= 28 (0.361) shown in bold.

	Model		Eigenvalues		Apiaciae				Balsaminaceae				Boraginaceae				Caprifoliaceae			
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2
Apoidea	0.971	0.561	0.0783 (33.3%)	0.0483 (20.5%)	0.649	0.760	-0.0734	0.0852	0.973	0.439	-0.204	-0.152	1.15	0.313	-0.196	-0.195	1.22	0.254	0.238	-0.295
Syrphidae	1.00	0.479	0.0767 (25.0%)	0.0543 (16.4%)	1.09	0.340	0.304	0.279	1.01	0.495	-0.247	-0.232	1.25	0.245	**-0.464**	-0.187	0.76	0.733	-0.0829	-0.294
Eristalinae	0.855	0.770	0.0640 (27.1%)	0.0488 (19.3%)	0.996	0.433	0.287	-0.106	0.961	0.463	-0.264	-0.0652	0.229	0.994	0.0735	0.0156	0.378	0.922	-0.150	-0.0606
Syrphinae	**1.37**	**0.023**	0.103 (33.5%)	0.0662 (19.4%)	0.858	0.593	0.147	-0.101	1.60	0.161	-0.284	0.283	**2.26**	**0.017**	**-0.445**	**0.370**	1.13	0.343	-0.110	0.346

	Ericaceae				Grossulariaceae				Liliaceae				Onagraceae				Pyrolaceae			
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2
Apoidea	0.535	0.936	-0.151	0.0266	1.44	0.153	-0.255	-0.210	0.458	0.908	-0.0926	-0.128	1.84	0.062	**0.489**	-0.227	1.24	0.270	-0.166	-0.333
Syrphidae	1.59	0.063	-0.300	0.194	1.18	0.267	0.0583	**0.395**	0.683	0.825	-0.0224	0.155	0.757	0.751	0.135	**-0.406**	0.832	0.663	0.203	0.0395
Eristalinae	1.68	0.178	0.172	-0.0509	0.259	0.915	0.150	-0.0521	0.711	0.661	0.0252	-0.109	0.891	0.528	-0.239	-0.00364	0.774	0.602	0.0691	-0.184
Syrphinae	**2.06**	**0.015**	-0.301	0.121	1.39	0.199	-0.0591	-0.348	0.889	0.521	0.0823	-0.304	1.09	0.387	0.150	**0.422**	1.81	0.065	**0.374**	-0.114

	Ranunculaceae				Rosaceaa				Rubiaceae				Saxifragaceae				R^2 Model
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	Adj. R^2
Apoidea	0.798	0.577	-0.188	-0.166	0.800	0.559	0.00686	-0.330	0.501	0.863	-0.000388	**0.401**	1.02	0.414	0.154	-0.145	-0.0131
Syrphidae	0.962	0.493	0.179	-0.230	0.870	0.590	0.0983	-0.206	1.15	0.358	**-0.422**	0.115	0.907	0.565	0.139	-0.142	0.000892
Eristalinae	1.43	0.186	-0.305	-0.335	0.871	0.509	-0.199	**-0.417**	0.620	0.693	-0.00605	**0.434**	1.32	0.231	-0.0514	-0.220	-0.0695
Syrphinae	0.915	0.537	0.108	0.254	1.05	0.366	0.0106	0.283	**1.91**	**0.034**	-0.304	**-0.405**	0.860	0.597	0.0952	0.227	0.143

Table A.9: Redundancy Analysis showing the effect of the abundance of flowers of each colour on assemblages of bees and hoverflies caught by net. Colours with a variance inflation factor over 10 were removed prior to analysis and the best model was selected using adjusted R^2 values with the function ordiR2step. In all cases, the best model included all of the flower colours. Eigenvalues are included for the first two axes (RDA 1 and 2) along with the corresponding proportion of explained variation that is due to each axis. Interset correlations are also provided for RDA 1 and RDA 2 with each factor with values above the critical value for Pearson's r for d.f.= 28 (0.361) shown in bold.

	Model		Eigenvalues		White				Yellow			
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2
Apoidea	**1.69**	**0.006**	0.0700 (42.9%)	0.0425 (26.0%)	**2.53**	**0.012**	**-0.457**	**0.480**	0.865	0.536	**-0.485**	**0.481**
Syrphidae	1.29	0.053	0.0590 (32.3%)	0.0544 (29.8%)	**2.13**	**0.006**	**-0.658**	0.233	0.572	0.919	**-0.389**	0.329
Eristalinae	1.16	0.255	0.0554 (41.0%)	0.0456 (33.8%)	**2.22**	**0.042**	**0.480**	0.216	0.882	0.557	**0.434**	0.117
Syrphinae	**1.58**	**0.009**	0.0734 (39.2%)	0.0595 (31.8%)	**2.51**	**0.007**	0.182	**0.710**	0.476	0.888	-0.004865	**0.447**

	Pink				Purple				Blue			
	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2	F value	P value	RDA 1	RDA 2
Apoidea	**2.33**	**0.025**	**0.558**	-0.172	**2.79**	**0.008**	0.101	0.545	0.724	0.645	-0.0488	**-0.423**
Syrphidae	0.870	0.605	**0.397**	**-0.418**	1.25	0.204	-0.0859	**0.420**	1.53	0.105	-0.263	**-0.440**
Eristalinae	0.718	0.657	-0.311	0.162	0.792	0.580	0.282	0.299	0.629	0.744	0.0498	-0.0548
Syrphinae	1.03	0.371	0.0272	**-0.601**	1.66	0.080	-0.241	0.243	**2.49**	**0.016**	**0.488**	-0.239

	Green				R^2 Model
	F value	Pvalue	RDA 1	RDA 2	Adj. R^2
Apoidea	0.895	0.529	0.202	0.0903	0.125
Syrphidae	1.40	0.132	0.00524	0.354	0.057
Eristalinae	1.73	0.126	0.0291	**-0.631**	0.032
Syrphinae	1.29	0.250	-0.309	0.175	0.106

Table A.10: Indicator species analysis for flowers recorded during net capture showing the specificity and the fidelity of the species to the given group. Only species with a p-value less than 0.05 are included in the table.

Group	Species	Specificity	Fidelity	Sqrt(IndVal)	P value
Agricultural Roads	*Solidago canadensis* *Melilotus alba*	0.983 0.957	1.00 1.00	0.991 0.978	0.003 0.012
All Roads	*Melilotus officinales* *Taraxacum officinale*	1.00 0.986	1.00 1.00	1.00 0.993	≤0.001 ≤0.001
Roads and CDOM Clearcut	*Achillea millefolium*	0.885	1.00	0.941	0.010
CDOM Clearcut, 20%, 50% and DDOM Control	*Chamerion angustifolium*	0.920	0.917	0.918	0.006
CDOM 20%, 50%, Control and DDOM 20%	*Linnaea borealis*	0.927	0.917	0.922	0.039
CDOM 50%, Clearcut and DDOM Control and Roads	*Trifolium* spp.	0.988	1.000	0.994	≤0.001
CDOM stands, DDOM Control, Agricultural Roads	*Lathyrus ochroleucus*	0.934	0.889	0.911	0.050
CDOM Clearcut, Control and DDOM stands	*Pyrola asarifolia*	0.975	0.778	0.871	0.049
DDOM and CDOM stands	*Cornus canadensis* *Rosa acicularis*	1.00 0.993	1.00 1.00	1.00 0.996	≤0.001 ≤0.001
CDOM Clearcut, 20%, 50%, and DDOM stands and Roads	*Eurybia* spp.	1.00	0.926	0.962	0.040

Table A.11: Comparison of the abundance of bees and hoverflies (including all subgroups) caught at forest versus agricultural roadsides and between forest roadsides and forest compartments. Analyses for forest road versus agricultural road were by two-sample t-tests except were indicated. For forest road versus forest comparisons all analyses were by Mann-Whitney tests. I used mean abundance/sampling period/site for net capture data and mean abundance/day/site for pan trap data with total raw abundance included in parentheses. Results were considered significant at p-value < 0.05. [a] Data did not meet assumption of normality, value represents U value from a Mann-Whitney test.

	Forest Road vs. Agricultural Road (Net)				Forest Road vs. Agricultural Road (Pan)			
	Forest Road	Ag. Road	t value	P value	Forest Road	Ag. Road	t value	P value
Apoidea	6.44 (59)	9.75 (95)	1.58	0.188	3.44 (217)	2.24 (127)	-1.38	0.239
Long-Tongued Bees	6.44 (59)	9.25 (89)	1.16	0.311	3.27 (206)	1.70 (98)	-1.91	0.128
Short-Tongued Bees	0 (0)	0.5 (6)	6[a]	0.505	0.175 (11)	0.545 (29)	1.71	0.163
Bombus spp.	6.08 (56)	5.39 (52)	-0.499	0.644	1.32 (83)	0.966 (55)	-0.956	0.393
B. terricola	1.5 (15)	0.417 (4)	-1.24	0.284	0.349 (22)	0.021 (1)	-2.61	0.059
Megachilidae	0.250 (2)	0.194 (2)	-0.316	0.768	**1.70 (107)**	**0.428 (26)**	**-3.57**	**0.023**
Syrphidae	6.86 (61)	1.28 (13)	0[a]	0.100	0.492 (31)	0.0317 (2)	1[a]	0.184
Eristalinae	0.972 (9)	0.667 (6)	-0.405	0.706	0.413 (26)	0 (0)	1.5[a]	0.197
Syrphinae	5.89 (52)	3.2 (7)	0[a]	0.100	0.0794 (5)	0.0317 (2)	3	0.643
Xylota spp.	0 (0)	0 (0)	N/A	N/A	0.302 (19)	0 (0)	1.5[a]	0.197
Temnostoma spp.	0.333 (3)	0 (0)	-1.00[a]	0.374	0.0159 (1)	0 (0)	3[a]	0.505
Syrphus spp.	2.25 (21)	0.0833 (1)	-2.39	0.074	0.0159 (1)	0 (0)	3[a]	0.505

	Forest Road vs. Forest (Net)				Forest Road vs. Forest (Pan)			
	Forest Road	Forest	U value	P value	Forest Road	Forest	U value	P value
Apoidea	**6.44 (59)**	**1.33 (98)**	**0**	**0.005**	**3.44 (217)**	**0.260 (175)**	**0**	**0.006**
Long-Tongued Bees	**6.44 (59)**	**1.32 (97)**	**0**	**0.006**	**3.27 (206)**	**0.242 (163)**	**0**	**0.006**
Short-Tongued Bees	0 (0)	0.0139 (1)	37.5	0.814	**0.175 (11)**	**0.0179 (12)**	**1**	**0.002**
Bombus spp.	**6.08 (56)**	**0.74 (55)**	**0**	**0.006**	**1.32 (83)**	**0.126 (85)**	**0**	**0.006**
B. terricola	**1.5 (15)**	**0.0278 (2)**	**12.5**	**0.001**	**0.349 (22)**	**0.00298 (2)**	**0**	**≤0.001**
Megachilidae	0.250 (2)	0.542 (39)	36	1	**1.70 (107)**	**0.0995 (67)**	**0**	**0.005**
Syrphidae	**6.86 (61)**	**1.68 (123)**	**6**	**0.022**	0.492 (31)	0.207 (139)	22.5	0.315
Eristalinae	0.972 (9)	0.785 (57)	23.5	0.351	0.413 (26)	0.120 (81)	19.5	0.205
Syrphinae	**5.89 (52)**	**0.899 (66)**	**1**	**0.007**	0.0794 (5)	0.0865 (58)	37.5	0.938
Xylota spp.	0 (0)	0.0556 (4)	42	0.491	0.302 (19)	0.0905 (61)	20	0.215
Temnostoma spp.	0.333 (3)	0.562 (41)	43	0.602	0.0159 (1)	0.0164 (11)	34	0.886
Syrphus spp.	**2.25 (21)**	**0.226 (17)**	**1**	**0.005**	0.0159 (1)	0.00298 (2)	26	0.179

Table A.12: *Bombus* spp. recorded in 1998 before harvest and in 1999 following harvest (Cartar 2005) and in 2007 and 2008 (Pengelly and Cartar 2010) at EMEND and whether or not they were present in DDOM compartments in my study in 2013. In the earlier studies bumble bees had been sampled in clearcut, 10% retention, 20% retention, 50% retention, 75% retention, and control compartments in deciduous dominated (DDOM) and deciduous dominated with a spruce understory (DDOMU) stands.

Species	Study	Present in 2013
B. flavifrons	Cartar (2005) Pengelly and Cartar (2010)	Yes
B. mixtus	Cartar (2005) Pengelly and Cartar (2010)	Yes
B. perplexus	Cartar (2005) Pengelly and Cartar (2010)	Yes
B. rufocinctus	Pengelly and Cartar (2010)	Yes
B. sylvicola	Cartar (2005) Pengelly and Cartar (2010)	No
B. terricola	Cartar (2005) Pengelly and Cartar (2010)	Yes
B. vagans	Cartar (2005) Pengelly and Cartar (2010)	Yes

Table A.13: Abundance of each bee species caught by net and pan traps in the EMEND landscape prior to standardization with total species richness (s) and abundance (a) given for each family and genus. Bees from sampling described in Chapter 2 were caught in clearcut, 20% retention, 50% retention, and control compartments in DDOM and CDOM stands in 2013 (Table A.1). Additional bee abundance data come from captures in DDOMU and MIXED control compartments in 2013 and sites sampled in 2012 (control compartments (DDOM, DDOMU, MIXED, CDOM), 50% retention compartments (853, 863, 898, 929, 953), clearcut compartments (892, 941), burn compartments (926, 943), a slash-harvest burn compartment (9251), roadsides, pan traps at the EMEND camp in 2012). Melittidae was identified to the family level, *Colletes* and *Protandrena* were identified to genus, and *Lasioglossum* was identified to subgenus. A few specimens (*) could not be identified to species and were not included in the species totals or analyses. Taxon names to genus level follow Michener (2007).

Family	Genus	Species	DDOM/CDOM Harvest (Chapter 2)	Additional Bee Abundance	Total Abundance
Colletidae (3s,10a)	*Colletes* (1s,1a)	*Colletes sp.*	1	0	1
	Hylaeus (2s,9a)	*H. annulatus*	5	0	5
		H. modestus	4	0	4
Andrenidae (7s,30a)	*Andrena* (6s,24a)	*A. algida*	9	0	9
		A. canadensis	1	0	1
		A. frigida	3	0	3
		A. nigrihirta	4	0	4
		A. nivalis	2	0	2
		A. thaspii	5	0	5
	Protandrena (1s,6a)	*Protandrena sp.*	6	0	6
Halictidae (5s,19a)	*Halictus* (2s,3a)	*H. rubicundus*	1	0	1
		H. confusus	2	0	2
	Lasioglossum (3s,16a)	*L. (Dialictus)* spp.	5	1	6
		L. (Evylaeus) spp.	3	1	4
		L. (Lasioglossum) spp.	6	0	6
Melittidae (1s,2a)			2	0	2
Megachilidae (22s,263a)	*Hoplitus* (2s,13a)	*H. albifrons*	8	0	8
		H. producta	5	0	5
	Osmia (3s,40a)	*O. bucephala*	15	4	19
		O. proxima	0	1	1
		O. simillima	19	1	20
	Anthidium	*A. clypeodentatum*	2	0	2

	(1s,2a)				
	Stelis (3s,3a)	*S. foederalis*	1	0	1
		S. nitida	1	0	1
		S. subemarginata	1	0	1
	Ceolioxys (3s,9a)	*C. funeraria*	4	0	4
		C. porterae	3	1	4
		C. sodalis	1	0	1
	Megachile (10s,196a)	*M. brevis*	1	0	1
		M. circumcincta	8	0	8
		M. frigida	11	3	14
		M. gemula	5	0	5
		M. inermis	64	7	71
		M. lapponica	1	0	1
		M. melanophaea	6	0	6
		M. pugnata	1	0	1
		M. relativa	79	1	80
		M. rotundata	7	0	7
		*M. relativa/lapponica**	2	0	2
Apidae (19s,774a)	*Eucera* (1s,1a)	*E. frater*	1	0	1
	Anthophora (2s,51a)	*A. bomboides*	3	0	3
		A. terminalis	35	13	48
	Bombus (15s,678a)	*B. appositus*	0	1	1
		B. bifarus	1	0	1
		B. borealis	3	1	4
		B. fervidus	3	0	3
		B. flavidus	5	0	5
		B. flavifrons	141	135	276
		B. frigidus	6	3	9
		B. melanopygus	0	1	1
		B. mixtus	13	8	21
		B. nevadensis	2	0	2
		B. perplexus	2	10	12
		B. rufocinctus	62	0	62
		B. ternarius	7	0	7
		B. terricola	46	30	76
		B. vagans	95	100	195
		Unknown male *B. sp.**	0	3	3
	Apis (1s,44a)	*A. mellifera*	44	0	44
Total	**57 species**		**773**	**325**	**1098**

Table A.14: Abundance of each hoverfly species caught by net and pan traps in the EMEND landscape prior to standardization with total species richness (s) and abundance (a) given for each subfamily and genus. Hoverflies from sampling described in Chapter 2 were sampled in clearcut, 20% retention, 50% retention, and control compartments in DDOM and CDOM stands in 2013 (Table A.2). Additional hoverfliy abundance data come from captures in DDOMU and MIXED control compartments in 2013, and sites sampled in 2012 (control compartments (DDOM, DDOMU, MIXED, CDOM), 50% retention compartments (853, 863, 898, 929, 953), clearcut compartments (892, 941), burn compartments (926, 943), a slash-harvest burn compartment (9251), roadsides, pan traps at the EMEND camp in 2012). *Lejops*, *Heringia*, *Pipiza*, and *Platycheirus* were only identified to genus. A few specimens (*) could not be identified to species and were not included in the species totals or analyses. Taxon names follow Miranda et al. (2013).

Subfamily	Genus	Species	DDOM/CDOM Harvest (Chapter 2)	Additional Hoverfly Abundance	Total Abundance
Eristalinae	*Blera* (1s,1a)	*B. nigra*	1	0	1
	Brachyopa (1s,3a)	*B. notata*	2	1	3
	Chalcosyrphus (1s,2a)	*C. nemorum*	2	0	2
	Cheilosia (1s,3a)	*C. sialia*	2	0	2
		*C. sp.**	0	1	1
	Eristalis (7s,25a)	*E. anthophorina*	0	2	2
		E. bardus	0	2	2
		E. compactus	1	0	1
		E. dimidiatus	0	2	2
		E. hirta	0	1	1
		E. interrupta	4	4	8
		E. rupium	4	5	9
	Helophilus (4s,29a)	*H. fasciatus*	1	0	1
		H. hybridus	3	1	4
		H. intentus	1	1	2
		H. obscurus	13	9	22
	Lejops (1s,1a)	*L. (Anasimyia) sp.*	1	0	1
	Rhingia (1s,11a)	*R. nasica*	0	11	11
	Sericomyia (5s,18a)	*S. chalcopyga*	1	0	1
		S. chrysotoxoides	0	2	2

		S. lata	1	4	5
		S. militaris	0	8	8
		S. sexfasciata	0	2	2
	Temnostoma (3s,111a)	*T. alternans*	5	3	8
		T. balyras/obscurus	10	16	26
		T. excentrica	41	36	77
	Volucella (1s,2a)	*V. facialis*	2	0	2
	Xylota (9s,162a)	*X. analis*	0	1	1
		X. annulifera	5	12	17
		X. barbata	0	3	3
		X. confusa	3	0	3
		X. flavitibia	1	1	2
		X. flukei	0	1	1
		X. naknek	6	4	10
		X. quadrimaculata	1	0	1
		X. subfasciata	68	55	123
		*X. sp.**	0	1	1
	Total Eristalinae	**35 species**	**179**	**189**	**368**
Syrphinae	*Baccha* (1s,6a)	*B. elongata*	3	3	6
	Chrysotoxum (1s,22a)	*C. derivatum*	9	13	22
	Dasysyrphus (1s,2a)	*D. venustus*	2	0	2
	Doros (1s,1a)	*D. aequalis*	1	0	1
	Epistrophe (1s,37a)	*E. grossularia*	25	12	37
	Epistrophella (1s,2a)	*E. emarginata*	0	2	2
	Eupeodes (3s,8a)	*E. americanus*	1	3	4
		E. curtus	1	0	1
		E. luniger	0	3	3
	Heringia (1s,23a)	*Heringia* spp.	7	16	23
	Lapposyrphus (1s,4a)	*L. lapponicus*	4	0	4
	Leucozona (1s,2a)	*L. lucorum*	0	2	2
	Melangyna (3s,27a)	*M. fisherii*	0	1	1
		M. labiatarum/subfasciata	1	0	1
		M. umbellatarum	19	6	25
	Melanostoma (1s,16a)	*M. mellinum*	11	5	16
	Meliscaeva (1s,3a)	*M. cinctella*	2	1	3

	Paragus (1s,1a)	*P. haemorrhous*	1	0	1
	Parasyrphus (4s,5a)	*P. genualis*	2	0	2
		P. macularis	0	1	1
		P. relictus	0	1	1
		P. new sp. Thompsoni	1	0	1
	Pipiza (1s,8a)	*Pipiza* spp.	7	1	8
	Platycheirus (1s,44a)	*Platycheirus* spp.	37	7	44
	Scaeva (1s,3a)	*S. pyrastri*	3	0	3
	Sphaerophoria (1s,14a)	*S. philanthus*	11	3	14
	Syrphus (3s,97a)	*S. ribesii*	37	34	71
		S. torvus	1	0	1
		S. vitripennis	4	20	24
		*S. sp.**	0	1	1
	Unknown Syrphinae (4a)	*Unknown* spp.*	0	4	4
	Total Syrphinae	**29 species**	**190**	**139**	**329**
Total	**64 species**		**369**	**328**	**697**

Table A.15: Abundance of flowering plant species recorded in the EMEND landscape prior to standardization with total species richness (s) and abundance (a) given for each family and flower colour given for each species. Flowers recorded by sampling described in Chapter 2 were from clearcut, 20% retention, 50% retention, and control compartments in DDOM and CDOM stands in 2013 (Table A.6). Additional flower abundance comes from sampling in DDOMU and MIXED control compartments in 2013, and sites sampled in 2012 (control compartments (DDOM, DDOMU, MIXED, CDOM), 50% retention compartments (853, 863, 898, 929, 953), clearcut compartments (892, 941), burn compartments (926, 943), and a slash-harvest burn compartment (9251). Taxon names follow the USDA Natural Resource Conservation Service plant database (USDA, NRCS 2015).

Family	Species	Colour	DDOM/CDOM Harvest (Chapter 2)	Additional Flower Abundance	Total Abundance
Liliaceae (2s,266a)	*Maianthemum canadense*	White	187	36	223
	Maianthemum stellatum	White	43	0	43
Orchidaceae (3s,329a)	*Corallorhiza maculata*	Pink	47	0	47
	Goodyera repens	White	81	157	238
	Platanthera spp.	Green	12	32	44
Caryophyllaceae (1s,5a)	*Stellaria longifolia*	White	4	0	4
	Stellaria sp.	White	1	0	1
Ranunculaceae (2s,393a)	*Delphinium glaucum*	Purple	252	135	387
	Ranunculus macounii	Yellow	6	0	6
Saxifragaceae (3s,20a)	*Chrysoplenium tetrandum*	Green	0	3	3
	Mitella nuda	Green	4	3	7
	Parnassia palustris	White	10	0	10
Grossulariaceae (1s,10a)	*Rhibes oxyacanthoides*	White	10	0	10
Rosaceae (5s,852a)	*Fragaria* spp.	White	138	15	153
	Geum aleppicum	Yellow	12	0	12
	Potentilla norvegica	Yellow	7	0	7
	Rosa acicularis	Pink	479	120	599
	Rubus idaeus	White	60	21	81
Fabaceae (8s,8756a)	*Astragalus agrestis*	Purple	138	0	138
	Astragalus americanus	White	20	0	20
	Caragana arborescens	Yellow	18	0	18
	Lathyrus ochroleucus	White	151	13	164
	Melilotus alba	White	579	0	579
	Melilotus officinalis	Yellow	3209	0	3209
	Trifolium spp.	White	3968	86	4054
	Vicia americana	Purple	481	93	574

Balsaminaceae (1s,20a)	*Impatiens noli-tangere*	Yellow	20	0	20
Onagraceae (2s,2256a)	*Chamerion angustifolium*	Pink	266	1974	2240
	Circaea alpina	White	0	16	16
Apiaceae (1s,154a)	*Heracleum maximum*	White	152	2	154
Cornaceae (1s,3501a)	*Cornus canadensis*	White	2231	1270	3501
Pyrolaceae (3s,363a)	*Moneses uniflora*	White	40	21	61
	Orthilia secunda	Green	36	5	41
	Pyrola asarifolia	Pink	221	40	261
Ericaceae (2s,27a)	*Ledum groenlandicum*	White	13	4	17
	Vaccinium vitis-idaea	White	0	10	10
Polemoniaceae (1s,3a)	*Polemonium acutiflorum*	Blue	1	2	3
Boraginaceae (1s,184a)	*Mertensia paniculata*	Blue	97	87	184
Lamiaceae (2s,100a)	*Lycopus uniflorus*	White	0	1	1
	Mentha arvensis	Purple	0	99	99
Scrophulariaceae (1s,210a)	*Rhinanthus minor*	Yellow	210	0	210
Rubiaceae (2s,740a)	*Galium boreale*	White	563	174	737
	Galium triflorum	White	3	0	3
Caprifoliaceae (3s,776a)	*Linnaea borealis*	Pink	554	24	578
	Viburnum edule	White	194	3	197
	Viburnum opulus	White	1	0	1
Asteraceae (11s,2501a)	*Achillea millefolium*	White	494	104	598
	Achillea sirbirica	White	11	0	11
	Arnica sp.	Yellow	2	2	4
	Cirseum arvense	Purple	82	0	82
	Erigeron glabellus	Purple	14	0	14
	Eurybia sp.	Purple	217	1040	1257
	Packera paupercula	Yellow	4	0	4
	Solidago canadensis	Yellow	373	10	383
	Taraxacum officinale	Yellow	73	0	73
	Composite sp. 1	Yellow	36	11	47
	Composite sp. 2	Yellow	4	24	28
	Unknown White Flower	White	50	0	50
	Unknown White Branched Flower	White	14	0	14
	Unknown sp. 1		1	0	1
	Unknown sp. 2		1	0	1
	Unknown sp. 3		1	0	1
Total	**56 species**		**15896**	**5637**	**21533**

Table A.16: List of plant species seen at EMEND at permanent sample plots from 1998-2018. Betulaceae, Cyperaceae, Equisetaceae, Graminae, Juncaceae, Lycopodiaceae, Pinaceae, Polypodiaceae, Salicaceae, mosses and lichens have been excluded from the table.

Family	**Species**	**Family**	**Species**
Adoxaceae	*Adoxa moschatellina*	Ophioglossaceae	*Botrychium lunaria*
Araliaceae	*Aralia nudicaulis*	Ophioglossaceae	*Botrychium virginianum*
Balsaminaceae	*Impatiens capensis*	Orchidaceae	*Calypso bulbosa*
Balsaminaceae	*Impatiens noli-tangere*	Orchidaceae	*Corallorhiza maculata*
Boraginaceae	*Mertensia paniculata*	Orchidaceae	*Corallorhiza trifida*
Caprifoliaceae	*Linnaea borealis*	Orchidaceae	*Goodyera repens*
Caprifoliaceae	*Lonicera dioica*	Orchidaceae	*Habenaria hyperborea*
Caprifoliaceae	*Lonicera involucrata*	Orchidaceae	*Habenaria obtusata*
Caprifoliaceae	*Symphoricarpos albus*	Orchidaceae	*Habenaria orbiculata*
Caprifoliaceae	*Viburnum edule*	Orchidaceae	*Habenaria viridis*
Caryophyllaceae	*Moehringia lateriflora*	Polemoniaceae	*Polemonium acutiflorum*
Caryophyllaceae	*Stellaria calycantha*	Polygonaceae	*Rumex occidentalis*
Caryophyllaceae	*Stellaria longifolia*	Primulaceae	*Trientalis borealis*
Compositae	*Achillea millefolium*	Primulaceae	*Trientalis europaea*
Compositae	*Arnica chamissonis*	Pyrolaceae	*Moneses uniflora*
Compositae	*Arnica cordifolia*	Pyrolaceae	*Orthilia secunda (Pyrola secunda)*
Compositae	*Aster ciliolatus*	Pyrolaceae	*Pyrola asarifolia*
Compositae	*Aster conspicuus*	Pyrolaceae	*Pyrola chlorantha (P. virens)*
Compositae	*Cirsium arvense*	Ranunculaceae	*Actaea rubra*

Compositae	*Crepis tectorum*	Ranunculaceae	*Anemone canadensis*
Compositae	*Hieracium umbellatum*	Ranunculaceae	*Aquilegia brevistyla*
Compositae	*Petasites palmatus*	Ranunculaceae	*Delphinium glaucum*
Compositae	*Petasites sagittatus*	Ranunculaceae	*Ranunculus abortivus*
Compositae	*Petasites vitifolius*	Ranunculaceae	*Ranunculus gmelinii*
Compositae	*Senecio pauperculus*	Ranunculaceae	*Ranunculus lapponicus*
Compositae	*Solidago canadensis*	Ranunculaceae	*Ranunculus macounii*
Compositae	*Taraxacum officinale*	Ranunculaceae	*Thalictrum sparsiflorum*
Cornaceae	*Cornus canadensis*	Ranunculaceae	*Thalictrum venulosum*
Cornaceae	*Cornus stolonifera*	Rosaceae	*Amelanchier alnifolia*
Cruciferae	*Cardamine pensylvanica*	Rosaceae	*Fragaria vesca*
Elaeagnaceae	*Sherpherdia canadensis*	Rosaceae	*Fragaria virginiana*
Empetraceae	*Empetrum nigrum*	Rosaceae	*Geum macrophyllum*
Ericaceae	*Arctostaphylos uva-ursi*	Rosaceae	*Geum rivale*
Ericaceae	*Ledum groenlandicum*	Rosaceae	*Potentilla gracilis*
Ericaceae	*Oxycoccus microcarpus*	Rosaceae	*Potentilla norvegica*
Ericaceae	*Vaccinium caespitosum*	Rosaceae	*Rosa acicularis*
Ericaceae	*Vaccinium vitis-idaea*	Rosaceae	*Rubus arcticus (R. acaulis)*
Fumariaceae	*Corydalis aurea*	Rosaceae	*Rubus chamaemorus*
Gentianaceae	*Gentianella amarella*	Rosaceae	*Rubus idaeus*
Gentianaceae	*Halenia deflexa*	Rosaceae	*Rubus pubescens*
Geraniaceae	*Geranium bicknelli*	Rosaceae	*Sorbus scopulina*
Grossulariaceae	*Ribes glandulosum*	Rubiaceae	*Galium boreale*
Grossulariaceae	*Ribes hudsonianum*	Rubiaceae	*Galium triflorum*

Grossulariaceae	*Ribes lacustre*	Santalaceae	*Geocaulon lividum*
Grossulariaceae	*Ribes oxyacanthoides*	Saxifragaceae	*Chrysosplenium iowense*
Grossulariaceae	*Ribes triste*	Saxifragaceae	*Chrysosplenium tetrandrum*
Hydrophyllaceae	*Phacelia franklinii*	Saxifragaceae	*Mitella nuda*
Labiatae	*Dracocephalum parviflorum*	Scrophulariaceae	*Pedicularis labradorica*
Labiatae	*Mentha arvensis*	Scrophulariaceae	*Veronica americana*
Leguminosae	*Astragalus alpinus*	Umbelliferae	*Heracleum lanatum*
Leguminosae	*Astragalus americanus*	Umbelliferae	*Osmorhiza depauperata*
Leguminosae	*Lathyrus ochroleucus*	Umbelliferae	*Sium suave*
Leguminosae	*Trifolium hybridum*	Urticaceae	*Urtica dioica*
Leguminosae	*Trifolium pratense*	Valerianaceae	*Valeriana dioica*
Leguminosae	*Vicia americana*	Violaceae	*Viola adunca*
Liliaceae	*Disporum trachycarpum*	Violaceae	*Viola canadensis*
Liliaceae	*Maianthemum canadense*	Violaceae	*Viola palustris*
Liliaceae	*Smilacina stellata*	Violaceae	*Viola renifolia*
Liliaceae	*Smilacina trifolia*		
Onagraceae	*Circaea alpina*		
Onagraceae	*Epilobium angustifolium*		
Onagraceae	*Epilobium ciliatum*		
Onagraceae	*Epilobium palustre*		

Appendix B: Supplementary Figures

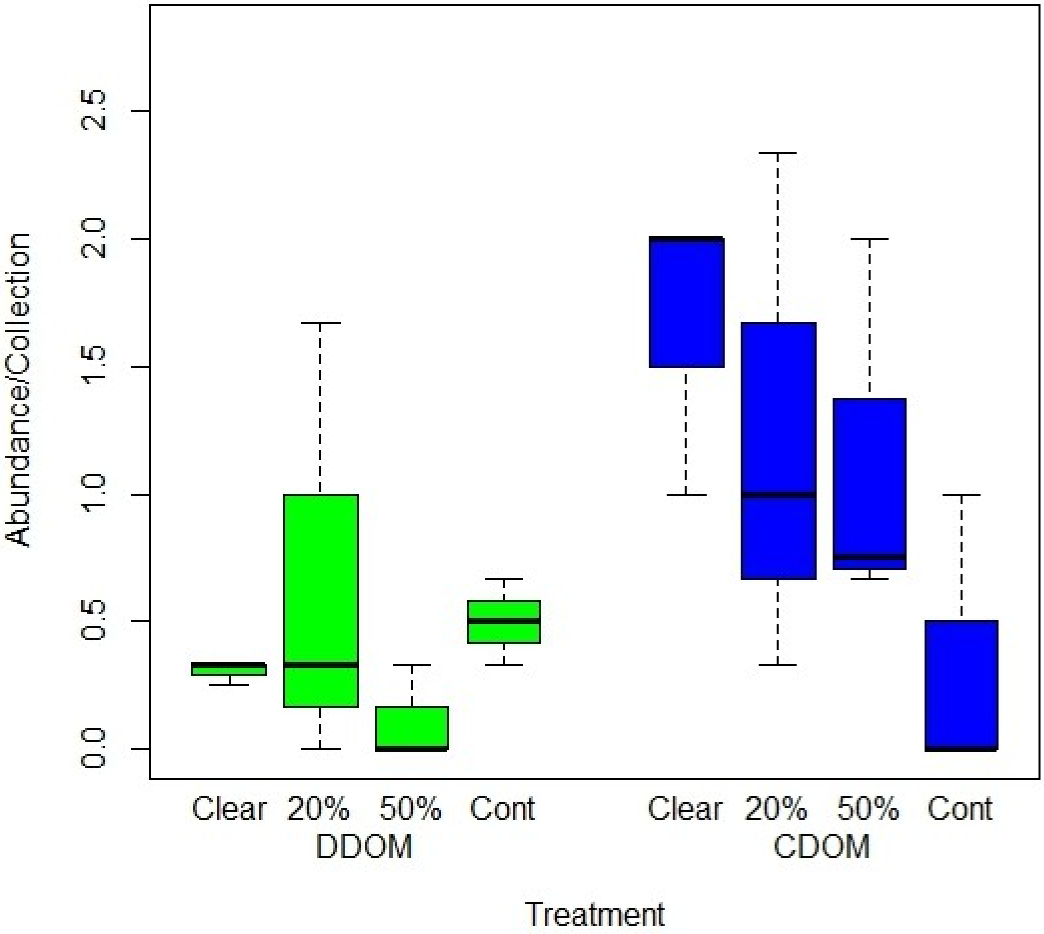


Figure B.1: Boxplot of the abundance of *Bombus* spp. caught by net (abundance/collection) in each harvest treatment. The central horizontal line is the median, the upper and lower edge of the boxes represent 1st and 3rd quartiles, respectively, and the whiskers represent data extremes. Significantly more bees were caught in CDOM compartments than DDOM compartments ($F_{(1,16)}$=7.45, *p*=0.016). (Clear= clearcut, 20%= 20% retention, 50%= 50% retention, Cont= control, DDOM= deciduous-dominated, CDOM= coniferous-dominated)

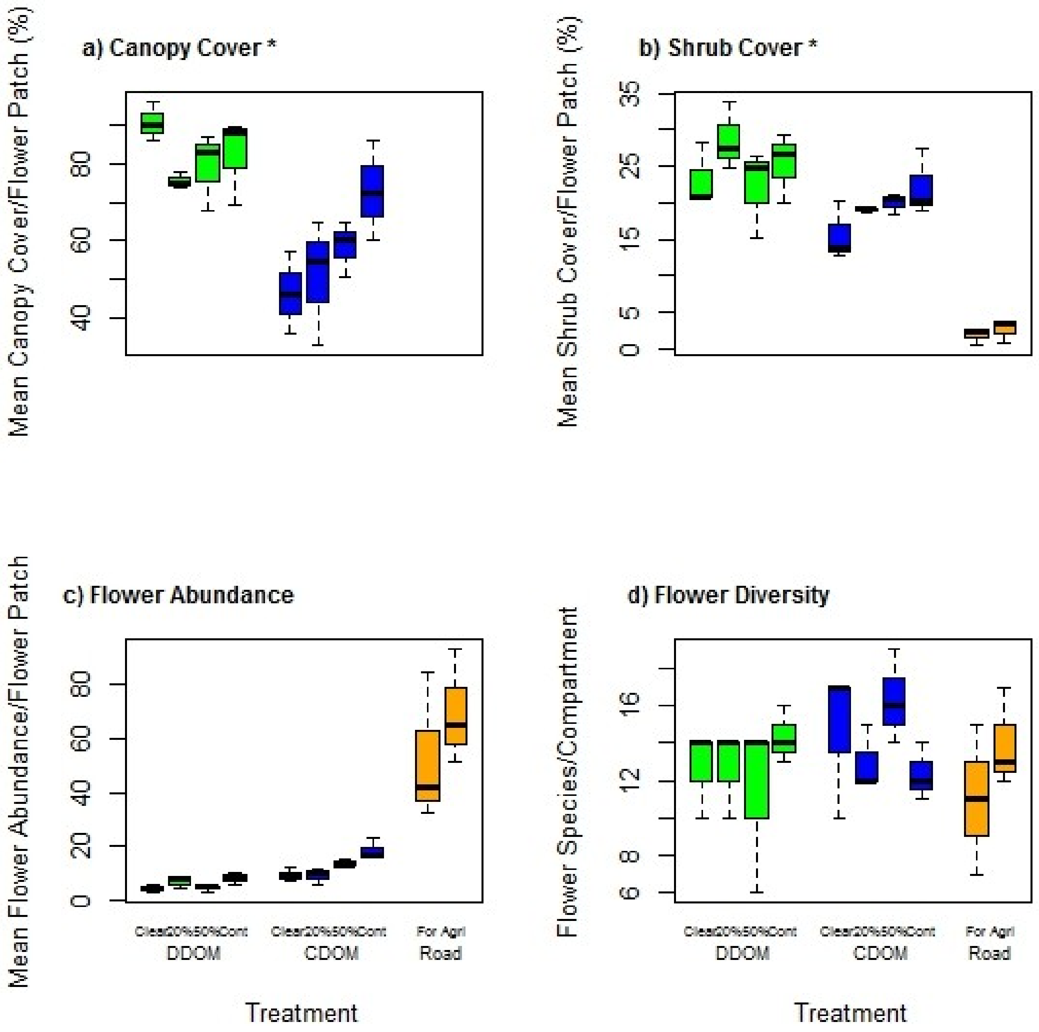


Figure B.2: Boxplots of percent canopy cover per flower patch (a), percent shrub cover per flower patch (b), flower abundance per flower patch (c), and flower species richness per compartment (d) in each harvest treatment. The central horizontal line is the median, the upper and lower edge of the boxes represent 1st and 3rd quartiles, respectively, and the whiskers represent data extremes. Significant differences between cover types (*p*≤0.05) are denoted by ***** (Table A.5). Differences in shrub cover and flower abundance between harvest treatments were not significant after a Bonferroni correction (Table A.6). (Clear= clearcut, 20%= 20% retention, 50%= 50% retention, Cont= control, DDOM= deciduous-dominated, CDOM= coniferous-dominated).

Appendix C: Effect of forest cover type on pollinator assemblages

Methods

Study Site

Field work was carried out at the Ecosystem Management Emulating Natural Disturbance (EMEND) study site located approximately 90km northwest of Peace River, Alberta, Canada. Located in the boreal mixedwood forest, EMEND encompasses four forest cover types: deciduous dominant (DDOM) in which over 70% of the trees in the canopy are deciduous, deciduous dominant with a spruce understory (DDOMU) in which over 70% of the trees in the canopy are deciduous over an understory of white spruce, mixedwood (MIXED) in which the canopy is composed of 40-60% spruce and aspen, and coniferous dominant (CDOM) in which over 70% of the trees in the canopy are coniferous. Harvesting treatments were applied during the winter of 1998/1999 by cutting machine corridors through each 10 ha block and then removing trees from the retention strips to reach the desired level of retention: clearcut, 10%, 20%, 50%, 75%, and unharvested control stands. Each treatment was replicated three times in each forest cover type.

Sampling Procedure

Pollinators were sampled at EMEND during the summer of 2012 and 2013 using both net capture and pan traps. We sampled control stands from all four forest cover types in both years of the study. In 2012, sampling began on July 4 and was completed August 29. In 2013, sampling began on May 31 and was completed on August 15.

In 2012, I sampled each stand three times by net. However, methods were changed and some stands were sampled twice during the first collection so only the last two collections were analyzed (July 25- August 29). Net capture was carried out in pairs by stopping at flower patches that fell along the baseline transects that ran through each compartment and catching all pollinators that flew into the flower patch during a five minute period. The first and last 10m of the baseline were excluded to reduce any edge effect with other compartments and trails. A flower patch was defined as having at least two species of flowers and at least five individuals and the size of the patch was a diamond with a length of 1.5m on each side (Figure C.2a). Sampling in each compartment continued for an hour plus an additional five minutes for each patch that we stopped at to account for the processing of caught insects or until the far edge of the compartment was reached. Net capture methods were changed in 2013 to increase efficiency and to increase the number of flower patches visited. In 2013, each person sampling pollinators worked separately to stop at flower patches adjacent to the baseline. Flower patches were considered regardless of the number of species or abundance and the shape of the patch was a half-circle with a diameter of 3m (Figure C.1b). Sampling in each compartment continued for an hour regardless of how many flower patches were sampled and whether the boundary was reached. We sampled all stands three times throughout the season except stand 852 which was sampled a fourth time early in the season. We killed insects caught by net using ethyl acetate and placed them in glassine envelopes to be pinned within a couple days.

Pan traps were constructed using 4oz Solo© translucent polystyrene soufflé portion cups that were subsequently painted white (Tremclad® semi-gloss white high-performance rust-enamel), yellow (Rona© fluorescent yellow), and blue (Devflex™ HP semi-gloss high performance waterborne acrylic from Dulux 42076 150000). Pan traps were placed in a line adjacent to the two EMEND permanent sample plots (PSPs) closest to the centre of the compartment to avoid edge effects. Each line of traps was placed approximately 5m south of the west end of the PSP and ran directly east. All traps were a minimum of 10m from the nearest compartment edge. A line of pan traps was created using thirty traps placed in ten groups of three traps (one of each colour) with each group separated by a 3m interval (Figure C.1c). In 2012, the traps were filled 2/3 full with soapy water and, in collection 2 and 3, boric acid as a preservative. These traps were set out by 10am and retrieved after 4pm and retrieved the next day (Collection 1) or two days later (Collection 2 and 3). In 2013, traps were filled 2/3 with propylene glycol and retrieved one week later to catch more pollinators than the previous year. Some ethylene glycol was also accidentally mixed in with the propylene glycol. Glycol was re-used throughout the season with new glycol added as needed to prevent the glycol from becoming too diluted from rainfall. We placed insects caught by pan traps in vials full of ethanol. Subsequently in the lab, we washed and dried bees (Droege 2015) and gave hoverflies a bath in ethyl acetate to facilitate identifications. Each stand was sampled three times in 2012 and four times in 2013.

Analysis

The taxonomy used in this study follows that of Michener (2007) for bees, Miranda et al. (2013) for hoverflies and the USDA plant database (USDA, NRCS 2015) for flowers. I identified pollinators to species with the exception of *Colletes*, *Mellisodes*, *Protandrena*, *Platycheirus*, *Pipiza*, and *Heringia* which were identified to genus and *Lasioglossum* which was identified to subgenus. Some hoverfly individuals could not be identified to species and these were not included in analyses abundance or richness. In addition to analyzing total hoverfly abundance, the assemblages of Eristalinae and Syrphinae were analyzed separately due to differences in larval life history.

Analysis was performed using R (version 3.1.1) using $\alpha=0.05$ to define significance throughout. We analyzed pollinators caught by net and pan trap separately to avoid confounding results due to different methodologies. The abundance of netted pollinators was standardized among sites by dividing their respective abundances by the number of times each site was sampled. Catches from pan traps at each site were standardized by dividing the abundance by the number of days that traps were left out at each site.

To analyze differences in abundance among cover types, between years and due to a cover type by year interactions, I performed perANOVA tests using adonis. Separate analyses were conducted for abundance of aall bees (Apoidea), all hoverflies (Syrphidae) and for Eristalinae and Syrphidae, separately. After applying Hellinger distances to abundance data (Legendre and Gallagher 2001), I also created constrained ordinations using a redundancy analysis (RDA) to explore variation in pollinator assemblages among the four forest cover types. Standardized pollinator abundance was contrained by forest cover type and year using the rda function in the Vegan package and the adjusted R^2 value for each model was obtained using the function RsquareAdj, also from the Vegan package. Eigenvalues and the percent data explained by them were obtained using the summary function and examining the importance of components and proportion explained for RDA1 and RDA2. Separate ordinations were done for assemblages of Apoidea, Syrphidae, Eristalinae, and Syrphinae.

Total species richness of bees and hoverflies, separately, was compared among forest cover types by combining data from both net capture and pan trap samples. Additionally, species richness at equal sample coverage (sample completeness) was compared among forest cover types for each sampling method following Chao et al. (2014) using iNEXT and ggiNEXT in the iNEXT package in R with Hill number set to q=0 (representing species richness). Hill numbers support easy comparison of different measures of species diversity (Chao et al. 2014). Raw abundance data were used for this analysis since calculations require integers.

Results

I caught 158 bees from at least 16 different species (Table C.1). Of the total abundance, all but three individuals (98.1%) were long-tongued bees with 90.5% of the total belonging to a single genus (*Bombus* sp.). In addition, I caught 213 hoverflies from at least 38 species (Table C.2). Hoverflies were represented somewhat equally by two subfamilies: Eristalinae and Syrphinae. I caught 126 hoverflies (59.2%) from 22 species belonging to the subfamily Eristalinae. I also caught 87 individuals (40.3%) from at least 15 species belonging to the subfamily Syrphinae. The most abundant genera of hoverflies were

Xylota spp. (71 individuals (32.9%)), *Temnostoma spp.* (33 individuals (15.3%)), and *Syrphus spp.* (20 individuals (9.3%)).

More pollinators were caught by pan traps than by net capture. More than twice as many bees were caught by pan traps than net capture (107 vs. 51 bees). Additionally, 8 species were caught exclusively by pan traps while only 1 species was caught exclusively by net capture. More hoverflies were also caught by pan traps than net capture with nearly three times as many hoverflies (160 vs. 53), more than three times as many Eristalinae (99 vs. 27), and more than twice as many Syrphinae (61 vs. 26) caught by pan traps. More species were caught exclusively by pan trap than net capture with 19 species (11 Eristalinae and 8 Syrphinae) caught exclusively by pan traps and 10 species (7 Eristalinae and 3 Syrphinae) caught exclusively by net capture.

Pollinator abundance differed between sampling years, especially for pan trap data (Figure C.2, Table C.3). More bees were caught in 2012 than in 2013 (101 vs. 57) for both sampling methods (Net: 35 vs. 16, $F_{(1.16)}$=4.80, p=0.030, Pan: 66 vs. 41, $F_{(1,16)}$=11.2, p=0.004). However, 11 species of bees were caught in each year with 4 species exclusively caught in each year. While more Eristalinae were caught in 2012 than in 2013 (67 vs. 59), the total abundance of hoverflies (110 vs. 103) and the abundance of Syrphinae (51 vs. 36) was higher in 2013 than 2012. However, the same trends were not found for each sampling method for hoverflies. While not statistically significant, more total hoverflies (40 vs. 13, $F_{(1,16)}$= 2.75, p= 0.114), Eristalinae (23 vs. 4, $F_{(1,16)}$= 2.92, p=0.105), and Syrphinae (17 vs. 9, $F_{(1,16)}$= 0.169, p=0.721) were caught by net capture in 2013 than in 2012. For pan traps, more total hoverflies (90 vs. 70, $F_{(1,16)}$= 8.55, p=0.008) and Eristalinae (63 vs. 36, $F_{(1,16)}$= 11.2, p=0.007) were caught in 2012 than in 2013, while more Syrphinae were caught in 2013 (34 vs. 27, $F_{(1,16)}$=2.06 , p=0.128). A similar number of species of hoverflies were caught in each year (2012: 21 sp., 2013: 22 sp.) with 6 species caught exclusively in 2012 and 13 species caught exclusively in 2013.

Hence, sampling with both techniques and over multiple years is essential to completely characterize pollinator communities, especially for hoverflies.

Effect of Forest Cover Type

Forest cover type did not have a statistically significant effect on pollinator abundance (Figure C.2, Table C.3). Assemblages of pollinators also did not differ among cover types, as indicated by the lack of significance of the RDA models (overall and the influence of cover type) (Table C.4).

In contrast, species richness differed between forest cover types. For bees, CDOM compartments had the highest total observed species richness (with 11 species) with 5 species caught exclusively in these compartments (Figure C.3a). DDOM and MIXED compartments each had 7 species, with 2 species caught exclusively in MIXED compartments, and DDOMU compartments had 6 species. Likewise, CDOM compartments also had the highest species richness of hoverflies (27 species) with 9 species caught exclusively in this forest cover type (Figure C.3d). DDOM and DDOMU compartments each had 17 species (4 caught exclusively in DDOM compartments and 5 caught exclusively in DDOMU compartments) and MIXED compartments had 14 species, one of which was caught exclusively in this cover type.

However, species richness did not differ significantly between most forest cover types when compared at equal sample coverage for either sampling method (Figure C.3b,c,e,f). The coverage-based rarefaction analysis suggested that species richness of hoverflies caught by net was greater in CDOM compartments than other forest cover types (Figure C.3e). Additionally, it suggested species richness of bees caught by net was greater in DDOMU compartments, although only three individuals were caught by net in this cover type (Figure C.3b).

Tables

Table C.1: Abundance of each species of bee caught by net and by pan trap in control compartments prior to standardization. *Lasioglossum* was only identified to subgenus. Taxon names to genus level follow Michener (2007).

Family	Genus	Species	Abundance caught by Net Capture	Abundance Caught by Pan Trap	Total Abundance
Andrenidae	*Andrena*	*A. nivalis*	0	1	1
Halictidae	*Lasioglossum*	*L. (Evylaeus) spp.*	0	1	1
		L. (Lasioglossum) spp.	0	1	1
Megachilidae	*Osmia*	*O. bucephala*	0	2	2
		O. proxima	0	1	1
		O. simillima	0	2	2
	Megachile	*M. inermis*	1	2	3
		M. relativa	1	0	1
Apidae	*Anthophora*	*A. terminalis*	0	3	3
	Bombus	*B. borealis*	0	1	1
		B. flavifrons	16	67	83
		B. mixtus	2	7	9
		B. perplexus	4	1	5
		B. terricola	1	5	6
		B. vagans	26	13	39
Total			**51**	**107**	**158**

Table C.2: Abundance of each species of hoverfly (Syrphidae) caught by net and pan trap in control compartments prior to standardization. *Heringia*, *Pipiza*, and *Platycheirus* were only identified to genus. Some individuals (*) could not be identified to species and were not included in total abundance or richness analyses. Taxon names follow Miranda et al. (2013).

Subfamily	Genus	Species	Abundance Caught by Net Capture	Abundance Caught by Pan Trap	Total Abundance
Eristalinae	*Brachyopa*	*B. ferruginea*	1	0	1
		B. notata	0	2	2
	Eristalis	*E. hirta*	1	0	1
		E. interrupta	1	0	1
		E. rupium	3	0	3
	Helophilus	*H. hybridus*	0	1	1
	Rhingia	*R. nasica*	1	0	1
	Sericomyia	*S. chalcopyga*	1	0	1
		S. chrysotoxoides	0	1	1
		S. lata	0	1	1
		S. militaris	1	6	7
		S. sexfasciata	0	2	2
	Temnostoma	*T. alternans*	2	0	2
		T. balyras/obscurus	2	14	16
		T. excentrica	13	2	15
	Xylota	*X. analis*	0	1	1
		X. annulifera	0	6	6
		X. barbata	0	3	3
		X. flukei	0	1	1
		X. naknek	0	2	2
		X. quadrimaculata	0	1	1
		X. subfasciata	1	56	57
	Total Eristalis		**27**	**99**	**126**
Syrphinae	*Baccha*	*B. elongata*	0	3	3
	Chrysotoxum	*C. derivatum*	5	6	11
	Epistrophe	*E. grossularia*	3	2	5
	Eupeodes	*E. americanus*	0	1	1
	Heringia	*Heringia* spp.	0	16	16
	Lapposyrphus	*L. lapponicus*	2	0	2
	Melangyna	*M. fisherii*	0	1	1
		M. umbellatarum	2	0	2
	Melanostoma	*M. mellinum*	0	9	9
	Meliscaeva	*M. cinctella*	1	0	1
	Pipiza	*Pipiza spp.*	0	1	1
	Platycheirus	*Platycheirus* spp.	3	12	15

	Syrphus	*S. ribesii*	8	8	16
		S. vitripennis	2	2	4
		S. sp.*	0	1	1
	Unkown Syrphinae	Unknown spp.*	0	2	2
	Total Syrphinae		**26**	**61**	**87**
Total			**53**	**160**	**213**

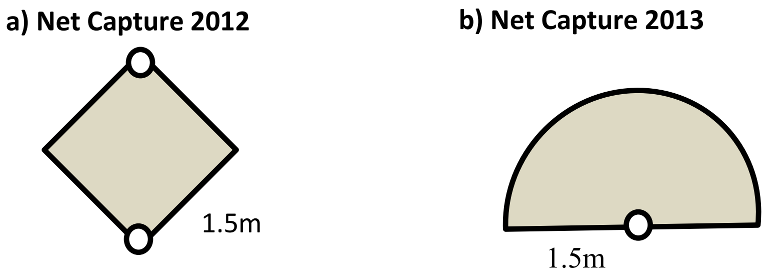
Table C.3: Permutational Analysis of Variance (perANOVA) results showing the effect of forest cover type and year on the abundance of Apoidea, Syrphidae, Eristalinae, and Syrphidae caught by net capture and pan trap. Results with a p-value less than 0.05 are considered significant and shown in bold.

Net Capture						
	Cover		Year		Cover * Year	
	F value	P value	F value	P value	F value	P value
Apoidea	2.16	0.107	**4.80**	**0.030**	1.77	0.156
Syrphidae	2.16	0.125	2.75	0.114	0.755	0.532
Eristalinae	1.55	0.207	2.92	0.105	0.502	0.723
Syrphinae	1.78	0.182	0.169	0.721	0.585	0.692
Pan Trap						
	Cover		Year		Cover * Year	
	F value	P value	F value	P value	F value	P value
Apoidea	1.44	0.249	**11.2**	**0.004**	1.41	0.294
Syrphidae	1.31	0.301	**8.55**	**0.008**	0.880	0.473
Eristalinae	1.13	0.378	**11.2**	**0.007**	0.722	0.550
Syrphinae	1.02	0.412	2.06	0.128	0.861	0.533

Table C.4: Redundancy analysis (RDA) showing the effect of forest cover type and year on assemblages of Apoidea, Syrphidae, Eristalinae, and Syrphinae. Results with a p-value less than 0.05 are shown in bold. Eigenvalues are included for the first two axes (RDA 1 and 2) along with the corresponding proportion of the explained variation that is due to each axis.

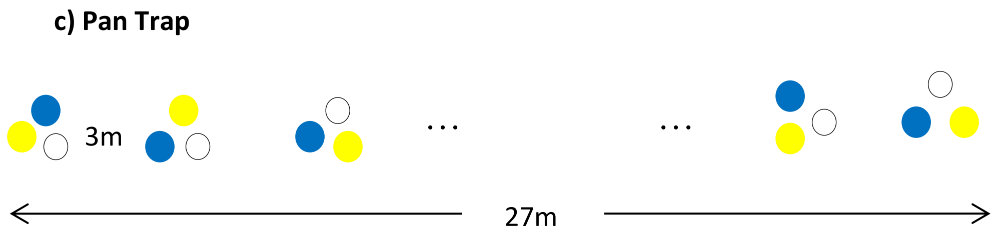
Net Capture											
	Model		Cover		Year		Cover * Year		R^2 Model	Eigenvalues	
	F value	P value	F value	P value	F value	P value	F value	P value	Adj. R^2	RDA 1	RDA 2
Apoidea	1.35	0.189	2.03	0.064	1.23	0.280	0.700	0.703	0.0954	0.0907 (64.5%)	0.0293 (20.8%)
Syrphidae	1.25	0.085	1.15	0.248	**1.77**	**0.050**	1.19	0.201	0.0714	0.0899 (42.8%)	0.0382 (18.2%)
Eristalinae	1.35	0.055	1.07	0.318	**3.08**	**0.007**	1.07	0.332	0.0973	0.0837 (52.7%)	0.0295 (18.6%)
Syrphinae	1.37	0.071	1.36	0.127	1.02	0.421	1.49	0.073	0.101	0.0904 (44.1%)	0.0526 (25.7%)
Pan Trap											
	Model		Cover		Year		Cover * Year		R^2 Model		
	F value	P value	F value	P value	F value	P value	F value	P value	Adj. R^2	RDA 1	RDA 2
Apoidea	0.885	0.632	0.820	0.639	1.63	0.131	0.704	0.799	-0.0362	0.0604 (44.9%)	0.0400 (29.7%)
Syrphidae	1.07	0.327	0.869	0.713	**2.49**	**0.004**	0.793	0.830	0.0202	0.0751 (36.5%)	0.0424 (20.6%)
Eristalinae	0.844	0.773	0.737	0.836	1.40	0.167	0.768	0.794	-0.0499	0.0434 (36.0%)	0.0277 (23.0%)
Syrphinae	1.07	0.383	0.904	0.593	**2.75**	**0.010**	0.671	0.865	0.0201	0.0925 (43.4%)	0.0686 (32.2%)

Figures



a) Net Capture 2012

b) Net Capture 2013



c) Pan Trap

Figure C.1: Diagram of a) flower patch sampling approach for net capture in 2012 with field technicians standing on opposite corners of a diamond with sides that measure 1.5m b) flower patch sampling approach for net capture in 2013 with a field technician standing at the centre of a half circle of radius 1.5m and c) set-up of 30 pan traps as ten sets of groups of 3 at 3m intervals for a total length of 27m.

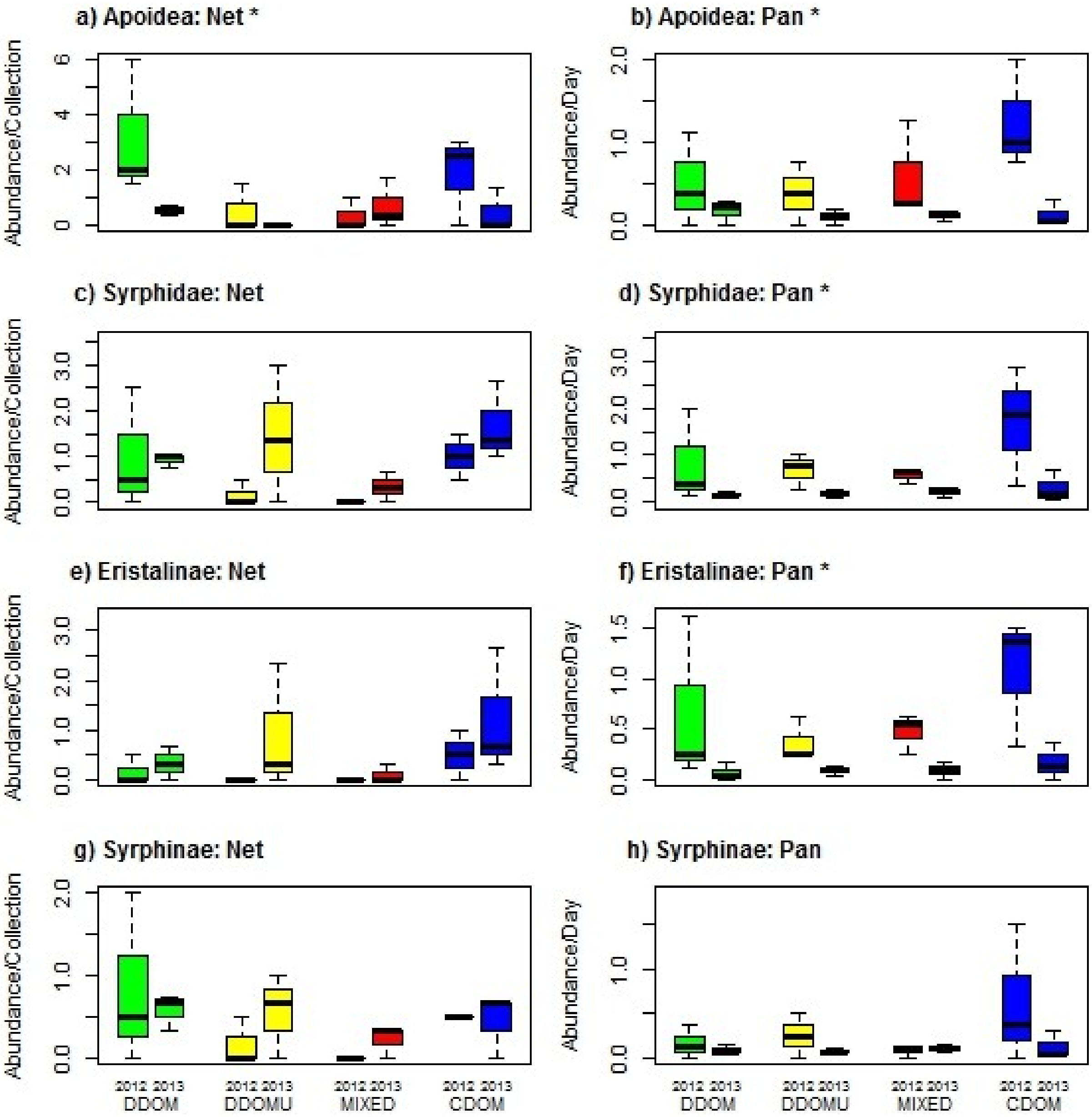


Figure C.2: Boxplot of the abundance of all bees (a-b), all hoverflies (c-d), Eristalinae (e-f), and Syrphinae (g-h) caught by net (abundance/collection) and by pan trap (abundance/day) in each forest cover type. The central horizontal line is the median, the upper and lower edge of the boxes represent 1st and 3rd quartiles, respectively, and the whiskers represent data extremes. Pollinators were sampled in undisturbed control compartments. Significant differences in sampling year ($p \leq 0.05$) are denoted by * (Table C.3). (DDOM= deciduous-dominated, DDOMU=deciduous-dominated with spruce understory, MIXED= mixedwood, CDOM=coniferous-dominated). There were no significant differences among cover types.

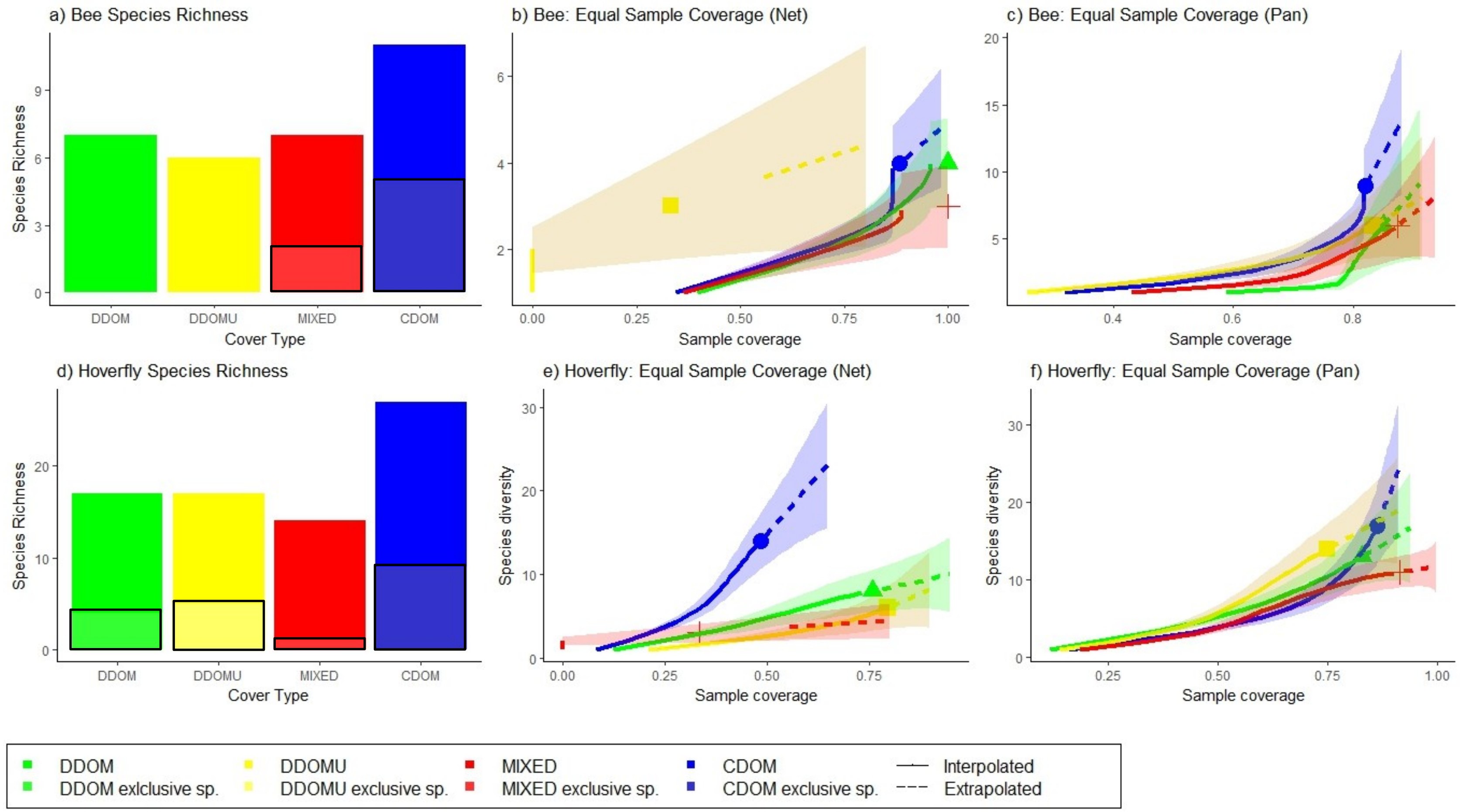


Figure C.3: Species richness of bees (a-c) and hoverflies (d-f) in control compartments of each forest cover type represented by both raw species richness using the combined number of species observed by net capture and pan traps and including the number of species exclusive to each treatment (a,d) and coverage-based rarefaction curves of species richness (q=0) for pollinators caught by net capture (b,e) and pan traps (c,f) with 95% confidence intervals.