Pollinator biodiversity and interaction networks in anthropogenic systems – roadside verges and transmission line easements as pollinator habitat in Manitoba, Canada

By

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ABSTRACT

The loss of natural and semi-natural habitats resulting from human activities is a global driver of wild pollinator declines and disruption of mutualistic plant-pollinator networks. Despite the negative effects of landscape conversion on biodiversity, green spaces within anthropogenic systems – including road verges, powerline easements, crop margins, and city parks – may be managed to serve as refuge habitats for insect pollinators. Road and powerline rights-of-way (ROWs) are widespread, long linear areas that connect and intersect multiple habitats, and are composed of vegetation that is continuously maintained in an early-successional state. Successful management requires detailed ecological information, but significant gaps exist in understanding how ROWs can benefit plant-pollinator communities and interactions. I investigated the effects of various local and landscape-level variables on pollinator communities and plant-pollinator networks within ROWs across sub-taiga Manitoba, Canada, to inform management for conserving wild pollinators and network functionality. Over two years, I recorded 9,190 bees, flies, and wasps foraging on flowers within 18 road verges and along a 300 km section of a major north-south powerline easement. Using generalized linear mixed-effects models, I found that blooming plant richness and abundance had positive effects on pollinator biodiversity in the powerline, but not in the roadsides, possibly due to the weedy nature of the latter. ROWs located within landscapes with a greater proportion of natural or semi-natural land hosted greater biodiversity. I found contrasting effects of landscape diversity, which had positive effects on pollinator biodiversity in the road verges, but negative effects in the powerline. The latter effect was region-dependent, probably due to the different identity of the dominant land-cover types between ecoclimatic regions. Finally, I found that integrated vegetation management allowed the powerline ROW to host more biodiverse and robust pollination networks. My results show that roadside verges and powerline easements in Manitoba are harbouring significant biodiversity of insect pollinators, including several rare or uncommon species that were previously unknown from the province, and one which had never been described before. My findings confirm that these ROWs have a considerable conservation potential, as they can host biodiverse and resilient plant-pollinator communities within Manitoba's disturbed and homogeneous landscapes.

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*with permission from the museum curator

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INTRODUCTION

In this thesis, I investigate the role of roadside verges and transmission line easements as habitats for insect pollinators in Manitoba, Canada, and evaluate their potential for the conservation of these animals and the ecosystem service they provide. My thesis is composed of four chapters. The first chapter is a literature review where I explore insights from past publications on the relationships that insects (with particular attention towards pollinators) have with road and powerline rights-of-way (ROWs). The second chapter is a research manuscript that focuses on quantifying the pollinator biodiversity that is found along roadside verges in south-eastern Manitoba. In this chapter, I explore the effects of local (flowering plant richness and abundance) and landscape-level (e.g., forested area, disturbed area, and landscape diversity) variables on the pollinator biodiversity within the verges. Concurrently, this manuscript focuses on testing and evaluating a roadside survey methodology that could be applied at a large scale for the monitoring of pollinator populations. Chapter three is the second research manuscript, which focuses on measuring the pollinator biodiversity found within a major powerline corridor in Manitoba. In this chapter, I explore the effects that local and landscape variables have both on pollinator biodiversity as well as on the size, structure (connectance, nestedness, modularity, and specialization) and stability (using plant extinction simulations) of pollination networks in the easement. Finally, chapter four, consists of a general conclusion to the thesis where I explore the implications of my findings.

The objectives of this thesis are:

i. Document the biodiversity of flower-visiting bees, wasps, and flies within roadside verges and powerline easements in sub-taiga Manitoba.

- ii. Determine what environmental variables at the local and landscape-scale are affecting pollinator biodiversity and plant-pollinator network structure and stability in these rights-of-way (ROWs).
- iii. Gather insights from my findings as well as from past research to provide informed suggestions for ROW vegetation management for pollinator conservation.

Based on the published literature reviewed in chapter one, I expect to find significant pollinator biodiversity within the surveyed ROWs. I predict that pollinator abundance and rarefied richness will respond positively to increased flowering plant biodiversity as well as to lower-intensity management strategies such as integrated vegetation management (IVM). I expect that landscape effects on pollinators will be weaker, however, I predict a positive effect of landscape heterogeneity on insect biodiversity. I also predict that the amount of natural area in the surrounding landscape (forest and meadow) will positively influence the pollinator abundance and richness in the ROWs. Finally, I predict that vegetation management strategy will have a strong impact on pollination networks, with IVM sites hosting larger and more robust webs.

CHAPTER 1. LITERATURE REVIEW

1.1 Pollination Ecology of Bees, Wasps, and Flies

Bees (Hymenoptera: Apoidea: Anthophila) are a monophyletic insect clade that originated approximately 123 million years ago, most likely from within the apoid wasp family Crabronidae, coinciding with the diversification of flowering plants (Michener 2007; Cardinal and Danforth 2013). Bees are dependent on floral resources (pollen, nectar, and for some species oils) for nutrition. Nectar contains sugars and is the main source of carbohydrates for bees. It is an energy source for adults and is mixed with pollen to make larval food (Michener 2007). For the vast majority of bees, pollen is the main protein source. It is carried to the nest to be used as larval food and is also consumed by egg-producing adult females (Michener 2007). Nest-building females have morphological and behavioural adaptations for collecting and transporting pollen from flowers to their nest, including hairs (usually plumose) which cover their head, bodies, and legs that are used for pollen transport (Portman et al. 2019). While foraging, bees disperse pollen between intraspecific flowers, aiding plant sexual reproduction. Approximately 87% of all angiosperm species reproduce with the aid of insects, the majority and most effective of which are bees (Ollerton et al. 2011). Bees pollinate garden flowers, fruits, vegetables, fibre crops such as flax and cotton, and forage crops including alfalfa and clover (Michener 2007). These insects, provide a huge global ecosystem service, valued at about €153 billion (~\$170 billion) (Gallai et al. 2009).

Over 20,000 bee species have been recorded worldwide (Orr et al. 2021) and over 800 in Canada (Canadian Endangered Species Conservation Council 2016). Six of the seven extant bee families have been recorded in Manitoba: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae. Only a single melittid species, *Macropis nuda* (Provancher), has been observed in Manitoba (Gibbs et al. 2021). Bees have a great variety of nesting and provisioning behaviours as well as social structures. All nest-building bees are central-place foragers, returning repeatedly to their nests to provision enough pollen and nectar for their larvae (Michener 2007). The vast majority of species burrow into the ground to build their nests, others nest in cavities or stems or build nests attached to various surfaces (Michener 2007; Packer et al. 2007). In terms of sociality, most bees are solitary, with single females individually laying eggs in

nests built by themselves, replenishing them with nectar and pollen (Michener 1974, Danforth et al. 2019). Solitary nests can be found in aggregations. Communal living instead involves multiple females independently laying eggs and provisioning cells in a common nest that is defended collectively. Subsociality occurs when the species produces larvae that require parental care, but there is no division of labour. Eusociality involves the production of worker daughters by a single fertile queen. The workers provision and defend the nest and tend to their queen and hatching siblings. Some bee lineages such as the genera *Nomada* and *Sphecodes* perform brood parasitism (kleptoparasitism), laying their eggs in solitary bee nests, while social parasites such as *Bombus* (*Psithyrus*) bumblebees lay their eggs in social colonies, which are subsequently taken over (Michener 2007).

Nest-building bees stock their nests with pollen and nectar from a diversity of flowering plants. Some species are generalists, visiting flowers of many species, while others specialize on pollen from one (monolectic) or a few (oligolectic) plant species (Packer et al. 2007; Sheffield et al. 2014). Generalist bee species such as *Apis* and *Bombus* species may show a behaviour called 'floral constancy', where, during a single trip or an extended period of time, individuals preferentially visit flowers of the same species (Michener 2007, Brosi 2016). Bee floral lecty (specialization) may be due to the species' phenological or morphological constraints, floral constancy on the other hand can vary between individuals of the same species at the same time and location, and may change based on floral resource availability and distribution (Brosi 2016). The most likely determinant of floral constancy is the quality of the reward, where bees will repeatedly visit flowers with a high level of reward, investigating alternatives only as the reward decreases (Grüter and Ratnieks 2011).

Nest-building bees can only reproduce if their habitat contains suitable nesting sites, specific nest-building materials (for certain species), and sufficient floral resources (Westrich 1996). Given these requirements, in temperate regions most bee species thrive in moderately disturbed, early successional habitats dominated by herbaceous plants or perennials, shrubs, and young trees (Russell et al. 2018). Habitats such as prairies, pastures and meadows benefit bees by providing floral resources over much of the growing season as well as a variety of nesting substrates (Ibbe et al. 2011; Tonietto et al. 2017). As central-place foragers, bee foraging is constrained to a certain distance from their nests, which is limited by their relative body size and the metabolic demands of flight (Greenleaf et al. 2007). This distance can be substantial, especially

for large-bodied bees (up to 1400 m) (Zurbuchen et al. 2010). In fragmented landscapes, the entire home range of a species can cover an area consisting of several habitats, each of which may contain only one of the required resources (Westrich 1996). The loss of one partial habitat may lead to the local extirpation of bee populations. Generally, landscape heterogeneity and proximity to semi-natural habitat benefit bee biodiversity (Murray et al. 2009; Kennedy et al. 2013). In highly modified landscapes, bee populations may be highly dependent on marginal habitats such as road verges, ditches and powerline easements (Jalkotzy et al. 1997; Michener 2007).

Bees are the predominant pollinators because they are obligate florivores, with both larval and adult stages feeding on floral products, whereas for other insect pollinators taxa florivory is often facultative and is mostly confined to the adult stage (Winfree et al. 2011). Flies (Diptera) are generally the second most frequent floral visitors (Larson et al. 2001), and often become the dominant pollinators in low-temperature and/or wet environments such as at high latitudes and altitudes (Elberling and Olesen 1999; Inouye et al. 2015). For instance, flies consisted of up to 60% of all floral visitors in the Manitoba tallgrass prairie (Robson 2008). There are over 150,000 species of flies globally, and in North America species from over 70 families have been identified as floral visitors (Larson et al. 2001). The frequent flower visitors are mainly from three families: Syrphidae (hoverflies or flower flies), Bombyliidae (bee flies), and Tachinidae. Nearly all syrphid species use flowers as an adult food source. Pollen provides egg-laying females with proteins and sterols, while both sexes feed on nectar for energy for flight (Moquet et al. 2018). Although specialization levels vary between species, syrphids tend to be fairly generalized foragers compared to other pollinator groups such as bees (Klecka et al. 2018). Syrphids can be important pollinators for many plant species under varying environmental conditions, including many crops (Jauker and Wolters 2008; Orford et al. 2015; Hodgkiss et al. 2018). Syrphids have been shown to carry pollen loads comparable to honeybees and some bumblebee species, and significantly greater than those of Lepidoptera and Coleoptera (Kendall and Solomon 1973; Free et al. 1975; Orford et al. 2015). Syrphid larvae are saprophagous or insectivorous, providing additional waste decomposition and pest control services (Moquet et al. 2018). The different resource requirements between the larval and adult stage of syrphids means that in fragmented landscapes their biodiversity is reliant on complementary partial habitats (Moquet et al. 2018). Finally, wasps (Hymenoptera: Apocrita, excluding bees and ants) are carnivorous but may forage on flowers for nectar as a sugar source and pollinate plants as they do so (Wojcik and Buchmann 2012).

1.2 Linear Rights-of-Way as Early-Successional Habitats

Linear rights-of-way (ROWs) cover an expansive area across the globe used for the transportation of people, goods, and energy. The green area associated with roads, powerlines, pipelines, and railways needs to be continuously managed by the authority or the adjacent landowner to meet regulatory and safety standards (Licensing and Environmental Assessment Department 2019). ROWs have been identified as potential habitat for early-successional plants (Maclellan and Stewart 1986; Rubino et al. 2002; Leston and Koper 2016; Eldegard et al. 2017; Vanneste et al. 2020), birds (Jalkotzy et al. 1997; King and Byers 2002; Yahner 2004; Berger 2010; Tryjanowski et al. 2014), mammals (Johnson et al. 1979; Yahner 2004; Clarke et al. 2006), and insects (Free et al. 1975; Munguira and Thomas 1992; Eversham and Telfer 1994; Smallidge et al. 1996; Swengel 1996; Lanham and Nichols 2000; Russell et al. 2005; Wagner et al. 2019). ROWs are uniquely influential because they are widespread, long linear areas that connect and intersect multiple habitats, and contain vegetation that is kept in an early-successional stage (Berger 2010; Wojcik and Buchmann 2012; Gardiner et al. 2018).

ROWs are corridors with a high edge-to-area ratio, and may have various effects on wildlife (Jalkotzy et al. 1997). In general, the creation of edge causes variation in microclimate, shifts in the composition of plant and animal communities, and changes in biotic interactions including predation, parasitism, competition, herbivory, and seed dispersal (Willyard et al. 2004). ROWs may act as i) habitats for wildlife by providing requisites for survival such as food and shelter (Hopwood et al. 2010; Schaffers et al. 2012; Moroń et al. 2014; Russell et al. 2018; Villemey et al. 2018; Wagner et al. 2019); ii) conduits, when wildlife moves along them (Eversham and Telfer 1994; Zink et al. 1995; Brunzel et al. 2004; Villemey et al. 2018; Nelson et al. 2021); iii) filters or barriers when wildlife movement across them is hindered or blocked (Keller et al. 2004; Muñoz et al. 2015; Andersson et al. 2017); iv) sources, when wildlife reproducing in the corridor moves out into the surrounding land (Berg et al. 2016); and v) sinks, if wildlife is attracted to the corridor and dies or fails to reproduce as a result (Jalkotzy et al. 1997; McKenna et al. 2001; Willyard et al. 2004; Muñoz et al. 2015). Whether ROWs are beneficial or detrimental to wildlife is highly dependent on the type of corridor, how it is managed, the surrounding environment, and the species' traits (Gates 1991; Willyard et al. 2004; Villemey et al. 2018). For instance, the species richness of habitat generalist and open-habitat specialist spiders and beetles increased with proximity to a highway ROW in both forested and open habitats, while forest-specialist beetle species were negatively impacted (Knapp et al. 2013). Similar patterns emerge in many ROW biodiversity studies, as the climatic and vegetational variations brought by the corridors tend to favour edge and habitat generalists to the detriment of habitat specialists that rely on undisturbed landscape (Jalkotzy et al. 1997; Berger 2010; Vanneste et al. 2020; Nelson et al. 2021). Similarly, whether a ROW acts as a conduit, filter or barrier depends on the mobility and dispersal capabilities of the observed organism (Muñoz et al. 2015; Andersson et al. 2017).

Most high-income nations across the globe have been experiencing a dramatic decrease in the amount of early-successional habitat for the past few centuries in both agricultural and forested landscapes. Agricultural expansion in many prairie regions has caused the almost complete collapse of natural grassland ecosystems (Samson and Knopf 1994). Furthermore, the intensification of production practices in the past decades (annual monoculture plantations made possible with the use of pesticides and fertilizers) has reduced the amount of extensively farmed land, which includes meadows, pastures, long-term set-aside, and field margins (Brown et al. 2005; Stoate et al. 2009; Vickruck 2021). At the same time, other regions have been experiencing significant farmland abandonment, with a decrease in the number of rural farms as communities have migrated towards more populated areas (Brown et al. 2005; Stoate et al. 2009; Queiroz et al. 2014). With the removal of recurring disturbance regimes such as livestock grazing, having, and controlled burns, large areas that were previously managed as meadows have experienced rapid vegetational succession and returned to a forested state (Ibbe et al. 2011; Queiroz et al. 2014). Furthermore, forest management practices from logging activities in northern Europe and Canada have reduced forest heterogeneity (King and Schlossberg 2014; Rodríguez and Kouki 2017). Tree plantations and fire suppression activities have decreased forest biodiversity, reducing the provision of important ecosystem services including pollination (Brown et al. 2005; Nilsson and Wardle 2005; Rodríguez and Kouki 2015, 2017). All of these events have caused a significant loss of early-successional habitats and a homogenization of landscapes, leading to a global decline of many open-habitat species (Willyard et al. 2004; Forrester et al. 2005; Winfree et al. 2009; Potts et al. 2010; Cameron et al. 2011; King and Schlossberg 2014).

Within these highly modified landscapes, marginal habitats such as roadside verges and powerline easements can become an important tool for the conservation of insect biodiversity. Linear ROWs are commonly seen as detrimental to local ecosystems, as they may fragment natural

habitats into smaller patches (Keller et al. 2004; Willyard et al. 2004). However, in landscapes lacking sufficient quality early-successional habitats due to reforestation or agricultural intensification, this land can become a valuable resource for many sun-loving insect species. In these landscapes, ROWs may be managed to act as 'remnant corridors': long strips of semi-natural habitat in an otherwise disturbance-dominated area (Jalkotzy et al. 1997). ROWs can act as habitat and ecological refugia for early-successional insects within agricultural (Munguira and Thomas 1992; Raemakers et al. 2001; Hopwood 2008; Moroń et al. 2014; Cole et al. 2017; Cariveau et al. 2019; Phillips et al. 2019), urban (Baldock et al. 2015, 2019; Leston and Koper 2016, 2017; Twerd et al. 2021) and forested landscapes (Wagner et al. 2014a, 2019; Hill and Bartomeus 2016; Riva et al. 2018a; Nelson et al. 2021). Even rare and stenotopic (habitat specialist) species have been observed using the corridors (Eversham and Telfer 1994; Forrester et al. 2005; Noordijk et al. 2008; Schaffers et al. 2012; Wagner et al. 2014a). ROWs add heterogeneity to modified landscapes: a key driver of beneficial insect diversity (Murray et al. 2009; Kennedy et al. 2013; Moquet et al. 2018; Neumüller et al. 2020). Furthermore, ROWs may increase connectivity and link habitat patches together, potentially acting as dispersal routes for insects and plants and promoting community interactions across the landscape (Tewksbury et al. 2002; Willyard et al. 2004; Thiele et al. 2018; Nelson et al. 2021).

1.3 Effects of roads on insects

Roads are a ubiquitous infrastructure that extends for over 64 million kilometres across the globe (Central Intelligence Agency 2021). The United States of America ranks 1st in terms of total road network length, with over six million kilometres, while Canada is in 6th position with just over 1 million kilometres (Wojcik and Buchmann 2012). Road verges are strips of grass and other plants, sometimes also trees, situated between roads and sidewalks, hedges, crop fields, forests, or other. This land is usually public property, with maintenance being a municipal responsibility. In North America, roadside maintenance usually involves frequent mowing and the occasional application of herbicides to uphold motorist safety (Hopwood 2008). Roadside verges occupy an estimated 4 million and 0.6 million hectares of land in the USA and Canada respectively, a vast amount of land that may potentially act as good habitat for insects (Wojcik and Buchmann 2012). Of all ROW corridors, roads probably have the greatest impact on wildlife. The most important negative effects are mortality due to traffic, and the loss of habitat effectiveness as a result of

wildlife avoiding lands in the vicinity of roads due to continuous disturbance (light and noise) (Jalkotzy et al. 1997). However, unlike agricultural fields, roadsides are not disturbed by heavy equipment nor are they plowed, and therefore may be an important conservation resource for insects in farmed landscapes despite the inherent negative aspects of roads (Hopwood 2008). Furthermore, in forested landscapes road verges can represent much of the managed early-successional habitat which, unlike forest clear-cuts, is continuously maintained in that stage, providing resources to open habitat species through time (Phillips et al. 2020).

Detrimental Effects: Filters and Sinks

Whether roads act as filters or barriers is highly dependent on the species' dispersal capabilities. Roads do not seem to act as filters to large-scale movements by insects (such as migration), which tend to cover large distances at heights of up to hundreds of metres (Phillips et al. 2020). However, small-scale movement might be affected, especially for smaller, less mobile species. A study found that species composition of bees and wasps differed on two sides of a wide highway – a relationship that strengthened when larger species were excluded from analyses (Andersson et al. 2017). Since both sides of the road had similar vegetation and equivalent bee and wasp species richness, these results suggest that the highway was acting as a barrier to the movement of the insects, particularly so for smaller species. Hopwood et al. (2010) found that fewer bumblebees crossed roads than would be expected if the roads had no effect on movement, however, the authors note that the high site fidelity of the insects confounded the issue. Similarly, another study suggests that roads can act as a filter to the movement of some butterfly species, but found that the range of species and proportions of populations crossing the busy wide roads greatly exceeded the threshold that geneticists believe is necessary for gene flow to be maintained between isolated populations (Munguira and Thomas 1992). Less mobile insects such as flightless beetles might be more severely impacted by the barrier effect of roads, leading to genetic differentiation and possibly local extinctions (although less likely for species with large population sizes) (Keller et al. 2004). Muñoz et al. (2015) established in their literature review that roads were considerable barriers for small or flightless insect species, while the effects on flying species varied.

Among the different types of ROWs, roads are those that have the greatest direct effect on wildlife due to light, noise, and chemical pollution and, most importantly, traffic collisions. In general, there seems to be a positive correlation between road traffic intensity and the amount of

insect collisions (Muñoz et al. 2015). However, studies on the magnitude and severity of insect mortality due to collisions along roads have varying conclusions. Some studies have reported negligible mortality of flying insects such as bees, butterflies, moths, and flies (Munguira and Thomas 1992; Hopwood et al. 2010). Others, however, have reported high levels of insect mortality, especially if scaled to larger geographical ranges. Based on collected data, one study estimated that the number of Lepidoptera killed along roads in all of Illinois (United States) during a single week was greater than 20 million individuals (McKenna et al. 2001). Data extrapolations from a study conducted along the Trans-Canada Highway in Ontario show the possible loss of hundreds of thousands (on the surveyed highway) to hundreds of billions (across all North America) of pollinating butterflies, moths, bees, wasps, and flies each summer (Baxter-Gilbert et al. 2015). For certain insect groups, there seems to be a relationship between the type of habitat in the verge and bordering land, and mortality on the road. A study conducted in Northeastern USA found that insect mortality in general, and in particular of bees and butterflies, was consistently lower when roadsides were bordered by woodlots than when they were bordered by lawn or meadows (Keilsohn et al. 2018). Regardless of the bordering habitat, the authors deemed insect mortality unacceptably high for areas being considered for conservation. In another study, tracking butterflies revealed that they were less likely to exit prairie roadside verges compared to weedy or non-native grass verges, suggesting that the mortality rate may be lower in higher-quality verges (Ries et al. 2001). The proportion of butterflies killed by traffic (compared to the abundance in the verges) was also shown to be negatively correlated with the richness of plants in the roadsides and with the amount of grassland area in the surrounding landscape (Skórka et al. 2013). This indicates that the verges which are valuable for butterfly conservation are less impacted by road mortality. Finally, the high site fidelity of bumblebees in road verges is potentially limiting their mortality rate (Hopwood et al. 2010). Another potential threat to insects in roadside verges is the chemical pollution caused by vehicles and de-icing salt (Muñoz et al. 2015). Soil in road verges, and consequently the plants growing in them can have relatively high concentrations of lead, cadmium, and nickel, however there is no evidence of this affecting insects in the verges (Muskett and Jones 1980; Swaileh et al. 2004).

Beneficial Effects: Habitat, Conduits, and Sources

Roadside verges are usually characterized by a rich and abundant flowering plant community, often more biodiverse than the surrounding landscapes (Rotholz and Mandelik 2013; Hanley and Wilkins 2015; Cole et al. 2017; Phillips et al. 2019, 2020; Vanneste et al. 2020). Plants benefit from rainwater harvesting on the paved surface and channelling to the verges, as well as abundant light, nutrients, and reduced competition from trees and shrubs (Wojcik and Buchmann 2012). These communities can include grassland specialists, and can overall be very similar in species composition to local natural grasslands, especially if managed accordingly (e.g., by sowing native seed mixes) (Hopwood 2008; Vanneste et al. 2020). Roadsides can also have high richness and cover of introduced plant species, which thrive along the verges due to the favourable conditions and reduced competition (Valtonen et al. 2006; Hopwood 2008; Hopwood et al. 2015; Cariveau et al. 2019). Whether by native or exotic species, roadside verges accommodate rich plant communities that provide suitable habitat for a wide variety of insect species. Roadside verges have been shown to attract many beneficial insects including pollinators such as bees, butterflies, wasps, and flies by providing ample floral resources that are often lacking in modified landscapes (Free et al. 1975; Munguira and Thomas 1992; Ries et al. 2001; Raemakers et al. 2001; Saarinen et al. 2005; Hopwood 2008; Hopwood et al. 2010; Hanley and Wilkins 2015; Cole et al. 2017; Heneberg et al. 2017; Riva et al. 2018a; Ste-Marie et al. 2018; Cariveau et al. 2019; Phillips et al. 2019). Road verges are also characterized by relatively high levels of exposed ground, which can benefit ground-dwelling or nesting arthropods such as many bee species (Hopwood 2008; Heneberg et al. 2017).

The habitat quality of roadside verges can be enhanced with relatively low effort through specific management strategies. These include reducing mowing to once or twice during the growing season (preferentially avoiding mid-season mowing), using targeted herbicidal treatment rather than untargeted spraying, and planting native forbs and grasses (Ries et al. 2001; Hopwood 2008; Noordijk et al. 2009, 2010; Hopwood et al. 2015; Jakobsson et al. 2018; Phillips et al. 2020). Higher-quality road verge habitats, defined by the high density and richness of flowers and larval host plants, host greater pollinator richness and abundance, and tend to benefit a greater number of stenotopic species (Munguira and Thomas 1992; Ries et al. 2001; Saarinen et al. 2005; Hopwood 2008; Noordijk et al. 2009; Andersson et al. 2017; Cole et al. 2017; Phillips et al. 2020). Verge width seems to contribute towards greater butterfly biodiversity (Munguira and Thomas

1992; Saarinen et al. 2005; Phillips et al. 2020), but this effect was not found for other insect groups (Samways et al. 1997; Raemakers et al. 2001; Hopwood 2008). There does not seem to be a consensus on the effect of road width and traffic volume on insect biodiversity within the verges. Some authors have reported no negative effects on the richness and abundance of certain insect groups (Munguira and Thomas 1992; Saarinen et al. 2005; Hopwood 2008). However, Villemey et al. (2018) in their meta-analysis did find that pollinator and primary consumer abundance was higher in non-highway verges compared to landscapes away from ROWs, whereas there was no difference in abundance between highway verges and the controls. The authors suggest that this might be due to a greater number of insect collisions in highways as well as a greater edge effect that lowers the carrying capacity of the verges. Another study found that road traffic did significantly reduce the abundance of insect pollinators within the verges, suggesting that management for pollinators should target wide road verges along roads with less traffic (Phillips et al. 2019). Finally, multiple studies have shown that road verges that are near natural habitats, such as grasslands and forests, tend to have greater insect richness and abundance (Saarinen et al. 2005; Villemey et al. 2018; Cariveau et al. 2019; Phillips et al. 2020). However, beneficial insects such as pollinators are likely more dependent on road verges in landscapes lacking high-quality habitats, where the vegetated corridors might be one of the few remaining sources of forage and nesting resources (Phillips et al. 2020).

Roadside verges could act as conduits for plants and insects in fragmented landscapes, however, the current knowledge is still too limited to draw general conclusions (Phillips et al. 2020). Carabid beetles, including habitat specialists, may use road verges as corridors to a certain extent, however, this behaviour is species-dependent (Eversham and Telfer 1994; Vermeulen 1994). An analysis of landscape features in western Germany revealed that the Cinnabar moth *Tyria jacobaeae* (L.) used valleys with roads and sparsely plant-covered verges to lay eggs and disperse to higher altitudes in the study area (Brunzel et al. 2004). A mark-recapture study on bumblebees revealed that they moved within roadsides an average of 132 m, while the maximum distance moved was 900 m, which is within known bumblebee flight ranges (Hopwood et al. 2010). However, bees that were marked and recaptured on the same day were most often found within 50 m from the original location. The dispersal corridors for invasive plant species, accelerated by long-distance seed transport by vehicles, and can enable their spread into adjacent habitats (Von

Der Lippe and Kowarik 2007). These invasive plants can alter the plant community in the verge and subsequently negatively impact pollinators via bottom-up effects (Valtonen et al. 2006). However, some alien plant species such as *Trifolium pratense* L., commonly found along roadsides of North America, are highly attractive to pollinators (Hopwood et al. 2010).

Despite the inherent risks that roads pose to arthropods, quality habitat within the verges can support breeding populations of many insect groups and therefore can act as sources in the landscape. Many carabid, moth, and butterfly species have been found to breed in roadside verges (Eversham and Telfer 1994; Vermeulen 1994; Brunzel et al. 2004), and the range of breeding habitats within verges seems to be an important driver of the butterfly biodiversity within them (Munguira and Thomas 1992). Many insect species seem to be overwintering in roadside verges as well. Schaffers et al. (2012) in the Netherlands found that for certain insect groups there was a high overlap between species found in the summer and those in the winter: up to 88% for Carabidae. For Apidae and Syrphidae, the overlap was rather low at 20%, however, this might be explained by their high dispersal ranges, clustered overwintering, or absence of adult overwintering for many species (Schaffers et al. 2012). The authors conclude that their study site provided resources for the persistence of insect species and functioned as year-round habitat.

Overall, most of the evidence indicates that the benefits to insects from the management of suitable habitat on road verges outweigh the risks from potential impacts with vehicles (Hopwood et al. 2015). However, more research needs to be done to be certain. A study in Sweden looking at landscape-scale effects of linear infrastructure habitats did not find a negative effect of road density on plant and pollinator biodiversity (Dániel-Ferreira et al. 2020). This suggests that any negative effects of roadways on insect populations are probably being countered by the increased grassland area from the verges.

1.3 Effects of powerlines on insects

Electric power transmission lines are ubiquitous and necessary for the transportation and distribution of electricity. The Canadian transmission network extends over 160,000 km and is characterized mostly by major powerlines which transport electricity from large hydropower projects in mid/northern Canada to the populous cities in the south (International Energy Agency 2009). Transmission lines consist of towers (made of wooden poles or steel), and conductors (wires) designed to carry specific electrical voltages (Berger 2010). This infrastructure is located

within a cleared strip of land (ROW) which is generally 40-80 m wide and is continuously managed by the utility authority (usually Crown-owned companies) to ensure that electricity is supplied safely and reliably (Berger 2010). The vegetation community within the powerline easement needs to be kept at a low stature to avoid contact of tall-growing plants with the conductors. Generally, this is achieved through either mechanical control (via drum or rotary cutters, mulcher, fellerbunchers, bulldozers with modified brush blades, mowers, etc.), herbicides, manual control (chain saws, brush saws, and axes), or a combination of the three (Licensing and Environmental Assessment Department 2019). Powerline ROWs share many similarities with roads in how they affect biodiversity, however, a major difference exists with the absence of a direct threat posed by moving traffic. The biggest negative impacts that powerlines may have on wildlife are fragmentation and edge effects brought by the creation and maintenance of the ROWs in previously-undisturbed landscapes (Willyard et al. 2004; Wojcik and Buchmann 2012). Similar to road verges, however, powerline ROWs can be managed as remnant corridors and act as earlysuccessional habitats and conduits for many insect species in agricultural, urban and forested landscapes (Wojcik and Buchmann 2012).

Detrimental Effects: Filters and Sinks

Filtering effects of powerline ROWs are less severe than those of roads, however, these corridors can still impede the movement of wildlife across them, particularly where they intersect forested areas (Gates 1991; Willyard et al. 2004). Powerlines probably do not act as filters to the large-scale movements of bigger, more mobile species. However, local-scale movements of smaller, less mobile species may be affected, especially for many plants, insects, reptiles and amphibians (Willyard et al. 2004; Berger 2010). Unfortunately, research on filtering and fragmentation effects of powerlines on insects is lacking. In general, it seems that width has a major influence on wildlife movements: the wider the corridor and the greater the contrast between the corridor and adjacent habitat, the stronger its filtering effect and more likely the interior will have a distinct community composition (Gates 1991). Overall, Willyard et al. (2004) conclude in their literature review that powerline ROWs are likely isolating only a small number of species. Forest specialists may be averse to crossing powerline ROWs and risk being exposed to potential dangers that exist in the open (Willyard et al. 2004). However, the filtering effect of powerline ROWs can be mitigated by keeping the width of the corridor to a minimum, reducing or buffering

the habitat contrast between the interior and exterior of the corridor, and leaving uncleared forest strips where trees do not pose a threat to the conductors (e.g., if the powerline crosses a valley or depression) (Berger 2010).

Research on sink and source effects of powerline ROWs on insect populations is limited. In general, due to the absence of traffic, we expect powerlines to pose less of a direct mortality threat to insects when compared to roads. In contrast, fragmentation and edge effects can cause indirect insect mortality through changes in biotic interactions such as increased predation, parasitism and competition (Willyard et al. 2004). Furthermore, the abundant exotic plants found in ROWs can potentially diminish the reproductive success of natives by reducing their pollinator visitation rates and increasing heterospecific pollination (Bjerknes et al. 2007). In terms of direct threats, a couple of studies found that the electromagnetic fields from high-voltage wires can lower the productivity and increase the aggression of honeybees (Wellenstein 1973; Lee and Reiner 1983), however, these results are far from identifying this as a potential cause of mortality to insects nesting within powerline ROWs.

Beneficial Effects: Habitats, Conduits and Sources

The creation and management of powerline ROWs produces habitats dominated by graminoids, herbs, and shrubs which can support many early-successional insect species (Wagner et al. 2014b). Similar to roadside verges, powerline ROWs have been shown to host distinct plant communities that are often more biodiverse than the surrounding landscape (Rubino et al. 2002; Wagner et al. 2014b; Eldegard et al. 2015, 2017). These communities may include native grassland species and act as substitute prairie habitats within agricultural lands (Leston and Koper 2016). In forested landscapes, ROWs maintain open areas in various successional stages. In these clearings there is a fall in evaporation and shading, and an increase in moisture, light intensity, and openness, favouring early-successional plant and animal species (Lensu et al. 2011). New powerline ROWs in forests are structurally similar to clear-cuts, which have been comprehensively studied in regards to their effects on wildlife (Johnson et al. 1979). However, ROWs are continuously kept in an early-successional state, and over time they develop into a novel habitat that is qualitatively different from clear-cuts (Eldegard et al. 2017). Within the ROW itself, the plant community composition can vary between the centre of the corridor and the edges (Eldegard et al. 2015). Plant richness can be much greater in the corridor centre compared to the edges (Eldegard et al. 2015).

Powerline ROWs constitute a large portion of the managed early-successional habitat in the forests of the United States and Canada and therefore play a valuable role in preserving biodiversity in these regions (King and Schlossberg 2014; Wagner et al. 2019). Similar to road verges, powerline ROWs may also host high richness and cover of exotic plant species (Rubino et al. 2002; Leston and Koper 2016, 2017). However, this is not always the case, with some studies finding low cover of exotics compared to that of native plants (Wagner et al. 2014b; Eldegard et al. 2017). The percentage of exotic species may increase following vegetation management but tends to decrease over time as woody cover increases (Forrester et al. 2005). The biodiverse plant communities within powerline easement corridors provide ample food and shelter resources for wildlife and act as refuges for many beneficial insects including rare and stenotopic species (Swengel 1996; Smallidge et al. 2014; Wagner et al. 2019; Hill and Bartomeus 2016; Leston and Koper 2016, 2017; Steinert et al. 2014a, 2019; Hill and Bartomeus 2016; Leston and Koper 2016, 2017; Steinert et al. 2020).

Management strategies aimed at improving the habitat quality within powerline ROWs can increase the biodiversity of insects and benefit a greater number of native stenotopic species. These strategies include reducing the frequency of mowing and herbicidal application, avoiding using only manual control (ineffective in minimizing tree growth), combining mowing with selective herbicidal treatment (rather than mowing-only), and promoting the growth of floral and larval host plants to benefit insects (Swengel 1996; Bramble et al. 1999; Forrester et al. 2005; Wagner et al. 2014b, 2019; Leston and Koper 2016, 2017; Russo et al. 2021). Some authors note however that the impact of management practices on insects can be dependent on the environmental context, and therefore treatment selection should reflect the environmental conditions within the ROW and surrounding landscape (Sydenham et al. 2016; Russell et al. 2018; Steinert et al. 2018). Irrespective of management, however, an abundance and diversity of flowering plants seem to be the major factor affecting butterfly and bee biodiversity within powerline ROWs (Yahner 2004; Berg et al. 2013; Steinert et al. 2020; Russo et al. 2021; Twerd et al. 2021). Integrated vegetation management strategies (IVM) for powerline ROWs have been receiving increasing attention, as they are effective in reducing long-term management costs while also benefiting biodiversity in the corridors (Licensing and Environmental Assessment Department 2019). IVM practices involve selectively targeting tall-growing woody plant species with a combination of manual and herbicidal treatments while promoting a stable community of native low or medium-stature plants

that inhibit the establishment and spread of the undesirable species (Russell et al. 2018). These methods ideally result in a lasting mosaic of meadow and scrub habitats predominated by native forbs and shrubs (Russell et al. 2018; Licensing and Environmental Assessment Department 2019). Powerline ROWs that have already experienced multiple decades of IVM management have significantly greater floral richness and abundance compared to mowing-only sites and new IVM sites (Russell et al. 2018). This allows these old IVM sites to host a significantly greater abundance and diversity of bees, including kleptoparasites, which are considered indicator species (Sheffield et al. 2013; Russell et al. 2018).

Powerline ROWs have the potential to act as conduits for many plant and insect species between habitat patches, which can be particularly beneficial to biodiversity in fragmented landscapes (Willyard et al. 2004). Research on insect movements within powerline ROWs is unfortunately still lacking. Studies have found that bumblebees and butterflies in the boreal forest of Alberta used seismic lines (narrow corridors used for the transportation of geophysical survey equipment) as dispersal corridors (Riva et al. 2018b; Nelson et al. 2021). Although these studies were not on transmission lines, the close structural similarity between the two types of infrastructure allows us to gather some insight into the potential role of powerline ROWs as conduits for insects in forested landscapes. Similar insights can be gathered from the roadside verge studies reviewed previously. Overall, however, the limited research prevents us from drawing general conclusions on the use of powerline ROWs as conduits by insects. Although the increased connectivity brought by powerline ROWs may boost the movement of native wildlife in the landscape, it also allows for the spread of exotic species in previously uninvaded areas. This is particularly relevant for alien plants, with ROWs often acting as conduits for the invasion of weedy species into previously unavailable sites such as the northern forests of Canada (Maclellan and Stewart 1986). This is facilitated by the removal of forest, which aids the wind dispersal of pollen and seeds (Maclellan and Stewart 1986). This ease of dispersal causes powerline ROWs to have relatively high richness and cover of exotic plant species (Rubino et al. 2002; Leston and Koper 2016, 2017) and could facilitate the invasion of adjacent natural habitats (Zink et al. 1995). However, Rubino et al. (2002) found that the majority of invasive plant species present in powerline corridors were shade-intolerant and absent from adjacent riparian forests, and therefore argues that in forested areas powerline ROWs should not serve as invasion foci for exotic plants.

By hosting a healthy diversity of food and nesting resources, transmission line easements can allow the establishment of stable breeding insect populations. Management can help this establishment. Powerline ROWs that have been managed via IVM for an extensive period are characterized by greater floral biodiversity as well as a larger amount of dead woody stems and live and dead woody cover (Russell et al. 2018). This increase in nesting resources allows these sites to contain a higher proportion of cavity-nesting bees, suggesting that they harbour breeding bee populations. Furthermore, these IVM sites also host a greater number of small bees, which can't travel long distances to forage and must nest near floral resources. This is interpreted as an indication that some of these bees are residents of the easement, rather than simply foragers from the surrounding landscape (Russell et al. 2018). Finally, butterfly abundance and richness in forest roads and pastures were negatively related to distance from powerline ROW habitats – a non-linear relationship that levelled off at 500 m from the powerlines (Berg et al. 2016). This supported the hypothesis that powerline ROWs act as source habitats for butterflies. At the landscape-scale, Dániel-Ferreira et al. (2020) did not find an effect of the amount of linear infrastructure habitats (including powerline ROWs) on butterfly or bumblebee richness in the landscape. They also found that landscapes with powerlines had on average 6 (±2.36 SD) more plant species than landscapes without them. The authors suggest that this could be due to the greater amount of grassland area in the landscape (following the species-area relationship), or because the additional area given by powerlines is slowing down the extinction rate of plants (meaning that these landscapes have an extinction debt) (Dániel-Ferreira et al. 2020).

1.4 Pollination Networks

Biotic interactions play an essential role in the organization and persistence of biodiversity (Ferreira et al. 2020). By describing interactions between species, ecological networks reveal community structure and the function and stability of ecosystems (Thébault and Fontaine 2010). By studying networks, we can evaluate the effects of human activities on complex ecological interactions (Memmott et al. 2007; Evans et al. 2013; Tylianakis and Morris 2017). Habitat management can have cascading effects within ecological networks, affecting multiple species and interactions simultaneously across trophic levels (Tylianakis et al. 2008). The study of mutualistic interaction networks pushes ecological knowledge beyond species diversity studies to assess the impacts of environmental change on ecological processes, such as pollination (Forup et al. 2008;

Ferreira et al. 2020). In recent years this has been increasingly recognized in conservation policy, which is moving away from targeting individual vulnerable species to managing entire communities, particularly if they provide ecosystem services (Tylianakis et al. 2010; Evans et al. 2013).

Network Structure

Pollination networks are the most biodiverse of all mutualistic systems, involving 88% of all flowering plant species, over one million insect species, and several bird, mammal and lizard species (Hagen et al. 2012). Plant-pollinator communities can be graphed as bipartite (two-node) networks where pollinators and plants are connected via mutualistic links (Figure 1). These networks are defined by their size (number of species) and structure (frequency and pattern of the links). Network structure has important implications for the stability and coexistence of species (Bascompte and Jordano 2007) and can be described through various metrics (Dormann et al. 2009). Despite relationships existing between many metrics, they can provide complementary information on the organization of interactions (Thébault and Fontaine 2010). Mutualistic systems such as pollination networks are non-randomly assembled and share some general structural properties, including a skewed link distribution (most species have few interactions while a few species have many), a nested organization of the interaction matrix, and the frequent occurrence of asymmetric interactions (Vazquez et al. 2009). A nested network (Figure 1) is one where specialist species interact with a core of linked generalist species while failing to interact frequently with other specialists (Bascompte et al. 2003). Nested networks are highly cohesive: generalist species interact with each other and generate a dense core of interactions to which the rest of the community is attached (Bascompte et al. 2003). This structure makes pollination networks highly asymmetric so that if a pollinator species depends strongly on a plant, the plant depends weakly on the pollinator. This facilitates species coexistence in the community, reduces interspecific competition, and promotes the maintenance of biodiversity (Bascompte et al. 2006; Bastolla et al. 2009). A nested structure and lower mutual dependencies promote functional robustness to local species loss or temporal population declines and facilitate the persistence of rare species with few links (Bascompte et al. 2003; Tylianakis et al. 2010; Kaiser-Bunbury et al. 2017). This occurs because, in the face of species loss, a nested structure allows alternative routes in response to disturbance, reducing the spread of secondary extinction cascades (Bascompte et al. 2003). For instance, if a specialist pollinator goes extinct from a nested network, the plant species that it interacted with will still be pollinated by other more generalist species (Tylianakis et al. 2010).

Besides nestedness and interaction asymmetry, network structure can be described by its connectance and modularity. Connectance is a binary metric that indicates the fraction of links in the network that are realized compared to the total possible number of links (Figure 1). For a given network size, higher connectance indicates higher generalization levels and redundancy within the network (Nielsen and Totland 2014). It is commonly suggested that a higher connectance promotes the rate of ecosystem processes (e.g., increased seed set in plant-pollinator networks due to a higher functional complementarity), and stabilizes them through time under fluctuating environmental conditions (Tylianakis et al. 2010). For instance, higher connectance may provide a buffer in the responses of pollinators to fluctuations in plant species abundances, and vice-versa, since generalists can rely on other partners to maintain their populations (Tylianakis et al. 2010). However, connectance is dependent on network size, decreasing exponentially as the number of species in the web increases even though the absolute number of established interactions increases (Jordano 1987). Therefore, although network connectance can be considered a positive characteristic, it is not positive when resulting from species or interaction loss. A simplified system is not desirable even if more stable or resilient (Ferreira et al. 2020). Plant-pollinator communities also tend to be divided into modules (Figure 1), which are subsets of the interaction network in which species interact frequently with one another, but little with other species outside of the compartment (Olesen et al. 2007). Modularity may be a result of co-evolution (e.g., tubular flowers and long-tongued bees), and it tends to increase the stability of interaction networks by slowing down the spread of disturbance across the web (although disturbance might spread quickly within single compartments) (Tylianakis et al. 2010). Generally, producer/resource species at lower trophic levels (e.g., plants) tend to be more compartmentalized across habitats, while mobile consumers link them together (Rooney et al. 2008).



Figure 1. Visualization of three network metrics based on hypothetical qualitative (presence/absence) networks of equal size. Letters indicate pollinator species; roman numerals indicate flowering plant species. Black boxes in the matrices indicate the presence of an interaction.

Pollination network modularity is brought by reciprocal specialization arising from biological constraints including flower symmetry, pollinator size, and sociality; traits that lead to morphological or phenological mismatching between species (Villalobos et al. 2019). Generalist species are important for linking individuals within modules and keeping compartments connected in a network. These generalists connect subsets of the network, and their extinction may lead to community fragmentation (Biella et al. 2017). These species are therefore vital to the overall network structure, functioning and resilience, promoting the cohesiveness of pollination

communities beyond what would be expected by number of interactions alone (Martín González et al. 2010). They have the potential to alter the abundance of others and the state of the community, and are the ones most responsible for the stable coexistence of species in their communities, making them keystones in the network (Cagua et al. 2019). Keystone species may play different roles in the network, based on how they connect the rest of the community (Tylianakis et al. 2010). Highly connected species within a module are known as "module hubs" and are very important for the coherence of their compartment. Species that link several modules together are called "connectors" and are responsible for the cohesion of the whole network. Finally, "network hubs" are species that are both highly connected in their compartment, and which link different modules together, providing stability to the entire system. These keystone species have high conservation importance, as their extinction can lead to the fragmentation of compartments or entire networks, with cascading extinctions ensuing. A loss of module hubs increases the probability of secondary extinctions within compartments (reducing web stability), while a loss of connectors decreases the probability of trophic cascades across compartments (increasing web stability), but may lead to network fragmentation (Tylianakis et al. 2010). Therefore, if the goal is to maintain ecosystem function and services, or overall diversity, conservation efforts should be directed towards the preservation of keystone species, whereas if the goal is to retain rare species of concern, efforts should be focused on the species of interest and its few interaction partners (Zografou et al. 2020).

Mutualistic networks may disassemble through a process where specialists, which are more vulnerable to extinction, are lost from a network before generalist species (Figure 2) (Spiesman and Inouye 2013). Low interaction frequency and high specialization between mutualistic partners contribute additively in increasing the vulnerability of interactions to disruption (Aizen et al. 2012). This implies that, in most cases, only the most generalized species will remain in small networks. The disassembly of ecological networks leads to a threshold whereupon the web collapses. Here, the consequences of species extinctions are amplified and self-reinforcing as species continue to be lost from the system (Bascompte and Stouffer 2009). Furthermore, in real-life an increased mortality rate and reduced abundance of a species' population can lead to its functional extinction well before it is truly extinct (Säterberg et al. 2013). Functional extinction occurs when the abundance of a species is too low to fulfill its interactive role in the ecosystem, leading to the true extinction of other species (Sellman et al. 2016). Hence, the extinction of

ecological interactions can occur well before the extinction of the organisms themselves. Network robustness measures the resistance of the web to secondary extinctions following the sequential removal of individual species and has been used to understand the threat of species loss to ecosystem functioning and services (Grass et al. 2018; Sritongchuay et al. 2019). In general, the heterogeneous distribution of interactions and the nested structure of mutualistic networks confer them high robustness to the random extinction of species, but also increase web sensitivity to the extinction of generalists (Bascompte and Stouffer 2009). When calculating robustness of pollination networks, most studies assume bottom-up effects of species loss at the lower trophic level (flowering plants), justified by the strong effects that resources have on consumers in plant-pollinator interactions (Weiner et al. 2014; Goulson et al. 2015). For instance, pollinators are more sensitive to the loss of their plant partners due to climate change than vice versa (Schleuning et al. 2016).



Figure 2. Pollination network disassembly. As networks disassemble in response to environmental change, pollinator specialists (bottom left) and plant specialists (top right) go extinct due to their low abundance. Links are lost following the concave curve inwards. As the matrix shrinks, the links concentrate in the upper left corner and only generalist species persist.

Sampling & Analysis

The high generalization of ecological networks, as well as a high temporal and spatial turnover, and complexity of interaction patterns, makes adequate sampling of ecological interactions challenging and calls for a large sampling effort (Jordano 2016). Interaction network studies always have a high inherent degree of uncertainty due to the stochasticity of ecological communities and to the variation generated by finite sampling effort (Cirtwill et al. 2019). Number of partner species detected, number of links, and some metrics describing network patterns are sensitive to sampling bias (Jordano 2016). The majority of potential interactions in a network are usually not observed, and this could be due to either them actually not existing ("forbidden links"), existing but not occurring during sampling, or existing and occurring during sampling but not being detected (Cirtwill et al. 2019). Forbidden links are potential pairwise interactions that do not exist because of biological constraints, such as spatio-temporal uncoupling, foraging constraints, and physiological or biochemical constraints (Jordano 2016). Forbidden links can explain much of the unobserved relationships, potentially up to 80% of missing interactions (Olesen et al. 2011). Nonetheless, sampling of interactions requires strong and even effort. Heterogeneity in sampling effort per species or network can influence the estimation of most metrics, however, the sensitivity varies among them (Rivera-Hutinel et al. 2012). Nestedness and modularity, for example, seem to be less influenced by insufficient sampling compared to connectance and the number of species and links in the network (Nielsen and Bascompte 2007; Rivera-Hutinel et al. 2012). Overall, it seems that qualitative descriptors (metrics based on binary data, i.e. presence-absence of species and interactions) are highly sensitive to varying levels of sampling effort. Quantitative metrics (which describe both the pattern and frequency of interactions) were found to be much more robust against variable sampling effort and therefore able to better represent interaction networks (Banašek-Richter et al. 2004). Moreover, in binary networks common and rare species are attributed with the same weight, meaning that differences in partner availability are not taken into account (Miranda et al. 2019). Therefore, network ecologists tend to agree that quantitative data is best for network representation and analysis, even though theoretical treatment is less established than it is for binary networks.

Isolated networks are the result of ecological drivers including forbidden links, functional composition, abundance, morphology, and phylogeny. The interaction matrix (Y) of a mutualistic network is a function of the relative species abundance (N), temporal (T) and spatial overlap (S),

and phenotypic traits of interacting species (K). The effects of these factors are constrained by the phylogenetic relationships among plants (Pp) and animals (Pa), with detection probabilities of interactions resulting from sampling effects (E) also playing a role (Vazquez et al. 2009).

Y = f(N, T, S, K, Pp, Pa, E)

The task of comparing pollinator diversity estimates among different networks based on raw species counts is susceptible to the same sampling pitfalls and biases of plant and animal biodiversity studies. Without adequately accounting for variation in pollinator activity or abundance, comparisons of pollinator species richness - even when based on similar sampling efforts (such as a similar duration of observation intervals) – may be biased (Herrera 2005). Hence, Herrera (2005) suggests using sample-based rarefaction curves to estimate pollinator species richness for individual flower species or patches (in his case, shrubs). Network metrics suffer a similar fate due to relationships between network properties and the underlying variation in species abundance and richness. This means that the comparison of raw metrics is largely flawed (Blüthgen et al. 2008). The raw values of most network metrics depend to a varying degree on network size and connectance (Grass et al. 2018). Therefore, null models are frequently used to standardize network metrics by controlling for network size and connectance, facilitating the interpretation of variations in structural properties (Pellissier et al. 2018). Null models allow us to evaluate whether structural properties may be the result of chance alone in the absence of any ecological constraint. The raw value of the network metric is compared to expected values from the null models, where links within each network are randomized (randomization can be constrained, for example by fixing network size and connectance) (Pellissier et al. 2018).

Most pollination network studies concentrate on the quantitative component of the mutualistic relationship and focus on sampling the pattern – and sometimes frequency – of interactions between plants and animals. In contrast, the qualitative component is often not taken into consideration due to the high effort required in obtaining such data. This component represents the qualitative differences among pollinator or plant species in their effect on the fitness of their partners, irrespective of interaction frequency (Schleuning et al. 2015). Examples include the amount of pollen deposited on a flower by a pollinator in a single visit or the nutritional value of the pollen or nectar made available by the plant. The quantitative and qualitative contributions of a species to the ecosystem function (pollination) aggregately define their functional mutualistic importance through the concept of 'effectiveness' (Ne'Eman et al. 2010; Schleuning et al. 2015).

Some pollination studies take into consideration both the quantitative and qualitative components by building zoo-centric networks via the analysis of pollen samples recovered from the pollinator's body (pollen-transport networks) (Lopezaraiza-Mikel et al. 2007; Forup et al. 2008; Alarcón 2010). These contrast the phyto-centric method, which involves taking samples of focal plant species and recording which animals arrive to pollinate them (Jordano 2016). Overall, it's been shown that visitation frequency and total pollen deposition are correlated at the community level, and therefore there is good support behind the use of visitation as a surrogate for pollinator importance in the network (Vázquez et al. 2005, 2012; Ballantyne et al. 2017). This positive relationship between interaction frequency and total effect (total pollen deposited) occurs despite no general relationship between visitation and per-visit effect (pollen deposition per visit). Differences in per-interaction effects among animal mutualists are thus overridden by differences in their visitation frequencies. Highly frequent flower visitors usually contribute disproportionately to the plant's reproductive success, even if their pollination effectiveness is relatively low (Vázquez et al. 2005). The correlation between visitation and pollen deposition is rarely present at the individual level, with some frequent visitors being poor pollen depositors due to poor morphological matching with the flowers or the sole collection of nectar (Ballantyne et al. 2017). For a given flowering plant species, up to 78% of visitors may be ineffective pollinators, meaning that plant-pollinator relationships are substantially more specialized than is revealed by visitation alone (King et al. 2013; Ballantyne et al. 2017). This has been confirmed by pollentransport studies revealing a more specialized network compared to the visitation counterpart (Alarcón 2010).

Response to Environmental Drivers

1. Disturbance

A major goal of ecological research is to understand how interaction networks are affected by disturbance, and how biodiversity loss affects ecosystem functioning (Weiner et al. 2014). Habitat disturbance and degradation can have profound effects on networks at the species-level, causing the local extinction of plant and pollinator species. In general, rare species and specialistspecialist interactions are more susceptible to environmental change and are quickly lost from the network following disturbance (Spiesman and Inouye 2013; Soares et al. 2017). This changes the topology of the networks, with plant-pollinator interactions in disturbed sites consisting of generalized nodes connecting modules, whilst interactions in less disturbed sites are more specialized and symmetrical (Shinohara et al. 2019; Villalobos et al. 2019). Thus, disturbance leads to a concentration of interactions by generalist species and loss of interactions between reciprocal specialists, causing an increase in interaction asymmetry in the network (Soares et al. 2017). A large study conducted in Germany found that land-use intensification triggered losses in flower diversity, leading to non-random, resource-mediated losses of pollinators (Weiner et al. 2014). The study also confirmed that intensification had a disproportionate effect on the abundance of specialist pollinators, however this effect was not true for specialist plant species. There are situations where intermediate disturbance may increase network link diversity (Shinohara et al. 2019). However, disturbed habitats were found to have a lower link turnover than natural habitats, indicating a homogenization of plant-pollinator networks as a result of degradation (Nielsen and Totland 2014). Many network properties are (to varying extents) conserved after perturbation, however, metrics such as interaction asymmetry and network specialization (H2'), as well as species-level specialization (d') and species' functional roles in the web, can be greatly influenced by habitat disturbance due to the extinction of populations and interactions (Nielsen and Totland 2014; Soares et al. 2017; Villalobos et al. 2019). Additionally, as disturbance increases, the loss of specialist species and the concentration of links among generalists cause pollination networks to become more nested and less modular (Villalobos et al. 2019; Morrison et al. 2020).

2. Habitat Loss & Landscape Configuration

Habitat loss and fragmentation pose an important threat to pollination networks, with the expansion and intensification of human activities decreasing land and resources available to wild pollinators (Kearns et al. 1998). Following the species-area relationship, smaller habitat patches have been shown to host a reduced number of flowering plant and pollinator species (Grass et al. 2018; Jauker et al. 2019). Plant-pollinator networks in smaller habitat patches show an increased standardized connectance (standardized for network size), and a decrease in standardized specialization (H2') (Hagen et al. 2012; Jauker et al. 2019), indicating a more generalized system. Impoverished communities in small habitat patches also show a shift towards functional homogenization, with opportunistic interactions among generalists replacing the lost specialized links (Hagen et al. 2012; Jauker et al. 2019). While these networks are structurally robust, they are usually characterized by reduced visitation frequency and increased heterospecific pollen
deposition (Jauker et al. 2019), leading to a loss of ecosystem functioning (Wilcock and Neiland 2002). At the landscape-scale, habitat loss is associated with lower species richness, abundance, and number of interactions (Evans et al. 2013; Spiesman and Inouye 2013; Ferreira et al. 2020). Pollination networks within landscapes with reduced habitat have lower raw nestedness and higher connectance and modularity, however, no effect of habitat loss was found on standardized nestedness and modularity (Spiesman and Inouye 2013). This indicates that the changes in network structure following habitat loss are mostly brought by the decrease in network size. Network nestedness increases in fragmented, less-connected landscapes, while network specialization (H2') is positively influenced both by natural habitat cover as well as landscape connectivity (Ferreira et al. 2020). These effects may be related to the loss of specialist species, and a shift towards generalist foraging behaviour of pollinators due to lower resource availability and diversity (Ferreira et al. 2020). Enhanced landscape connectivity may rescue habitat specialists from extinction and increase resource availability for generalists (Grass et al. 2018). Corridors that connect habitat patches in the landscape benefit pollination networks by increasing habitat area in the landscape as well as facilitating interpatch movement and maintaining key interactions (Tewksbury et al. 2002). Finally, proximity to natural habitat in the landscape was shown to enhance plant-pollinator networks by increasing the number of interactions and boosting both interaction evenness and network robustness (Sritongchuay et al. 2019). Interaction richness and evenness of pollination networks were also shown to be greater in more heterogeneous landscapes, which offer a greater variety of foraging and nesting resources to pollinators (Martínez-Núñez et al. 2019).

3. Invasive Plant Species

Invasive species are one of the major drivers in global environmental change and can significantly impact local ecological interactions and network structure. Invasive flowering plant species are often highly attractive to pollinators because they tend to have large and colourful flowering displays, accessible flower morphology, prolific nectar production, high generalization, and are often highly abundant due to an absence of co-evolved enemies (Bjerknes et al. 2007; Stout and Morales 2009; Aslan 2019). At small spatial and temporal scales, invasive plants may compete for interactions and potentially reduce the reproductive output of natives (Kaiser-Bunbury et al. 2017; Tylianakis and Morris 2017). Pollen transport networks of invaded plant-pollinator systems

were shown to be dominated by alien pollen grains, meaning that native plants may experience greater levels of heterospecific pollination and thus reduced reproductive output (Lopezaraiza-Mikel et al. 2007). However, invasive plants may bring long-term benefits to natives by attracting more pollinators with their floral displays, and supporting larger pollinator communities in the landscape through their high abundance and density (Bjerknes et al. 2007; Tylianakis and Morris 2017). For the most part, invasive plants are more generalized with respect to their pollinators than natives (Albrecht et al. 2014). Plant invaders attracting pollinators into invaded modules tend to play important topological roles (network or module hubs, connectors), creating larger modules that are more connected among each other, and cause role shifts in native species (Albrecht et al. 2014). These super-generalist species, which play important network roles in their native ranges, are likely to play similar roles in the networks they invade (Emer et al. 2016). Invaded networks tend to have lower modularity, but more links on average, higher generality, as well as higher visitor richness, abundance, and flower visitation (Lopezaraiza-Mikel et al. 2007; Hagen et al. 2012; Aslan 2019). Invasive plants, therefore, enhance the functional redundancy within pollination networks and may bolster the persistence of ecosystem functioning in the face of disturbance (Aslan 2019). The altered interaction structure of invaded networks makes them more robust to the random extinction of species, but also vulnerable to the extinction of the highly connected invasives (Albrecht et al. 2014). Invasive plants, however, are unlikely to partner with native specialist pollinators, and thus fail to support the resilience of native species assemblages (Aslan 2019). Even though the integration of alien species may not alter overall network connectivity, a transferral of links from native species to alien super-generalists can cause significant declines in the connectivity among natives in invaded webs (Aizen et al. 2008). Therefore, although ecological functionality is maintained, taxonomic diversity may decline as alien species become established in networks worldwide (Aslan 2019). Removing alien plant species can have important desirable effects in plant-pollinator communities (Carvalheiro et al. 2008; Kaiser-Bunbury et al. 2017), but should be done with caution. It can be very difficult to predict the direction in which the system will change, and some communities may be extremely vulnerable to the eradication of core species (Carvalheiro et al. 2008; Cagua et al. 2019). When considering ecosystem management, there may therefore be tension between the desire to eradicate invasive species and the need to maintain robust pollination networks resilient to disturbance, climate change, and other perturbations (Larson et al. 2014).

4. Time and Space

Pollination networks tend to exhibit considerable spatial and temporal stability in several macroscopic features (network structure), while microscopic features (such as topology, species' roles, and individual specialization) show strong variability (Trøjelsgaard and Olesen 2013). At finer temporal scales (days to months), mutualistic interactions are highly dynamic, with considerable variation in network structure, while at intermediate scales (years to decades) interactions are still highly dynamic, but tend to influence network properties only weakly (CaraDonna et al. 2021). Spatio-temporal studies of mutualistic networks reveal a general pattern of high species and interaction turnover across space and time, but low variation in network structure (Dupont et al. 2009; Zografou et al. 2020; CaraDonna et al. 2021). The low inter-annual variation in network structure may be partly due to the relatively low turnover among generalist species forming the network core, with high turnover rates mainly occurring among specialist species at the network periphery (Zografou et al. 2020; CaraDonna et al. 2021). Despite high levels of interaction turnover, highly generalist species tend to be very stable and can be reliably found across space and time, unlike specialists (Zografou et al. 2020). Nonetheless, species' roles in the networks are also prone to temporal variability, therefore management actions should not be based on data from a single year (Larson et al. 2014). Rather, the suggestion is to identify the module hubs and connectors over several years and prioritize their conservation to produce more resilient pollination systems (Larson et al. 2014). At broader temporal scales (decades to centuries), continued shifts in interactions reshape network structure, leading to significant changes in the community, including the loss of species and functionality (CaraDonna et al. 2021). When comparing data from the late 1800s to 2009 and 2010, Burkle et al. (2013) found that modern networks were less nested, had reduced redundancy, weakened interaction strengths, and a declined quantity and quality of pollinator services. Reasons for shifts in interactions included the extirpation of species (particularly of specialists, parasites, cavity-nesters, and those involved in weak historic interactions), absence of spatial co-occurrence due to landscape fragmentation, and changes in phenology, abundance, behavior or physiology that alter the propensity for particular interactions to occur (Burkle et al. 2013).

1.5 Conclusion

The potential of roadside verges and powerline easements as pollinator habitat is being increasingly explored but remains a controversial topic. As natural habitats continue to decline worldwide, all opportunities for the conservation of wildlife and ecosystem functioning within anthropogenic systems must be explored. Despite this, there is still little information on how linear infrastructure ROWs affect pollinators and their mutualistic interactions with flowering plants. Existing studies have only focused on measuring the richness and abundance of insects within ROWs, and powerline easement studies have so far mostly been restricted to bees and butterflies. To properly evaluate the conservation potential of ROWs for pollinators, we must determine whether these linear systems can host healthy insect pollinator communities as well as stable plant-pollinator networks.

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CHAPTER 2. ASSESSING POLLINATOR BIODIVERSITY AND COMMUNITY COMPOSITION WITHIN ROADSIDE VERGES OF SOUTH-EASTERN MANITOBA

2.0 Abstract

Roadside verges occupy a huge area of land that is continuously maintained in an earlysuccessional state, is not disturbed by heavy equipment, is not plowed, and is precluded from further development. These verges provide diverse foraging and nesting resources to wild pollinators and thus have a high conservation potential. I surveyed roadsides in south-eastern Manitoba, Canada, to quantify the biodiversity of insect pollinators and evaluate the potential for these habitats to be used for pollinator monitoring and conservation in the region. Flower-visiting bees, flies, and wasps were sampled along 18 routes used for the North American Breeding Bird Survey, across an area encompassing three ecozones. I stopped ten times along each route to sample pollinators via ten minutes of targeted netting. I used satellite imagery and ground surveys to model how environmental variables affect pollinator biodiversity in the verges. I sampled and identified 4,232 insects belonging to 221 species or morphospecies. Roadside plant-pollinator communities were characterized by the dominance of a few eusocial generalist bee species foraging on floral assemblages dominated by introduced generalist plant species. Verges with greater plant biodiversity did not harbour greater pollinator biodiversity, probably due to the weedy nature of the surveyed roadsides not being attractive to specialists. Road verges surrounded by landscapes with greater patch diversity and with a greater proportion of open habitats hosted more abundant and rich pollinator communities. However, pollinator populations should benefit more from roadsides in homogeneous, disturbed landscapes where habitat resources are lacking. I determine that roadside verges are acting as habitats for a significant insect pollinator biodiversity and may be a good tool for conservation strategies in anthropogenic systems. Based on my results and previous studies, I suggest that management of road verges in south-eastern Manitoba should involve the restoration of original habitat via the sowing of native forbs and grasses in roadsides located within heavily modified, homogeneous landscapes.

2.1 Introduction

Marginal habitats such as hedgerows, roadside verges, powerline easements and crop margins become especially important for biodiversity conservation in highly human-impacted landscapes lacking quality early successional land. Roadside verges can be important habitat for beneficial insects including pollinating bees, butterflies, wasps and flies (Free et al. 1975; Munguira and Thomas 1992; Ries et al. 2001; Raemakers et al. 2001; Saarinen et al. 2005; Hopwood 2008; Hopwood et al. 2010; Hanley and Wilkins 2015; Cole et al. 2017; Heneberg et al. 2017; Riva et al. 2018; Ste-Marie et al. 2018; Cariveau et al. 2019; Phillips et al. 2019). Roadside verges are ubiquitous, occupying an estimated 4 million and 0.6 million hectares of land in the United States and Canada respectively (Wojcik and Buchmann 2012). Unlike clear cuts or abandoned fields, they are constantly maintained in an early successional state for the sake of driver and pedestrian safety and to provide a buffer to adjacent land. Furthermore, unlike agricultural fields, roadsides are only moderately disturbed by heavy equipment and aren't plowed. They are a permanent early successional habitat that is only moderately disturbed and usually precluded from further development. Roads tend to be considered ecologically negative since they can act as filters to animal movement, and have direct negative effects on wildlife through light, noise, chemical pollution, and traffic collisions (Muskett and Jones 1980; Munguira and Thomas 1992; McKenna et al. 2001; Keller et al. 2004; Baxter-Gilbert et al. 2015; Muñoz et al. 2015; Andersson et al. 2017). Nonetheless, the increased landscape heterogeneity brought by road verges may boost populations of beneficial insects due to an increased diversity of habitat resources within dispersal range (Kennedy et al. 2013; Steckel et al. 2014; Cole et al. 2017; Moquet et al. 2018). Road verges can benefit pollinators by providing abundant and diverse floral resources (Rotholz and Mandelik 2013; Hanley and Wilkins 2015; Cole et al. 2017; Phillips et al. 2019, 2020; Vanneste et al. 2020), shelter and nesting sites (Munguira and Thomas 1992; Brunzel et al. 2004; Schaffers et al. 2012), and connectivity in fragmented landscapes (Brunzel et al. 2004; Hopwood et al. 2010, 2015; Phillips et al. 2020).

Various roadside vegetation management regimes have been shown to enhance habitat quality for pollinators. In North America, conventional roadside maintenance involves planting non-native grasses and legumes, frequent mowing, and herbicidal treatment to control noxious weeds (Hopwood 2008). However, roadside verges may host greater pollinator biodiversity and a greater number of stenotopic (habitat specialist) species when mowing is kept to a minimum,

herbicidal treatment is targeted (as opposed to untargeted spraying), and when native forbs and grasses are planted (Ries et al. 2001; Hopwood 2008; Noordijk et al. 2009, 2010; Hopwood et al. 2015; Jakobsson et al. 2018; Phillips et al. 2020). Management strategies resulting in higher density and richness of flowers and larval host plants, especially natives, positively relates to pollinator biodiversity and benefits more stenotopic species (Munguira and Thomas 1992; Ries et al. 2001; Saarinen et al. 2005; Hopwood 2008; Noordijk et al. 2009; Andersson et al. 2017; Cole et al. 2017; Phillips et al. 2020). Landscape context also plays a role in determining roadside pollinator biodiversity. Road verges surrounded by more natural habitat, such as grassland and forest, tend to host a greater insect richness and abundance (Saarinen et al. 2005; Villemey et al. 2018; Cariveau et al. 2019; Phillips et al. 2020).

Increased awareness of the importance of wild insect pollinators and their global decline highlights the necessity for accurate distribution and population estimates. Unfortunately, rigorous pollinator monitoring projects in North America are lacking, with efforts directed towards species inventories (Kearns 2001; Woodard et al. 2020). With this study, I set out to test a roadside pollinator survey design and evaluate its potential to be used for the monitoring of pollinator populations. My objective was to quantify the pollinator biodiversity within roadside verges in southeastern Manitoba to determine their potential for pollinator conservation in the region. I also aimed to investigate what environmental factors within the verges and surrounding habitats might be affecting the pollinator biodiversity. I predict that the plant richness and abundance within the verges will have strong positive impacts on pollinator biodiversity. I also predict that landscape heterogeneity and the amount of natural land surrounding the verges will positively affect biodiversity, but to a lesser extent than local variables. Beyond assessing the viability of this survey design for large-scale pollinator monitoring, the primary goal of this study is to gather insights from my data as well as previous research to provide informed suggestions on roadside vegetation management for pollinator conservation.

2.2 Methods

Study Area

The study was carried out along 18 roadside verges scattered throughout south-eastern Manitoba, located below 51.7°N and between -95.2°W and -98.6°W (Figure 3). The climate in this area is moderately dry, with an average annual precipitation of 250-700 mm (Smith et al.

1998). Average monthly air temperatures span from -13°C in the winter to 27°C in the summer, but can reach extremes of -40°C and 38°C respectively, and snow covers the ground from November to April (Government of Canada 2021).

The roadside verges I surveyed were located within five of Manitoba's ecoregions (Smith et al. 1998), which vary greatly in their dominant soil types and vegetation: the Lac Seul Upland, Lake of the Woods, Mid-Boreal Lowland, Interlake Plain, and Lake Manitoba Plain ecoregions. The Lac Seul Upland and Lake of the Woods ecoregions are part of Canada's Boreal Shield ecozone. The Boreal Shield is mostly covered in dense forests of black and white spruce, jack pine, and balsam fir, mixed with innumerable bogs, marshes, lakes and other wetlands (Agriculture and Agri-Food Canada 1995). Broadleaf trees such as paper birch, trembling aspen, and poplar can be found in the southern range of this ecozone. The Mid-Boreal Lowland and Interlake Plain ecoregions are part of the Boreal Plains ecozone. This ecozone is a section of the flat Interior Plains of Canada and is largely covered by forests of white and black spruce, balsam fir, jack pine and tamarack, as well as aspen and poplar (Agriculture and Agri-Food Canada 1995). Unlike the boreal shield, it is also partially covered by swathes of mixed prairie. Finally, the Lake Manitoba Plain ecoregion is part of Canada's Prairie ecozone. Farmland dominates the Prairies, covering about 94% of the land and leaving little of the natural vegetation. Less than 1% of the Tall-Grass Prairie, 18% of the Short-Grass Prairie, and 24% of the Mixed-Grass Prairie remain (Agriculture and Agri-Food Canada 1995).

Study Sites

Study sites were located in verges along 18 established routes from the North American Breeding Bird Survey (BBS) program (USGS Patuxent Wildlife Research Center 2018). These are routes that have been surveyed repeatedly for breeding bird populations in Manitoba through a community science-based project. I used the BBS website to select routes for my study, targeting those that already had some baseline bird data (more than five years of surveys) and making sure that the routes were spread out throughout the study area to encompass different landscape types (agricultural, natural and semi-natural land) (Figure 3). To sample pollinators throughout the whole route I drove along the road and stopped 10 times every 4-5 km (road distance), with the first stop located at the start of the BBS route. Since I was sampling pollinators, site selection was also dependent on the distribution of floral resources. If there were little to no flowers at a stop, I

would continue driving until I reached the closest floral patch along the route. No standardized methodology was used to determine suitability of sites based on floral density and distribution. I prioritized locations with abundant floral resources and high pollinator activity. These observations were made while slowly driving along the road. I had 10 sampling sites for every survey route, totalling 180 sampling sites. My routes had a mean road length of 37.5 km (range = 31.2 - 43 km) from the first site to the last. The straight-line distance between sites of a route varied based on road topography (whether the road was straight or meandering) and floral patch distribution. The average straight-line distance between two consecutive sites of the same route was 3.81 km (range = 0.944 - 9.437 km). The minimum distance is smaller than the maximum flight distance of most bee species (Walther-Hellwig and Frankl 2000), and within reach of the maximum observed distance travelled by bumblebees along roadside verges (Hopwood et al. 2010). A study by Hopwood et al. (2010) revealed that bees in roadside verges showed high site fidelity, moving an average of 132 m across several days and 50 m or less in a single day, returning frequently to the flower patch where they were originally caught. I included route as a random factor in my models to account for relationships between sites. A list of the surveyed BBS routes and individual site coordinates is shown in Table S3 of the Appendix. All 18 routes (180 sites) were sampled once during the 2019 summer season, from July to August.



Figure 3. Breeding Bird Survey (BBS) routes used for pollinator sampling. Yellow lines indicate the routes, white text indicates the route name as given on the BBS website. Maps created with SimpleMappr (Shorthouse 2010) and Google Earth (Google Earth 7.3.4.8248 2021).

Sampling Procedure

At each of the 10 sites along a route, I set out a 50 m transect parallel to the road in the verge, at a minimum of 2 m away from the roadside. I would then conduct 10 minutes of active pollinator sampling using an insect net, collecting all bees, wasps, and flies (Hymenoptera and Diptera) that visited flowers located within 2 m of the transect on both sides (effectively sampling a 50 by 4 m plot). Pollinator handling time was excluded from the 10 minutes of sampling. Multiple researchers (maximum of three, in this study) could sample pollinators along the transect, providing that the combined sampling time totalled 10 minutes. All pollinators caught at a site were pooled together in a container with the route name and site number written on it. All routes were sampled between 0900 h and 1700 h during days without precipitation with air temperatures greater than 17°C and with low to moderate wind (below 15 km/h average, based on daily weather

reports). When arriving at the first site of a route, I recorded the air temperature and estimated the windspeed using the Beaufort wind force scale. At each site, I noted the sampling start and end time and recorded the coordinates using a Garmin GPS.

At each site, I gathered local flowering plant diversity data using 1 m sampling lines perpendicular to the road. The 50 m transect used to sample pollinators was divided into 10 sections of five metres each, and within each section I placed a 1 m transect using a 1-5 random numbers table. This method of stratified random sampling allowed me to gather plant diversity data along the entire transect while avoiding any potential bias. The 1 m sampling lines were placed perpendicular to the pollinator-sampling transect, on the side facing away from the road. Each 1 m sampling line was divided into five 20 by 20 cm squares (Figure 4), and for each square, the presence of all flowering plant species was recorded. Thus, an individual plant species could have a maximum presence count of 5 per sampling line, and 50 for the whole transect. Flowering plants were identified in the field using Newcomb's Wildflower Guide (1989) in combination with the plant-identifying iNaturalist phone application (iNaturalist 2021). If I was uncertain of any plant identification, I would take several pictures of the plant as well as sample some flowering branches for later identification in the laboratory with the use of Scoggan's "Flora of Manitoba" (1957). Vegetation was sampled along all routes except for the first one (Sandilands), therefore only 17 routes (170 sites) were used in our models.



Figure 4. Vegetation sampling procedure. For each 20 by 20 cm square a researcher recorded the presence of flowering plant species. For each sampling line, a plant species could have a maximum

presence count of 5, and therefore a maximum of 50 counts along the whole transect. Spatial arrangement of sampling lines along the transect in the figure is not intended to accurately represent the stratified design used.

Pollinator and Plant Community

I identified pollinators to the lowest possible taxonomic level using published identification keys (Cockerell 1903; Sandhouse 1939; Stephen 1954; LaBerge 1956b, 1956a, 1961, 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989; Mitchell 1962; Ribble 1968, 1974; LaBerge and Bouseman 1970; LaBerge and Ribble 1972, 1975; Baker 1975; Laverty and Harder 1988; Michener et al. 1994; Romankova 2003, 2007; Coelho 2004; Michener 2007; Packer et al. 2007; Rightmyer 2008; Kits et al. 2008; Buck et al. 2008; Arduser 2009a, 2009c, 2009b, 2009d; Gibbs 2011; Rightmyer et al. 2010; Gibbs 2010; Sheffield et al. 2011; Gibbs et al. 2012, 2013; Dumesh and Sheffield 2012; Miranda et al. 2013; Skevington et al. 2019) as well as reference materials (specimens from the J. B. Wallis/R. E. Roughley Museum of Entomology at the University of Manitoba). The collected bees belonged to the families Apidae, Andrenidae, Colletidae, Halictidae, and Megachilidae, and were all identified to species. For flies and wasps, only individuals from the most abundant families, and for which I could make confident identifications (based on availability of updated dichotomous keys and of reference specimens in the museum), were identified to species or morphospecies and included in the analyses. Therefore, only flies in the families Bombyliidae, Conopidae, Stratiomyidae, and Syrphidae; and only wasps in the families Braconidae, Crabronidae, Gasteruptiidae, Leucospidae, Perilampidae, Sphecidae, and Vespidae were identified to species or morphospecies. Apis mellifera L. individuals were not included in the biodiversity models, since their presence and abundance are dependent on the existence of beehives in the vicinity of study sites. Insect vouchers were deposited in the J. B. Wallis/R. E. Roughley Museum of Entomology at the University of Manitoba.

I used distance-based redundancy analysis (dbRDA) to compare the pollinator community composition across the three ecozones (Prairie, Boreal Plain, and Boreal Shield) with the Bray-Curtis index. The dbRDAs were performed on the relationship between route-specific community composition and ecozones using the 'capscale' function and then visualized with the 'ordiplot' function from the 'vegan' package in R (Oksanen et al. 2019). I used permutational multivariate analysis of variance (perMANOVA) to test for the effect of ecozone on pollinator communities using the Bray-Curtis index in the 'adonis' function (Oksanen et al. 2019). If the effect was

significant ($p \le 0.05$), I used the 'pairwise.adonis' function of the 'pairwiseAdonis' package (Arbizu 2017) to perform a post-hoc test. I then tested for the beta-dispersion among ecozones using the 'betadisper' function (Oksanen et al. 2019) to determine whether the three groups were equally dispersed. Identical analyses were conducted to compare the flowering plant community composition across ecozones.

Land-use Variables

I extracted land-use data from six circular buffers of increasing size around all 180 sites (250, 500, 750, 1000, 1500, and 2000 m radii). I used the 'landscapemetrics' R package (Hesselbarth et al. 2021) to extract land-use data from the Agriculture Canada Crop Inventory GEOTIFF layers (Agriculture and Agri-Food Canada 2020). These layers have a resolution of 30 m² and include 72 cover types. In Manitoba, they are at least 94% accurate for crop cover types and at least 70% accurate for non-crop cover. I measured five landscape variables for each site at each buffer size (Table 1): (i) 'open land' is the combined area (% cover) of exposed or barren land, shrubland, grassland, and fallow; (ii) 'forested land' includes the total area of broadleaf, coniferous, and mixedwood forests combined; (iii) 'disturbed land' represents the area covered by anthropogenic development (buildings, roads, greenhouses, and other) and crops; (iv) the Shannon Landscape Diversity Index (SHDI), derived from the Shannon entropy (Shannon 1948), retains the original landcover classifications and weighs each one by the number of patches in the landscape; and (v) the total Edge Density (ED). SHDI is a unitless metric that is only useful to compare landscapes with each other (Mcgarigal 2015). Edge density is calculated as:

$$ED = \frac{E}{A}(10,000)$$

E is the edge length (m) of the various patches combined, and A is the total area in the buffer (ha). Since ED represents total edge length per unit area (m/ha), it can be used to compare landscapes at differing spatial scales (Mcgarigal 2015).

Data Analysis

I ran separate models on pollinator abundance and rarefied species richness. Rarefied richness accounts for differences in richness estimates due to variation in species abundances (Hill 1973; Chao et al. 2014). To calculate rarefied richness I used the 'rarefy' function from the 'vegan'

R package (Oksanen et al. 2019). I used generalized linear mixed-effects models (GLMMs) to analyze the effects of environmental variables on the pollinator communities, using sites as individual data units and route as a random effect. Models for abundance were fitted to a negative binomial distribution using a log-link function, while those for rarefied richness were fitted to a Gaussian distribution. Model assumptions were evaluated through descriptive statistics and the visualization of residual distributions using quantile-quantile plots and histograms. In addition to running abundance and rarefied richness models on the whole pollinator community, I also ran the same models separately for bees, flies, and wasps. This allowed me to determine whether environmental variables had differing effects on the three insect groups (Jauker et al. 2019).

Landscape models for site-specific data included the main effects of day-of-year, ecozone, landscape (open land, forested land, disturbed land, SHDI and ED), and the interactions of ecozone with landscape (e.g. with SHDI); and included route as a random effect. The same model was run for each buffer size, and then I selected the best-fitting model with the lowest AICc score (Akaike 1998). If the model of best-fit had non-significant interactions, I excluded them and ran the model again, removing non-significant interactions until only significant ones remained or none at all. I also removed main effects that were correlated with others. For instance, amount of forested and disturbed land were correlated with each other and with ecozone, therefore they were excluded from the final model. Finally, the local variables – flowering plant abundance and richness – were added to run a final, global model. Only results from the global model are shown and reviewed. I made sure that my data met the model assumptions by checking the descriptive statistics and visualizing the distribution of residuals using the 'check_model' function of the 'performance' R package (Lüdecke et al. 2021).

Table 1.	Enviro	onmental	variable	s at the	e local	and	landscap	e scale.	Vegetatio	n data	was	gathe	ered
through	five 1	m sampli	ng lines	per site	e perpe	endic	cular to th	e verge	e transect.	Landsc	ape	data	was
gathered	l at six	buffer siz	zes (250,	500, 7	50, 10	00, 1	500, 200	0).					

Variable	Description
Local	
Floral richness	Total number of flowering plant species across all 1 m sampling lines per site.
Floral abundance	Total flowering plant presence across all 1 m sampling lines per site.
Landscape	

Open land	Area covered by exposed or barren land, shrubland, grassland, and
	fallow (%)
Forested land	Area covered by forest (%)
Disturbed land	Area covered by anthropogenic development and crops (%)
Shannon's Landscape	A measure of landcover diversity, where cover types are weighted by
Diversity Index	their relative patch abundance (unitless)
(SHDI)	
Total edge density	Sum of all edge lengths divided by the total landscape area (m/ha)
(ED)	

2.3 Results

Pollinator & Plant Biodiversity and Community Composition

I collected a total of 5,334 insects and subsequently identified 4,232 individuals to either species or morphospecies (Table S2). These insects consisted of 221 species within the three major pollinator groups (Table 2). Bees accounted for approximately 75% of the total pollinator abundance and 50% of the total richness (Figure 5). All collected bees were identified, consisting of 109 species. My total bee count represents just under 30% of the 369 species found in Manitoba, 23 out of 37 known genera, and five out of six families present in the province. Apids were dominant in terms of abundance (74% of all bee individuals, including A. mellifera L.) and codominant with halictids in terms of richness (29% of all bee species were either Apidae or Halictidae). Bombus was by far the most abundant genus, with 1,844 individuals sampled (58.6% of all bee individuals and 43.5% of all identified insects). Flies were the second most abundant and rich pollinator group (Figure 5), with 839 individuals sampled and identified, consisting of 65 species (19.8% and 29% of the total pollinator abundance and richness respectively). Syrphids were the most abundant fly family with 607 individuals sampled and were overall the most speciose family of all with 45 species identified (20% of all identified insects). Finally, 47 wasp species belonging to 7 families were identified from 247 individuals. Wasps only represented 5.8% of the total pollinator abundance but 21% of the total richness (Table 2). Overall, most pollinator species were rare (140 species were represented by five individuals or less), while a few were highly abundant (Figure 6). The ten most abundant species were, in descending order (Table 3): Bombus ternarius Say (25.9% of all insects caught and identified), Apis mellifera L. (9.8%),

Bombus sandersoni Franklin (5.9%), *Bombus vagans* Smith (5.2%), *Eristalis dimidiata* Wiedemann (3.3%), *Villa fulviana* (Say) (3.1%), *Toxomerus marginatus* (Say) (3.1%), *Megachile relativa* Cresson (2.1%), *Bombus rufocinctus* Cresson (2%), and *Heriades carinata* Cresson (1.8%). Four apid species, all generalists and eusocial, accounted for 46.8% of individuals captured in this study (Table 3).

Family	Total abundance	Genera	Species
Bees	3146	23	109
Andrenidae	105	3	10
Apidae	2336	8	32
Colletidae	128	2	11
Halictidae	217	5	32
Megachilidae	360	5	24
Flies	839	31	65
Bombyliidae	203	5	11
Conopidae	11	1	2
Stratiomyidae	18	2	7
Syrphidae	607	23	45
Wasps	247	29	47
Braconidae	41	1	3
Crabronidae	76	15	24
Gasteruptiidae	1	1	1
Leucospidae	1	1	1
Perilampidae	11	1	1
Sphecidae	16	3	4
Vespidae	101	7	13
Total	4232	83	221

Table 2. Families with individuals identified to species or morphospecies. Apis mellifera is included.

Table 3. Twenty-five most abun	lant pollinators sam	npled in roadside verges	across south-eastern
Manitoba, Canada.			

Species	Family	Abundance	% Of	Cumulative
			total	%
Bombus ternarius Say	Apidae	1096	25.9	25.9
Apis mellifera L.	Apidae	415	9.8	35.7
Bombus sandersoni Franklin	Apidae	249	5.9	41.6
Bombus vagans Smith	Apidae	221	5.2	46.8
Eristalis dimidiata Wiedemann	Syrphidae	139	3.3	50.1
Villa fulviana (Say)	Bombyliidae	133	3.1	53.2
Toxomerus marginatus (Say)	Syrphidae	131	3.1	56.3

Megachile relativa Cresson	Megachilidae	90	2.1	58.4
Bombus rufocinctus Cresson	Apidae	85	2.0	60.4
Heriades carinata Cresson	Megachilidae	77	1.8	62.2
Eristalis stipator Osten Sacken	Syrphidae	63	1.5	63.7
Bombus terricola Kirby	Apidae	59	1.4	65.1
Eristalis tenax L.	Syrphidae	57	1.3	66.4
Megachile latimanus Say	Megachilidae	44	1.0	67.4
Halictus rubicundus (Christ)	Halictidae	44	1.0	68.4
Megachile rotundata (Fabricius)	Megachilidae	43	1.0	69.4
Andrena lupinorum Cockerell	Andrenidae	40	0.94	70.3
Hylaeus mesillae (Cockerell)	Colletidae	39	0.92	71.3
Chelonus sp.ChA	Braconidae	38	0.9	72.2
Bombus borealis Kirby	Apidae	34	0.8	73.0
Bombus perplexus Cresson	Apidae	30	0.71	73.7
Eupeodes americanus (Wiedemann)	Syrphidae	30	0.71	74.4
Halictus confusus Smith	Halictidae	29	0.68	75.1
Systoechus vulgaris Loew	Bombyliidae	28	0.66	75.7
Megachile inermis Provancher	Megachilidae	27	0.64	76.4



Figure 5. Total pollinator biodiversity sampled and identified to species or morphospecies.



Figure 6. Pollinator rank-abundance curve for all combined routes, showing species in order of numerical dominance. Abundance axis is scaled logarithmically with base 10.

The Boreal Plain had the lowest average pollinator abundance per site (\pm SD) with 19.9 \pm 13.9 individuals/site, but the greatest average richness (8.6 \pm 4.1 species/site). Richness per site was equal in the Boreal Shield (8.6 \pm 4.1 species/site), but sites in this ecozone had a greater mean abundance (26.9 \pm 14 individuals/site). The Prairie ecozone hosted the lowest pollinator richness per site at 7.9 \pm 4.8 species/site, with a mean pollinator abundance of 21.5 \pm 16.4 individuals/site. Comparing the relative abundances of the three major pollinator groups (bees, flies, and wasps) reveals a variation between ecozones (Figure 7). In the Prairie and Boreal Plain ecozones, bees consisted of approximately 65% of the total insect abundance while flies were about 30% of the total. However, in the Boreal Shield, bees consisted of 83% of the total pollinator abundance while flies were at 12%. Despite this large difference in relative abundance, the relative richness of the three pollinator groups remained more stable throughout the three ecozones (Figure 7). Pollinator community composition was significantly different among the three ecozones (Table 4), with no overlap in ordination space (Figure 8). The post-hoc test revealed that the Prairie and Boreal Plain

ecozones' pollinator communities were significantly different from that of the Boreal Shield and were different from one another, although this last relationship was weaker (p = 0.057). The abundance and richness of the three pollinator groups also changed throughout the summer season, particularly for bees and flies (Figure 9). Bee abundance and richness both increased throughout July, with richness then slowly decreasing throughout August. Bee abundance also fell in early August but started rising again as the month progressed, reaching a second peak in mid/late August. Following a different pattern, fly abundance and richness remained relatively constant throughout the first month, only increasing in late July and reaching a peak in early August.



Figure 7. Pollinator biodiversity sampled and identified from each ecozone. Numbers inside the coloured bars show the raw abundance and richness values for each pollinator group.


Figure 8. Ordination plot of the dbRDA of all pollinator communities. Each point represents the community within a whole BBS route (18 total). Ecozone significantly affected the pollinator community composition (perMANOVA, F = 4.23, $R^2 = 0.36$, p = 0.001), resulting from a significant difference between the Boreal Shield and both the Prairie and Boreal Plain ecozones (Tukey's post-hoc test with a Bonferroni correction p = 0.015 and p = 0.003 for the relationship between Boreal Shield and, respectively, Boreal Plain and Prairie). Boreal Plain and Prairie ecozone communities were also different, although not statistically (adjusted p = 0.057). Singleton species were excluded from this analysis.



Figure 9. Abundance and richness of the three pollinator groups per sampling event throughout the sampling season. Shaded area represents 0.95 confidence interval.

I sampled 93 flowering plant species within the roadside verges, 61 of which were native to Manitoba while 32 were invasive. Although native species outnumbered invasives in terms of richness, alien plants were by far the most abundant (Figure 10). The ten most abundant plant species were, in descending order: Melilotus albus Medikus (18.9% of total vegetation counts), Cirsium arvense (L.) (12.1%), Medicago sativa L. (10.6%), Medicago lupulina L. (7.3%), Trifolium hybridum L. (7.3%), Trifolium pratense L. (4.5%), Sonchus arvensis L. (3.6%), Lotus corniculatus L. (3%), Melilotus officinalis (L.) (2.6%), and Galium boreale L. (1.9%). Only one species within the ten most abundant, Galium boreale, is native to Manitoba. Sites in the Prairie ecozone hosted the lowest average (\pm SD) flowering plant richness with 3.6 \pm 1.7 species/site, with an average plant abundance of 35.1 ± 15.7 counts/site. The Boreal Plain ecozone hosted the lowest average plant abundance at 30.2 ± 13.3 counts/site but hosted the second-highest mean plant species richness (5.5 \pm 2 species/site). Finally, the Boreal Shield ecozone hosted both the greatest mean plant abundance (42.1 ± 16.7 counts/site) and richness (6.2 ± 1.8 species/site) out of the three ecozones. Flowering plant community composition was significantly different among the three ecozones (Table 4), although there was overlap in ordination space (Figure 11). Plant communities in the Boreal Plain and Prairie were significantly different from each other (p = 0.033), while there were no significant differences with the community in the Boreal Shield (p = 0.228 and p = 0.249respectively). Finally, flowering plant abundance and richness varied throughout the sampling season (Figure 12). Overall, there was a decrease in the abundance of plants that were in bloom per site throughout the summer. Abundance started high in early July and steadily decreased throughout the month. In late July it started increasing, reaching a peak in early August, after which it once again decreased at a steady rate for the rest of the sampling season. Following an opposite pattern, blooming plant richness increased throughout the summer (Figure 12). Richness increased during July, reaching a first peak towards the end of the month. Richness then decreased during the first days of August, and then increased rapidly for the rest of the season, reaching its highest point at the very end.



Figure 10. Plant rank-abundance curve for all combined routes, showing species in order of numerical dominance. The abundance axis is scaled logarithmically with base 10.



Figure 11. Ordination plot of the dbRDA of all plant communities. Each point represents the community within a whole BBS route (17 total). Ecozone had a significant effect on the plant community composition (Table 4, perMANOVA, F = 1.80, $R^2 = 0.205$, p = 0.012), resulting from a significant difference between the Boreal Shield and the Prairie ecozone (Tukey's post-hoc test with a Bonferroni correction p = 0.033). Singleton species were excluded from this analysis.

Table 4. Summary of perMANOVA performed on the Bray-Curtis distance of the pollinator and plant communities. Post-hoc column shows the results of Tukey's post-hoc test with a Bonferroni correction. BS = 'Boreal Shield', BP = 'Boreal Plain', P = 'Prairie'.

Community	F model	R ²	p-value	BS-BP	BS-P	BP-P
				Post-hoc	Post-hoc	Post-hoc
Pollinators	4.234	0.3608	0.001	0.015	0.003	0.057
Flowering Plants	1.801	0.2046	0.012	0.228	0.249	0.033



Figure 12. Flowering plant richness and abundance throughout the sampling season.

Pollinator Abundance and Species Richness Modelling

The global models included land-use variables extracted from 500 m buffers around all sites, as this distance produced the lowest AICc scores in my landscape models. The landcover within the 500 m radius around all 180 sites was on average 23.8% open land (range = 0-87.4%), 34.4% forest (range = 0-93.3%), and 32.4% disturbed land (range = 2.9-100%). At the local scale, the average flowering plant abundance across all sites was 34.3 presence counts (9-98 counts) while the mean richness was 4.6 species (1-9 species). Both pollinator abundance and rarefied richness significantly increased throughout the sampling season (Table 5). This trend was however moderated by ecozone (Figure 15, Figure 16), which also had a significant effect on the two response variables (Figure 13D, Figure 14D). Pollinator rarefied richness was negatively affected by wind speed, while abundance was negatively affected both by increased wind speed and temperature (Figure 14B, Figure 13B-C). Plant abundance did not affect pollinator abundance (Figure 13F). Landscape-scale variables did not seem to affect pollinator biodiversity except for SHDI, which had a significant positive effect on pollinator rarefied richness (Figure 14G).

Building the same global models separately on bees, flies and wasps reveals differing trends between the three major pollinator groups. The abundance and richness of all three pollinator groups (rarefied richness for bees and flies) significantly increased over the sampling season, but for bees this trend was moderated by ecozone (Table 6). The interaction between

ecozone and Julian date was not significant in the fly and wasp models and was therefore excluded. Wind speed had a significant negative effect on bee abundance and rarefied richness, but a positive effect on flies (Table 7). Wasps were not affected by wind speed. Temperature only affected bee abundance, causing a slight but significant decrease in individuals sampled (Table 6). At the landscape-scale, fly abundance was negatively affected by edge density but responded positively to the amount of open land (Table 7). Besides Julian date, wasps were only affected by the landscape SHDI, with both abundance and richness responding positively (Table 8).

	Pollinator .	Abundance			Pollinator I	Rarefied Ric	hness	
Pseudo - R_M^2	0.09				0.152			
Pseudo - R_c^2	0.092				0.152			
Predictor	β	SE	Z	р	β	SE	Z	р
Intercept	-7.310	1.969	-3.71	0.0002	-23.1	9.511	-2.43	0.0151
Julian Date	0.0557	0.0094	5.94	<0.0001	0.1554	0.0457	3.4	0.0007
Beaufort Windspeed	-0.1639	0.0532	-3.08	0.0021	-0.6386	0.2597	-2.46	0.0139
Temperature	-0.0606	0.0193	-3.15	0.0017	-0.1476	0.0939	-1.57	0.116
Plant Abundance	0.001	0.0028	0.35	0.723	0.0041	0.0155	0.26	0.7917
Plant Richness	-0.0534	0.0253	-2.11	0.0346	-0.104	0.1393	-0.75	0.4557
SHDI	0.2031	0.1743	1.17	0.2439	1.742	0.8816	1.98	0.0481
Edge Density (m/ha)	0.0005	0.0008	0.62	0.5354	0.0011	0.0046	0.25	0.8052
Open Land	0.0031	0.003	1.04	0.2961	-0.006	0.0156	-0.39	0.6992
Ecozone – Boreal Plain	5.561	2.665	2.09	0.0369	15.8	13.05	1.21	0.226
Ecozone – Boreal Shield	13.54	2.628	5.15	<0.0001	47.94	13.03	3.68	0.0002
Boreal Plain : Julian Date	-0.0271	0.0097	-2.13	0.0332	-0.0711	0.0626	-1.14	0.2559
Boreal Shield : Julian Date	-0.0625	0.0127	-4.88	<0.0001	-0.2277	0.0636	-3.58	0.0003

Table 5. Results of the global GLMMs performed on pollinator abundance and rarefied richness per site. BBS route was included as a random effect. Landscape variables are based on landcover surrounding each site within a 500 m radius buffer. Variables that were correlated with others are excluded from the model. "Sandilands" route is excluded due to lack of vegetation data.



Figure 13. Effects of environmental variables on roadside pollinator abundance. Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and the p-values are shown in Table 5. Landscape variables were calculated from 500 m buffers around each site. Ecozone 'P' = Prairie, 'BP' = Boreal Plain, 'BS' = Boreal Shield.



Figure 14. Effects of environmental variables on roadside pollinator rarefied richness ("Rare Richness"). Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and the p-values are shown in Table 5. Landscape variables were calculated from 500 m buffers around each site. Ecozone 'P' = Prairie, 'BP' = Boreal Plain, 'BS' = Boreal Shield.



Figure 15. Pollinator abundance and richness over time per ecozone. Shaded area sows 95% confidence intervals.



Figure 16. Ecozone-dependent effects of Julian date on pollinator abundance. Points represent observations per sampling event. Regression lines represent predicted values from GLMM. Shaded areas represent 95% confidence intervals. Significant effects are shown in bold.

	Bee Abund	ance			Bee Rarefie	ed Richness		
Pseudo - R_M^2	0.167				0.166			
Pseudo - R_C^2	0.167				0.166			
Predictor	β	SE	Z	р	β	SE	Z	р
Intercept	-4.08	2.408	-1.69	0.0901	-8.542	7.234	-1.18	0.2377
Julian Date	0.0356	0.0114	3.12	0.0018	0.0724	0.0347	2.09	0.0369
Beaufort Windspeed	-0.2919	0.0641	-4.55	<0.0001	-0.7612	0.1975	-3.85	0.00012
Temperature	-0.0518	0.0237	-2.19	0.0286	-0.1293	0.0714	-1.81	0.0702
Plant Abundance	0.0035	0.0035	1.00	0.3165	0.0166	0.0117	1.41	0.1582
Plant Richness	-0.0425	0.0315	-1.35	0.1777	-0.0027	0.106	-0.03	0.9799
SHDI	0.2544	0.2089	1.22	0.2234	0.9414	0.6704	1.40	0.1602
Edge Density (m/ha)	0.0017	0.001	1.65	0.0988	0.0008	0.0035	0.24	0.8125
Open Land	-0.0014	0.0039	-0.37	0.7145	-0.0052	0.0119	-0.44	0.6595
Ecozone – Boreal Plain	4.937	3.177	1.55	0.1201	16.62	9.93	1.67	0.0943
Ecozone – Boreal Shield	12.11	3.143	3.85	0.00012	35.89	9.91	3.62	0.0003
Boreal Plain : Julian Date	-0.0217	0.0152	-1.42	0.1543	-0.0725	0.0476	-1.52	0.1278
Boreal Shield : Julian Date	-0.0538	0.0153	-3.51	0.00045	-0.1698	0.0483	-3.51	0.00044

Table 6. Results of global GLMMs performed on bee abundance and rarefied richness. BBS route is included as a random effect.

	Fly Abund	ance			Fly Raref	ied Richness		
Pseudo - R_M^2	0.362				0.216			
Pseudo - R_C^2	0.395				0.216			
Predictor	β	SE	Z	р				
Intercept	-10.14	2.524	-4.02	<0.0001	-7.54	2.296	-3.28	0.001
Julian Date	0.0637	0.0097	6.55	<0.0001	0.0477	0.0088	5.42	<0.0001
Beaufort Windspeed	0.3	0.1098	2.73	0.0063	0.2811	0.0968	2.90	0.0037
Temperature	-0.0563	0.0383	-1.47	0.1419	-0.0389	0.0355	-1.09	0.2736
Plant Abundance	-0.0085	0.0062	-1.37	0.1698	-0.005	0.0062	-0.81	0.42
Plant Richness	-0.0608	0.052	-1.17	0.2426	-0.0711	0.056	-1.27	0.204
SHDI	-0.0117	0.3473	-0.03	0.9731	0.1454	0.3433	0.42	0.672
Edge Density (m/ha)	-0.00354	0.0016	-2.16	0.0312	0.0001	0.0018	0.08	0.9369
Open Land	0.0123	0.0057	2.15	0.0312	0.0018	0.0063	0.29	0.7709
Ecozone – Boreal Plain	-1.035	0.3822	-2.71	0.0068	-0.7515	0.3592	-2.09	0.0364
Ecozone – Boreal Shield	-0.1125	0.328	-0.34	0.7316	0.0112	0.3092	0.04	0.9711
Boreal Plain : Julian Date	-	-	-	-	-	-	-	-
Boreal Shield : Julian Date	-	-	-	-	-	-	-	-

Table 7. Results of global GLMMs performed on fly abundance and rarefied richness. BBS route is included as a random factor.

	Wasp Abu	Indance			Wasp Ric	hness		
Pseudo - R_M^2	0.198				0.117			
Pseudo - R_C^2	0.4				0.163			
Predictor	β	SE	Z	р	β	SE	Z	р
Intercept	-10.32	4.609	-2.24	0.025	-7.334	3.298	-2.22	0.026
Julian Date	0.0363	0.0176	2.06	0.039	0.0258	0.0125	2.06	0.04
Beaufort Windspeed	-0.013	0.172	-0.08	0.94	-0.0567	0.1334	-0.42	0.671
Temperature	0.0614	0.0665	0.92	0.356	0.0399	0.0485	0.82	0.411
Plant Abundance	-0.0011	0.009	-0.12	0.902	-0.0107	0.0078	-1.37	0.171
Plant Richness	-0.0596	0.0812	-0.73	0.463	-0.0553	0.0656	-0.84	0.399
SHDI	1.103	0.559	1.97	0.048	0.9431	0.4466	2.11	0.035
Edge Density (m/ha)	-0.0014	0.0027	-0.51	0.61	0.0005	0.0021	0.23	0.816
Open Land	0.0099	0.0085	1.16	0.245	0.0009	0.0073	0.12	0.901
Ecozone – Boreal Plain	0.0654	0.6443	0.1	0.919	0.1331	0.4871	0.27	0.785
Ecozone – Boreal Shield	0.1158	0.5647	0.21	0.838	0.0017	0.4253	0.00	0.997
Boreal Plain : Julian Date	-	-	-	-	-	-	-	-
Boreal Shield : Julian Date	-	-	-	-	-	-	-	-

Table 8. Results of global GLMMs performed on wasp abundance and richness. BBS route is included as a random factor.

2.4 Discussion

Pollinator Fauna

The roadside verges I surveyed in south-eastern Manitoba were acting as partial habitats for a rich and abundant insect pollinator fauna. I identified 221 species of bees, flies, and wasps that were using the roadside verges as foraging sites for pollen and/or nectar resources. The 109 bee species observed constitute almost 14% of all bees recorded from Canada, and approximately 30% of the known fauna in the province of Manitoba (Gibbs et al. unpublished). Previous studies have also recorded a high richness of pollinator species in roadside verges, although differences in sampling effort and methodology make direct comparisons difficult (Free et al. 1975; Raemakers et al. 2001; Hopwood 2008; Heneberg et al. 2017; Cariveau et al. 2019; Phillips et al. 2019). I expect that increasing the sampling effort of the roadside surveys would result in an even greater number of observed species. Increasing netting time per site and sampling each site multiple times throughout the summer season, for instance, may allow us to capture greater pollinator biodiversity. Sampling each site only once did not allow us to capture local variation in pollinator populations due to seasonal emergence. Adding passive sampling methods such as bee bowls and blue vane traps would also be helpful given that certain pollinator taxa can be over or underrepresented depending on sampling methodology (Portman et al. 2020; Prendergast et al. 2020). Generally, a combination of active and passive sampling methods is ideal to sample a proper representation of the pollinator community (Prendergast et al. 2020). However, targeted net sampling outperforms passive sampling methods in terms of the pollinator abundance and richness captured (Prendergast et al. 2020). Netting enabled me to specifically target insects that were actively visiting flowers in the road verge, allowing me to be certain that they were using the floral resources on the ROW. Furthermore, passive sampling methods are not ideal for the nature of this community-science survey due to the high effort and time required to implement them. Biodiversity data from traps also tends to have unexpected interactions with floral variables (Portman et al. 2020), which are eliminated when we only use targeted netting.

The vast majority of the sampled pollinator species were native to Canada, but a few introduced species were observed in relatively high abundances. These include 24 *Andrena wilkella* (Kirby) individuals, a mining bee originally from Europe, and 43 individuals of *Megachile rotundata* (Fabricius), the alfalfa leafcutter bee purposefully imported from Europe for the

pollination of alfalfa and canola crop fields. Furthermore, *Apis mellifera* L. was the second most abundant pollinator within the roadside verges with 415 individuals sampled.

With 109 species sampled, bees accounted for almost 50% of the total insect richness in the roadside verges. Among the bees foraging in the verges, I report several rare or uncommon species. I observed regionally uncommon species such as Melissodes trinodis Robertson and *Colletes hyalinus* Provancher, which have only recently been added to Manitoba's provincial bee species record (Gibbs et al. unpublished). Just under 60 individuals of Bombus terricola Kirby, a species in decline across North America (Colla and Packer 2008; Cameron et al. 2011), were also observed foraging in the verges. One of the most interesting finds was that of *Calliopsis australior* Cockerell, a new national record for Canada. Additionally, I also found several kleptoparasitic bee species which have only been recently added to the provincial record. These include *Triepeolus* helianthi (Robertson) and T. obliteratus Graenicher, Coelioxys modestus Smith, and the blood bees Sphecodes confertus Say, S. coronus Mitchell, S. dichrous Smith, and S. prosphorus Lovell and Cockerell. Parasitic pollinators are considered indicator species of quality habitat, as they are thought to persist only where populations of their hosts reach a stable threshold (Sheffield et al. 2013; Russell et al. 2018). Furthermore, kleptoparasites are expected to spend less time foraging and more time near their hosts' nesting sites (Russell et al. 2005). Hence, the presence of kleptoparasitic bees in the roadside verges may be an indication that their hosts are using the verges for nesting, beyond simply foraging. Several insect clades such as butterflies, carabids and moths have been observed breeding in roadside verges (Eversham and Telfer 1994; Vermeulen 1994; Brunzel et al. 2004), and many, including bees, use roadside verges to overwinter (Schaffers et al. 2012). Although my sampling methodology precludes us from determining whether a sampled individual was nesting in the verge or simply passing by, I did have the occasion to observe many bee and wasp ground nests in the verges throughout the season. Furthermore, the well-drained sandy soil of many of the surveyed roadsides made them ideal spots for ground-nesting species. I presume that several of the sampled species were nesting in the verges. However, a proper study designed to explore this matter is necessary to confirm this.

Bees were overwhelmingly dominant in terms of abundance (75% of all the collected insects), but this was mostly brought by a few highly abundant, generalist eusocial species in the Apidae family. These were *Apis mellifera* L., *Bombus ternarius* Say, *B. sandersoni* Franklin, and *B. vagans* Smith, which were the four most abundant species overall. Combined, these species

encompassed almost 47% of the total insect abundance sampled. Bombus ternarius alone, the orange-belted bumblebee, consisted of 25% of all collected insects. Species evenness in the roadside verges was therefore quite low, with most species being rare or uncommon and a few species being disproportionately abundant. Similar results were found in a previous roadside pollinator biodiversity study from Europe, where a single bee species, Lasioglossum pauxillum (Schenck), comprised almost 20% of captured individuals (Heneberg et al. 2017). Cariveau et al. (2019) also found that common species dominated roadside bumblebee communities in Minnesota (U.S.A). In general, large habitat fragments are characterized by a high proportional abundance of habitat and resource specialists due to elevated resource heterogeneity that promotes species coexistence (Wiens 1989; Marini et al. 2014). On the other hand, small habitat patches tend to be dominated by generalists (Marini et al. 2014). Despite their considerable length, road verges are a small habitat patch due to being very narrow, therefore dominance of a few generalist species in the pollinator community was to be expected. ROW biodiversity studies confirm that the biotic and abiotic characteristics of these long, narrow corridors tend to favour habitat generalists to the detriment of specialists that rely on large areas of undisturbed landscape (Jalkotzy et al. 1997; Berger 2010; Knapp et al. 2013; Vanneste et al. 2020; Nelson et al. 2021). Species evenness alters the shape of species-area relationships: more species are found in a defined area if the assemblage has higher evenness (He and Legendre 2002). Therefore, dominance by a few apid species in the community may be limiting the pollinator richness within the roadside verges. This effect of evenness can potentially be explained by competition. Increasing dominance changes the relative importance of intraspecific vs. interspecific interactions, which in turn can significantly alter population dynamics. In uneven communities, species dominance generally leads to rare species experiencing greater importance of interspecific interactions, while the dominant species experience greater importance of intraspecific ones (Hillebrand et al. 2008). Assuming species compete for the same resource (pollen and/or nectar for pollinators), populations largely regulated by intraspecific interactions exhibit dynamics predicted by logistic growth models, growing to a certain carrying capacity. Those experiencing stronger interspecific interactions, on the other hand, are kept at lower abundances (Hillebrand et al. 2008; Wignall et al. 2020). The increased interspecific competition experienced by rare species in the roadside verges might thus be keeping their abundances at lower levels than if evenness had no effect. For the dominant species in my system, however, the importance of intraspecific interactions is mediated by their eusocial

behaviour. At any given site, individuals of *Bombus ternarius* were most likely workers originating from one or a few colonies established within or in the vicinity of the road verge. Solitary bee individuals represent single reproductive units working independently for the continuation of their lineages while competing with individuals from the same species and from others. The individual is the unit of evolutionary selection. In contrast, eusocial bee individuals from the same colony represent cooperating units which contribute aggregately to the survival and reproduction of a "superorganism". Individuals are integral parts of a colony, and selection primarily operates at the level of the colony (Moritz and Fuchs 1998). Eusocial bees, therefore, do not experience intraspecific competition at the individual-level, but only at the colony level. In eusocial groups, resources for survival are shared among entities, allowing for the survival of the colony (reduced variance in resource supply for survival). At the same time, there is an increase in variance in resource supply for reproduction, as these resources are destined only for a small number of individuals (the queens). When resources are scarce, these two methods of resource allocation allow both for the survival of a larger number of individuals as well as for reproduction (Fronhofer et al. 2018). In most environmental situations, this dramatic increase in resource use efficiency leads to supersaturation – a strong increase in carrying capacity (Fronhofer et al. 2018). Therefore, the marked dominance of some apid bees in my system was initially brought by favouring of resource and habitat generalists due to habitat characteristics of roadside verges, and further elevated by the high resource use efficiency associated with their eusocial behaviour. The combination of these competitive advantages over solitary and specialist species has allowed these apids to thrive within the roadside verges and supersaturate the habitat.

Vey little is known about the effects of dominance on aggregate community properties and ecosystem processes. Theoretically, if the dominant species perform plant pollination better than the mean of the community, this process will increase, and vice-versa if the dominants perform below average (Hillebrand et al. 2008). Since specialist pollinators possess inherent physiological, behavioural, and morphological adaptations to particular plant taxa, one might hypothesize that specialists should demonstrate higher per-visit pollination effectiveness (e.g., number of monospecific pollen grains deposited per visit) compared to generalists foraging on the same plant source (Larsson 2005). Since all dominant species in the road verges were generalists, it could be inferred that the reduction of species evenness is having negative effects on overall plant reproduction in this system. The higher per-visit pollination effectiveness of specialized visitors

on unspecialized plants has been demonstrated (Larsson 2005), however, this is not a universal rule (Motten et al. 1981). Furthermore, despite specialists being more effective pollinators during single floral visits, generalist species tend to contribute more to overall pollen flow due to a greater abundance and more frequent floral visitations (Larsson 2005). Visitation frequency has been shown to be so important for plant pollination that it overrides differences in per-interaction effects (Vázquez et al. 2005, 2012; Ballantyne et al. 2017). My study does not allow me to draw conclusions on the effect that an overwhelming dominance of a few generalist, eusocial species have on the rest of the pollinator community and on pollination rates through their high abundance and frequent floral visits, however at the same time they may be limiting the richness and abundance of other pollinators through high competitive pressures. As a result, specialist plant-pollinator interactions may be limited in the verges.

Flies were also important pollinators in the roadside verges. Flies accounted for almost 30% of the total insect richness sampled, and Syrphidae was the most speciose family of any pollinator group. Additionally, a few fly species were very abundant. Eristalis dimidiata Wiedemann, Villa fulviana (Say), and Toxomerus marginatus (Say) together comprised 9.5% of the total insect abundance. Flies are the second most frequent floral visitors, after bees, and a huge diversity of dipteran species are known to visit flowers (Larson et al. 2001). Syrphids in particular visit flowers often to consume nectar and pollen for flight and reproduction (Moquet et al. 2018). Several species within this clade have been shown to carry significant pollen loads comparable to certain bee species (Kendall and Solomon 1973; Free et al. 1975; Orford et al. 2015) and can be important pollinators for many plant species (Jauker and Wolters 2008; Orford et al. 2015). Syrphids have also been found to carry significant amounts of pollen while foraging in a roadside verge (Free et al. 1975). My results, therefore, suggest that flies are significantly contributing towards the provisioning of pollination services within the roadside verges. The verges also hosted a relatively high wasp diversity, consisting of 21% of the total richness. Abundance, however, was low at just under 6%. All recorded wasp species were observed in low abundance, with no individual wasp species representing more than 1% of the total insect abundance. Most wasps have carnivorous diets and only occasionally visit flowers (Patt et al. 1997). This explains the underrepresentation of wasps and the discrepancy between richness and abundance: many wasp species visited flowers, but none of them were frequent visitors.

Pollinator biodiversity and community composition in the roadside verges varied significantly between the three ecozones. The Boreal Shield hosted the greatest overall pollinator biodiversity as well as the greatest average richness and abundance per site. Average richness per site was equivalent in the Boreal Plain despite these sites hosting the lowest mean abundance, while verges in the Prairie ecozone hosted the least number of species. Sites within the Boreal Shield were surrounded by a reduced proportion of disturbed land, such as agricultural fields and urban development, and a greater proportion of forested land compared to sites in the other two ecozones. Furthermore, sites in the Boreal Shield had the greatest average plant abundance and richness. Pollinators respond positively to increased abundance and diversity of floral resources at the local scale (Hülsmann et al. 2015; Cole et al. 2017; Rollin et al. 2019) and benefit from a higher amount of natural and semi-natural land at the landscape-scale (Kennedy et al. 2013). A combination of these beneficial factors may be what is driving higher pollinator diversity in the roadside verges within the Boreal Shield. The pollinator community composition in the roadsides was significantly different between the three ecozones, indicating that the different landscape characteristics and environmental conditions found in each ecozone influenced the pool of pollinator species available to forage and nest in the roadsides. The differences were particularly large between the Boreal Shield and the other two ecozones. The plant community composition in the boreal shield roadsides however was not different from the Boreal Plain or Prairie, meaning that it was not what drove the difference in pollinator community composition.

Contrary to my expectations, relative bee abundance was greatest in road verges within the boreal shield ecozone. This ecozone is characterized by an abundant and dense distribution of wetlands such as lakes, bogs and marshes (Agriculture and Agri-Food Canada 1995), and bees (especially ground-nesters) tend to favour xeric areas (Michener 2007; Orr et al. 2021). On the other hand, dipterans can thrive in the vicinity of wetlands, and several, such as those in the genus *Eristalis*, require freshwater environments for reproduction. Therefore, I expected flies to be the dominant pollinator group in this ecozone, however this was not the case. Raw bee richness was also greatest in road verges within the boreal shield, however, the relative richness of bees compared to the other two clades was constant throughout all three ecozones. There was therefore a discrepancy in the variation between relative richness and abundance among ecozones. The increased abundance in the boreal shield was primarily brought by social bee species in the genus *Bombus*. Over 1400 *Bombus* individuals were sampled in the boreal shield (~20 individuals per

site), while 297 bumblebees were collected in the boreal plains ecozone (~6 individuals per site), and only 97 in the prairie ecozone (~2 per site, a ten-fold decrease). I am unsure as to why there was this marked increase in bumblebee abundance in the boreal shield. Potentially, there might have been a greater concentration of bees in these roadside verges due to the disproportionate attractiveness of the habitat compared to the surrounding environment. The landscape surrounding the verges in the boreal shield consisted mainly of forest or wetland, which tend to lack the plentiful floral resources and dry sandy soils which characterized the roadsides and are favoured by bumblebees. Being less dependent on these resources compared to bees, flies and wasps may have experienced less attractiveness towards the verges and remained more dispersed in the landscape. Furthermore, verges in the boreal shield ecozone hosted on average a greater flowering plant richness and abundance, and were surrounded by more forested area and less agriculture – all factors which have been shown to boost bumblebee abundance in roadside verges (Cariveau et al. 2019). Additionally, a couple of my boreal shield routes were situated within the Sandilands Moraine, an area characterized by its predominantly sandy soil which is favoured by ground-nesters such as bumblebees (Michener 2007).

Biodiversity Models

Greater flowering plant cover and richness generally boost pollinator biodiversity through greater availability and diversity of foraging resources (Hülsmann et al. 2015; Cole et al. 2017). However, contrary to my original expectations, I found that blooming plant abundance (measured as presence counts in my sampling lines) had no effect on roadside pollinator biodiversity, while blooming plant richness had a small but significant negative effect on pollinator abundance. Flower abundance and richness in the road verges were not related, meaning that some sites with high floral abundance were dominated by a few plant species. As with pollinators, although to a lesser extent, I found that the overall plant community within the verges was highly uneven, with a few species being highly abundant while the majority were uncommon. The most abundant plant, *Melilotus albus* Medikus, comprised just under 20% of the total presence counts across all sites. Together with the next four most abundant plants, *Cirsium arvense* (L.), *Medicago sativa* L., *M. lupulina* L. and *Trifolium hybridum* L., these plants amounted to 56% of the total abundance sampled. Flowering plant community evenness can have significant effects on pollination rates. Target plants can experience facilitative effects from greater species diversity since it tends to

attract a greater number and diversity of pollinators (Ghazoul 2006). However, these facilitative effects are conditional on the evenness of the floral mixture and can shift to competitive effects as relative abundances of dominant species increase (Ghazoul 2006). Furthermore, the dominant plants in the verges were mostly invasive weeds. Other studies have also reported high richness and cover of invasive plants in roadside verges (Valtonen et al. 2006; Hopwood 2008; Hopwood et al. 2015; Cariveau et al. 2019), which is aggravated by seed dispersal from vehicles (Von Der Lippe and Kowarik 2007). With their large and colourful floral displays, accessible flower morphology and prolific nectar production, invasive plants can compete for interactions with pollinators and consequently reduce the reproductive output of natives (Kaiser-Bunbury et al. 2017; Tylianakis and Morris 2017). Rare or uncommon native flowering plants in the roadside verges may therefore be experiencing high competitive pressures as the activity of pollinators is diverted away from them and towards the more attractive dominant species. The invasive nature of the dominant plants might be the reason why I found no relationship between plant abundance and pollinator biodiversity. In a similar roadside survey, Hopwood (2008) found positive effects of floral abundance on bee richness in restored roadsides (sowed with native forb and grass seeds). However, this relationship was no longer significant in weedy roadsides, where the primarily invasive flowers attracted a less diverse bee assemblage compared to the native floral communities of the restored verges. Weedy roadsides were characterized by the presence of non-native grasses and >50% cover of non-native forbs, including Melilotus species (Hopwood 2008). The author suggests that this difference might be explained by a reduced attraction of native insects by exotic flowers compared to native flowers (Memmott and Waser 2002; Frankie et al. 2005). Valtonen et al. (2006) found that roadside verges invaded by the invasive plant Lupinus polyphyllus Lindley harboured fewer butterflies due to bottom-up effects of changes in plant assemblages and a reduction of flowering plant richness and cover. Increased floral abundance within the surveyed roadsides was brought mainly by a few dominant, non-native species which are visited by generalists such as bumblebees (Memmott and Waser 2002). The dominance of these invasive generalist plants may have limited the growth of more specialist, native flowers in the verges. Furthermore, invasive plants are unlikely to partner with native specialist pollinators (Aslan 2019). The resulting plant community was therefore highly attractive to common generalist pollinators, but not to specialists. I hypothesize that this is the reason why I did not observe a relationship between flowering plant abundance and pollinator biodiversity. I am unsure as to what might

explain the small but significant negative effect that plant richness had on pollinator abundance. Perhaps sites with greater floral diversity, hosting more native plants, promoted a more even pollinator community and hence a reduced dominance of eusocial species, which may have resulted in an overall reduced abundance.

Following my original predictions, landscape diversity had a positive effect on pollinator rarefied richness. This indicates that more heterogeneous landscapes, containing more numerous and diverse patch types, provided various partial habitats containing the foraging and nesting resources necessary to host rich pollinator communities. These results are in line with other studies reporting positive effects of landscape heterogeneity on pollinator biodiversity (Kennedy et al. 2013; Steckel et al. 2014; Cole et al. 2017; Moquet et al. 2018). Wasps were highly affected by the landscape SHDI both in terms of abundance and richness. Landscape diversity was the only environmental factor that affected wasp biodiversity in the verges. Wasps only occasionally visit flowers for the metabolic support provided by pollen and nectar (Patt et al. 1997), therefore it is not surprising that they were not affected by variation of floral abundance or richness in the roadsides. Rather, the carnivorous or parasitic lifestyle of most wasp species makes them highly dependent on the distribution and abundance of their prey or host species (Szczepko et al. 2012b), which in turn is dependent on the distribution and abundance of the host requisites. Wasps, therefore, lie at higher levels (secondary and tertiary consumers) of complex multi-trophic networks. This means that wasp biodiversity is hypothetically less dependent on the local availability of primary producers (plants), and more on the combined distribution of primary producers and primary consumers in the landscape. Studies have shown that plant diversity has strong bottom-up effects on multitrophic interaction networks, however, these effects are stronger on lower trophic levels (Scherber et al. 2010). Effects on higher trophic levels are indirectly mediated through bottom-up trophic cascades (Scherber et al. 2010; Fenoglio et al. 2012). Uniform landscapes limit the diversity of resources available within the mobility ranges of primary consumers, reducing their biodiversity which in turn negatively affects their highly-specialized predators and parasites/parasitoids (Szczepko et al. 2012b). This is confirmed by reports from several studies on a positive relationship between landscape heterogeneity and wasp biodiversity (Steffan-Dewenter 2003; Bianchi et al. 2006; Szczepko et al. 2012b, 2012a; Steckel et al. 2014).

Flies did not respond to habitat diversity. Instead, verges surrounded by a greater proportion of open habitats such as fallow land, shrubland and grassland tended to host a greater

abundance of flower-visiting dipterans. Many fly species, particularly syrphids, thrive in seminatural open habitats such as grasslands, heathlands and other open-space environments which are rich in floral resources (Gittings et al. 2006; Meyer et al. 2009; Moquet et al. 2018). Therefore, road verges that are in the vicinity of these habitats may be experiencing a stronger influx of hoverflies compared to verges that are surrounded by less open-space habitats. I also found a slight negative effect of edge density on fly abundance. Increased edge density indicates a reduction of habitat patch size, and syrphids tend to be associated more with large open spaces rather than small open spaces (Gittings et al. 2006). Therefore, I interpret these results as an indication that syrphid abundance in roadside verges is influenced both by the amount of surrounding open habitats, as well as the size of these habitat patches. Roadside verges in landscapes containing a greater amount of open habitats that are less fragmented should host the greatest abundance of flower-visiting flies. Verges in heterogeneous landscapes with greater amounts of open land may therefore host a greater abundance and diversity of pollinators. However, since these landscapes already contain plentiful resources for wasps, bees, and flies; these pollinators would probably benefit more from road verges in homogeneous areas lacking sufficient early-successional habitats.

I found that pollinator biodiversity was significantly different between the three ecozones, with verges in the boreal shield hosting significantly more abundance and rarefied richness. However, these differences were moderated by the Julian date, meaning that they were dependent on when the sites were sampled. I found that there was an overall increase in pollinator abundance and richness over the sampling season. However, verges in the three ecozones experienced different rates and patterns of biodiversity growth through time, which explains the significant relationship of ecozone and Julian date. I hypothesize that the different rates of biodiversity growth may be a result of the difference in pollinator community composition between all three ecozones. This may be due to different phenologies of the species within the three separate pollinator communities.

Implications for Management and Monitoring

I have shown that roadside verges in south-eastern Manitoba are attracting many pollinator species as they provide ample floral resources which are often lacking in the surrounding agricultural and forested landscapes. These results are in line with several other studies investigating insect biodiversity along roadsides (Free et al. 1975; Munguira and Thomas 1992;

Ries et al. 2001; Raemakers et al. 2001; Saarinen et al. 2005; Hopwood 2008; Hopwood et al. 2010; Hanley and Wilkins 2015; Cole et al. 2017; Heneberg et al. 2017; Riva et al. 2018; Ste-Marie et al. 2018; Cariveau et al. 2019; Phillips et al. 2019). Investigating the effects of roadside vegetation management on pollinators was beyond the scope of this study. Nonetheless, roadside management can affect the capacity of road verge habitats to support pollinators. Results from previous studies suggest that the quality of the verge habitat can be enhanced with relatively loweffort strategies. These include reducing mowing to a minimum and avoiding mid-summer mowing, using targeted herbicidal treatment rather than untargeted spraying, and planting native forbs and grasses (Ries et al. 2001; Hopwood 2008; Noordijk et al. 2009, 2010; Hopwood et al. 2015; Jakobsson et al. 2018; Phillips et al. 2020). My study did not reveal a positive relationship between roadside flowering plant and pollinator biodiversity. I attribute this to the predominantly weedy nature of the surveyed verges, with plant communities mostly dominated by invasives. Other studies report positive effects, with higher densities and richness of flowers and larval host plants positively relating to pollinator abundance and richness and supporting a greater number of stenotopic species (Munguira and Thomas 1992; Ries et al. 2001; Saarinen et al. 2005; Hopwood 2008; Noordijk et al. 2009; Andersson et al. 2017; Cole et al. 2017; Phillips et al. 2020). Additionally, road verges that are restored with native prairie vegetation have been shown to support 2x greater density and 1.5x greater richness of bees compared to weedy verges, despite little difference in floral density (Hopwood 2008); and 5x greater density and 2x greater species richness of stenotopic butterflies compared to weedy or grassy (low forb cover) verges (Ries et al. 2001). Verges dominated by invasive species, on the other hand, are characterized by low diversity and cover of other flowering plant species, as well as reduced pollinator biodiversity due to bottomup effects (Valtonen et al. 2006).

To improve the quality of roadside verge habitats in Manitoba I believe that the best strategy is to restore them to an original native prairie plant community. This would involve the removal of invasive species such as *Melilotus* and the sowing of native forbs and grasses. The restored verges would host a diverse and even flowering plant community which would provide pollen and nectar resources to a diverse assemblage of native pollinators, including rare and specialist species. I also suggest reducing mowing to only once or twice a year and to avoid midsummer mowing to keep disturbance to a minimum. However, I also found that there were significant differences in roadside pollinator community composition between ecozones, and that these communities increased in richness and abundance throughout the summer at different rates (potentially due to varying phenologies of species). This suggests that verge management should not be blindly calendar-based but should take into consideration the community composition and phenology of the local plant and insects. Land managers should therefore make informed decisions based on locality. Finally, in line with previous studies, I found that roadside pollinator biodiversity was greatest in verges within heterogeneous landscapes with larger habitat patches and a greater proportion of open and forested land. Therefore, if the goal is to increase the value of verges to existing pollinator populations, focusing on habitat improvements in these landscapes would be most productive. However, these landscapes already contain abundant and diverse foraging and nesting resources for pollinators. Increasing road verge attractiveness here might actually be detrimental if pollinators from adjacent lands are drawn in and die as a result of vehicle collisions (Keilsohn et al. 2018). I hence suggest targeting road verges within highly modified and/or homogeneous landscapes lacking sufficient early successional habitats, such as in highly agricultural or densely forested areas. Here, restored road verges may constitute the only quality habitat for early-successional species. This would allow promotion of pollinator conservation in these landscapes and expand the range of species into areas that were historically occupied.

If the roadside survey design were to be applied at a large scale for the monitoring of pollinator populations, I suggest a few modifications. In my study, I sampled each route only once during the summer period. However, as I have observed, pollinator biodiversity varies through time and at different rates depending on locality. Different pollinator species have different peaks in abundance within a single summer season, therefore I believe routes should be surveyed more than once to capture this variation. Being a community-based project, there is an issue of observer variability built in. For instance, there will be variability in the ability of volunteers to detect and catch pollinators, and the speed at which they process specimens. With my design, I eliminated the latter factor by excluding pollinator handling time from the 10 minutes of sampling. However, this inevitably increases the time necessary to complete a survey, which is not desirable if we wish for the project to be appealing to volunteers. To understand what factors were affecting pollinators in the roadside verges, I added a flowering plant sampling protocol to the survey. Plant data are very useful since they can reveal whether observed changes in roadside pollinator populations are due to internal or external factors. I believe gathering more detailed plant data, such as floral cover as a proxy of abundance rather than presence counts, would be helpful. This would allow us to

better understand plant-pollinator relationships within road verges. For instance, detailed plant data might allow us to comprehend the interspecific effects (facilitative or competitive) that generalist invasive plants, which tend to dominate unrestored roadsides, have towards native species. However, this increases the training (for plant species identification) and effort required to complete the survey. Therefore, although gathering plant data would be useful, I don't think it is realistic to expect volunteers to sample the floral community. Nonetheless, surveyors could be asked to take pictures and notes of the flowering plants they observe in the verge. These could either be sent to experts for later identification or could be uploaded on applications such as iNaturalist ("iNaturalist" 2021). The data gathered this way would not be very detailed, but it could help unveil general plant-pollinator biodiversity patterns in the road verges.

In general, roads are considered detrimental for wildlife due to the associated edge, barrier and habitat fragmentation effects, as well as noise, light and chemical pollution (Jalkotzy et al. 1997). With this study, I do not wish to justify the construction of new roads, especially through natural areas where they would only bring adverse effects to the local wildlife. I instead argue that improving the habitat characteristics of already existing road verges within modified or homogeneous landscapes can increase habitat diversity and provide foraging and nesting resources to pollinators. Roadside verges will never be a substitute for natural habitats, however they are excluded from further development and continuously maintained in an early-successional state. If managed properly, they may constitute a valuable conservation resource for native pollinator and flowering plant communities.

2.5 Conclusion

The pollinator roadside survey I designed and tested allowed me to determine that road verges in south-eastern Manitoba are acting as habitats for a significant biodiversity of pollinating bees, flies, and wasps. With this study, I was able to determine that the pollinator biodiversity and community composition within road verges varied between ecozones and was greatest in sites surrounded by heterogeneous landscapes with larger habitat patches and with greater amounts of forest and open habitats. I found no relationship between pollinators and roadside floral resources but argue that this was due to a dominance of invasive plants in the verges. Overall, I found that both plant and pollinator communities in the verges were highly uneven with a few generalist species dominating the environment – potentially reducing the abundance and richness of less

common, specialist species through competitive pressures. I believe that management regimes aimed at maintaining native prairie vegetation in the verges would allow for the conservation of a diverse wild pollinator community.

I believe this type of pollinator survey has a strong potential to be applied at a much broader scale for the monitoring of pollinator populations in Canada and throughout the rest of North America. Currently, there is a lack of rigorous pollinator monitoring programs in place in Canada or the United States. However, increased awareness of the importance of wild pollinators and the declines they are experiencing calls for more data collection. Roadside pollinator surveys might be a useful method to monitor populations across space and time due to the ease of implementation and attractiveness to volunteers. The model and sampling frame for a continent-wide roadside survey already exist in the form of the North American Breeding Bird Survey (USGS Patuxent Wildlife Research Center 2018), and the North American Amphibian Monitoring Program (USGS Eastern Ecological Science Center 2016). The application towards pollinator surveys should be relatively straightforward. Roadside surveys do not require landowner permission since they are conducted on public roads. Furthermore, travel between sampling sites is quick and easy, enabling the coverage of large areas in little time. Roadside surveys are also inexpensive and require relatively little training, but specimens need to be sent to experts for identification. Applying this survey to a larger area and conducting it on an annual basis would allow us to capture variations in pollinator populations.

2.6 Appendix

Route	Ecozone	Day-of-Year
Sandilands	Boreal Shield	190
Saint Claude	Prairie	193
Grunthal	Boreal Plain	196
Bird River	Boreal Shield	197
Saint F. Xavier	Prairie	199
Braintree	Boreal Shield	200
Woodroyd	Boreal Plain	203
Graysville	Prairie	204
Whitemouth Lake	Boreal Shield	205
Traverse Bay	Boreal Shield	211

Table S1. Ecozone of the BBS routes and day-of-year in which they were sampled.

Elma	Boreal Shield	212
Hecla Island	Boreal Plain	212
Jordan	Prairie	214
Delta Beach	Prairie	220
Springer Lake	Boreal Shield	224
Camper	Boreal Plain	225
Red Rose	Boreal Plain	227
Bissett	Boreal Shield	228

Table S2. Abundance of all identified pollinator species

Species	Author	Abundance
Andrenidae		105
Andrena canadensis	Dalla Torre 1896	1
Andrena chromotricha	Cockerell 1899	4
Andrena hirticincta	Provancher 1888	5
Andrena lupinorum	Cockerell 1906	40
Andrena miranda	Smith 1879	4
Andrena nubecula	Smith 1853	1
Andrena thaspii	Graenicher 1903	24
Andrena wilkella	(Kirby 1802)	24
Calliopsis australior	Cockerell 1897	1
Protandrena aestivalis	(Provancher 1882)	1
Apidae		2336
Anthophora terminalis	Cresson 1869	9
Apis mellifera	Linnaeus 1758	415
Bombus bimaculatus	Cresson 1863	14
Bombus borealis	Kirby 1837	34
Bombus fervidus	(Fabricius 1798)	12
Bombus flavidus	Eversmann 1852	12
Bombus frigidus	Smith 1854	2
Bombus griseocollis	(DeGeer 1773)	12
Bombus huntii	Greene 1860	1
Bombus melanopygus	Nylander 1848	17
Bombus perplexus	Cresson 1863	30
Bombus rufocinctus	Cresson 1863	85
Bombus sandersoni	Franklin 1913	249
Bombus ternarius	Say 1837	1096
Bombus terricola	Kirby 1837	59
Bombus vagans	Smith 1854	221
Ceratina dupla	Say 1837	3
Ceratina mikmaqi	Rehan and Sheffield 2011	9

Epeolus compactus	Cresson 1878	1
Melissodes agilis	Cresson 1878	2
Melissodes confusus	Cresson 1878	23
Melissodes druriellus	(Kirby 1802)	4
Melissodes illatus	Lovell and Cockerell 1906	3
Melissodes trinodis	Robertson 1901	2
Melissodes wheeleri	Cockerell 1906	4
Nomada aquilarum	Cockerell 1903	1
Nomada arenicola	Swenk 1913	1
Nomada composita	Mitchell 1962	1
Nomada crawfordi	Cockerell 1905	7
Triepeolus helianthi	(Robertson 1897)	1
Triepeolus obliteratus	Graenicher 1911	5
Triepeolus pectoralis	(Robertson 1897)	1
Bombyliidae		203
Hemipenthes morio	(Linnaeus 1758)	3
Lepidophora lutea	Painter 1962	1
Poecilanthrax alcyon	(Say 1824)	5
Poecilanthrax tegminipennis	(Say 1824)	22
Systoechus vulgaris	Loew 1863	28
Villa alternata	Say 1823	1
Villa fulviana	(Say 1824)	133
Villa lateralis	(Say 1823)	2
Villa nigra	Cresson 1916	4
Villa nigropecta	Cresson 1916	2
Villa pretiosa	(Coquillett 1887)	2
Braconidae		41
Chelonus sp.ChA		38
Chelonus sp. ChB		2
Chelonus sp.ChD		1
Colletidae		128
Colletes brevicornis	Robertson 1897	1
Colletes hvalinus	Provancher 1888	7
Colletes kincaidii	Cockerell 1898	17
Colletes simulans	Cresson 1868/Patton 1879	8
Hylaeus affinis	(Smith 1853)	15
Hylaeus annulatus	(Linnaeus 1758)	16
Hylaeus basalis	(Smith 1853)	1
Hylaeus gaigei	(Cockerell 1916)	5
Hylaeus illinoisensis	(Robertson 1896)	1
Hylaeus mesillae	(Cockerell 1896)	39
	· · · · · · · · · · · · · · · · · · ·	57

Hylaeus modestus	Say 1837	18
Conopidae		11
Physocephala furcillata	(Williston 1882)	10
Physocephala texana	(Williston 1882)	1
Crabronidae		
(Bembicidae, Crabronidae,		
Pemphredonidae, Philanthidae)		76
sp.PB		3
sp.PC		1
Anacrabro ocellatus	Packard 1866	5
Bembix americana	Fabricius 1793	9
Bicyrtes ventralis	Say 1824	6
Cerceris arelate	Banks 1912	1
Cerceris clypeata	Dahlbom 1844	1
Cerceris halone	Banks 1912	1
Ectemnius arcuatus	(Say 1837)	3
Ectemnius continuus	(Fabricius 1804)	1
Ectemnius lapidarius	(Panzer 1804)	3
Ectemnius maculosus	(Gmelin 1790)	7
Gorytes atricornis	Packard 1867	3
Larropsis sp.LB	$(\mathbf{D}_{1}, 1, 1, 0, \mathbf{c})$	3
Lestica producticollis	(Packard 1866)	5
Oxybelus emarginatus	Say 1837	6
Oxybelus uniglumis	(Linnaeus 1758)	5
Pemphredon sp.PA	C 1965	4
Philanthus bilunatus	Cresson 1865	1
Philanthus lepidus	Cresson 1865	2
Philanthus solivagus	Say 1837 (S_{22})	2
Khopalum coarctatum	(Scopoli 1/63)	1
Saygorytes phaleratus	(Say 1837) (Estricius 1804)	2
Tacnytes auruientus	(Fablicius 1804)	1
Gasteruptiidae		1
Gasteruption assectator	(Linnaeus 1758)	1
Halictidae		217
Agapostemon texanus	Cresson 1872	1
Augochlorella aurata	(Smith 1853)	21
Halictus confusus	Smith 1853	29
Halictus rubicundus	(Christ 1791)	44
Lasioglossum admirandum	(Sandhouse 1924)	2
Lasioglossum albipenne	(Robertson 1890)	2

(Sandhouse 1933)	1
(Provancher 1888)	3
(Robertson 1890)	5
(Cockerell 1916)	5
(Smith 1853)	14
(Lovell 1908)	2
(Schrank 1781)	8
(Crawford 1906)	1
(Graenicher 1911)	8
(Mitchell 1960)	1
McGinley 1986	1
(Ellis 1913)	10
(Smith 1853)	1
(Lovell 1905)	4
(Crawford 1907)	7
(Cockerell 1938)	4
(Robertson 1901)	1
(Lovell 1905)	3
(Robertson 1902)	7
(Lovell 1905)	5
(Smith 1853)	3
(Smith 1848)	11
Say 1837	1
Mitchell 1956	4
Smith 1853	6
Lovell and Cockerell 1907	2
	1
Say 1824	1
	360
Smith 1854	2
Smith 1854	3
Cresson 1864	2
Cockerell 1900	1
Smith 1854	2
Cresson 1878	4
Cresson 1864	77
(Cresson 1872)	10
(Cresson 1864)	3
(Cresson 1864)	10
(Provancher 1888)	5
(Robertson 1903)	2
Smith 1853	10
	(Sandhouse 1933) (Provancher 1888) (Robertson 1890) (Cockerell 1916) (Smith 1853) (Lovell 1908) (Schrank 1781) (Crawford 1906) (Graenicher 1911) (Mitchell 1960) McGinley 1986 (Ellis 1913) (Smith 1853) (Lovell 1905) (Crawford 1907) (Cockerell 1938) (Robertson 1901) (Lovell 1905) (Robertson 1902) (Lovell 1905) (Smith 1853) (Smith 1853) (Smith 1848) Say 1837 Mitchell 1956 Smith 1853 Lovell and Cockerell 1907 Say 1824 Say 1824 Smith 1854 Cresson 1864 (Cresson 1878 Cresson 1864) (Cresson 1872) (Cresson 1864) (Cresson 1864) (Cresson 1872) (Cresson 1864) (Cresson 1864) (Cresson 1864) (Cresson 1872) (Cresson 1864) (Cresson 1903) Smith 1853

Megachile gemula	Cresson 1878	3
Megachile inermis	Provancher 1888	27
Megachile latimanus	Say 1823	44
Megachile melanophaea	Smith 1853	5
Megachile montivaga	Cresson 1878	2
Megachile pugnata	Say 1837	6
Megachile relativa	Cresson 1878	90
Megachile rotundata	(Fabricius 1787)	43
Osmia bucephala	Cresson 1864	1
Osmia proxima	Cresson 1864	2
Osmia simillima	Smith 1853	6
Perilampidae		11
Perilampus hyalinus	Say 1829	11
Sphecidae		16
Ammophila azteca	Cameron 1888	7
Prionyx atratus	(Lepeletier 1845)	4
Prionyx canadensis	(Provancher 1887)	4
Sceliphron caementarium	(Drury 1773)	1
Stratiomyidae		18
Hedriodiscus binotatus	(Loew 1866)	3
Hedriodiscus sp.L		1
Hedriodiscus sp.M		6
Hedriodiscus vertebratus	(Say 1824)	2
Stratiomys badia	Walker 1842	2
Stratiomys obesa	(Loew 1866)	2
Stratiomys sp.A		2
Syrphidae		607
Cheilosia pallipes	(Loew 1863)	1
Cheilosia shannoni	Curran 1923	1
Epistrophe emarginata	(Say 1823)	1
Eristalis brousii	Williston 1882	1
Eristalis dimidiata	Wiedemann 1830	139
Eristalis flavipes	Walker 1849	16
Eristalis stipator	Osten Sacken 1877	63
Eristalis tenax	(Linnaeus 1758)	57
Eupeodes americanus	(Wiedemann 1830)	30
Eupeodes perplexus	(Osburn 1910)	2
Helophilus fasciatus	Walker 1849	6
Helophilus hybridus	Loew 1846	5
Helophilus latifrons	Loew 1863	2

Helophilus obscurus	Loew 1863	1
Heringia canadensis	Curran 1921	1
Lapposyrphus lapponicus	(Zetterstedt 1838)	2
Melanostoma mellinum	(Linnaeus 1758)	1
Neocnemodon rita	(Curran 1921)	7
Ocyptamus fascipennis	(Wiedemann 1830)	7
Orthonevra pulchella	(Williston 1887)	3
Paragus angustifrons	Loew 1863	4
Paragus haemorrhous	Meigen 1822	2
Parasyrphus genualis	(Williston 1887)	4
Platycheirus granditarsis	(Forster 1771)	3
Platycheirus immarginatus	(Zetterstedt 1849)	4
Platycheirus rosarum	(Fabricus 1787)	1
Scaeva affinis	Say 1823	2
Sericomyia militaris	(Walker 1849)	2
Sphaerophoria contigua	Macquart 1847	1
Sphaerophoria novaeangliae	Johnson 1916	1
Sphaerophoria philanthus	(Meigen 1822)	9
Sphaerophoria pyrrhina	Bigot 1884	1
Syritta pipiens	(Linnaeus 1758)	17
Syrphus attenuatus	Hine 1922	1
Syrphus rectus	Osten Sacken 1875	5
Syrphus ribesii	(Linnaeus 1758)	25
Syrphus torvus	Osten Sacken 1875	1
Syrphus vitripennis	Meigen 1822	10
Toxomerus geminatus	(Say 1823)	11
Toxomerus marginatus	(Say 1823)	131
Tropidia quadrata	(Say 1824)	21
Volucella facialis	Williston 1882	1
Xylota annulifera	Bigot 1884	1
Xylota flavifrons	Walker 1849	2
Xvlota hinei	(Curran 1941)	1
<u>,</u> ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	×	
Vespidae		101
Ancistrocerus albophaleratus	(de Saussure 1855)	6
Ancistrocerus antilope	(Panzer 1798)	2
Ancistrocerus catskill	(de Saussure 1853)	7
Dolichovespula adulterina	(de Buysson 1905)	1
Dolichovespula arenaria	(Fabricius 1775)	23
Dolichovespula maculata	(Linnaeus 1763)	27
Dolichovespula norvegicoides	(Sladen 1918)	12
Eumenes crucifera	Provancher 1888	4
Euodynerus foraminatus	(de Saussure 1853)	1
Euodynerus planitarsis	(Bohart 1945)	4
✓ 1		

Polistes fuscatus	(Fabricius 1793)	2
Stenodynerus kennicottianus	(de Saussure 1870)	2
Vespula consobrina	(de Saussure 1864)	10

Grand Total

Table S3. Site codes and coordinates for all eighteen BBS routes. Route name and length are indicated (road distance from first to tenth site).

Route Name & Site Code	Latitude	Longitude
Bird River – 38.7 km		
BR1	50.413	-95.676
BR2	50.414	-95.618
BR3	50.433	-95.561
BR4	50.463	-95.528
BR5	50.468	-95.463
BR6	50.462	-95.415
BR7	50.459	-95.375
BR8	50.471	-95.319
BR9	50.469	-95.265
BR10	50.468	-95.208
Bissett – 42.6 km		
BS2	51.023	-95.471
BS3	51.029	-95.535
BS4	51.032	-95.606
BS5	51.026	-95.663
BS6	51.039	-95.720
BS7	51.051	-95.778
BS8	51.068	-95.850
BS9	51.069	-95.909
BS10	51.076	-95.979
BS11	51.092	-96.033
Braintree – 37.2 km		
BT1	49.439	-95.404
BT2	49.441	-95.483
BT3	49.444	-95.496
BT4	49.468	-95.536
BT5	49.504	-95.554
BT6	49.536	-95.564
BT7	49.562	-95.597
BT8	49.554	-95.651
BT9	49.554	-95.703

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BT10	49.556	-95.760
<i>Camper</i> – 38.1 km		
CA1	51.067	-98.114
CA2	51.067	-98.155
CA3	51.067	-98.216
CA4	51.067	-98.284
CA5	51.067	-98.344
CA6	51.067	-98.396
CA7	51.082	-98.435
CA8	51.096	-98.467
CA9	51.134	-98.467
CA10	51.140	-98.541
Delta Beach – 37.7 km		
DB1	50.173	-98.313
DB2	50.147	-98.330
DB3	50.119	-98.330
DB4	50.079	-98.331
DB5	50.051	-98.331
DB6	50.048	-98.400
DB7	50.048	-98.445
DB8	50.019	-98.460
DB9	50.019	-98.511
DB10	50.019	-98.595
<i>Elma</i> – 35.8 km		
EL1	49.875	-95.975
EL2	49.856	-95.956
EL3	49.856	-95.911
EL4	49.837	-95.884
EL5	49.799	-95.884
EL6	49.764	-95.881
EL7	49.732	-95.879
EL8	49.707	-95.899
EL9	49.670	-95.895
EL10	49.644	-95.881
Grunthal – 37.5 km		
GR1	49.561	-96.889
GR2	49.539	-96.889
GR3	49.512	-96.872
GR4	49.471	-96.871
GR5	49.439	-96.871
GR7	49.378	-96.849
GR8	49.348	-96.849
GR9	49.319	-96.849
CP 10	49 281	-96.849
UKIU	17.201	,

GR11	49.249	-96.848
Graysville – 42.4 km		
GV1	49.510	-98.160
GV2	49.531	-98.175
GV3	49.531	-98.228
GV4	49.532	-98.285
GV5	49.531	-98.300
GV7	49.572	-98.414
GV8	49.591	-98.456
GV9	49.576	-98.482
GV10	49.606	-98.507
GV11	49.606	-98.556
<i>Hecla Island</i> – 31.4 k	m	
HI2	51.097	-96.908
HI3	51.057	-96.841
HI4	51.051	-96.789
HI5	51.066	-96.730
HI6	51.079	-96.687
HI7	51.117	-96.687
HI8	51.142	-96.659
HI9	51.159	-96.641
HI10	51.052	-96.773
HI11	51.081	-96.861
Jordan – 43 km		
JO1	49.389	-98.024
JO2	49.412	-98.024
JO4	49.459	-98.024
JO5	49.515	-98.023
JO6	49.524	-98.069
JO7	49.567	-98.073
JO8	49.594	-98.073
JO9	49.621	-98.028
JO10		
JO11	49.650	-98.073
	49.650 49.685	-98.073 -98.073
Red Rose – 34.8 km	49.650 49.685	-98.073 -98.073
<u>Red Rose – 34.8 km</u> RR1	49.650 49.685 51.624	-98.073 -98.073 -97.428
<u>Red Rose – 34.8 km</u> RR1 RR2	49.650 49.685 51.624 51.601	-98.073 -98.073 -97.428 -97.417
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3	49.650 49.685 51.624 51.601 51.568	-98.073 -98.073 -97.428 -97.417 -97.418
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3 RR4	49.650 49.685 51.624 51.601 51.568 51.527	-98.073 -98.073 -97.428 -97.417 -97.418 -97.425
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3 RR4 RR5	49.650 49.685 51.624 51.601 51.568 51.527 51.491	-98.073 -98.073 -97.428 -97.417 -97.418 -97.425 -97.462
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3 RR4 RR5 RR6	49.650 49.685 51.624 51.601 51.568 51.527 51.491 51.476	-98.073 -98.073 -97.428 -97.417 -97.418 -97.425 -97.462 -97.482
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3 RR4 RR5 RR6 RR7	49.650 49.685 51.624 51.601 51.568 51.527 51.491 51.476 51.476	-98.073 -98.073 -97.428 -97.417 -97.418 -97.425 -97.462 -97.482 -97.532
<u>Red Rose – 34.8 km</u> RR1 RR2 RR3 RR4 RR5 RR6 RR7 RR8	49.650 49.685 51.624 51.601 51.568 51.527 51.491 51.476 51.476 51.450	-98.073 -98.073 -97.428 -97.417 -97.418 -97.425 -97.462 -97.482 -97.532 -97.522
RR10	51.411	-97.470
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Sandilands – 31.2 km		
SDL2	49.631	-96.091
SDL3	49.597	-96.089
SDL4	49.567	-96.067
SDL5	49.548	-96.036
SDL6	49.537	-96.061
SDL7	49.539	-96.095
SDL8	49.498	-96.143
SDL9	49.483	-96.145
SDL10	49.469	-96.149
SDL11	49.426	-96.144
Saint F. Xavier – 39.6 km		
SFX2	49.950	-97.521
SFX3	49.919	-97.535
SFX4	49.898	-97.551
SFX5	49.913	-97.572
SFX6	49.931	-97.615
SFX7	49.950	-97.686
SFX8	49.960	-97.711
SFX9	49.960	-97.759
SFX10	49.975	-97.802
SFX11	49.986	-97.849
Springer Lake – 36 km		
SL1	50.507	-95.466
SL2	50.532	-95.466
SL3	50.56	-95.452
SL4	50.581	-95.419
SL5	50.613	-95.456
SL6	50.642	-95.447
SL7	50.646	-95.418
SL8	50.669	-95.405
SL9	50.673	-95.372
SL10	50.686	-95.325
Saint Claude – 38 km		
STC1	49.576	-98.300
STC2	49.607	-98.301
STC3	49.648	-98.301
STC4	49.682	-98.301
STC5	49.709	-98.285
STC6	49.746	-98.278
STC7	49.785	-98.278
STC8	49.811	-98.278
STC9	49.861	-98.278

STC10	49.901	-98.284		
<i>Traverse Bay</i> – 36.6 km				
TB1	50.665	-96.529		
TB2	50.664	-96.483		
TB3	50.633	-96.478		
TB4	50.614	-96.432		
TB5	50.618	-96.369		
TB6	50.620	-96.321		
TB7	50.596	-96.281		
TB8	50.567	-96.236		
TB9	50.560	-96.183		
TB10	50.533	-96.155		
Whitemouth Lake – 37.6 km	l			
WL2	49.266	-95.485		
WL3	49.281	-95.533		
WL4	49.281	-95.600		
WL5	49.281	-95.643		
WL6	49.280	-95.702		
WL7	49.289	-95.759		
WL8	49.299	-95.838		
WL9	49.309	-95.879		
WL10	49.311	-95.932		
WL11	49.311	-95.986		
<i>Woodroyd</i> – 36.7 km				
WR2	50.300	-97.488		
WR3	50.314	-97.524		
WR4	50.348	-97.529		
WR5	50.385	-97.529		
WR6	50.421	-97.529		
WR7	50.463	-97.529		
WR8	50.502	-97.529		
WR9	50.506	-97.576		
WR10	50.527	-97.598		
WR11	50.561	-97.598		

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Preface to Chapter 3

In Chapter 2, I explored pollinator biodiversity in roadside verges in Manitoba to assess their potential use for pollinator monitoring and conservation. I found that a significant portion of the local pollinator biodiversity was using the abundant floral resources provided by the verges. I also found positive effects of heterogeneity and proportion of open land in the surrounding landscapes on pollinator biodiversity. Contrary to my expectations I did not find a positive relationship between local vegetation variables and pollinators, which I attributed to the weedy nature of the plant community in the verges. Simple biodiversity measures such as abundance and richness, however, did not allow me to evaluate whether the pollinator communities in these narrow linear habitats were healthy and resilient. The persistence of biodiversity is highly dependent on the frequency and patterns of biotic interactions. Studying plant-pollinator networks is essential to properly evaluate whether ROWs can host stable pollinator communities. My objectives for Chapter 3 were to explore the pollinator biodiversity found in a major powerline ROW in Manitoba (another type of linear, man-made widespread system) and investigate how various environmental variables - including vegetation management strategy - affected both pollinator biodiversity and the robustness of plant-pollinator interaction networks. I associated host plants with pollinators to build flower visitation networks and test for effects of local and landscape-level variables on these interactions. Knowing the status of pollinator communities and networks within ROWs, and how environmental variables can affect both, can allow us to manage these marginal habitats to promote pollinator conservation whilst maintaining their anthropogenic utility.

CHAPTER 3. NETWORKS IN THE GRID: PLANT-POLLINATOR INTERACTIONS IN A POWERLINE EASEMENT CORRIDOR OF MANITOBA, CANADA

3.0 Abstract

The loss of natural and semi-natural open habitats is a leading cause of global insect pollinator declines. Electric transmission line easements provide large linear expanses of managed habitat that is continuously maintained in an early-successional state. This land is potentially important wild pollinator habitat and may be a valuable tool for biodiversity conservation, especially within heavily disturbed or homogeneous landscapes such as agricultural or densely forested areas. However, there is a lack of evidence of whether these narrow linear habitats can host healthy and stable plant-pollinator communities. I quantified the biodiversity of flowervisiting insects within a major powerline corridor in Manitoba and described the plant-pollinator interaction networks to evaluate the potential of these habitats for the conservation of pollinators and the ecosystem service they provide. I sampled all bees, flies, and wasps visiting flowers at 15 sites along a 300 km powerline easement section stretching over a 2.5° latitudinal gradient. I used satellite imagery and ground surveys to model how environmental variables affect pollinator biodiversity and network structure in the easements. I also investigated the effects of integrated vegetation management (IVM) on the plant-pollinator networks relative to other management practices such as mowing, grazing, and fallowing. I recorded 4,958 links between 80 plant and 259 pollinator species, forming 1,431 unique interactions. I found that increased cover and richness of flowering plants in the easement positively affected pollinator biodiversity. Furthermore, vegetation management strategy had a significant impact on both pollinator biodiversity and the interaction network structure. IVM sites hosted the largest pollination networks, which were more modular and specialized due to a greater number of specialized species and interactions. IVM networks were also more robust to random plant species extinction simulations, potentially due to aggregate buffering effects of specialists and reduced dependency on few generalist species. Management practices that increase floral cover and richness lead to greater pollinator biodiversity and more robust networks, regardless of the surrounding landscape. I show that powerline ROWs can host biodiverse pollinator communities that form robust plant-pollinator interaction networks, and therefore have a high conservation potential.

3.1 Introduction

In homogeneous, modified landscapes lacking sufficient natural and semi-natural early successional habitats, powerline rights-of-way (ROWs) could constitute a valuable resource for the conservation of insect pollinator biodiversity. Wild pollinator diversity has been declining globally throughout the past few decades (Kearns et al. 1998; Biesmeijer et al. 2006; Colla and Packer 2008; Potts et al. 2010; Cameron et al. 2011a; Goulson et al. 2015). The principal cause for these declines is the loss of natural and semi-natural habitats as a result of human activity (Kearns et al. 1998; Goulson et al. 2008; Winfree et al. 2009). In North America, there has been a significant decrease in open, early-successional habitats due to agricultural intensification, urban development, and forest logging practices (Samson and Knopf 1994; Brown et al. 2005; Ellis et al. 2010; Vickruck 2021). This has resulted in the decline of many plant and animal species that rely on these open habitats (Willyard et al. 2004; Forrester et al. 2005; Winfree et al. 2009; Potts et al. 2010; Cameron et al. 2011a; King and Schlossberg 2014). Although this landscape conversion is a major cause of pollinator decline, correctly managed green spaces within anthropogenic systems – including road verges, powerline easements, crop margins, and city parks - may serve as refuge habitats for insect pollinators (Russell et al. 2005; Wojcik and Buchmann 2012; Baldock et al. 2015, 2019a; Hopwood et al. 2015; Hall et al. 2017; Leston and Koper 2017; Twerd et al. 2021). An increasing set of studies suggest that powerline ROWs are important habitats for many beneficial insects such as pollinating bees, butterflies and moths (Swengel 1996; Smallidge et al. 1996; Lanham and Nichols 2000a; Forrester et al. 2005; Russell et al. 2005, 2018; Lensu et al. 2011; Wagner et al. 2014a, 2019; Hill and Bartomeus 2016; Leston and Koper 2016, 2017; Steinert et al. 2020). These include rare, endangered species such as the Karner blue butterfly (Lycaeides melissa samuelis Nabokov) (Smallidge et al. 1996; Forrester et al. 2005), the frosted elfin (Callophrys irus (Godart)) (Swengel 1996), and Epeoloides pilosulus (Cresson), a cleptoparasite of the oil-collecting melittid bees of the genus Macropis (Wagner et al. 2014a, 2019), among others. Powerline ROWs occupy a vast area of land that is continuously maintained at various early-successional stages to prevent vegetation from interfering with the conductors (Berger 2010). It has been estimated that in the United States, powerline easements cover an area of about four million hectares, not including small low-voltage lines (Russell et al. 2018). In Canada, the electrical transmission network extends for over 160,000 km, occupying vast stretches

of land (International Energy Agency 2009). This land represents a permanent open habitat that is only moderately disturbed periodically and is usually excluded from future development.

Powerline ROWs can constitute good quality habitat for pollinators, as they often host distinct plant communities that are more biodiverse than the surrounding landscapes (Rubino et al. 2002; Wagner et al. 2014b; Eldegard et al. 2015, 2017). Additionally, powerline ROWs have been shown to provide a healthy diversity of nesting resources for insects, which allow for the establishment of stable breeding populations, such as large amounts of exposed ground, dead woody stems, and live and dead woody cover (Russell et al. 2018). By hosting breeding populations, powerline ROWs may act as source habitats for pollinators in the landscape (Berg et al. 2016). Finally, these corridors have the potential to act as conduits for plant and animal species between habitat patches, which can be particularly beneficial to pollinator biodiversity in fragmented landscapes (Willyard et al. 2004). Some studies recommend specific vegetation management practices that can improve the quality of ROW habitat and are likely to have positive effects on the abundance and richness of pollinators in the easements. These include reducing the frequency of mowing and herbicidal application, combining mowing with selective herbicidal treatment (rather than only mowing), and promoting the growth of larval host and floral plants (Swengel 1996; Bramble et al. 1999; Forrester et al. 2005; Wagner et al. 2014b, 2019; Leston and Koper 2016, 2017; Russo et al. 2021). Generally, an abundance and diversity of floral resources is the major factor affecting bee and butterfly biodiversity within powerline ROWs (Yahner 2004; Berg et al. 2013; Steinert et al. 2020; Russo et al. 2021; Twerd et al. 2021). Recently more attention has been given to the implementation of integrated vegetation management (IVM) practices within powerline ROWs. IVM strategies involve selectively removing tall-growing woody species through a combination of manual and herbicidal treatments, while maintaining a stable community of low and medium-growing plants (Russell et al. 2018). These methods result in a mosaic of meadow and scrub habitat, composed of forbs and shrubs which inhibit the establishment and growth of undesirable woody species (Russell et al. 2018). IVM strategies therefore have the advantage of reducing long-term management costs – since vegetation needs to be controlled less frequently - while benefiting biodiversity in the ROWs (Wojcik and Buchmann 2012; Russell et al. 2018; Licensing and Environmental Assessment Department 2019).

The organization and persistence of biodiversity are highly dependent on the patterns and frequencies of complex and dynamic biotic interactions (Ferreira et al. 2020). By describing

interactions between species, ecological networks allow us to understand the functioning and stability of ecosystems, and to quantify the effects of human activities on ecological interactions (Memmott et al. 2007; Thébault and Fontaine 2010; Evans et al. 2013; Tylianakis and Morris 2017). A pollination network is a mutualistic system where plants and animals co-exist by benefiting each other (Bascompte and Jordano 2007). Pollinators receive rewards such as nectar and pollen from their host plants, which they use for nourishment and reproduction, while the foraging action of pollinators aids plant sexual reproduction. About 87% of flowering plants depend on animal pollinators – the majority of which are insects – for sexual reproduction (Ollerton et al. 2011). Preserving the species and interactions within pollination networks is essential for maintaining pollination services and for the stability of healthy plant populations. Sampling pollination networks within powerline ROWs may allow us to determine if these narrow habitats can host healthy and stable pollinator communities, and whether management practices such as IVM can benefit the whole system rather than individual species.

Environmental disturbance and habitat loss resulting from anthropogenic activities can cause pollinator and flowering plant population declines and extinctions (Biesmeijer et al. 2006; Potts et al. 2010). There can also be severe consequences on ecosystem functioning, as the reduction of species' abundances can lead to a loss of their ecological functionality well before their own existence is threatened (Säterberg et al. 2013; Sellman et al. 2016). The loss of species and interactions inevitably results in changes to the size, structure, and stability of networks (Kearns et al. 1998; Spiesman and Inouye 2013). Various aspects of network structure can be quantified through several commonly-used metrics (Bascompte et al. 2003; Blüthgen et al. 2006; Olesen et al. 2007; Vazquez et al. 2009; Thébault and Fontaine 2010). "Connectance" represents the proportion of links in the network that exist compared to the total number of possible interactions, "nestedness" explains the extent to which specialist species in one level of the bipartite network interact with generalists in the other level, "modularity" describes the extent to which species interactions are organized into compartments (densely connected, non-overlapping subsets of species), and "H2" represents the network-level specialization (the degree of niche partitioning across species). Generally, pollination networks are characterized by a periphery of specialist species interacting mostly with a central core of interlinked generalists, thus creating a highly cohesive, nested structure (Bascompte et al. 2003). Asymmetric dependencies in pollination networks facilitate coexistence, reduce interspecific competition, and promote biodiversity

maintenance (Bascompte et al. 2006; Bastolla et al. 2009). Generalist species play important roles in pollination networks as they link individuals within modules and keep compartments connected (Martín González et al. 2010; Biella et al. 2017; Cagua et al. 2019). In general, rare species and specialist-specialist interactions are the first to be lost following disturbance and habitat loss (Spiesman and Inouye 2013; Soares et al. 2017). This loss of specialist species and a concentration of links among generalists causes pollination networks to become smaller, more nested, and less modular (Villalobos et al. 2019; Morrison et al. 2020).

Changes in size and structure can alter network stability. Networks have inherent disassembly thresholds whereupon the system rapidly collapses. At this threshold, the consequences of species and interaction extinctions are amplified and self-reinforcing (Bascompte and Stouffer 2009). Network "robustness" is a measure of resistance to secondary extinctions following the successive removal of single species from the web. This metric has been used to understand the threat that species loss poses towards ecosystem functioning and services (Grass et al. 2018; Sritongchuay et al. 2019). A heterogeneous distribution of interactions and nested structure confers pollination networks high robustness to the random extinction of species, but also a fragility to the extinction of generalists (Bascompte and Stouffer 2009). Theoretically, networks that are smaller and more modular, and have lower connectance and nestedness, are more prone to secondary extinction following species losses (Thébault and Fontaine 2010; Evans et al. 2013; Moreira et al. 2015; Grass et al. 2018). Powerline ROWs are small, narrow habitat patches often surrounded by modified habitat that is inhospitable for pollinators. Evaluating whether these corridors can host healthy, stable pollination networks will allow us to determine their potential for pollinator conservation.

With this study, my objectives were to quantify the extent to which a major powerline ROW is serving as habitat for pollinators in Manitoba and investigate its potential for use in conservation efforts. I also aimed to explore what environmental factors in the easement and the surrounding landscape are affecting the pollinator biodiversity and network structure in the ROW. I predict that increased flowering plant abundance and richness in the easement will have positive effects on pollinator biodiversity as well as on network specialization and modularity. Furthermore, I predict sites where vegetation is controlled with IVM strategies will host larger, more modular networks that are more robust to random plant species extinctions. The main goal of this study is to provide informed suggestions on powerline ROW management for the conservation of pollinator biodiversity and pollination services within anthropogenic systems.

3.2 Methods

Study System

The study system is a section of a continuous double-line width transmission line ROW extending between the towns of Woodlands and Grand Rapids in Manitoba, Canada (Figure 17). This corridor is part of Manitoba's Nelson River high-voltage direct current transmission system and includes two lines known as Bipoles I and II. Completed in 1971 and 1978 respectively, Bipoles I and II run parallel to each other along their 895 km route. The two lines originate in northern Manitoba at the Radisson and Henday Converter Stations near Gillam (56.35 N, -94.71 W) and run southwards through the Interlake Region, ending at the Dorsey Converter Station (49.99 N, -97.43 W) just north of Winnipeg. The width of the ROW for Bipoles I and II varies slightly from 115 m in southern sections to 125 m in central and northern ones. The construction and maintenance of the ROW have resulted in a cleared linear corridor that traverses six latitudinal degrees, two geo-morphological regions (Precambrian Shield and Manitoba Lowland Region), and five natural vegetation zones (Maclellan and Stewart 1986).

The plant community within the ROW significantly differs from that in the surrounding landscapes, as it originates from the initial disturbance of clear-cutting, followed by various management strategies used to maintain a low-stature community (Berger 2010). Vegetation control on Manitoba Hydro ROWs is primarily achieved through mechanical means (felling and mowing), herbicides, or manual control with chainsaws and axes (Licensing and Environmental Assessment Department 2019). Integrated Vegetation Management (IVM) is sometimes used by the corporation to reduce long-term management costs while also benefiting biodiversity within the ROW (Licensing and Environmental Assessment Department 2019). IVM practices involve the selective topping and/or selective herbicide treatment of tall-growing woody species, while encouraging a stable community of low-growing native plants that inhibit the establishment and spread of the undesirable species (Russell et al. 2018). Traditional vegetation management cycles vary between 2 to 10 years, depending on local plant growth conditions. However, the use of IVM practices can dramatically increase the period between management activities, reducing disturbance on wildlife (Licensing and Environmental Assessment Department 2019). ROW

management practices result in habitats dominated by shrubs, forbs and grasses, however considerable variation in species composition can occur due to soil type and latitude (Maclellan and Stewart 1986).

Study Area and Sites

In summer 2020, 15 sites were established along a 304 km section of the transmission line, stretching over a 2.5° latitudinal gradient between 50.2° and 52.7°N (Table S6). The sites were separated into three clusters of five, situated within different ecoclimatic regions (Figure 17). The southern cluster was located within Manitoba's transitional grassland region (GT). This is a region where the moisture deficit is sufficiently large to stress out woody plant species in favour of herbaceous ones, and the soil is characterized by nutrient and humus-rich Chernozem topsoils (Scott 1996). The dominant ecosystem surrounding my sites in this region was aspen parkland, however much of the land had been converted for the production of cereals, oilseeds, and hay by continuous cropping, or altered to pastureland (Smith et al. 1998). The middle sites were situated in the subhumid low boreal ecoclimatic region (LBs). Here, coniferous trees start to appear, but deciduous species remain important components of the ecosystem, and well to imperfectly drained Chernozemic Dark Gray soils are predominant (Scott 1996; Smith et al. 1998). Despite considerable logging activity, less of the natural vegetation has been disturbed here compared to the GT region (Scott 1996). The five northern sites were in the subhumid mid boreal region (MBs), where the typical northern coniferous forests prevail. Eutric Brunisols on loamy glacial till, and Organic Mesisols and Fibrisols co-dominate the landscape and are often superficially covered by feather and sphagnum mosses (Scott 1996; Smith et al. 1998). Along my study area, which is mainly located in Manitoba's Interlake Plain region, the average annual precipitation ranges from 400 – 700 mm (Government of Canada 2021). Air temperatures can reach extremes of -40°C in winter and 38°C in the summer, with average monthly temperatures spanning -13 to 27°C respectively (Government of Canada 2021). The average number of frost-free days is around 110 - 80, falling with increasing latitude (Maclellan and Stewart 1986).

To avoid spatial correlation, the sites within each ecoclimatic region were more than 6 km apart (mean = 11.51 km, range = 6.48 - 26.69 km), while the GT and MBs clusters were respectively 78.8 and 79 km away from the middle LBs cluster (distance between sites 5 and 6, and 10 and 11 respectively). I conducted non-random stratified sampling to select study sites based

on ecoclimatic region, accessibility (presence of roads in the vicinity of the powerline and entry points into the corridor), and land use underneath the line (wetlands, crop fields, and developed areas were avoided). I completed an initial survey with the use of satellite maps to identify 30 potential study sites and subsequently scouted each one to narrow the selection down to 15 based on the requirements.



Figure 17. Study sites along a section of the Nelson River Hydroelectric Project Bipole I and II right-of-way (yellow line). Study sites are sequentially numbered 1 to 15 from south to north. Maps created with SimpleMappr (Shorthouse 2010) and Google Earth (Google Earth 7.3.4.8248 2021).

Sampling Procedure

I collected data on plant-pollinator interactions in a 50 by 50 m plot centred in the middle of the ROW. I surveyed each square plot for flower-visiting insects between 0900 h and 1700 h during days without precipitation with temperatures above 17°C, and with average wind speed never above 15 km/h. I started each sampling session by identifying the plant species in bloom within the plot and taking note of floral patch distribution. Using this information I proceeded to conduct a sampling circuit via active netting (Ferreira et al. 2020). For each plant species, I would sample for 10 minutes all Hymenoptera, excluding ants, and Diptera that visited the flowers of the focal species. To avoid unequal sampling effort between patches of the same floral species, I stopped in front of a patch/individual for a maximum of two minutes before moving to a different one, circling the plot. The 10 minutes only included time spent actively searching for pollinators, thus excluding time required for handling pollinators and walking between floral patches. I sequentially repeated the 10-minute sampling procedure for each blooming plant species within the plot, until all species were sampled once. Multiple researchers could sample the same plant species providing the cumulative time of active sampling totalled 10 minutes. Pollinators caught from the same floral species were pooled together in a container with the plant name, site number, and date written on it. I collected samples of individuals of all flowering plant species that were being observed for the first time, using a plant press, such that they could later be confirmed and/or identified in the lab (Ferreira et al. 2020). I also re-sampled individuals if I was uncertain of the species, a common occurrence when asters and goldenrods started flowering. The sampled plants were identified using Scoggan's "Flora of Manitoba" (1957). In the field, I would check my plant identifications using Newcomb's Wildflower Guide (Newcomb 1989) in combination with the iNaturalist app ("iNaturalist" 2021).

Each site was sampled five times from June to August 2020 at one of three time periods of the day; either AM: 0900 - 1130 h, midday: 1130 - 1400 h, or PM: 1400 - 1700 h. I sampled each site at least once in each period, and never sampled the same site in the same time-period twice in a row. This allowed me to measure changes in flowering plant and pollinator communities throughout the summer season, as well as capture any variation due to the time of day. I used a Kestrel 2000 Wind Meter to record air temperature and wind speed data at every site at the end of each sampling session. Temperature was taken while holding the Kestrel in the shade, waiting a minute or two to allow the reading to stabilize. For wind speed, I angled the meter such that the fan was perpendicular to the wind direction and held it steady for one minute. I then recorded the average and maximum wind speed that occurred in that period. Finally, the start and end time of each sampling session and the date were noted as well. Average and maximum wind speed were highly correlated (Spearman rho = 0.92), so only average wind speed and temperature data were used in my models.

Pollinator Communities

Pollinators were identified to the lowest possible taxonomic level using published identification keys (Cockerell 1903; Sandhouse 1939; Stephen 1954; LaBerge 1956b, 1956a, 1961, 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989; Mitchell 1962; Ribble 1968, 1974; LaBerge and Bouseman 1970; LaBerge and Ribble 1972, 1975; Baker 1975; Laverty and Harder 1988; Michener et al. 1994; Romankova 2003, 2007; Coelho 2004; Michener 2007; Packer et al. 2007; Rightmyer 2008; Kits et al. 2008; Buck et al. 2008; Arduser 2009a, 2009c, 2009b, 2009d; Gibbs 2011; Rightmyer et al. 2010; Gibbs 2010; Sheffield et al. 2011; Gibbs et al. 2012, 2013; Dumesh and Sheffield 2012; Miranda et al. 2013; Skevington et al. 2019) and reference material (specimens from the J. B. Wallis/R. E. Roughley Museum of Entomology at the University of Manitoba). All collected bees were identified to species. For flies and wasps, I identified individuals from the families that were most abundant and for which I could make confident identifications (based on availability of updated dichotomous keys and of reference specimens in the museum). Bees belonged to the families Apidae, Andrenidae, Colletidae, Halictidae, Megachilidae, and Melittidae. With the flies, only individuals in the families Bombylidae, Conopidae, Stratiomyidae, and Syrphidae were identified to species or morphospecies. Finally, only wasps in the families Braconidae, Crabronidae, Gasteruptiidae, Perilampidae, Sphecidae, and Vespidae were identified to species or morphospecies. Overall, 92% of all collected flower visitors were identified to species or morphospecies and included in my biodiversity and network analyses. Insect vouchers were deposited in the J. B. Wallis/R. E. Roughley Museum of Entomology at the University of Manitoba.

I used distance-based redundancy analysis (dbRDA) to compare pollinator community composition across the three ecoclimatic regions with the Bray-Curtis index. The dbRDAs were performed on the relationship between site-specific community composition and ecoclimatic regions using the 'capscale' function and then visualized with the 'ordiplot' function; both in the R 'vegan' package (Oksanen et al. 2019). I then used permutational multivariate analysis of variance (perMANOVA) to test for effect of ecoclimatic region on pollinator communities using the Bray-Curtis index in the 'adonis' function (Oksanen et al. 2019). If the effect was significant ($p \le 0.05$), I performed a post-hoc test using the 'pairwise.adonis' function of the 'pairwiseAdonis' package (Arbizu 2017). Finally, I tested for the beta-dispersion among ecoclimatic regions using the 'betadisper' function (Oksanen et al. 2019) to check that the three groups were equally

dispersed, to ensure that the observed effect was not due to differences in dispersion. The same analysis procedure was conducted to compare the host plant community across ecoclimatic regions.

Floral Surveys

During each sampling session, I gathered local landcover and flowering plant diversity data using 1 by 1 m quadrats. The 50 by 50 m plot was divided into four 25 by 25 m subplots, and for each one a random numbers table (1-25) was used to determine four coordinates where the quadrat would be placed. This made for a total of 16 quadrat placements within the whole plot. For each quadrat, the researcher recorded the species of flowering plants that were in bloom and estimated the percent cover of each species, as well as the percent bare ground using the charts provided by Anderson (1986) as reference. Additionally, the number of floral units per species – defined as individual stems with open flowers - was recorded as well. Values for plant cover, ground cover, and number of floral units were averaged across the 16 samples, while the plant species recorded were pooled to calculate floral richness per sampling event (Table 9). Quadrat surveys were conducted in four of the five sampling rounds per site except for site 3, which was only sampled three times due to it having been recently mowed before one of the sampling events. To eliminate any potential variation in cover estimates due to different observers, the same researcher recorded the quadrat data throughout the season. The mean number of plant species sampled with quadrats per sampling event across all sites was 9.12. The mean values for the three other quadrat variables were: floral cover 12.87% (range = 0.99%), bare ground 7.13% (range = 0.100%), and 6.81 stems (range = 0-130). Because plant species overlapped with each other and with the ground, the total area covered by both could be greater than 100%. Floral cover and number of floral units were moderately correlated (Spearman rho = 0.75), so only floral cover was used in my models.

Landscape Variables

Landscape data was obtained for six circular buffers of increasing radius length around my sites (250, 500, 750, 1000, 1500, and 2000 m radii). I used the "landscapemetrics" R package (Hesselbarth et al. 2021) to extract land-use data from the Agriculture Canada Crop Inventory GEOTIFF layers (Agriculture and Agri-Food Canada 2020). These layers, freely available online through an open government license, have a resolution of 30 m² and include 72 cover types. They

are at least 94% accurate for crop cover types and at least 70% accurate for non-crop cover in Manitoba. I measured five landscape variables (Table 9):

(i) 'Open land' represented the total area (%) covered by exposed or barren land, shrubland, grassland, and fallow. In a buffer of radius 2000 m around my 15 sites, open land covered an average of 45.21% of the total area (range = 13.44 - 77.01%).

(ii) 'Forested land' included the combined area of broadleaf, coniferous, and mixedwood forests. Within the 2000 m buffers, forested land covered an average of 33.5% of the total area (range = 3.52 - 69.51%).

(iii) 'Disturbed land' represented the area in the buffers covered by anthropogenic development (buildings, roads, greenhouses, and other) as well as crops such as canola, barley and wheat. On average, disturbed land occupied 8.88% of the area within the 2000 m buffers (range = 0.9 - 37.34%).

The Shannon's Landscape Diversity Index (SHDI) was also measured – a metric derived from the Shannon entropy (Shannon 1948) – as well as the total edge density (ED). The SHDI retains the original landcover classifications and weighs each one by the number of patches in the landscape. It is a unitless metric that is only useful to compare landscapes with each other (Mcgarigal 2015). Edge density is calculated as $ED = \frac{E}{A}$ (10,000), where E is the edge length (m) of the various patches combined, and A is the total area in the buffer (ha). ED standardizes total edge length per unit area (m/ha) and can therefore be used to compare landscapes of different spatial scales (Mcgarigal 2015).

Biodiversity Models

I ran separate models on abundance and rarefied species richness (Table 10). Abundance is here defined as the number of pollinators collected per site per day. Rarefied richness accounts for differences in richness estimates due to variation in abundance (Hill 1973; Chao et al. 2014). To calculate rarefied richness I used the 'rarefy' function (Oksanen et al. 2019). I used generalized linear mixed-effect models (GLMMs) to analyze the effects of several environmental variables on the pollinator biodiversity, using sampling event as individual data units and site as a random effect. Abundance models were fit to a negative-binomial distribution using a log-link function, while rarefied richness models were fit to a Gaussian distribution. I evaluated whether my data met model assumptions with the use of descriptive statistics and by visualizing residual distributions with quantile-quantile plots and histograms. The 'check-model' function of the 'performance' R package was used for this task (Lüdecke et al. 2021).

To select the landscape buffer size, I first ran landscape models for sampling event-specific data that included the main effects of Julian date, ecoclimatic region, landscape (open, disturbed, and forested land, SHDI and ED), and the interactions of ecoclimatic region with landscape (e.g. with SHDI); and included site as a random effect. I ran the same GLMM for each of the six buffer sizes and selected the best fitting model with the lowest Akaike Information Criterion with small sample size correction (AICc) (Akaike 1998). If the model of best-fit had non-significant interactions, these were excluded. I then proceeded to run the models again, removing nonsignificant interactions until I only had significant interactions or none at all. I also removed main effects that were correlated with others. ED and SHDI were strongly correlated (Spearman rho = 0.91), so only SHDI was kept in the models. Additionally, ecoclimatic region was strongly correlated with forest cover (rho = 0.90), and moderately correlated with open land (rho = 0.74), so these two variables were not included in the global model. Once again, I made sure that my data met the model assumptions by checking the descriptive statistics and visualizing the distribution of residuals. Once the best-fit landscape buffer was selected, I ran a global GLMM by adding local variables to the existing model. Only results from the final, global model are shown and discussed. In addition to running global abundance and rarefied richness models on the whole pollinator community, I also ran the same models separately for bees, flies, and wasps, to analyze whether environmental variables had differing effects on the three insect groups (Jauker et al. 2019).

Variable	Description
Local	
Floral richness	Total number of flowering plant species across all 1x1 m quadrat
	placements per sampling event. Plant individuals within the quadrats
	did not need to have open flowers to be counted, as long as the
	species in question was actively in bloom during that period and
	within the 50 by 50 m plot.

Table 9. Environmental variables at the local and landscape scale. Landscape data was gathered at six buffer sizes (250, 500, 750, 1000, 1500, and 2000 metre radius).

Floral abundance	Combined number of flowering plant species presence counts across	
	all 1 by 1 m quadrat placements per sampling event. A single plant	
	species could have a maximum of 16 presence counts per sampling	
	event (one per quadrat).	
Floral cover	Average area covered by flowering plant species in a 1 by 1 m	
	quadrat (%) per sampling event. Plants within the quadrats did not	
	need to have open flowers to be measured for cover, as long as the	
	species in question was actively in bloom during that period and	
	within the 50 by 50 m plot.	
Floral units	Average number of stems with open flowers in a 1 by 1 m quadrat	
	per sampling event.	
Bare ground	Average exposed ground in a 1 by 1 m quadrat (%) per sampling	
	event.	
Vegetation	Vegetation management strategies were pooled under three	
management strategy	categories:	
	a. Cattle grazing or annual mowing	
	b. Pasture fallow or abandoned field	
	c. Integrated Vegetation Management (IVM)	
Landscape		
Open land	Area covered by exposed or barren land, shrubland, grassland, and	
	fallow (%)	
Forested land	Area covered by forest (%)	
Disturbed land	Area covered by anthropogenic development and crops (%)	
Shannon's Landscape	Measure of landcover diversity, where cover types are weighted by	
Diversity Index	their relative patch abundance (unitless)	
(SHDI)		
Total edge density	Sum of all edge lengths divided by the total landscape area (m/ha)	

Pollination Networks

By pooling the net data obtained at each sampling session, I constructed 15 quantitative pollination networks (one per site). The architecture of these networks was described by the abundance and pattern of plant-pollinator interactions, using link frequency as surrogate of functional dependency between species as justified by Vázquez et al. (2005; 2012), and Sahli and Conner (2006). I used six commonly-used qualitative and quantitative metrics (Bascompte et al. 2003; Blüthgen et al. 2006; Olesen et al. 2007; Vazquez et al. 2009; Thébault and Fontaine 2010) to interpret the structure of the networks: network size, connectance, nestedness, modularity, specialization (H2') and robustness (Table 10). These six indices were calculated for each network using the "bipartite" package in R (Dormann et al. 2009, 2020).

Modularity was calculated using Beckett's 'DIRTLPAwb+' algorithm (Beckett 2016) through the 'ComputeModules' function in the bipartite R package (Dormann et al. 2020). I ran the algorithm 10 times per network and selected the network partition where modularity was maximized. Robustness was measured as the area underneath the pollinator species co-extinction curve resulting from the sequential removal of plant species. To generate these secondary extinction curves, I simulated the random loss of plant species from the networks without replacement, and considered a pollinator or plant co-extinct when it was left without interaction partners (Memmott et al. 2004; Evans et al. 2013; Sritongchuay et al. 2019). I assumed bottom-up regulation because plant-pollinator interactions are strongly driven by effects of resources on consumers (Scherber et al. 2010; Goulson et al. 2015; Schleuning et al. 2016). The robustness value for each network was calculated as the mean value resulting from 1000 repetitions of random plant extinction sequences per network.

The values of most network metrics are dependent on network size, so to directly compare the 15 networks I standardized all metrics (connectance, nestedness, H2', modularity and robustness) relative to a null expectation (Dormann et al. 2009; Thébault and Fontaine 2010; Spiesman and Inouye 2013). These standardized metrics reflect the extent to which the network structure differs from random given a network size (Tylianakis and Morris 2017; Grass et al. 2018), and were calculated using the formula:

 $metric_{z} = \frac{metric_{obs} - \overline{metric_{null}}}{\sigma metric_{null}}$

The standardized metric is calculated by subtracting the mean metric value of null networks from the observed value, divided by the standard deviation of the metric values from null networks. One thousand null networks were created per site to calculate the metric z-scores. For connectance values, null models were created using Patefield's algorithm, which shuffles interactions while maintaining species richness and number of interactions per species constant (Patefield 1981). For nestedness, H2', modularity, and robustness z-score calculations I used Dormann's 'SwapWeb' algorithm in the "bipartite" package to build null models that not only kept species richness and number of interactione constant as well (Tylianakis and Morris 2017; Dormann et al. 2020; Morrison et al. 2020).

To determine which environmental variables were affecting the network structure and robustness, I used a model selection approach using the Akaike Information Criterion (AIC). This was done to reduce the number of variables in the models as much as possible, given the low sample size (15 network metric values, one per site). For each network metric, I initially ran the same global model that was used for the biodiversity data. I then proceeded to obtain the optimal model by using the 'drop1' function to test the significance of the fixed effects, and sequentially removing non-significant variables with the highest AIC score (Hodgkiss et al. 2018). The optimal model was obtained once all remaining variables were significant, or when non-significant variables had lower AIC scores than the significant effects (and therefore could not be dropped). All models performed on standardized (z) metrics were fitted to a Gaussian distribution, while the model performed on network size was fitted to a negative binomial distribution. As above, I made sure that the data met model distribution assumptions.

A significant challenge for ecological network studies is the adequate sampling of species interactions, particularly so when looking at environmental gradients (Dormann et al. 2009; Chacoff et al. 2012; Rivera-Hutinel et al. 2012; Grass et al. 2018). Therefore, I estimated the sampling completeness across my networks to exclude potential sampling bias that could affect the metrics. I estimated sampling completeness for each network by dividing the observed richness of pairwise interactions by the estimated link richness. I calculated the estimated link richness using the Chao1 estimator of asymptotic richness (Chao 1984). I used R code provided by Macgregor et al. (2017), available for use in the server 'bioRxiv' (Cold Spring Harbor Laboratory 2021) along with the preprint version of their article, to calculate sampling completeness. Note that asymptotic diversity estimators such as Chao1 tend to overestimate the total number of

possible interactions, and do not differentiate between missing links (due to under-sampling) and forbidden links from morphological or phenological mismatches among species (Grass et al. 2018). These mismatches can explain up to 80% of unobserved interactions (Olesen et al. 2011).

Variable	Description
Community Metrics	
Abundance	Total number of pollinator individuals caught by net per sampling
	event. Also calculated separately for bees, wasps, and flies.
Rarefied species	Total number of species caught by net per sampling event, rarefied to
richness	the mean pollinator abundance along a species accumulation curve.
	Also calculated separately for bees, wasps, and flies.
Network Metrics	
Network size	Total number of pollinator and plant species in the network
Connectance (z score)	Fraction of links in the network that are realized compared to the total
	possible number of links
Nestedness (z score)	The extent to which specialists interact with proper subsets of the
	species interacting with generalists
Modularity (z score)	The extent to which species interactions are organized into modules:
	densely-connected, non-overlapping subsets of species
H2' (z score)	Network-level specialization: the degree of niche partitioning across
	all species
Robustness (z score)	Tolerance of the network to species extinctions. Robust networks are
	less prone to co-extinction cascades following sequential species loss

Table 10. Response variables description.

Species' strength and role in the networks

To identify keystone species within the various networks, I evaluated the relative importance of each insect and plant species by determining their 'strength' and their role in the modular network. In quantitative networks the importance of one species to another is calculated as 'dependence': the link abundance between a species and one of its partners relative to the abundance of links between that species and all of its partners combined (Jordano 1987). By summing up the dependencies of all interaction partners of a species, we calculate the 'species
strength', an index that expresses the importance of that species for the entire network (Bascompte et al. 2006; Dátillo and Rico-Gray 2018).

Pollinator and host species within the networks were classified into different functional roles with respect to their position within and among modules. Following the weighted approach described by Dormann (2019), based on the methods developed by Guimerà & Amaral (2005) and Olesen et al. (2007), I calculated standardized connection and participation values (c and z) for each species based on species strength. The within-module degree z is the standardized number of links that a species has with others in the same module, while the among-module connectivity cdescribes the level to which the species links different modules together (Olesen et al. 2007). With these two parametres, I identified the roles of each species in the networks. 'Module hubs' were species that interacted with most of the species within their module, but with few species outside it (high z, low c); 'connector' species linked multiple modules together (low z, high c); 'network hubs' were super-generalists that interacted extensively both within their module and among other modules (high z and c); and 'peripheral' species interacted with few species within a single module (low z and c) (Olesen et al. 2007; Larson et al. 2014). As proposed by Dormann (2019), to objectively define the thresholds used to determine species' role I employed the 95% quantiles of c and z values calculated through 1000 null models per network (the same null models created to calculate modularity z-scores). The quantiles were calculated individually for each network, meaning that the thresholds varied slightly between communities.

3.3 Results

Pollinator & Plant Biodiversity and Community Composition

I sampled 5,107 insects in the powerline easement and subsequently identified 4,958 to species or morphospecies (Table S4). In total, I identified 259 species belonging to the three major pollinator groups (Table 11). Bees accounted for approximately 50% of the total insect abundance and richness, with 130 species identified out of 2322 individuals (Figure 18). These represent 35% of the 369 species found in Manitoba, 27 out of 37 genera, and 6 out of 6 families present in the province (Gibbs et al. unpublished).



Figure 18. Total pollinator biodiversity sampled and identified to species or morphospecies.

I found several rare and uncommon bee species within the powerline easement, some of which represented new provincial and national records. Two species in the genus Protandrena, P. albitarsis (Cresson), and P. cf. piercei albertensis (Cockerell), which have recently been added as new Canadian records, were found in the ROW. Additionally, I caught several uncommon parasitic bee species including Triepeolus obliteratus Graenicher, Nomada quadrimaculata Robertson, Sphecodes coronus Mitchell and Sphecodes dichrous Smith. I also caught an individual of Stelis nitida Cresson and of Triepeolus grindeliae Cockerell, both cleptoparasites, as well as two individuals of Osmia subaustralis Cockerell, which represent new records for the province of Manitoba. These records of O. subaustralis are also the first records of the subgenus Cephalosmia in Manitoba. They are particularly relevant as they also help fill a gap in the known distribution of the species, joining eastern and western populations which previously seemed disjunct (Gibbs, personal communication). A large population of *Macropis nuda* (Provancher), an oil-collecting bee, was found in the northern-most site, where its host plant Lysimachia ciliata L. was present. M. nuda is the only Melittid known to be present in Manitoba. One of the most significant findings was that of Lasioglossum immigrans Gardner, a bee species which had never been described before my study and that had only been previously recorded in southern and mid-U.S.A. My find led to the description of this species and represents a major range extension of the known distribution.



Figure 19. *Lasioglossum immigrans*. Female (left) and male (right). Reprinted from Gardner and Gibbs (2021).

Apidae was the most abundant bee family with 836 individuals caught (36% of all bees). Megachilidae was the richest family with 36 species identified, closely followed by Halictidae with 33 species. *Bombus* was the most abundant genus with 667 individuals sampled (13.4% of all insects) consisting of 14 species. Flies were the second-most abundant and rich group (Figure 18), with 80 species identified out of 2100 individuals (30.8% of the total richness and 42% of the total abundance sampled). The majority of flies belonged to Syrphidae, consisting of 1748 individuals (35.2% of all collected insects were syrphids) and 58 species (22.4% of the total insect richness) belonging to 28 genera. *Eristalis* and *Toxomerus* were the second and third most abundant genera of all, with 517 and 451 individuals collected respectively. Finally, 49 wasp species were identified from 536 individuals, representing about 19% of the total pollinator richness and 11% of the abundance. Most insect species were rare (147 species were represented by 5 individuals or less), with a few being very abundant (Table S4). The ten most abundant species were, in descending order (Table 12): *Eristalis dimidiata* Wiedemann (8.2% of the total insect abundance), *Bombus ternarius* Say (8%), *Toxomerus marginatus* (Say) (7.8%), *Helophilus fasciatus* Walker (5.1%), *Dolichovespula arenaria* (Fabricius) (4.9%), *Megachile rotundata* (Fabricius) (3%), *Megachile*

relativa Cresson (2.7%), *Syrphus ribesii* (L.) (2.7%), *Hylaeus affinis* (Smith) (2.4%), and *Bombus sandersoni* Franklin (2.1%).

Family	Total abundance	# Genera	# Species
Bees	2322	27	130
Andrenidae	110	3	20
Apidae	836	8	30
Colletidae	268	2	10
Halictidae	310	5	33
Megachilidae	750	8	36
Melittidae	48	1	1
Flies	2100	40	80
Bombyliidae	260	8	13
Conopidae	6	1	1
Stratiomyidae	86	3	8
Syrphidae	1748	28	58
Wasps	536	26	49
Braconidae	71	1	4
Crabronidae	71	10	17
Gasteruptiidae	6	1	1
Perilampidae	7	2	2
Sphecidae	33	3	4
Vespidae	348	9	21
Total	4958	93	259

Table 11. Families with individuals identified to species or morphospecies.

Table 12. Twenty-five most commonly sampled pollinator taxa (listed in decreasing abundance) in a 300-km transmission line ROW section in Manitoba, Canada (all sampling events).

Species	Family	Abundance	% Of	Cumulative
			total	%
Eristalis dimidiata Wiedemann	Syrphidae	406	8.19	8.19
Bombus ternarius Say	Apidae	397	8.01	16.2
Toxomerus marginatus (Say)	Syrphidae	388	7.82	24.0
Helophilus fasciatus Walker	Syrphidae	254	5.12	29.1
Dolichovespula arenaria (Fabricius)	Vespidae	246	4.96	34.1
Megachile rotundata (Fabricius)	Megachilidae	147	2.96	37.1
Megachile relativa Cresson	Megachilidae	136	2.74	39.8
Syrphus ribesii (L.)	Syrphidae	134	2.70	42.5
Hylaeus affinis (Smith)	Colletidae	117	2.36	44.9
Bombus sandersoni Franklin	Apidae	104	2.1	47
Syritta pipiens (L.)	Syrphidae	89	1.79	48.8
Heriades variolosa (Cresson)	Megachilidae	84	1.69	50.5
Systoechus vulgaris Loew	Bombyliidae	68	1.37	51.8

Villa lateralis (Say)	Bombyliidae	67	1.35	53.2
Toxomerus geminatus (Say)	Syrphidae	63	1.27	54.4
Eristalis interrupta (Poda)	Syrphidae	63	1.27	55.7
Villa fulviana (Say)	Bombyliidae	62	1.25	57
Megachile latimanus Say	Megachilidae	59	1.19	58.2
Bombus rufocinctus Cresson	Apidae	58	1.17	59.3
Hylaeus mesillae (Cockerell)	Colletidae	52	1.05	60.4
Heriades carinata Cresson	Megachilidae	51	1.03	61.4
Bombus vagans Smith	Apidae	48	0.97	62.4
Macropis nuda (Provancher)	Melittidae	48	0.97	63.3
Anthophora terminalis Cresson	Apidae	45	0.91	64.2
Tropidia quadrata (Say)	Syrphidae	45	0.91	65.1

I sampled the greatest average (±SD) pollinator abundance and richness per sampling event in the subhumid mid-boreal ecoclimatic region, with 86.5 ± 47.9 individuals/event and 27.4 ± 8.4 species/event. The ROW section within the transitional grassland ecoclimatic region was the second-most biodiverse, with 58.9 ± 43.6 individuals/event and 19.6 ± 10.8 species/event. Finally, the subhumid low-boreal ecoclimatic region hosted the least pollinator biodiversity with 53 ± 29.1 individuals/event and 18.8 ± 6 species/event. The relative abundance and richness of bees, compared to the total pollinator biodiversity, diminished moving northwards, going from 52% and 53% respectively in the GT region to 42% abundance and 46% richness in the MBs region (Figure 20). On the other hand, flies experienced an increase in relative abundance and richness moving northwards, from 36% and 25% of the total in the GT region to 46% and 37% in the MBs region. Flies, therefore, replaced bees as the dominant pollinator group in terms of abundance in the five northern-most sites, however bees remained the most diverse group throughout all three ecoclimatic regions despite a 7% fall in relative richness. The pollinator community composition between the three ecoclimatic regions was significantly different (Table 13), with no overlap in ordination space (Figure 21). The MBs region's pollinator community was significantly different from those of the LBs and GT ecoregions, while the communities in the latter two were not significantly different from each other (Table 13, p = 0.525).



Figure 20. Pollinator biodiversity sampled at each ecoclimatic region and identified to species or morphospecies. GT = transitional grassland; LBs = subhumid low-boreal region; MBs = subhumid mid-boreal region.



Figure 21. Ordination plot of the dbRDA of all pollinator communities. Each point represents the community within a site (15 total). Ecoclimatic region had a significant effect on the pollinator community composition (Table 13, perMANOVA, F = 3.202, $R^2 = 0.348$, p = 0.002), resulting from a significant difference between the MBs and both the GT and LBs regions (Tukey's posthoc test with Bonferroni correction p = 0.021 and p = 0.033 for the relationship between MBs and, respectively, GT and LBs). The GT and LBs communities were not different (adjusted p = 0.525). Singleton species were excluded from this analysis.

Table 13. Summary of perMANOVA performed on the Bray-Curtis distance of the pollinator and plant communities. Post-hoc column shows the results of Tukey's post-hoc test with a Bonferroni correction. 'GT' = transitional grassland, 'LBs' = subhumid low-boreal, 'MBs' = subhumid mid-boreal.

Community	F model	R ²	p-value	GT-LBs	GT-MBs	LBs-MBs
				Post-hoc	Post-hoc	Post-hoc
Pollinators	3.202	0.348	0.002	0.525	0.021	0.033
Flowering Plants	2.256	0.273	0.001	0.024	0.048	0.069

Grazed and mowed sites had the lowest average (\pm SD) abundance and richness, with 35.9 \pm 20.2 individuals and 13.8 \pm 5 species per sampling event. Fallowed sites had a mean pollinator abundance of 58.5 \pm 30.9 individuals/event, and an average richness of 19.4 \pm 6.9 species/event. IVM sites had the greatest average abundance and richness, with 83.6 \pm 47.7 individuals and 26.9 \pm 9 species per sampling event. IVM sites hosted the most cleptoparasites, with 128 individuals representing 30 species (3.75 species/site average). Fallowed sites hosted the second greatest cleptoparasite biodiversity with 10 species (2.5/site) identified out of 36 individuals. Finally, I found the fewest cleptoparasitic species in the grazed and mowed sites, with only 18 individuals representing 6 species (2/site). Furthermore, IVM hosted on average the greatest abundance of stem-nesting species (43.9 individuals/site), including bees in the genus *Ceratina*, *Heriades*, *Hoplitis*, and *Hylaeus*. IVM sites also had a much greater number of unique species (115 species were only found in sites of this management category) compared to fallowed (12) and grazed or mowed sites (4).

Total pollinator abundance increased throughout the summer season, reaching a plateau in late July, and remaining stable during August despite large variation among sampling sites (Figure 22). Analyzing the three pollinator groups separately reveals that bee abundance peaked in late July and subsequently fell throughout August, while both fly and wasp abundance increased in August, following a somewhat stable initial period (Figure 23). On the other hand, total pollinator richness steadily increased from June to late July, at which point it reached a peak and started decreasing (Figure 22). This trend was mostly brought by bees, with fly and wasp richness only slightly increasing throughout the sampling season (Figure 23).



Figure 22. Pollinator rarefied richness and abundance per sampling event over the sampling season. Day of year is displayed as Julian date. Shaded area represents the 95% confidence intervals.



Figure 23. Abundance and rarefied richness per sampling event of the three pollinator groups throughout the sampling season. Day of year is displayed as Julian date. Shaded area represents the confidence intervals.

Combining network and quadrat survey data, I found a total of 94 flowering plant species in the powerline easement, with an average of 21.9 species per site (range = 16 - 28). Out of the 94 flowering plant species, 77 were native to Manitoba while 17 were introduced. Quadrat surveys alone yielded 65 plant species (69% of the total plant richness observed in the ROW). The ten flowering plant species with the greatest overall ground cover were, in descending order: *Dasiphora fruticosa* (L.) (15.5% of the total sampled plant cover), *Sonchus arvensis* L. (11.4%), *Cirsium arvense* (L.) (8.1%), *Symphyotrichum ericoides* (L.) (6.6%), *Solidago nemoralis* Aiton (5.5%), Symphyotrichum laeve (L.) (5%), Apocynum androsaemifolium L. (3.9%), Achillea millefolium L. (3.6%), Mentha canadensis L. (3.5%), and Campanula rotundifolia L. (3.2%). Note that plant species cover is dependent both on the plant's abundance (number of individual organisms) and structure (average size and number of branches per single organism). Per sampling-event, I recorded the greatest average (±SD) flowering plant richness in the MBs ecoclimatic region with 10 ± 2.2 species/site. However, the mean plant cover per quadrat per site in this region was lowest, at 10.6% \pm 6.6. The LBs region hosted the second highest plant richness with 9.35 ± 3.2 species/site, as well as the second highest plant cover per quadrat per site at 11.7% \pm 5.2. Finally, although the GT region hosted the greatest plant cover per quadrat per site, at 16.4% \pm 16.6, it had the lowest richness, with 7.9 \pm 3.6 species/site. Note that the standard deviation for the average plant cover per quadrate per site in the GT region is greater than the mean, indicating a large variation between sites. The plant communities between the three ecoclimatic regions were significantly different from one another (Table 13), with little overlap in ordination space (Figure 24). The GT plant community was significantly different from those in the LBs and MBs regions (corrected p = 0.024 and p = 0.048 respectively). The difference in community composition between the LBs and MBs regions was instead only marginal (corrected p = 0.069). Both plant species richness and presence count (presence/absence of a species within a quadrat) increased throughout the summer season, reaching a peak in late August (Figure 25). Average flowering plant cover instead did not show any trend through time, with large variation between sampling events (Figure 25).



Figure 24. Ordination plot of the dbRDA of all plant communities. Each point represents the community within a site (15 total). Ecoclimatic region had a significant effect on the plant community composition (Table 13, perMANOVA, F = 2.256, $R^2 = 0.273$, p = 0.001), resulting from a significant difference between the GT and both the MBs and LBs regions (Tukey's posthoc test with Bonferroni correction p = 0.024 and p = 0.048 for the relationship between GT and, respectively, LBs and MBs). The MBs and LBs communities were only marginally different (adjusted p = 0.069). Singleton observations were excluded from this analysis.



Figure 25. Flowering plant species richness, abundance (presence counts), and mean cover per sampling event over the sampling period. Day of year is shown as Julian date.

When comparing flowering plant biodiversity among the three management categories (Figure 26), I found that grazed and mowed sites had the lowest average richness, with 13.8 ± 5 plant species per sampling event. Mean plant cover per quadrate per sampling event, however, was the second highest at $13.2\% \pm 15.6$. Fallowed sites had the lowest mean plant cover per quadrat per sampling event, at $11.3\% \pm 6.7$, but had the greatest average plant richness with 10.1 ± 3.5

species/event. In terms of mean richness, IVM sites were not far behind with 9.7 ± 2.7 species/event, but had the greatest mean plant cover per quadrat per sampling event, at 13.55 ± 10.5 . Overall, differences in local variables between management categories were not statistically significant.



Figure 26. Differences in local-scale variables per sampling event between the three management categories. Mean plant cover and bare ground are measured as percentage cover within 1 by 1 m quadrats.

ROW sites within the GT ecoclimatic region were surrounded by landscapes composed on average of only 3% forested land, 67% open land and 21% disturbed land (Figure 27). Sites in the LBs region were on average surrounded by more forest (24%), less open land (58%) but also less disturbed land (15%). Finally, ROW sites within the MBs region were surrounded by landscapes that had on average 46% forested land, 35% open land and only 3% disturbed land. The MBs region also had the greatest average SHDI and ED values, at 1.66 and 286 m/ha respectively (Figure 27). The landscapes surrounding sites within the LBs region had the second highest average SHDI and ED values, at 1.44 and 210 m/ha respectively. Landscapes in the GT ecoclimatic region had the lowest diversity, with an average SHDI value of 1.19 and mean ED of 171 m/ha.



Figure 27. Landscape characteristics of the three ecoclimatic regions. The dark line is the median value, box edges are the upper and lower quantiles, whiskers are 50% from the median, and closed circles are outliers, i.e. values smaller or larger than 1.5 times.

Pollinator Abundance and Species Richness Modelling

Global models included landscape variables extracted from 500 m buffers around the 15 sites since this distance resulted in the lowest AICc scores in my landscape models. Landcover within 500 m around my sites was on average 53.4% open land (range = 30.2-88.2%), 24.5% forest (0.2-61.9%), and 13.4% disturbed land (0-61.6%). At the local-scale, the average flowering plant richness across all sampling events was 9.1 species (3-17 species/event), and the average abundance was 30.1 counts (7-62 counts/event). The average mean plant cover across all sampling events was 12.9% (0.4-59.7%), and the average mean bare ground was 7.1% (0-24.5%). Finally, the average mean number of stems across the sampling events was 6.8 stems/quadrat (0.4-43.7 stems/quadrat). Overall, plant richness had a positive effect on both pollinator abundance (Figure 28A) and rarefied richness (Figure 29D). Pollinator abundance also responded positively to mean plant cover (Figure 28F). Both pollinator abundance and rarefied richness responded negatively to the surrounding landscape SHDI (Figure 28I, Figure 29I), however, this effect was moderated by ecoclimatic region (Table 14, Figure 32). Vegetation management strategy had a strong effect on

pollinator biodiversity, with fallowed sites and IVM sites hosting significantly greater abundance and rarefied richness than mowed sites (Table 14).

When we conduct the same global analyses separately on bees, flies, and wasps we observe that the three groups respond differently to the environmental factors. The plant richness and mean cover positively affected bee abundance but had no effect on rarefied richness (Table 15). Bee rarefied richness did however respond positively to the mean bare ground (Figure 31G). Both bee abundance and rarefied richness responded negatively to landscape SHDI, however for bee abundance this trend was strongly moderated by ecoclimatic region (Table 15). The effect of the interaction between ecoclimatic region and SHDI on bee rarefied richness was strong but not significant (p = 0.0606 for the interaction between MBs and SHDI). Bee rarefied richness responded positively to IVM management strategies compared to mowing, but not to fallowing, while abundance significantly increased for both categories when compared to mowing (Figure 30H, Figure 31H). Flies responded positively to mean plant cover both in terms of abundance and rarefied richness (Table 16). Fly rarefied richness also increased significantly with plant richness $(\beta = 0.454, p = 0.018)$. Finally, wasp biodiversity was not affected by any local-scale variables (Table 17). Both wasp abundance and rarefied richness responded negatively to SHDI, however once again this effect was moderated by ecoclimatic region. Additionally, wasp rarefied richness increased slightly with the amount of surrounding disturbed land ($\beta = 0.0739$, p = 0.0037). Finally, management strategy significantly affected wasp abundance, with both fallowed and IVM sites hosting a greater number of wasp individuals compared to mowed sites. IVM sites also hosted a greater number of species compared to mowed sites, but this effect was only marginally significant (p = 0.056).

	Pollinator	linator Abundance				Pollinator Rarefied Richness			
Pseudo - R_M^2	0.0595				0.535				
Pseudo - R_C^2	0.0595				0.535				
Predictor	β	SE	Z	р	β	SE	Z	р	
Intercept	5.523	1.566	3.53	0.00042	40.3	15.01	2.68	0.0073	
Julian Date	-0.0015	0.0054	-0.28	0.777	-0.1057	0.0538	-1.96	0.0497	
Temperature	-0.0009	0.0241	-0.04	0.9708	0.3736	0.234	1.60	0.1103	
Average Windspeed	-0.0357	0.0289	-1.24	0.2161	-0.0412	0.2812	-0.15	0.8835	
Plant Richness	0.1105	0.0405	2.73	0.0063	0.9609	0.402	2.39	0.0168	
Plant Abundance	-0.0208	0.011	-1.88	0.06	-0.1433	0.1072	-1.34	0.1812	
Mean Plant Cover	0.0251	0.0097	2.58	0.0098	0.1115	0.1054	1.06	0.29	
Mean Bare Ground	-0.0036	0.015	-0.24	0.8089	0.2241	0.1517	1.48	0.1396	
SHDI	-1.852	0.7657	-2.42	0.0156	-19.87	7.857	-2.53	0.0114	
Disturbed Land	0.0048	0.0087	0.55	0.5797	0.0662	0.0905	0.73	0.4648	
Mgmt. – Pasture Fallow	0.6736	0.3344	2.01	0.0439	7.319	3.637	2.01	0.0442	
Mgmt. – IVM	0.7028	0.3151	2.23	0.0257	9.926	3.242	3.06	0.0022	
Ecoclimate – LBs	-2.138	1.131	-1.89	0.0587	-11.58	11.69	-0.99	0.3222	
Ecoclimate – MBs	0.3849	1.546	0.25	0.8033	-43.44	16.41	-2.65	0.0081	
LBs : SHDI	1.756	0.8557	2.05	0.0402	11.46	8.803	1.30	0.1931	
MBs : SHDI	0.4188	1.063	0.39	0.6935	32.585	11.17	2.92	0.0035	

Table 14. Results of global GLMMs performed on pollinator abundance and rarefied richness per sampling event. Site is included as a random factor. Landscape buffer used is of 500 m radius. Sampling events lacking vegetation data are excluded. Variables strongly correlated with others are excluded.



Figure 28. Effects of environmental variables on pollinator abundance. Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and p-values are shown in Table 14. Landscape variables were calculated from 500 m buffers around each site. Management 'g/m' = grazed/mowed, 'pf' = pasture fallow, 'IVM' = integrated vegetation management.



Figure 29. Effects of environmental variables on pollinator rarefied richness. Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and p-values are shown in Table 14. Landscape variables were calculated from 500 m buffers around each site. Management 'g/m' = grazed/mowed, 'pf' = pasture fallow, 'IVM' = integrated vegetation management.

	Bee Abun	Abundance				Bee Rarefied Richness			
Pseudo - R_M^2	0.0721				0.553				
Pseudo - R_C^2	0.0721				0.553				
Predictor	β	SE	Z	р	β	SE	Z	р	
Intercept	6.756	1.798	3.76	0.00017	19.65	9.455	2.08	0.0377	
Julian Date	-0.0119	0.0064	-1.85	0.0647	-0.0675	0.0339	-1.99	0.0464	
Temperature	0.0368	0.0279	1.32	0.187	0.4583	0.1474	3.11	0.0019	
Average Windspeed	0.0105	0.0322	0.33	0.7439	-0.0308	0.1771	-0.17	0.8619	
Plant Richness	0.1258	0.0461	2.73	0.0063	0.2706	0.2532	1.07	0.2851	
Plant Abundance	-0.0241	0.0126	-1.92	0.0547	-0.1094	0.0675	-1.62	0.105	
Mean Plant Cover	0.0281	0.011	2.55	0.0108	0.1203	0.0664	1.81	0.0698	
Mean Bare Ground	-0.0061	0.0168	-0.36	0.7155	0.1954	0.0955	2.05	0.0408	
SHDI	-2.679	0.879	-3.05	0.0023	-12.44	4.949	-2.51	0.012	
Disturbed Land	0.0052	0.0098	0.53	0.5943	-0.049	0.057	-0.86	0.3898	
Mgmt. – Pasture Fallow	0.5978	0.3961	1.51	0.1313	7.172	2.291	3.13	0.0017	
Mgmt. – IVM	0.7528	0.3622	2.08	0.0376	9.116	2.042	4.46	<0.0001	
Ecoclimate – LBs	-4.433	1.279	-3.46	0.0005	-8.725	7.366	-1.18	0.2362	
Ecoclimate – MBs	-3.095	1.743	-1.78	0.0757	-16.93	10.34	-1.64	0.1015	
LBs : SHDI	3.527	0.9705	3.63	0.0003	8.031	5.544	1.45	0.1475	
MBs : SHDI	2.62	1.212	2.16	0.0307	13.21	7.038	1.88	0.0606	

Table 15. Results of global GLMMs performed on bee abundance and rarefied richness. Site is included as a random factor.



Figure 30. Effects of environmental variables on bee abundance. Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and p-values are shown in Table 15. Management 'g/m' = grazed/mowed, 'pf' = pasture fallow, 'IVM' = integrated vegetation management.



Figure 31. Effects of environmental variables on bee rarefied richness. Points represent observation per sampling event. Regression lines represent predicted values from the GLMM. Shaded area shows the 95% confidence intervals. Significant effects are shown with bold p-values. Significant effects of categorical variables are indicated with a star, and p-values are shown in Table 15. Management 'g/m' = grazed/mowed, 'pf' = pasture fallow, 'IVM' = integrated vegetation management.

	Fly Abund	Abundance				Fly Rarefied Richness			
Pseudo - R_M^2	0.121				0.301				
Pseudo - R_C^2	0.121				0.378				
Predictor	β	SE	Z	р	β	SE	Z	р	
Intercept	5.261	2.128	2.47	0.013	12.02	6.913	1.74	0.082	
Julian Date	-0.0018	0.0079	-0.23	0.818	-0.0195	0.0266	-0.73	0.465	
Temperature	-0.0395	0.0354	-1.11	0.265	-0.143	0.1108	-1.29	0.197	
Average Windspeed	-0.1066	0.0423	-2.52	0.012	-0.229	0.1339	-1.71	0.087	
Plant Richness	0.0667	0.0579	1.15	0.249	0.454	0.1921	2.36	0.018	
Plant Abundance	-0.0116	0.016	-0.73	0.467	-0.0845	0.051	-1.66	0.098	
Mean Plant Cover	0.0295	0.0132	2.23	0.026	0.092	0.0459	2.01	0.045	
Mean Bare Ground	-0.0058	0.0232	-0.25	0.802	0.0112	0.075	0.15	0.882	
SHDI	-1.139	0.6082	-1.87	0.061	-0.105	2.286	-0.05	0.963	
Disturbed Land	-0.0008	0.0131	-0.06	0.953	-0.0379	0.0467	-0.81	0.417	
Mgmt. – Pasture Fallow	0.9324	0.4497	2.07	0.038	1.638	1.645	1.00	0.319	
Mgmt. – IVM	0.4825	0.4464	1.08	0.28	0.499	1.537	0.32	0.745	
Ecoclimate – LBs	0.1281	0.3176	0.4	0.687	0.6095	1.184	0.51	0.607	
Ecoclimate – MBs	1.046	0.5599	1.87	0.062	0.8993	2.078	0.43	0.665	
LBs : SHDI	-	-	-	-	-	-	-	-	
MBs : SHDI	-	-	-	-	-	-	-	-	

Table 16. Results from global GLMMs performed on fly abundance and rarefied richness. Site is included as a random factor.

	Wasp Abu	sp Abundance				Wasp Rarefied Richness			
Pseudo - R_M^2	0.406				0.453				
Pseudo - R_C^2	0.406				0.453				
Predictor	β	SE	Z	р	β	SE	Z	р	
Intercept	0.9366	3.458	0.27	0.7865	6.51	4.22	1.54	0.1227	
Julian Date	0.0299	0.0121	2.47	0.0136	-0.0005	0.0151	-0.03	0.9756	
Temperature	0.0363	0.0526	0.69	0.4898	0.0738	0.0658	1.12	0.2614	
Average Windspeed	-0.03	0.0562	-0.53	0.5938	0.0647	0.079	0.82	0.4132	
Plant Richness	0.0328	0.0853	0.38	0.7007	0.115	0.113	1.02	0.3075	
Plant Abundance	-0.0089	0.0239	-0.37	0.709	0.0012	0.0301	0.04	0.9688	
Mean Plant Cover	0.0266	0.0205	1.30	0.1945	-0.0064	0.0296	-0.22	0.8285	
Mean Bare Ground	-0.0042	0.0323	-0.13	0.8972	0.0389	0.0426	0.91	0.3611	
SHDI	-7.229	2.048	-3.53	0.00042	-8.3	2.21	-3.76	0.0002	
Disturbed Land	0.0262	0.0171	1.54	0.1244	0.0739	0.0254	2.91	0.0037	
Mgmt. – Pasture Fallow	1.897	0.8945	2.12	0.034	1.53	1.02	1.49	0.135	
Mgmt. – IVM	2.401	0.777	3.09	0.002	1.74	0.911	1.91	0.056	
Ecoclimate – LBs	-8.957	2.852	-3.14	0.0017	-7.75	3.29	-2.36	0.0183	
Ecoclimate – MBs	-7.229	3.443	-2.21	0.0269	-0.128	4.61	-2.77	0.0056	
LBs : SHDI	6.97	2.151	3.24	0.0012	6.57	2.47	2.66	0.0079	
MBs : SHDI	6.433	2.491	2.58	0.0098	0.107	3.14	3.4	0.0007	

Table 17. Results of global GLMMs performed on wasp abundance and rarefied richness. Site is included as a random factor.



Figure 32. Ecoclimate-dependent effects of SHDI within a 500 m buffer on the pollinator abundance and rarefied richness. Points represent observations per sampling event. Regression lines represent predicted values from GLMM. Shaded areas represent 95% confidence intervals. Significant effects are shown in bold. "GT" = Transitional Grassland, "LBs" = subhumid Low-Boreal, "MBs" = subhumid Mid Boreal.

To compare pollinator biodiversity between the three management strategy groups, I performed type III ANOVA analyses (Table 18). This allowed me to compare all three categories with each other, which could not be done with the GLMM analyses. I compared the abundance and rarefied richness of all three pollinator groups, and of the whole community, between IVM, fallowed, and grazed/mowed sites. All tests revealed significant differences among the management categories, with IVM sites hosting greater abundance and rarefied richness of all three pollinator groups and of the whole community. The differences in pollinator biodiversity between management categories were plotted so that they may be easily visualized (Figure 33, Figure 34).



Management Strategy

Figure 33. Abundance of the three pollinator groups per management strategy.

Per Sampling Event

Total



Management Strategy

Figure 34. Rarefied richness of the three pollinator groups per management strategy.

pasture fallow, "IVM" = integrated vegetation management.											
Response	F	R ²	p-value	g/m	pf	IVM					
Variable	value			mean	mean	mean					
Pollinator	12.5	0.301	<0.0001	35.9 (a)	58.5 (b)	83.6 (c)					
Abundance											
Pollinator	16.1	0.304	<0.0001	13.7 (a)	17.9 (b)	22.9 (c)					
Rarefied											
Richness											
Bee Abundance	7.57	0.201	0.001	18.3 (a)	27 (b)	38.7 (c)					
Bee Rarefied	13.4	0.265	<0.0001	6.73 (a)	9.14 (a)	11.9 (b)					
Richness											
Fly Abundance	5.6	0.203	0.0055	14.2 (a)	27.4 (b)	34.5 (c)					
Fly Rarefied	3.23	0.0802	0.0455	5.23 (a)	6.66 (ab)	7.39 (b)					
Richness											
Wasp	7.57	0.238	0.00103	3.29 (a)	4.1 (a)	10.5 (b)					
Abundance											
Wasp Rarefied	7.7	0.172	0.0009	1.32 (a)	2.14 (ab)	3.05 (b)					
Richness											

Table 18. Results of ANOVA Type III tests performed on pollinator abundance and rarefied richness variables between the three management categories. "g/m" = grazed or mowed, "pf" = pasture fallow, "IVM" = integrated vegetation management.

Pollination Network Analysis

Across the 15 networks (Figure S1-S15), I found 1,431 unique plant-pollinator interactions out of the 4,958 observed links. The ten plant species with the greatest number of interactions across all networks were *Sonchus arvensis* L. (9.5% of all interactions), *Dasiphora fruticosa* (L.) (8.7%), *Cirsium arvense* (L.) (7.8%), *Melilotus albus* Medikus (6.2%), *Solidago nemoralis* Aiton (4.3%), *Solidago canadensis* L. (4.1%), *Apocynum androsaemifolium* L. (3.6%), *Solidago rigida* L. (3.4%), *Symphyotrichum laeve* (L.) (3.3%) and *Solidago gigantea* Aiton (2.7%). Plants were with the greatest pollinator richness: *Dasiphora fruticosa* (L.) (85 pollinator species), *Melilotus albus* Medikus (83), *Sonchus arvensis* L. (74), *Cirsium arvense* (L.) (67), *Solidago canadensis* L. (52), *Solidago nemoralis* Aiton (49), *Apocynum androsaemifolium* L. (47), *Hieracium umbellatum* L. (45), *Solidago rigida* L. (42), and *Solidago ptarmicodes* (Torrey & A. Gray) (41). Most pollinators had low partner richness (184 pollinator species had 5 or less plant species partners), but a few had many. The ten insects visiting the greatest number of plant species were, in descending order: *Toxomerus marginatus* (Say) (55 plant species), *Bombus ternarius* Say (32), *Eristalis dimidiata* Wiedemann (32), *Megachile relativa* Cresson (32), *Helophilus fasciatus* Walker (27), *Systoechus vulgaris* Loew (25), *Bombus sandersoni* Franklin (24), *Hylaeus affinis*

(Smith) (24), *Toxomerus geminatus* (Say) (24), and *Heriades variolosa* (Cresson) (23). In general, the plants and pollinators with the greatest link abundance also had greater link richness compared to others. The networks had an average size (±SD) of 87.3±19 species and were all dominated by pollinators (mean web asymmetry = 0.48±0.11). On average, networks were composed of 65.5 pollinator and 21.8 plant species. Mean link abundance was 330.5±146, and the average link richness was 147.7±48.6 (Table 19). The estimated sampling completeness across my 15 networks was 55.75±7.7, in line with other pollination network studies (Chacoff et al. 2012; Devoto et al. 2012; Grass et al. 2018; Martínez-Núñez et al. 2019). Furthermore, sampling completeness was not significantly related to the sites' vegetation management strategy (Type III ANOVA, F = 1.3, p = 0.3, $r^2 = 0.18$), or to the ecoclimatic region (Type III ANOVA, F = 0.72, p = 0.5, $r^2 = 0.11$). Therefore, even if some links in the networks remained unobserved, no systematic bias in sampling completeness affected the network metrics between the different management strategies or ecoclimatic regions.

The model selection process revealed that network size was mainly influenced by the vegetation management strategy (Table 20), with fallowed sites hosting larger networks than grazed or mowed sites, and IVM sites hosting the largest networks overall (Figure 35F). Connectance was also strongly affected by management, with IVM and 'pf' sites having significantly smaller connectance compared to 'g/m' sites (Figure 35A). Connectance was additionally affected by ecoclimatic region, with the LBs region hosting networks with greater connectance compared to the others (Figure 35B). No environmental variable influenced network nestedness (Table 20). Network specialization (H2') was significantly greater in IVM and 'pf' sites when compared to 'g/m' sites, and was greatest in the MBs region (Figure 35C, D). Additionally, H2' was positively affected by the mean flowering plant cover (Figure 35F) and negatively affected by the landscape SHDI (Figure 35E). Network modularity followed a similar pattern, being positively affected by mean plant cover and negatively by SHDI (Figure 35I, H). And as with network specialization, modularity was also greatest in the MBs ecoclimatic region (Figure 35G). Finally, networks in IVM sites were the most robust to random plant species extinctions (Figure 35J). Furthermore, network robustness was positively affected by mean plant cover, and negatively affected by bare ground (Figure 35K, L).

Site	Size	Link richness	Link abundance	Connec- tance z	Nodf z	Linkage density z	H2' z	Modularity z	Robustness random z
1	57	82	171	-8.201	-0.952	-1.88	3.356	2.131	1.478
2	87	166	373	-12.62	-0.139	-3.488	5.736	6.339	2.384
3	78	136	223	-7.476	-0.737	-2.272	3.812	3.129	-0.592
4	112	196	482	-17.02	0.633	-4.507	7.579	6.259	2.825
5	81	118	222	-13.62	-2.299	-1.171	2.108	1.253	1.277
6	85	148	361	-12.63	2.094	-1.875	3.465	2.609	2.968
7	64	110	266	-9.769	1.511	-0.799	1.559	2.136	0.0875
8	82	112	226	-10.62	-2.017	-2.902	3.283	1.243	1.967
9	55	71	151	-4.019	1.846	0.386	0.622	3.882	-0.0117
10	87	151	321	-12.60	1.444	-2.407	5.063	4.523	1.726
11	96	135	307	-11.66	-3.024	-4.732	10.181	7.769	1.687
12	113	210	420	-15.85	0.0836	-2.828	5.424	4.909	1.363
13	93	131	229	-12.04	0.913	-1.605	5.28	3.629	0.224
14	105	239	535	-12.61	-3.249	-5.585	7.207	4.644	3.698
15	114	210	671	-17.54	-3.944	-7.424	11.098	7.152	4.183

Table 19. Network metrics. 'z' indicates metrics that have been standardized via null models.

Table 20. Results of GLMMs performed on the network metrics. Model selection was performed by sequentially dropping non-significant variables from an initial global model using the "drop1" function in R statistical software. All standardized (z) metric models were fit with a Gaussian distribution. Network size model was fit with a negative binomial distribution.

Response	R^2	Predictor	β	SE	Z	р
Network Size	0.532	Intercept	4.148	0.081	51.23	<0.0001
		Mgmt. – Pasture Fallow	0.224	0.103	2.17	0.03
		Mgmt. – IVM	0.459	0.091	5.04	<0.0001
Connectance (z)	0.685	Intercept	-7.655	1.072	-7.14	<0.0001
		Mgmt. – Pasture Fallow	-6.951	1.408	-4.94	<0.0001
		Mgmt. – IVM	-6.854	1.408	-4.87	<0.0001
		Ecoclimate – LBs	3.27	1.195	2.74	0.0062
		Ecoclimate – MBs	0.568	1.321	0.43	0.6669
NODF (z)	0.328	Intercept	-0.699	0.686	-1.02	0.308
		Ecoclimate – LBs	1.674	0.97	1.73	0.084
		Ecoclimate – MBs	-1.145	0.97	-1.18	0.238
H2' (z)	0.824	Intercept	8.72	1.544	5.65	<0.0001
		Mean Plant Cover	0.133	0.0389	3.42	0.0006
		Mgmt. – Pasture Fallow	2.536	0.8739	2.9	0.0037
		Mgmt. – IVM	3.744	0.9905	3.78	0.0002
		Ecoclimate – LBs	-0.0086	0.7184	-0.01	0.9905
		Ecoclimate – MBs	5.176	0.9228	5.61	<0.0001
		SHDI	-6.74	1.368	-4.93	<0.0001
Modularity (z)	0.586	Intercept	5.576	1.798	3.1	0.00192
		Mean Plant Cover	0.1554	0.0428	3.63	0.0003
		Ecoclimate – LBs	0.2178	0.8371	0.26	0.7947
		Ecoclimate – MBs	3.85	1.034	3.72	0.0002
		SHDI	-3.279	1.456	-2.25	0.0243
Robustness to	0.755	Intercept	1.062	0.4915	2.16	0.031
random plant		Mean Plant Cover	0.0981	0.0215	4.55	<0.0001
species loss (z)		Mean Bare Ground	-0.1409	0.0293	-4.8	<0.0001
		Mgmt. – Pasture Fallow	-0.0402	0.4966	-0.08	0.935
		Mgmt. – IVM	1.05	0.4223	2.49	0.013



Figure 35. Effects of environmental variables on network connectance (A-B), specialization (C-F), modularity (G-I), robustness (J-L), size (M) and nestedness (N). Regression lines represent predicted values from the selected GLMMs. Shaded area and whiskers show 95% confidence intervals. Significant effects are shown in bold p-values. Significant effects of categorical variables are indicated with a star, and p-values are shown in Table 20. Management 'g/m' = grazed/mowed, 'pf' = pasture fallow, 'IVM' = integrated vegetation management.

To compare network structure among the three management strategies or ecoclimatic regions, I performed type III ANOVA tests (Table 21). This allowed me to compare all three categories of either variable with each other. This was not possible in the GLMMs, which only allowed me to determine whether two categories were different from the third (eg. 'IVM' and 'pf' against 'g/m'). Only significant relationships revealed through the model-selection process were explored. For instance, since I found no significant relationship between ecoclimatic region and network size in the selected GLMM, I did not perform an ANOVA to explore this relationship further. Finally, I created box plots to visualize the differences in network size and structure between the three management categories (Figure 36).

Table 21. Summary of ANOVA type III tests to compare network metrics among the three management strategies or ecoclimatic regions. Tests were completed based on the results from the model selection process, shown in Table 20. Only significant relationships were explored. "g/m" = grazed or mowed, "pf" = pasture fallow, "IVM" = integrated vegetation management. "GT" = transitional grassland, "LBs" = subhumid low-boreal, "MBs" = subhumid mid-boreal.

Predictor	Response	F value	R^2	<i>p</i> value	Groups	& Means
Management	Size	11.79	0.532	0.0015	g/m – a	63.33
					pf - b	79.25
					IVM - c	100.2
Management	Connectance (z)	10.05	0.589	0.0027	g/m - a	-6.565
					pf - b	-12.15
					IVM - b	-13.74
Management	H2' (z)	6.219	0.47	0.014	g/m - a	2.597
					pf - ab	3.049
					IVM - b	6.974
Ecoclimate	H2' (z)	6.62	0.486	0.0115	GT - ab	4.518
					LBs - b	2.799
					MBs - a	7.838
Ecoclimate	Modularity (z)	2.798	0.285	0.1006	GT - a	3.822
					LBs - a	2.878
					MBs - a	5.62
Management	Robustness (z)	2.963	0.297	0.0899	g/m - a	0.2914
					pf - a	1.515
					IVM - a	2.291



Figure 36. Effect of management strategy on network structure. z-score metrics have been standardized using null networks to control for network size.

Many network metrics are inherently related, in various degrees, with each other (Dormann et al. 2009). To visualize the relationships between the calculated metrics I plotted the smoothed conditional means on scatter plots using the 'stat_smooth' function of the 'ggplot2' package (Wickham et al. 2021). We observe a positive relationship between standardized network specialization (H2') and modularity, while standardized connectance, nestedness and linkage density all have negative relationships with H2' (Figure 37). Standardized H2' and modularity had a positive relationship with standardized network robustness, while standardized connectance and nestedness were negatively related to robustness (Figure 38).



Figure 37. Relationships of standardized network modularity, linkage density, connectance and nestedness (NODF) with standardized specialization (H2').



Figure 38. Effect of standardized network modularity, specialization (H2'), connectance and nestedness (NODF) on standardized robustness.

Species' Network Roles

Across the 15 sampled networks I identified 39 pollinator species (15% of the total) that played a key role in at least one network (Table 22). Out of these, 27 species were module hubs and 19 were connectors in one or more of the networks. Only four species were identified as network hubs: the bees Bombus ternarius Say, which was a network hub in two sites, Lasioglossum laevissimum (Smith), Megachile rotundata (Fabricius), and the syrphid Eristalis dimidiata Wiedemann. The other 85% of identified pollinator species were peripherals and played no key network roles. Bees were the group with the most species playing important network roles, with 22 species being module hubs, connectors and/or network hubs in at least one site. Species' roles were variable across space, with most species only playing key network roles in one or two sites. However, a few species were consistently important for the preservation of the stability of the networks in which they were present. For the bees, these species included B. ternarius, which was a keystone species in nine of the fifteen networks. Bombus ternarius was consistently important throughout most of the latitudinal gradient, from the southern sites to the northern ones. Other notable species include Megachile relativa Cresson, which was a module hub or connector in four networks, and Megachile rotundata (Fabricius), the introduced alfalfa leafcutter bee, which was a module hub, connector, or network hub in three networks within the LBs ecoclimatic region, where this species was being managed for crop pollination. The Lysimachia specialist oil-collecting bee Macropis nuda (Provancher) was a module hub in the northern-most site, where it was most abundant. Thirteen fly species played a key network role in at least one site. Notable species which were consistently important include *Toxomerus marginatus* (Say) (module hub or connector in six networks) and Syritta pipiens (L.) (module hub or connector in five networks). These two species played key network roles in the southern and middle sites along the latitudinal gradient but were not important in maintaining network stability within northern sites, where they were much less abundant if not absent. On the other hand, syrphids Eristalis dimidiata Wiedemann and Helophilus fasciatus Walker consistently played key roles in northern sites but were only peripheral in the southern sites. Besides syrphids, among the flies playing key network roles I also identified four species in the Bombyliidae family, and one in the Stratiomyidae family. Only four wasp species played a key network role in at least one site: Dolichovespula arenaria (Fabricius), which was a module hub in two networks, Ammophila azteca Cameron, and two Chelonus morphospecies (which I named A and B for simplicity).

I identified 17 flowering plant species (18.1% of the total) that played a key network role in at least one site (Table 22). Ten species were module hubs while seven were connectors in at least one of the sampled networks. No flowering plant species ever played the role of network hub. Plant species network roles were not consistent across space. Most of the 17 species were only important in maintaining the stability of a single network out of the fifteen sampled. The only species which played a key role in more than one network was *Dasiphora fruticosa* (L.), which was a module hub in two networks. Overall, plant species were less likely than pollinators to be critical in the maintenance of network structure. In four networks out of fifteen, all the plant species were peripheral, with none playing a key role. Although most of the identified keystone plant species were natives, a few were introduced species. These were *Melilotus albus* Medikus (white sweet clover), *Medicago sativa* L. (alfalfa), *Sonchus arvensis* L. (field sow-thistle), and *Trifolium hybridum* L. (alsike clover). In the northern-most site, in conjunction with the bee *Macropis nuda* (Provancher) being a module hub, I identified its host plant species *Lysimachia ciliata* L. as a connector species.

Species Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Bees															
Anthophora terminalis	-	-	-	-	-	-	-	-	-	-	-	-	-	Μ	-
Augochlorella aurata	-	-	-	-	-	-	-	С	-	-	-	-	-	-	-
Bombus ternarius	C	Μ	С	-	С	Μ	-	Ν	С	-	С	-	Ν	-	-
B. rufocinctus	-	Μ	-	-	-	-	-	С	-	-	-	-	-	-	-
B. griseocollis	-	-	-	-	-	-	-	-	Μ	-	-	-	-	-	-
B. sandersoni	C	-	-	-	-	-	-	-	-	-	-	Μ	-	-	-
Colletes hyalinus	-	-	-	-	-	-	-	-	-	-	С	-	С	-	-
C. simulans	-	-	-	-	С	-	-	-	-	-	-	-	-	-	-
Dufourea harveyi	-	-	-	-	-	-	-	-	-	-	Μ	-	-	-	-
D. maura	-	-	-	-	-	-	-	-	-	-	-	-	Μ	-	-
Halictus confusus	-	-	С	-	-	-	-	-	-	-	-	-	-	-	-
Heriades variolosa	-	-	-	Μ	-	-	-	-	-	-	-	Μ	-	-	-
H. carinata	-	-	Μ	-	-	-	-	-	-	-	-	-	-	-	-
Hylaeus mesillae	-	-	-	Μ	-	-	-	-	-	-	-	-	-	-	-
H. affinis	-	-	-	-	-	-	-	-	-	-	-	Μ	-	-	-
Lasioglossum laevissimum	-	-	-	-	-	-	-	-	-	-	-	-	-	Ν	-
Macropis nuda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	М
Megachile relativa	-	С	-	-	-	-	-	-	-	-	Μ	-	-	Μ	Μ
M. latimanus	-	-	Μ	-	-	-	-	-	-	Μ	-	-	-	-	-
M. rotundata	-	-	-	-	-	С	Ν	Μ	-	-	-	-	-	-	-
Nomada florilega	-	-	-	-	-	-	-	-	-	-	С	-	-	-	-
Osmia proxima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Μ
Flies															
Eristalis dimidiata	-	-	-	-	-	-	-	-	-	Μ	Ν	Μ	-	-	-
E. interrupta	-	-	-	-	-	-	-	-	-	-	-	-	Μ	-	-
Hedriodiscus binotatus	-	-	-	-	-	-	-	-	-	-	С	-	-	-	-
Helophilus fasciatus	-	-	-	-	-	-	-	-	Μ	Μ	-	Μ	-	-	Μ
Poecilanthrax alycon	-	-	-	-	Μ	-	-	-	-	-	-	-	-	-	-
Sphaerophoria philanthus	-	-	-	-	-	-	-	-	-	-	-	-	Μ	-	-
Syritta pipiens	Μ	М	-	-	С	Μ	-	-	С	-	-	-	-	-	-
Systoechus vulgaris	-	-	-	-	Μ	-	-	-	-	-	-	-	Μ	-	-
Toxomerus marginatus	Μ	М	-	Μ	Μ	-	С	-	-	С	-	-	-	-	-

Table 22. Module hubs, connectors and network hubs of each network. "M" = module hub, "C" = connector, "N" = network hub.

T. geminatus	-	-	-	-	-	-	С	-	-	-	-	-	-	-	С
Villa fulviana	-	-	-	Μ	-	-	-	С	-	-	-	-	-	-	-
V. lateralis	-	-	-	-	С	-	-	-	-	-	-	-	-	-	-
Xylota naknek	-	-	-	-	-	-	-	-	-	-	-	-	-	-	М
Wasps															
Ammophila azteca	-	-	-	-	-	-	-	-	-	-	-	-	С	-	-
Dolichovespula arenaria	-	-	-	Μ	-	-	-	Μ	-	-	-	-	-	-	-
Chelonus sp. ChB	-	-	-	-	-	-	С	-	-	-	-	-	-	-	-
Chelonus sp. ChA	-	-	-	-	-	-	-	С	-	-	-	-	-	-	-
Flowering Plants															
Campanula rotundifolia	-	Μ	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium flodmanii	Μ	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dasiphora fruticosa	-	-	-	-	-	-	-	-	-	Μ	-	-	Μ	-	-
Erigeron glabellus	-	-	-	-	-	-	-	-	Μ	-	-	-	-	-	-
Euthamia graminifolia	-	-	-	-	-	-	-	-	-	-	С	-	-	-	-
Galium boreale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	С
Lysimachia ciliata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	С
Melilotus alba	-	-	-	-	-	-	-	-	-	-	-	-	-	М	-
Mentha canadensis	-	-	-	М	-	-	-	-	-	-	-	-	-	-	-
Medicago sativa	-	-	-	-	-	-	-	-	С	-	-	-	-	-	-
Monarda fistulosa	-	-	-	-	-	-	-	-	-	-	-	С	-	-	-
Solidago sp.X	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solidago gigantea	-	-	-	М	-	-	-	-	-	-	-	-	-	-	-
Sonchus arvensis	-	-	-	Μ	-	-	-	-	-	-	-	-	-	-	-
Symphoricarpos occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	С	-
Trifolium hybridum	-	Μ	-	-	-	-	-	-	-	-	-	-	-	-	-
Zizia aurea	-	-	-	-	-	-	Μ	-	-	-	_	-	-	-	-
3.4 Discussion

Pollinator Fauna

The ~300 km section of double-line transmission ROW that I surveyed in Manitoba provided habitat for a rich fauna of wild insect pollinators. Among the three pollinator groups sampled (bees, flies, and wasps) I identified 259 species. The 130 observed bee species constitute ~16% of the known bee fauna of Canada and ~35% of the 369 described bee species recorded from Manitoba (Gibbs et al. unpublished). I expect that greater sampling effort would further increase the number of species observed. This could be done by increasing netting time per flower species, the number of sites and sampling events per site, and by adding passive sampling methods such as bee bowls and blue vane traps. A few exotic bee species were present in the samples, including Andrena wilkella (Kirby), a ground-nesting European bee, a single individual of Apis mellifera L., the European honeybee, and over 140 individuals of Megachile rotundata (Fabricius), the alfalfa leafcutter bee. Megachile rotundata was mostly present in the LBs ecoclimatic region, where the introduced species was being actively managed for the pollination of alfalfa and canola crop fields. Other studies have also found significant pollinator biodiversity within powerline ROWs, although differences in methodologies make direct comparisons difficult (Lanham and Nichols 2000a; Russell et al. 2005, 2018; Lensu et al. 2011; Wagner et al. 2014a, 2019; Hill and Bartomeus 2016; Steinert et al. 2020). These studies all focus on sampling the biodiversity of either bees or butterflies and moths. Leston and Koper (2017) sampled butterflies in urban powerline ROWs within 70 km of Winnipeg (Manitoba) and recorded 46 species over three years of observations. Wagner et al (2014, 2019) recorded 163 and 197 bee species from powerline ROWs in Connecticut and New Hampshire (USA), respectively. Meanwhile, Russell et al. (2005, 2018) reported 98 and 146 species respectively from easements in Maryland (USA). To my knowledge, the study by Russo et al. (2021), conducted in Pennsylvania, is the only published study where the whole flower-visiting insect community was sampled, with 126 bee species and 179 non-bee morphospecies recorded. All pollinator-related research conducted within powerline ROWs however has focused only on sampling abundance and richness. This study is the first to investigate pollination networks within transmission-line easements.

I documented several rare native bee species. For instance, a large population of *Macropis nuda* (Provancher), the only melittid found in Manitoba, was observed in the northern-most site, where its host plant *Lysimachia ciliata* L. was present. This bee species is considered a

conservation target due to its rarity. Given the presence of a large *Macropis* population within the ROW, I hoped to detect the species' cleptoparasite *Epeoloides pilosulus* (Cresson), an exceptionally rare, endangered bee which has recently been rediscovered within the province of Manitoba (Gibbs et al. 2021). I failed to observe this rare species but believe that its presence within the surveyed ROW is possible given its known distribution and the presence in high numbers of its host. Furthermore, the presence of this species within powerline ROWs has already been recorded previously in Connecticut, USA (Wagner et al. 2014a, 2019), and in Manitoba (Gibbs et al. 2021). In the ROW, I observed species such as Triepeolus obliteratus, Nomada quadrimaculata, Sphecodes coronus and Sphecodes dichlorus – cleptoparasites which have only recently been included in Manitoba's bee record (Gibbs et al. unpublished). Furthermore, I added four bee species to the record which had previously never been observed in the province: Osmia subaustralis Cockerell (also the first Cephalosmia subgenus record for Manitoba), Stelis nitida Cresson, Triepeolus grindeliae Cockerell (two cleptoparasitic species), and Lasioglossum *immigrans* Gardner (Figure 19) - a species that was undescribed before my study and which had never been recorded in Canada before. Bombus terricola Kirby, a bumblebee species in decline across North America (Colla and Packer 2008; Cameron et al. 2011b), was also recorded from the powerline ROW. Diversity and the presence of rare species tend to be the most frequently used criteria for the selection of conservation-worthy sites (Prendergast et al. 1993). Rare, at-risk species are an excellent biodiversity indicator group and have a high potential to be used to select areas for conservation when information about species distributions is scarce (Lawler et al. 2003). Our observations of many rare (in terms of abundance and/or spatial distribution) species within the powerline easements, therefore, is a promising indication that these ROWs may have a strong conservation value. Among the wasp species sampled, a noteworthy find was that of Dolichovespula adulterina (de Buysson), a social parasite of other wasps of the same genus. Dolichovespula adulterina females parasitize nests of host species by usurping the queen and assuming the reproductive responsibility while simultaneously leading the pre-existing workers (Archer 2006). Parasitic species such as cleptoparasites are expected to spend less time foraging and more time near potential nesting sites (Russell et al. 2005). The presence of many parasitic species within the powerline ROW, therefore, suggests that many pollinators may be using the easement for nesting, rather than only for foraging. Parasitic species also indicate good quality of the habitat in the powerline ROW, as they only persist in areas where populations of their hosts

reach a stable threshold (Sheffield et al. 2013; Russell et al. 2018). Occupying a higher trophic level, cleptoparasites may be similarly considered indicator taxa to top predators and parasites; their presence is dependent on the distribution of their hosts and the resources available to these hosts (Sheffield et al. 2013). Cleptoparasites respond to environmental pressures in ways that are reflective of the entire bee community, and thus serve as sensitive indicator taxa (Sheffield et al. 2013). The presence of a diverse cleptoparasitic community within the powerline ROW is further indication of the quality of this early-successional habitat and of its conservation potential.

Bees were overall the dominant pollinator group in the powerline ROW both in terms of abundance and richness. A few abundant generalist bee species comprised a significant portion of the observed plant-pollinator links. Five bee species, *Bombus ternarius* Say, *Bombus Sandersoni* Franklin, *Megachile relativa* Cresson, *Megachile rotundata* (Fabricius), and *Hylaeus affinis* (Smith) combined were involved in 18.2% of all observed interactions. *Bombus ternarius* alone was involved in 8% of all links. *Bombus* species tended to be highly abundant due to their eusocial behaviour – building colonies that increased in size as the summer progressed. To build and sustain these colonies, bumblebees require highly abundant and diverse floral resources – a requirement that scales with increasing colony size (Moquet et al. 2017; Kaluza et al. 2018). The presence of *Bombus* in a large proportion of plant-pollinator interactions in the ROW suggests that this habitat contains a rich and diverse floral community that can sustain the resource requirements of large eusocial bee colonies. The high observed richness and floral visitation rate of bees, and their known high pollination efficiency (Jauker et al. 2012; Orford et al. 2015) suggest that they were the most dominant and effective pollinator group within the surveyed powerline ROW. This highlights the importance of bees in maintaining a key ecosystem service within anthropogenic systems.

Flies were also highly involved in the pollination of plants within the powerline ROW. The species with the greatest number of links overall was a syrphid, *Eristalis dimidiata* Wiedemann, which was involved in 8.2% of all observed interactions. This fly was particularly important in the northern sites (within the MBs ecoclimatic region), where most of its interactions were observed. Together with *Toxomerus marginatus* (Say), and *Helophilus fasciatus* Walker, two other supergeneralist, highly abundant syrphids, these three fly species were involved in 21.1% of all sampled interactions. Furthermore, Syrphidae was overall the family with the greatest number of species and with the greatest frequency of interactions with flowering plants in the ROW. Syrphids, and in particular species within the genus *Eristalis*, have been shown to be effective pollinators, as they

carry pollen loads that are comparable to some bee species (e.g. *Apis mellifera*) and visit flowers at a high frequency (Kendall and Solomon 1973; Sahli and Conner 2007; Rader et al. 2009; Orford et al. 2015). My results, therefore, suggest that syrphids were also playing an important role in the pollination system within the ROW. In particular, I highlight the importance of the genera *Toxomerus, Eristalis, Helophilus*, and *Syrphus*, which were involved in a significant portion of the total observed interactions. The latter three taxa were especially important in the northern-most ecoclimatic region (MBs) where they took part in 32.6% of network links.

Finally, my results show that wasps were not as involved in flower pollination as bees and flies, only partaking in 11% of the observed links. However, despite the low visitation numbers, the richness of this pollinator clade was relatively high, consisting of 19% of all recorded species in the ROW. Only one wasp species was a highly frequent flower visitor: Dolichovespula arenaria (Fabricius), the common yellowjacket, which was involved in almost 5% of all observed interactions. Commonly misjudged due to its highly defensive nature, my results show that this species may be contributing highly towards the provisioning of a beneficial ecosystem service. Besides its frequent flower visitations, this species has a relatively large body size, which is positively associated with pollination effectiveness (Sahli and Conner 2007). Furthermore, this species can be highly abundant due to its eusocial nesting behaviour and may potentially carry high pollen loads due to an abundance of long hairs covering its body. This suggests that *Dolichovespula arenaria* may be an effective pollinator species in the surveyed powerline ROW. Unfortunately, the lack of data on the quantity and quality (monospecific deposition) of pollen transfer precludes us from fully quantifying pollination effectiveness. In general, however, wasps played a minor role in the pollination system. Most wasps are carnivores or parasitoids, visiting flowers only occasionally to consume nectar and pollen for gamete development (Patt et al. 1997). Since my study only focused on sampling the pollination network within the ROW, it was to be expected that wasps would not be highly involved. This however highlights the lack of exploration of multitrophic networks and the provisioning of multiple ecosystem services. Beyond pollination, wasps provide critical ecosystem services such as pest control through their predatory and parasitic behaviour (Bianchi et al. 2006; Steckel et al. 2014). The conservation of natural enemies within anthropogenic systems is, together with pollinators, also a management priority (Redlich et al. 2018). Biotic and abiotic changes resulting from anthropogenic activity, such as declines in plant biodiversity and habitat fragmentation, can have complex and compounding effects on species and

interactions within multitrophic networks (Scherber et al. 2010; Fenoglio et al. 2012; Steckel et al. 2014; Grass et al. 2018). The plants and pollinators in the ROW form a mutualistic network which is part of a much larger ecosystem composed of other trophic levels connected through both mutualistic and antagonistic relationships. This includes herbivores eating the plants and carnivores eating or parasitizing both the herbivores and the pollinators. Studying an entire multitrophic network, even if "contained" within a powerline ROW, is virtually impossible. However, given the important ecosystem service provided by natural pest enemies in agricultural areas, I believe future studies should focus on quantifying host-parasite trophic networks within ROWs and evaluate how they are affected by different environmental variables and management strategies (Kruess 2003; Grass et al. 2018). This would allow us to determine whether ROWs have the potential to be used for the conservation of natural enemies, along with pollinators.

Pollinator biodiversity and community composition changed markedly within the ROW as I moved northwards through the three ecoclimatic regions. A well-known trend of biogeography is a decrease in species richness with increasing distance from the equator (Fischer 1960). However, contrary to my original expectations and this general biogeographical trend, my results reveal that pollinator biodiversity was greatest in the northern-most stretch of the surveyed powerline section. The five sites in the subhumid mid-boreal (MBs) region hosted the greatest average abundance and richness. This may be the result of a combination of environmental factors that benefited pollinator biodiversity in this region. The MBs ecoclimatic region was characterized by reduced anthropogenic disturbance both within the ROW and in the surrounding landscape. All five sites were managed IVM and hosted the greatest average flowering plant species richness (compared to sites in the other ecoclimatic regions). Additionally, anthropogenic disturbance in the landscape surrounding these sites was minimal (Figure 27), while forested land was higher than in the other regions. Finally, the MBs region was also characterized by a greater landscape diversity, with higher SHDI and ED levels than the LBs and GT regions. All of these factors may be contributing to the increased pollinator biodiversity in the powerline section within this region. At the local scale, pollinators respond positively to increasing flowering plant cover and richness (Hülsmann et al. 2015; Cole et al. 2017; Rollin et al. 2019). Studies examining the effect of landscape-scale variables on pollinator biodiversity instead report positive effects of amount of natural and semi-natural land, while effects of landscape configuration tend to be weaker (Kennedy et al. 2013). Sites within the MBs ecoclimatic region also had a significantly different pollinator

community composition compared to the LBs and GT sites. The flowering plant community in the MBs was significantly different from that in the GT region, but not in the LBs region. I therefore believe that it was the variability in the surrounding vegetation and the abiotic characteristics (average temperature, moisture, soil type, etc.) to cause the difference in pollinator community composition, rather than variability in local flowering plant communities.

The proportion of bees in terms of total pollinator abundance and richness diminished moving northwards along the ROW, while that of flies increased. Bee relative abundance and richness fell by 10% and 7% respectively moving northwards along the powerline from the GT to the MBs ecoclimatic region. Flies, on the other hand, experienced an increase in relative abundance and richness of 10% and 12% respectively moving northwards. In the northern-most ecoclimatic region flies were the dominant pollinator group in terms of abundance and participated in 46% of all sampled interactions, compared to bees which were involved in 42% of the links. Even though bees remained the most species-rich clade in the northern stretch of the surveyed ROW, I expect flies to become dominant in terms of richness as well moving further north. This general trend of a decrease in relative bee biodiversity in proportion to the total pollinator fauna, and increase in relative fly biodiversity with increasing latitude is well-established (Elberling and Olesen 1999). The reason behind this is that most bee species thrive in warmer, xeric environments and therefore are not as prevalent in cold, wet environments such as high altitudes and latitudes (Michener 2007; Orr et al. 2021). Many fly species, on the other hand, are well-adapted to cold environments, and some require the presence of wetlands for the development of the larval stage (e.g. Eristalis). Hence the observed drop in bee and increase in fly biodiversity in proportion to the total visitor fauna in the higher-latitude sites. These were situated within the boreal forest, characterized by a cold environment and a high density of wetlands. Nonetheless, in terms of raw numbers, bee richness was greatest in the MBs region compared to the other two. Several pollinator taxa were associated with different ecoclimatic regions. Eristalis, Helophilus and Syrphus were dominant fly genera in the northern MBs region, while genera such as Syritta and Villa were abundant flower visitors in the GT and LBs regions. The two recorded *Toxomerus* species followed completely different patterns. Toxomerus marginatus (Say) (the most abundant of the two species) diminished moving northwards, while Toxomerus geminatus (Say) increased. Bombus species were most abundant in the southern region and diminished moving northwards. Meanwhile, other eusocial species in the genera Dolichovespula and Lasioglossum, particularly L. planatum (Lovell) and L.

viridatum (Lovell), increased markedly in abundance in the MBs compared to the southern and middle ecoclimatic regions.

Overall, these findings demonstrate that the surveyed transmission line ROW is serving a role in the conservation of wild insect pollinators, including rare species, in the agricultural and forested landscapes of southern and mid-Manitoba where early-successional habitats and the associated species are known to be in decline. Other studies have reported high biodiversity of bees and butterflies in powerline ROWs in the United States and Canada (Russell et al. 2005, 2018; Wagner et al. 2014a, 2019; Leston and Koper 2016, 2017), however, I have shown that these linear habitats can also host abundant and rich flower-visiting fly and wasp assemblages. Although it has been suggested that powerline ROWs can be used as conduits by insects (Phillips et al. 2020), I found distinct pollinator communities along the length of the easement, suggesting that many species did not disperse along the corridor beyond their latitudinal maxima. I also found that pollinator biodiversity increased mowing northwards, which goes against the general global trend (Fischer 1960). I determined that this was likely due to reduced anthropogenic pressure within the corridor and in the surrounding landscape.

Biodiversity Models

Following my original predictions, I found that local vegetation management and floral resource availability and diversity in the powerline ROW had positive influences on pollinator biodiversity. Both flowering plant species richness and cover positively affected pollinator biodiversity in the ROW. Pollinator rarefied richness was significantly affected by the flowering plant richness in the easement, while pollinator abundance was affected both by plant richness and cover. The positive bottom-up relationship between flowering plant and pollinator biodiversity is well-established (Nicholls and Altieri 2013). It has been observed within small, isolated habitat patches, in anthropogenic environments (e.g. city parks), and within narrow linear environments such as floral strips, roadside verges, and powerline easements (Hopwood 2008; Hülsmann et al. 2015; Cole et al. 2017; Russell et al. 2018; Baldock et al. 2019b; Rollin et al. 2019; Phillips et al. 2020; Russo et al. 2021). My study confirms that this general trend occurs within powerline ROWs, regardless of latitudinal location, surrounding landscape characteristics, or local vegetation management strategy. When analyzing the three pollinator groups separately the GLMMs show that bee abundance was positively affected by both plant richness and cover, however rarefied

richness was not. Instead, I found that bee rarefied richness was positively affected by the amount of bare ground in the ROW. Most bee species burrow in the soil to build their nests (Michener 2007) and therefore benefit from habitats with high amounts of exposed ground. Other studies have also found a positive relationship between the amount of bare ground in ROWs and bee biodiversity (Hopwood 2008; Moroń et al. 2014). These results suggest that increasing exposed ground within powerline ROWs can help increase bee richness. Furthermore, although my net collecting method does not allow me to determine whether foragers were also residents in the ROW, these results suggest that several bee species are using the easement for nesting, and not just for foraging. These results are encouraging because they suggest that powerline ROWs provide both foraging and nesting resources to pollinators, which are otherwise lacking in many agricultural or forested areas. These ROWs may therefore act as a source of pollinators for the surrounding landscapes, a beneficial aspect that has been suggested by other studies as well (Berg et al. 2016; Russell et al. 2018). Flies and wasps responded differently to local environmental variables. Fly biodiversity responded positively to flowering plant richness and cover, while wasp biodiversity did not. Flies, particularly syrphids and bombyliids, are frequent flower visitors and therefore just like bees are positively affected by a high richness and density of floral resources (Cole et al. 2017). Wasps are carnivorous, they hunt or parasitize other insects and visit flowers only occasionally to consume some nectar (Patt et al. 1997; Wojcik and Buchmann 2012). They are much less dependent on floral resources than bees, syrphids and bombyliids, hence the lack of relationship between floral resource availability and diversity, and wasp biodiversity in my study. In contrast, by occupying higher trophic levels, wasps tend to be more dependent on the distribution and abundance of their prey or hosts species (Szczepko et al. 2012). Wasps, therefore, thrive in heterogeneous landscapes, where they can find greater biodiversity of their hosts (primary consumers) due to a large diversity of resources (primary producers) (Steffan-Dewenter 2003; Bianchi et al. 2006; Szczepko et al. 2012; Steckel et al. 2014).

Following my original predictions, local vegetation management strategy had a significant effect on pollinator biodiversity. Results from the GLMMs indicate that vegetation management strategy had a significant effect on both abundance and rarefied richness. Separating the three pollinator groups reveals that the effect is significant for the abundance of bees, flies and wasps, but only for the rarefied richness of bees. Wasp and fly rarefied richness did not respond significantly to management. Nonetheless, the results from the ANOVA analyses comparing the pollinator biodiversity among the three management categories (Table 18, Figure 33, and Figure 34) show that IVM sites hosted the greatest mean abundance and rarefied richness of bees, flies and wasps, and of all three combined. Results from the GLMMs and ANOVAs regarding effect of management on pollinator biodiversity are inconsistent due to the different nature of the analyses. GLMM analyses explain whether pollinator rarefied richness or abundance in the fallowed or IVM sites are significantly different from the grazed or mowed sites, while also taking into consideration the effects of the other variables in the models. The ANOVA analyses only consider management as the independent variable and explain whether pollinator rarefied richness or abundance are significantly different among all three categories. Therefore, by only considering vegetation management, the biodiversity of the three pollinator groups is significantly different in all three categories. These results are in line with other insect biodiversity studies conducted within ROWs, which have found that integrated vegetation management strategies have positive effects on insect richness and abundance (Russell et al. 2018). My study, therefore, confirms that ROW vegetation management strategy can have a significant impact on insect pollinator biodiversity, with lessdisturbing methods such as IVM positively affecting abundance and rarefied richness. IVM sites hosted greater pollinator biodiversity and were home to a greater number of parasitic species as well as unique, spatially-rare species – both indicators of greater habitat quality (Russell et al. 2005, 2018; Sheffield et al. 2013).

Landscape diversity had a negative effect on pollinator abundance and rarefied richness, which contradicts my predictions. Several studies argue that heterogeneous landscapes, containing more numerous and diverse patch types, provide increased habitat resources for species to exploit and allow for greater insect biodiversity (Kennedy et al. 2013; Cole et al. 2017; Moquet et al. 2018). I did not find this relationship in my study, with bees, flies and wasps all responding negatively to the SHDI in a 500 m radius buffer. However, GLMMs also revealed a significant relationship between SHDI and ecoclimatic region, indicating that the effect of landscape diversity on the pollinators was region-dependent. To explore this relationship, I performed GLMMs separately on the three regions and focused on the effect of SHDI on pollinator abundance and rarefied richness (Figure 32). In the GT ecoclimatic region, SHDI had a strong negative effect on pollinators was weak (non-significant). Nonetheless, we observe no trend in the LBs region and a weak positive trend with both abundance and rarefied richness in the MBs region. In addition to

these differences among ecoclimatic regions, I also note that overall landscape diversity (as well as edge density) levels were highest in the MBs, lower in the LBs, and lowest in the GT region (Figure 27). Therefore, within the region with the lowest landscape diversity, increased levels of SHDI negatively affected pollinator abundance and rarefied richness. Within the region with the highest landscape diversity, we observe an opposite effect where greater SHDI levels positively affected pollinator abundance and rarefied richness. Finally, in the region with intermediate levels of landscape diversity, increased SHDI did not affect pollinators. Landscape diversity estimates depend on regional context, such that similar levels of SHDI between landscapes dominated by different cover types are not biologically equivalent (Martin et al. 2020). In the GT region, dominated by agriculture, increasing levels of SHDI are probably the result of a greater diversity of crop fields. On the other hand in the MBs region, which is dominated by forests, an increase in SHDI is probably an indication of a greater diversity of natural and semi-natural habitats. Nonetheless, we would still expect crop diversity to benefit insect richness/abundance, a trend that has been reported in several studies (Palmu et al. 2014; Novotný et al. 2015; Redlich et al. 2018). However, Hass et al. (2018) found that high crop diversity reduced wild bee abundance, probably due to an increase of crop types with intensive management. In some cases, the effect of crop diversity depends on the amount of farmland in the landscape. Crop diversity can have positive effects on biodiversity in landscapes with low crop cover, but negative effects in landscapes dominated by crops (Wilson et al. 2017; Sirami et al. 2019). This might explain why we observe a decrease in pollinator richness and abundance with increasing landscape SHDI in the GT region. A greater diversity of natural and semi-natural habitats in the northern MBs region may instead be providing increased resources to pollinators and thus boosting their biodiversity.

Pollination Networks

One of the most important findings of my study is that vegetation management strategy has a significant effect on the structure and resiliency of pollination networks within the powerline ROW. As I predicted, IVM sites hosted larger networks (a greater number of insect and plant species), which had greater link abundance and richness compared to fallowed or grazing/mowing site networks (Figure 36A, B, C). Networks in IVM sites were also significantly more specialized (Table 21) and tended to be more modular – although this last relationship was weak due to the low sample size and some variation in modularity values among IVM networks (Figure 36E). Networks within IVM sites, together with 'pf' networks, were also significantly less connected than those in 'g/m' sites. Grazed and mowed sites hosted smaller networks due to a loss of species following disturbance. Rare species and specialist-specialist interactions tend to be more susceptible to environmental change and are the first to disappear after disturbance (Spiesman and Inouye 2013; Soares et al. 2017). This loss of specialists and the concentration of links among generalists causes pollination networks to become more nested and less modular (Villalobos et al. 2019; Morrison et al. 2020). The higher standardized connectance and the lower standardized specialization (H2') and modularity of the networks within grazed and mowed sites indicates that these disturbed sites have experienced a loss of specialist species, resulting in more generalized systems with higher interaction asymmetries. On the other end of the spectrum, IVM networks were larger, had lower standardized connectance but higher standardized H2' and modularity, indicating more specialized systems. Theoretically, networks with higher connectance also have a greater functional redundancy due to their generalized state (Tylianakis et al. 2010; Schleuning et al. 2015) and are therefore expected to be more robust to future species extinctions. However, this theoretical increased robustness often comes at the cost of a simplified network and therefore is not necessarily desirable. Nevertheless, my results show that the more complex, larger networks in the IVM sites, despite the higher specialization, were also more robust to random sequential extinctions of plant species. I presume that this phenomenon was brought by the greater modularity of networks in IVM sites, which helps slow down the spread of extinction cascades in the system (Tylianakis et al. 2010). The higher robustness observed in the IVM networks indicates that the higher diversity and complexity of these systems grant them a higher resiliency to species loss before the threshold of web collapse is reached (Bascompte and Stouffer 2009). Networks in fallowed sites had intermediate levels of standardized robustness (Figure 35H), although they weren't significantly different from either the 'g/m' or IVM networks. I believe that this is a result of the low number of sites in each management category and predict that increasing this would allow for the detection of significant differences between all three categories.

Ecoclimatic region was also a factor that affected network structure. Ecoclimatic region was included as an explanatory variable in the selected models for standardized connectance, modularity, H2' and nestedness (NODF), and had a significant effect on all metrics but one (NODF). Certain macroscopic network features such as nestedness and connectance tend to remain stable across space (Trøjelsgaard and Olesen 2016; Zografou et al. 2020). Instead, microscopic

network features such as species identity, partner affiliations, individual specialization levels and network roles show strong variability across space (Trøjelsgaard and Olesen 2016). My results show significant variation in both micro and macroscopic network features among the three ecoclimatic regions. I believe this variation to be a result of the different species composition of pollinators and plants among the three regions. For instance, species composition is an important driver of network modularity (Spiesman and Inouye 2013). Differences in land-use type and levels of anthropogenic disturbance between each region may also have caused variation in network features (Morrison et al. 2020). Mean plant cover was also present in the selected models and had a significant positive effect on standardized network modularity, H2', and robustness. Increased availability of floral resources may be attracting a greater number of specialist species and may also be causing a shift towards specialized foraging behaviour (floral constancy and/or reduced diet breath) in generalist species (Grüter and Ratnieks 2011; Valdovinos et al. 2012; Ferreira et al. 2020). These changes would boost network stability by increasing specialization and modularity (slower spread of extinction cascades). Finally, my results show that SHDI within a 500 m radius had a negative effect on both network modularity and specialization. I believe that this is due to the strong negative effect that SHDI had on pollinator biodiversity in the GT region, where increased SHDI indicated a greater diversity of crops. The increased crop diversity and associated farming intensity may be pushing rare and specialist species towards local extinction, resulting in poorer, more generalized networks.

We can visualize the effects of management on network structure by taking as an example two of the sampled networks. The land within the powerline easement at site 9 (LBs region) was used as cattle pasture throughout the entire summer season. Here, cows applied continuous pressure on the pollination network through grazing and trampling, limiting floral resources. Plant-pollinator interactions are strongly driven by effects of resources on consumers (Scherber et al. 2010; Goulson et al. 2015; Schleuning et al. 2016), therefore I predicted that cattle activity would negatively affect the entire local pollination network. This was confirmed by my results. Network 9 (Figure S9) was the smallest sampled network (55 species), with the lowest link richness and abundance (Table 19). This network was essentially devoid of spatially rare species (species that were only recorded from a single site). Only a single pollinator species, the syrphid *Orthonevra nitida*, was unique to this site. On the other hand, common generalist species dominated the network. At the pollinator level two species, *Bombus ternarius* and *Toxomerus marginatus*,

accounted for 37% of all interactions in the network. At the plant level, a single species, Dasiphora *fruticosa*, participated in 57.6% of all links. This network is a clear example of how disturbance may cause a loss of rare species and specialist-specialist interactions, and lead to generalized systems. Network 9 had the highest connectance, indicating a reduced number of total potential links, and the second highest nestedness, suggesting a high dependence of specialist species from one level on generalists from the other (Bascompte et al. 2003). This network also had the lowest specialization of all (Table 19), confirming its highly generalized state. On the opposite side of the spectrum, the land at site 15 (MBs region) was being managed with IVM techniques, meaning that the local ecosystem only experienced mild disturbance (selective cutting and herbicidal spraying) once every several years. Network 15 was the largest (114 species) and had the highest link abundance and second highest link richness (Table 19). This site hosted fourteen spatially rare pollinator species, and abundant generalist species were less dominant than in network 9. The two most abundant pollinator species participated in 29% of all sampled interactions, while the most visited plant, Sonchus arvensis, participated in 23% of all links. Compared to network 9 we observe a greater number of rare species and specialist-specialist interactions, and a reduced concentration of links by generalists. Network 15 had the lowest connectance and lowest nestedness, indicating lower asymmetry of interactions and species dependencies. Network 15 also had the greatest H2' and modularity values of all, suggesting a highly specialized system.

Network theory states that greater connectance, nestedness, and generalization (at equal network size) lead to more robust networks due to greater functional redundancy (Tylianakis et al. 2010; Schleuning et al. 2015). However, my results show that network 9 had the second lowest robustness value, while network 15 was the most robust of all. Overall, throughout all my networks we observe a trend where robustness was negatively correlated with connectance and nestedness but positively correlated with modularity and specialization (Figure 38). These network metrics are, to a varying degree, related to each other (Figure 37). This is because, at equal network size, it is the generalist-specialist ratio and the pattern of interactions between these two groups that determine network structure. Therefore, I suggest that the decrease in rare species and specialist-specialist interactions, following disturbance, is leading to higher connectance and nestedness, lower modularity and specialization, and ultimately lower robustness of the networks. Rare species and specialist-specialist interactions are highly prone to extinction following disturbance (Aizen et al. 2012; Spiesman and Inouye 2013). On the other hand, abundant generalists tend to be stable

through time and space and to be resilient towards environmental disturbances (Spiesman and Inouye 2013; Soares et al. 2017; Zografou et al. 2020). Usually, a few abundant species provide the vast majority of the community biomass (Schwartz et al. 2000), and abundant generalists participate in a large portion of ecological interactions (as we have observed within my networks). We therefore expect abundant generalists to contribute highly towards ecosystem functioning when compared to rare, specialist species. This was confirmed by the species' roles analysis, which revealed that species playing key roles tended to be abundant generalists such as Bombus ternarius, Toxomerus marginatus, and Dasiphora fruticosa. We would therefore expect that networks hosting a greater proportion of abundant, generalist species would be more robust to species extinctions. However, rare specialist species can also play keystone roles and can contribute disproportionately towards ecosystem functioning (Lyons et al. 2005; Leitão et al. 2016; Dee et al. 2019). And I did find that certain uncommon or specialist species were also playing key network roles, such as Macropis nuda (Provancher), Nomada cf. florilega Lovell and Cockerell, and Lasioglossum laevissimum (Smith). Macropis nuda and Lasioglossum laevissimum are species that were geographically restricted in my system but locally abundant, contributing significantly to the functioning of the ecosystem and the provisioning of services where they did occur (Dee et al. 2019). More importantly, even though abundant generalists tend to contribute more, individually, towards ecosystem functioning, the aggregate effect of uncommon or specialist species on the whole system may be much larger (Lyons et al. 2005). Minor species that are functionally similar to dominant species but with different environmental requirements increase resilience in ecosystem functioning under perturbations that favour them over the dominants (Lyons et al. 2005; Dee et al. 2019). For instance, low-abundance plant species in a lightly grazed site were found to compensate, collectively, for the functions provided by a few abundant species in a heavily grazed one (Walker et al. 1998). Similarly, the aggregate contribution of less common native bees towards pollination in row crops, compared to the highly abundant and generalist honeybee, was determined to be essential in sustaining a system with high annual variation in species composition and abundance (Kremen et al. 2002). I suggest that the numerous uncommon specialist pollinators within IVM networks are aggregately increasing functional redundancy and buffering against plant species extinctions. Individual losses of these species may only have small impacts on network structure, but their combined loss following disturbance may be severely affecting the ability of networks to resist disassembly following future extinctions.

Certain pollinator species were critically important for the functioning and cohesiveness of the networks beyond what would be expected by their interaction frequency alone. As a result of being highly connected within and/or among modules, many species were identified as module hubs, connectors, and network hubs. Bee species were the most likely to be identified as keystones in the networks. Given their high abundance, visitation frequency and known pollinating effectiveness (Jauker et al. 2012; Orford et al. 2015) it is clear that these bee species were critical in supporting the structure of the networks and maintaining their stability. Several syrphid species, as well as some bombyliids, were also identified through this process – highlighting the importance of flies in maintaining stable provisioning of pollination services. Many fly species have been identified as important pollinators in various systems due to their high abundance, visitation frequencies, and pollen loads (Elberling and Olesen 1999; Larson et al. 2001; Jauker and Wolters 2008; Orford et al. 2015). My results reveal that beyond the high visitation frequencies I observed, several fly species are particularly important due to how they connect species and compartments of a network with each other. In contrast, most wasp species were identified as peripheral in the networks except for a few species. This was predictable since I determined that wasps were, with the exception of Dolichovespula arenaria (Fabricius), infrequent floral visitors due to their primarily carnivorous diet. It is surprising that two Chelonus (Braconidae) morphospecies were identified as module connectors in two of my networks. However, I hesitate to consider them truly impactful towards network cohesiveness given their apparent low pollination effectiveness - their parasitoid lifestyle, small body size and absence of hairs likely makes them pollen/nectar thieves rather than pollinators. In a similar fashion, I hesitate to identify any Hylaeus (Colletidae) species as a true keystone given that they store pollen in their crop and therefore carry little to no pollen grains on their exterior (Michener 2007). Plant-pollinator interactions generally promote sexual reproduction for both trophic levels. Pollinator reproduction is benefited through the intake of energy (from nectar) and nutrients (from pollen), while plant reproduction is aided by the transferral and deposition of monospecific pollen grains. Keystone species in one trophic level are responsible for promoting and maintaining rich and abundant assemblages in the other level by enhancing their survival and reproductive success. This in turn will have cascading effects, benefiting the entire system. For instance, a connector plant species plays an important role in attracting and maintaining a healthy, biodiverse pollinator community, which in turn allows for more specialized or less abundant plant species to persist. Connector species therefore promote the

nestedness and functional redundancy within a network, while module hubs promote modularity and functional complementarity in the system. In a pollination web, species which do not positively contribute towards the reproductive success of their interaction partners (such as pollen/nectar thieves) should only be considered peripherals, no matter the pattern of interactions.

The networks roles that the various pollinator and plant species played were not consistent through space. Although a few pollinator species such as *Bombus ternarius* were consistently identified as keystones throughout the latitudinal gradient, the identity of their role was variable. Species could act as a module hub in certain networks but would be connectors or simply peripherals in other sites. Most species were identified as keystones only in one or two networks and were peripheral in the rest. Microscopic network features such as species' roles are highly variable both across space and time (Trøjelsgaard and Olesen 2013). My results follow this trend, showing a strong variability in species' roles across the latitudinal gradient. Spatially common, abundant generalist pollinators were more likely to be identified as keystone species across multiple networks, highlighting their importance in maintaining the cohesiveness of networks across space. However, due to the known variability in species' roles across time, I suggest that the importance of various species within the powerline ROW should be determined through multiple years of data collection, rather than a single summer season. This information could be very useful for eventual targeted plant or pollinator surveys and conservation strategies within the ROW.

Introduced Species

Although native pollinator and plant species greatly outnumbered invasive species in the surveyed powerline ROW, a few invasives were highly abundant and had a strong impact on the pollination networks. Most pollinator species were native, but introduced species such as *Andrena wilkella* (Kirby), *Apis mellifera* L., *Megachile rotundata* (Fabricius) were also observed foraging within the ROW. *Megachile rotundata*, the alfalfa leafcutter bee was involved in 3% of all observed interactions. A semi-domesticated introduced species, its involvement in the ROW networks was dependent on the presence of alfalfa and rapeseed fields, and associated artificial bee nests, in the surrounding landscape. This was the case in the LBs ecoclimatic region, where most *M. rotundata* individuals were sampled. Within this region, I identified this bee as a keystone species in three networks, acting as a module hub or connector in two, and as a network hub in the

third. This introduced species was therefore having a critical impact on the structure of the networks in which it was present. Invasive species tend to be highly generalized, and due to the absence of co-evolved enemies often can become highly abundant in the invaded areas (Stout and Morales 2009; Aslan 2019). Resource overlap between native and introduced bee species can have detrimental effects on the natives due to competitive pressures (Kearns et al. 1998; Stout and Morales 2009). The effects of invasive pollinator species on native plant/pollinator biodiversity and network structure are beyond the scope of this study. Nonetheless, I suggest that future studies should investigate the impact of *M. rotundata* on pollination networks within ROWs to evaluate whether this species can aid or limit pollination services in these anthropogenic systems. I hypothesize that the competitive pressure of *M. rotundata* on native bees is less intense than that of *Apis mellifera* since the leafcutter bee is a solitary species and thus is generally less abundant and requires much less pollen and nectar to reproduce.

A few invasive flowering plant species such as Sonchus arvensis L., Cirsium arvense (L.), and *Melilotus albus* Medikus were very abundant within the powerline ROW and were highly involved in the observed plant-pollinator interactions. Other studies have also reported high cover of invasive plants within powerline ROWs (Rubino et al. 2002; Leston and Koper 2016, 2017). Sonchus arvsensis, for instance, was the second most abundant plant sampled in the surveyed ROW in terms of ground cover, only surpassed by the native flowering shrub Dasiphora fruticosa (L.). Sonchus arvensis was also the plant species that participated in the greatest number of plantpollinator interactions and had the third greatest pollinator biodiversity. This is a clear example of how invasive plants can become dominant in local pollination networks. These plants are often highly attractive to pollinators due to their large and colourful floral displays, accessible flower morphology and copious nectar production (Bjerknes et al. 2007). Furthermore, invasive plants can become highly successful in invaded areas due to their often generalist nature and to the absence of natural enemies (Bjerknes et al. 2007; Stout and Morales 2009; Aslan 2019). My analyses revealed that some of these invasive plant species were also playing key roles in the networks. Sonchus arvensis, Melilotus albus and Trifolium hybridum L. were identified as module hubs in three separate networks, while Medicago sativa L. was a connector species in another. These highly abundant, generalist plants connect multiple species and compartments of the network in such a way that they have become critical for the cohesiveness and stability of the system they have invaded. Invasive plants can increase the functional redundancy within

pollination networks and may therefore increase robustness (Albrecht et al. 2014; Aslan 2019). However, they tend not to partner with native specialist pollinators and thus fail to support the resiliency of native species assemblages (Aslan 2019). Although I did not evaluate the effects of invasive plants on the local biodiversity and pollination network robustness, I have determined that a few alien plants were highly abundant in the surveyed ROW and have become fully integrated in the networks, even contributing significantly to maintaining the cohesiveness of the system.

Implications for Management

My results show that powerline easements in Manitoba are acting as habitat for a many pollinator species by providing abundant and diverse floral resources, which are often lacking in the province's intensively farmed or densely forested landscapes. This agrees with previous studies which have found powerline easements to host biodiverse insect communities as well as rare and stenotopic species (Swengel 1996; Smallidge et al. 1996; Lanham and Nichols 2000b; Forrester et al. 2005; Russell et al. 2005, 2018; Lensu et al. 2011; Wagner et al. 2014a, 2019; Hill and Bartomeus 2016; Leston and Koper 2016, 2017; Steinert et al. 2020). I also found that powerline ROW vegetation management can affect the capacity for this habitat to support biodiverse pollinator communities. IVM strategies involve selectively removing tall-growing woody plant species via targeted manual and herbicidal control, while leaving the understory intact (Russell et al. 2018). These practices allowed the ROW to host greater biodiversity of pollinators as well as more robust pollination networks. Other studies also report on the beneficial effects of targeted cutting and spraying, rather than mowing or untargeted, high-volume herbicidal application, on pollinator biodiversity (Wojcik and Buchmann 2012; Berg et al. 2013; Russell et al. 2018; Steinert et al. 2020; Russo et al. 2021). In general, promoting a rich and abundant floral community is the best way to promote pollinator biodiversity within powerline ROWs (Wojcik and Buchmann 2012), my results confirm this, and also show that increasing plant cover will enhance pollination network robustness. Based on my results and previous studies (Hopwood 2008; Moroń et al. 2014), it seems that a greater amount of exposed ground within ROWs can boost bee richness as well. Increasing the amount of exposed ground may allow powerline ROWs to become nesting sites for ground-nesting insects, including many bee species, and thus become a source of pollinators in the landscape.

Overall, local variables had a greater impact on pollinators in the ROW than landscape factors. Many pollinator species are small-bodied with low dispersal capabilities, therefore local factors tend to be more influential than the landscapes surrounding the ROW (Moroń et al. 2014). This is encouraging because it indicates that targeted management practices can have positive effects regardless of the land surrounding the easement. For instance, site 4 was located in the GT region and was surrounded by an intensely farmed, homogeneous landscape. However, it was managed with IVM practices and hosted a relatively high floral biodiversity. Consequently, site 4 hosted a significant pollinator biodiversity forming the third largest network of all (Figure S4). This network was also highly specialized, modular, and was among the most robust of all (Table 19). On the other hand, site 13, within the MBs region, was surrounded by natural habitat and located within a heterogeneous landscape. Despite this being an IVM site, it had been managed recently and hosted both the lowest plant richness and cover of any site. Even though this site hosted a large network, the web had relatively low modularity and was among the least robust to the random simulation of plant extinctions. Therefore, my results show that high diversity and cover of flowering plants is a key factor, strongly influencing pollinator biodiversity and network stability. A combination of IVM practices and a more biodiverse floral community allowed the powerline easement to host larger pollination networks with a greater number of rare species and specialist-specialist interactions. These networks were more specialized, modular, and less dependent on a few generalist species, allowing them to be more robust.

Conservation efforts aim at preserving biodiversity and ecosystem services. However, if rare species and specialists contribute little to ecosystem functioning, yet are those most in need of protection, then trade-offs may exist for these contrasting objectives (Dee et al. 2019). My study has revealed that these objectives work together in my system and are not exclusive. I observed that generalist species were responsible for a large proportion of floral visits and played important roles in the networks by connecting species within a module with each other and linking modules together. However, I also determined that larger networks hosting a greater number of rare and specialist species were more robust, probably due to the greater trait diversity and functional redundancy brought by these species. Specialist species aggregately contributed significantly to maintaining ecosystem stability. Therefore, conservation practices aimed at increasing pollinator biodiversity and preserving rare and specialist species within the ROW will also boost the stability of the networks and the provisioning of pollination services. Although pollinators were most strongly affected by local factors, my results also revealed that powerline sites located within landscapes with greater heterogeneity hosted lower pollinator biodiversity. This however was dependent on the region and dominant cover type in the landscape. Therefore, if the goal is to increase the value of powerline easements to existing pollinator populations, efforts to improve ROW habitat quality should focus on easements within landscapes with a greater diversity of natural and semi-natural habitats (as opposed to a greater diversity of disturbed land-use types). However, these landscapes would already contain abundant and diverse foraging and nesting resources for pollinators. Instead, I suggest focusing management efforts in powerline ROWs within homogeneous landscapes dominated by anthropogenic activity. This would promote pollinator conservation in areas where their required nesting and foraging resources are otherwise severely lacking.

Considerations for Future Studies

The small sample size of this study reduces the statistical power of some analyses and the ability to determine the significance of certain effects. Concurrently, the large amount of measured environmental variables included in the models makes it difficult to disentangle some of the effects, such as those of management and ecoclimatic region. The large sampling effort required to build ecological networks, and the limited resources at my disposal precluded me from having a greater number of sampling sites. Additionally, this research was based on an observational study design, while some of the questions I explored would require an experimental setup to be fully understood. These factors do not allow me to draw definitive conclusions from my GLMM and ANOVA models. The results from this study should rather be interpreted as indications of what environmental factors positively influence pollinator biodiversity and network stability within powerline ROWs. Experimental design studies should be conducted in the future to be able to fully determine causality between independent and response variables. A study exploring the effect of vegetation management on pollinator biodiversity (and networks) within powerline ROWs - for example - should have an equal number of study sites per category, should be performed over multiple separate easements, and control for regional variations of measured variables. Furthermore, I recommend collecting data over multiple years rather than a single sampling season given the high temporal stochasticity of biodiversity and microscopic network features such as species' roles. Nevertheless, the results from this study allow us to draw some insights on the

conservation potential of powerline ROWs, as well as on various management practices that can help maintain stable and biodiverse pollinator communities in these corridors.

3.5 Conclusion

The surveyed powerline ROW in Manitoba is acting as an early-successional habitat for a significant component of the region's pollinator biodiversity. The corridor provides abundant and diverse floral resources for foraging bees, wasps and flies, and may also act as a nesting site for many bee species by providing them with ample amounts of exposed ground and plant stems. ROWs may be playing a role in the conservation of local pollinator biodiversity within Manitoba's agricultural and forested landscapes. I showed that vegetation management practices in the corridor have strong effects on the pollinator biodiversity as well as the pollination network structure and robustness. Sites managed using integrated vegetation management techniques hosted more abundant and diverse pollinator communities. These communities formed pollination networks that were less connected and nested, but more modular and specialized due to a greater number of specialist-specialist links. IVM networks were the most robust towards random plant species extinction simulations in part due to a reduced reliance on few abundant super-generalist species and to the aggregate functional redundancy from uncommon specialist species which slowed down the rate of network disassembly. Pollinators responded more strongly to local plant variables (richness and cover) than to the surrounding landscape composition and configuration. Management practices (such as sowing of native wildflowers) in the ROW can therefore have important positive impacts on pollinator biodiversity and network structure regardless of the surrounding landscape. Invasive plants in the ROW are well-integrated in the pollination networks and are partially responsible for maintaining the cohesiveness and stability of the invaded systems. Land managers should be cautious if they plan to remove invasive species unless they can be replaced with native plants that can take over similar network roles.

Transmission line rights-of-way are an inevitable, permanent aspect of modern landscapes, and as energy demand increases everywhere their global network will keep expanding. As natural habitats continue to disappear, we must consider alternative ways to conserve wildlife and explore all potential approaches that would allow us to coexist with ecosystems rather than supplant them. Powerline ROWs occupy land which is continuously maintained in an early-successional state and is precluded from further development. Applying informed vegetation management practices to these corridors can allow us to simultaneously meet our energy transportation demands and preserve pollinator biodiversity and pollination services within anthropogenic systems.

3.6 Appendix

Table S4. Abundance of all identified pollinator species. Abbreviations were used for the creation of the bipartite network graphs.

Species	Abbreviation	Author	Abundance
Andrenidae			110
Andrena algida	And.alg	Smith 1853	2
Andrena barbilabris	And.bar	(Kirby 1802)	1
Andrena chromotricha	And.chr	Cockerell 1899	8
Andrena cressonii	And.cre	Robertson 1891	5
Andrena hirticincta	And.hir	Provancher 1888	8
Andrena lupinorum	And.lup	Cockerell 1906	1
Andrena miranda	And.mir	Smith 1879	6
Andrena nubecula	And.nub	Smith 1853	4
Andrena persimulata	And.per	Viereck 1917	1
Andrena robervalensis	And.rob	Mitchell 1960	5
Andrena thaspii	And.tha	Graenicher 1903	1
Andrena wilkella	And.wil	(Kirby 1802)	38
Andrena w-scripta	And.w-s	Viereck 1904	1
Andrena ziziae	And.ziz	Robertson 1891	7
Calliopsis coloradensis	Cal.col	Cresson 1878	1
Protandrena aestivalis	Pro.aes	(Provancher 1882)	1
Protandrena albitarsis	Pro.alb	(Cresson 1872)	5
Protandrena piercei albertensis	Pro.irr	(Cockerell 1922)	11
Protandrena parvus	Pro.par	(Robertson 1892)	2
Protandrena renimaculatus	Pro.ren	(Cockerell 1896)	2
Apidae			836
Anthophora terminalis	Ant.ter	Cresson 1869	45
Apis mellifera	Api.mel	Linnaeus 1758	1
Bombus bimaculatus	Bom.bim	Cresson 1863	2
Bombus borealis	Bom.bor	Kirby 1837	8
Bombus flavidus	Bom.fer	(Franklin 1911)	3
Bombus fervidus	Bom.fern	(Fabricius 1798)	3
Bombus frigidus	Bom.fri	Smith 1854	5
Bombus griseocollis	Bom.gri	(DeGeer 1773)	16
Bombus melanopygus	Bom.mel	Nylander 1848	2
Bombus perplexus	Bom.per	Cresson 1863	2

Bombus rufocinctus	Bom.ruf	Cresson 1863	58
Bombus sandersoni	Bom.san	Franklin 1913	104
Bombus sylvicola	Bom.syl	Kirby 1837	2
Bombus ternarius	Bom.ter	Say 1837	397
Bombus terricola	Bom.terri	Kirby 1837	17
Bombus vagans	Bom.vag	Smith 1854	48
Ceratina dupla	Cer.dup	Say 1837	1
-	_	Rehan and Sheffield	
Ceratina mikmaqi	Cer.mik	2011	33
Epeolus minimus	Epe.min	(Robertson 1902)	7
Melissodes agilis	Mel.agi	Cresson 1878	1
Melissodes confusus	Mel.con	Cresson 1878	14
		Lovell and Cockerell	
Melissodes illatus	Mel.ill	1906	35
Melissodes trinodis	Mel.tri	Robertson 1901	2
Melissodes wheeleri	Mel.whe	Cockerell 1906	11
Nomada aquilarum	Nom.aqu	Cockerell 1903	7
		Lovell and Cockerell	
Nomada florilega	Nom.flo	1905	3
Nomada quadrimaculata	Nom.qua	Robertson 1903	3
Nomada vincta	Nom.vin	Say 1837	1
Triepeolus cf. grindeliae	Tri.gri	Cockerell 1907	1
Triepeolus obliteratus	Tri.obl	Graenicher 1911	4
Bombyliidae			260
Anastoechus barbatus	Ana.bar	Osten Sacken 1877	1
Anthrax irroratus	Ant.irr	Say 1823	1
Bombylius incanus	Bom.inc	Johnson 1907	2
Hemipenthes morio	Hem.mor	(Linnaeus 1758)	5
Hemipenthes sinuosus	Hem.sin	(Wiedemann 1821)	3
Lepidophora lutea	Lep.lut	Painter 1962	2
Poecilanthrax alcyon	Poe.alc	(Say 1824)	19
Poecilanthrax tegminipennis	Poe.teg	(Say 1824)	21
Systoechus vulgaris	Sys.vul	Loew 1863	68
Villa alternata			
Vill - f. l	Vil.alt	Say 1823	4
ν πα fuiviana	Vil.alt Vil.ful	Say 1823 (Say 1824)	4 62
Villa fulviana Villa lateralis	Vil.alt Vil.ful Vil.lat	Say 1823 (Say 1824) (Say 1823)	4 62 67
Villa fulviana Villa lateralis Villa nigra	Vil.alt Vil.ful Vil.lat Vil.nig	Say 1823 (Say 1824) (Say 1823) Cresson 1916	4 62 67 5
Villa fulviana Villa lateralis Villa nigra Braconidae	Vil.alt Vil.ful Vil.lat Vil.nig	Say 1823 (Say 1824) (Say 1823) Cresson 1916	4 62 67 5 71
Villa fulviana Villa lateralis Villa nigra Braconidae Chelonus sp.ChA	Vil.alt Vil.ful Vil.lat Vil.nig	Say 1823 (Say 1824) (Say 1823) Cresson 1916	4 62 67 5 <u>71</u> 39
Villa fulviana Villa lateralis Villa nigra Braconidae Chelonus sp.ChA Chelonus sp.ChB	Vil.alt Vil.ful Vil.lat Vil.nig sp.ChA sp.ChB	Say 1823 (Say 1824) (Say 1823) Cresson 1916	4 62 67 5 71 39 21
Villa fulviana Villa lateralis Villa nigra Braconidae Chelonus sp.ChA Chelonus sp.ChB Chelonus sp.ChC	Vil.alt Vil.ful Vil.lat Vil.nig sp.ChA sp.ChB sp.ChC	Say 1823 (Say 1824) (Say 1823) Cresson 1916	4 62 67 5 71 39 21 5

Chelonus sp.ChD	sp.ChD		6
Colletidae			268
Colletes brevicornis	Col.bre	Robertson 1897	3
Colletes hyalinus	Col.hya	Provancher 1888	22
Colletes kincaidii	Col.kin	Cockerell 1898	3
Colletes simulans	Col.sim	Cresson 1868	13
Hylaeus affinis	Hyl.aff	(Smith 1853)	117
Hylaeus annulatus	Hyl.ann	(Linnaeus 1758)	15
Hylaeus basalis	Hyl.bas	(Smith 1853)	6
Hylaeus mesillae	Hyl.mes	(Cockerell 1896)	52
Hylaeus modestus	Hyl.mod	Say 1837	36
Hylaeus verticalis	Hyl.ver	(Cresson 1869)	1
Conopidae			6
Physocephala furcillata	Phy.fur	(Williston 1882)	6
Crabronidae			71
sp.PB	sp.PB		1
Cerceris nigrescens	Cer.nig	Smith 1856	3
Diodontus minutus	Dio.min	(Fabricius 1793)	1
Ectemnius arcuatus	Ect.arc	(Say 1837)	6
Ectemnius borealis	Ect.bor	(Zetterstedt 1838)	2
		(Lepeletier and Brulle	
Ectemnius dives	Ect.div	1834)	3
Ectemnius lapidarius	Ect.lap	(Panzer 1804)	3
Ectemnius maculosus	Ect.mac	(Gmelin 1790)	6
Ectemnius ruficornis	Ect.ruf	(Zetterstedt 1838)	2
Ectemnius trifasciatus	Ect.tri	(Say 1824)	5
Gorytes atricornis	Gor.atr	Packard 1867	1
Larropsis sp.LA	Larr.spLA		1
Larropsis sp.LB	Larr.spLB		4
Lestica producticollis	Les.pro	(Packard 1866)	24
Oxybelus emarginatus	Oxy.ema	Say 1837	2
Pemphredon sp.PA	sp.PA	C 10.75	3
Philanthus bilunatus	Phil.bil	Cresson 1865	4
Gasteruptiidae			6
Gasteruption assectator	Gas.ass	(Linnaeus 1758)	6
Halictidae			310
Augochlorella aurata	Aug.aur	(Smith 1853)	22
Dufourea harveyi	Duf.har	(Cockerell 1906)	9

Dufourea maura	Duf.mau	(Cresson 1878)	9
Halictus confusus	Hal.con	Smith 1853	38
Halictus ligatus	Hal.lig	Say 1837	1
Halictus rubicundus	Hal.rub	(Christ 1791)	39
Lasioglossum albipenne	Las.alb	(Robertson 1890)	8
Lasioglossum athabascense	Las.ath	(Sandhouse 1933)	3
, and the second s		(Knerer and Atwood	
Lasioglossum comagenense	Las.coma	1964)	2
Lasioglossum immigrans	Las.com	Gardner 2021	1
Lasioglossum coriaceum	Las.cor	(Smith 1853)	4
Lasioglossum cressonii	Las.cre	(Robertson 1890)	7
Lasioglossum ephilatum	Las.eph	Gibbs 2010	3
Lasioglossum inconditum	Las.inc	(Cockerell 1916)	1
Lasioglossum laevissimum	Las.lae	(Smith 1853)	36
Lasioglossum leucocomum	Las.leu	(Lovell 1908)	10
Lasioglossum leucozonium	Las.leucoz	(Schrank 1781)	12
Lasioglossum nigroviride	Las.nig	(Graenicher 1911)	1
Lasioglossum novascotiae	Las.nov	(Mitchell 1960)	2
Lasioglossum oblongum	Las.obl	(Lovell 1905)	4
Lasioglossum paraforbesii	Las.par	McGinley 1986	3
Lasioglossum perpunctatum	Las.per	(Ellis 1913)	4
Lasioglossum planatum	Las.pla	(Lovell 1905)	37
Lasioglossum quebecense	Las.que	(Crawford 1907)	1
Lasioglossum seillean	Las.sei	Gibbs and Packer 2013	4
Lasioglossum subversans	Las.subve	(Mitchell 1960)	1
Lasioglossum subviridatum	Las.sub	(Cockerell 1938)	5
Lasioglossum versans	Las.ver	(Lovell 1905)	2
Lasioglossum viridatum	Las.vir	(Lovell 1905)	30
Lasioglossum zonulum	Las.zon	(Smith 1848)	6
Sphecodes clematidis	Sph.cle	Robertson 1897	2
Sphecodes coronus	Sph.cor	Mitchell 1956	2
Sphecodes dichrous	Sph.dic	Smith 1853	1
Megachilidae			750
Anthidium chinaodantatum	Ant cly	Swenk 1914	2

Anthidium clypeodentatum	Ant.cly	Swenk 1914	2
Coelioxys modestus	Coe.mod	Smith 1854	2
Coelioxys moestus	Coe.moe	Cresson 1864	5
Coelioxys porterae	Coe.por	Cockerell 1900	2
Coelioxys rufitarsis	Coe.ruf	Smith 1854	15
Coelioxys sodalis	Coe.sod	Cresson 1878	3
Dianthidium pudicum	Dia.pud	(Cresson 1879)	3
Heriades carinata	Her.car	Cresson 1864	51
Heriades variolosa	Her.var	(Cresson 1872)	84

Hoplitis albifrons	Hop.alb	(Kirby 1837)	5
Hoplitis pilosifrons	Hop.pil	(Cresson 1864)	12
Hoplitis producta	Hop.pro	(Cresson 1964)	15
Hoplitis spoliata	Hop.spo	(Provancher 1888)	10
Hoplitis truncata	Hop.tru	(Cresson 1878)	1
Megachile campanulae	Meg.cam	(Robertson 1903)	6
Megachile frigida	Meg.fri	Smith 1853	27
Megachile gemula	Meg.gem	Cresson 1878	6
Megachile inermis	Meg.ine	Provancher 1888	42
Megachile lapponica	Meg.lap	Thomson 1872	6
Megachile latimanus	Meg.lat	Say 1823	59
Megachile melanophaea	Meg.mel	Smith 1853	8
Megachile montivaga	Meg.mon	Cressom 1878	1
Megachile perihirta	Meg.per	Cockerell 1989	4
Megachile pugnata	Meg.pug	Say 1837	8
Megachile relativa	Meg.rel	Cresson 1878	136
Megachile rotundata	Meg.rot	(Fabricius 1787)	147
Osmia atriventris	Osm.atr	Cresson 1864	11
Osmia bucephala	Osm.buc	Cresson 1864	5
Osmia inermis	Osm.ine	(Zetterstedt 1838)	33
Osmia nigriventris	Osm.nig	(Zetterstedt 1838)	1
Osmia proxima	Osm.pro	Cresson 1864	20
Osmia simillima	Osm.sim	Smith 1853	10
Osmia subaustralis	Osm.sub	Cockerell 1900	2
Osmia tersula	Osm.ter	Cockerell 1912	5
Stelis foederalis	Ste.foe	Smith 1854	2
Stelis nitida	Ste.nit	Cresson 1878	1
Melittidae			48
Macropis nuda	Mac.nud	(Provancher 1882)	48
Perilampidae			7
sp. PeA	sp. PeA		2
Perilampus hyalinus	Per.hya	Say 1829	5
Sphecidae			33
Ammophila azteca	Amm.azt	Cameron 1888	18
Podalonia luctuosa	Pod.luc	(Smith 1856)	1
Prionyx atratus	Pri.atr	(Lepeletier 1845)	5
Prionyx canadensis	Pri.can	(Provancher 1887)	9
Stratiomyidae			86
Hedriodiscus binotatus	Hed.bin	(Loew 1866)	31

Hedriodiscus vertebratus	Hed.ver	(Say 1824)	14
Odontomyia hirtocculata	Odo.hir	James 1936	5
Odontomyia pubescens	Odo.pub	Day 1882	7
Stratiomys badia	Str.bad	Walker 1842	9
Stratiomys obesa	Str.obe	(Loew 1866)	2
Stratiomys sp.1	Str.sp1		16
Stratiomys sp.2	Str.sp2		2
Syrphidae			1748
Allograpta obliqua	All.obl	(Say 1823)	4
Chalcosyrphus inarmatus	Cha.ina	(Hunter 1897)	1
Cheilosia latrans	Che.lat	Walker 1849	1
Cheilosia shannoni	Che.sha	Curran 1923	13
Chrysotoxum flavifrons	Chr.fla	Macquart 1842	3
Chrysotoxum plumeum	Chr.plu	Johnson 1924	2
Epistrophe emarginata	Epi.ema	(Say 1823)	2
Epistrophe grossulariae	Epi.gro	(Meigen 1822)	1
Eristalis anthophorina	Eri.ant	(Fallen 1817)	1
Eristalis dimidiata	Eri.dim	Wiedemann 1830	406
Eristalis flavipes	Eri.fla	Walker 1849	4
Eristalis interrupta	Eri.int	(Poda 1761)	63
Eristalis stipator	Eri.sti	Osten Sacken 1877	29
Eristalis tenax	Eri.ten	(Linnaeus 1758)	2
Eristalis transversa	Eri.tra	Wiedemann 1830	12
Eupeodes americanus	Eup.ame	(Wiedemann 1830)	6
Eupeodes luniger	Eup.lun	(Meigen 1822)	1
Eurimyia stipata	Eur.sti	(Walker 1849)	3
Helophilus fasciatus	Hel.fas	Walker 1849	254
Helophilus hybridus	Hel.hyb	Loew 1846	25
Helophilus latifrons	Hel.lat	Loew 1863	10
Helophilus obscurus	Hel.obs	Loew 1863	1
Heringia canadensis	Her.can	Curran 1921	10
Lapposyrphus lapponicus	Lap.lap	(Zetterstedt 1838)	8
Meligramma triangulifera	Mel.tria	(Zetterstedt 1843)	1
Neoascia tenur	Neo.ten	(Harris 1780)	1
Neocnemodon sp.	Neoc		3
Neocnemodon elongata		(Curran 1921)	1
Neocnemodon rita		(Curran 1921)	4
Ocyptamus fascipennis	Ocy.fas	(Wiedemann 1830)	5
Orthonevra nitida	Ort.nit	(Wiedemann 1830)	1
Paragus angustifrons	Par.ang	Loew 1863	11
Paragus haemorrhous	Par.hae	Meigen 1822	31
Parasyrphus nigritarsis	Par.nig	(Zetterstedt 1843)	1

Platycheirus immarginatus	Pla.imm	(Zetterstedt 1849)	2
Platycheirus inversus	Pla.inv	Ide 1926	1
Sericomyia lata	Ser.lat	(Coquillett 1907)	5
Sericomyia militaris	Ser.mil	(Walker 1849)	2
Sphaerophoria asymmetrica	Sph.asy	Knutson 1972	1
Sphaerophoria brevipilosa	Sph.bre	Knutson 1972	9
Sphaerophoria contigua	Sph.con	Macquart 1847	9
Sphaerophoria philanthus	Sph.phi	(Meigen 1822)	43
Spilomyia sayi	Spi.say	(Goot 1964)	2
Syritta pipiens	Syr.pip	(Linnaeus 1758)	89
Syrphus rectus	Syr.rec	Osten Sacken 1875	5
Syrphus ribesii	Syr.rib	(Linnaeus 1758)	134
Syrphus torvus	Syr.tor	Osten Sacken 1875	2
Syrphus vitripennis	Syr.vit	Meigen 1822	2
Temnostoma barberi	Tem.bar	Curran 1939	1
Temnostoma excentrica	Tem.exc	(Harris 1841)	1
Toxomerus geminatus	Tox.gem	(Say 1823)	63
Toxomerus marginatus	Tox.mar	(Say 1823)	388
Tropidia quadrata	Tro.qua	(Say 1824)	45
Xylota annulifera	Xyl.ann	Bigot 1884	8
Xylota confusa	Xyl.con	Shannon 1926	4
Xylota flavifrons	Xyl.fla	Walker 1849	2
Xylota flavitibia	Xyl.flavtib	Bigot 1884	1
Xylota naknek	Xyl.nak	Shannon 1926	8
Vespidae			348
Ancistrocerus adiabatus	Anc.adi	(de Saussure 1852)	2
Ancistrocerus albophaleratus	Anc.alb	(de Saussure 1855)	2
Ancistrocerus antilope	Anc.ant	(Panzer 1798)	3
Ancistrocerus catskill	Anc.cat	(de Saussure 1853)	6
Ancistrocerus waldenii	Anc.wal	(Viereck 1906)	1
Dolichovespula adulterina	Dol.adu	(de Buysson 1905)	1
Dolichovespula arenaria	Dol.are	(Fabricius 1775)	246
Dolichovespula maculata	Dol.mac	(Linnaeus 1763)	31
Dolichovespula norvegicoides	Dol.nor	(Sladen 1918)	2
Eumenes crucifera	Eum.cru	Provancher 1888	15
Euodynerus foraminatus	Euo.for	(de Saussure 1853)	3
Euodynerus leucomelas	Euo.leu	(de Saussure 1855)	1
Euodynerus planitarsis	Euo.pla	(Bohart 1945)	6
Odynerus dilectus	Ody.dil	de Saussure 1870	1
Parancistrocerus pensylvanicus	Par.pen	(de Saussure 1855)	7
Polistes fuscatus	Pol.fus	(Fabricius 1793)	2
Stenodynerus anormis	Ste.ano	(Say 1824)	6

Stenodynerus kennicottianus	Ste.ken	(de Saussure 1870)	1
Vespula consobrina	Ves.con	(de Saussure 1864)	10
Vespula vidua	Ves.vid	(de Saussure 1854)	1
Vespula vulgaris	Ves.vul	(Linnaeus 1758)	1
Total			4958

Table S5. Number of links observed for each plant species in the networks. Abbreviations were used to create bipartite graphs.

Species	Abbreviation	Author	Links
Achillea millefolium	Ach.mil	Linnaeus	89
Agoseris glauca	Ago.gla	(Pursh) Rafinesque	16
Allium stellatum	All.ste	Fraser	2
Anemonastrum canadense	Ane.can	(Linnaeus) Mosyakin	32
Anticlea elegans	Ant.ele	(Pursh) Rydberg	23
Apocynum androsaemifolium	Apo.and	Linnaeus	181
Astragalus laxmannii	Ast.lax	Jacquin	4
Brassica napus	Bra.nap	Linnaeus	7
Campanula rotundifolia	Cam.rot	Linnaeus	105
Carum carvi	Car.car	Linnaeus	29
Chamaenerion angustifolium	Cha.ang	(Linnaeus) Holub	65
Cicuta maculata	Cic.mac	Linnaeus	10
Cirsium arvense	Cir.arv	(Linnaeus) Scopoli	386
Cirsium flodmanii	Cir.flod	(Rydberg) Arthur	49
Cirsium muticum	Cir.mut	Michaux	3
Cirsium vulgare	Cir.vul	(Savi) Tenore	20
	Cre.run	(E. James) Torrey & A.	
Crepis runcinata		Gray	24
Dasiphora fruticosa	Das.fru	(Linnaeus) Rydberg	432
Drymocallis arguta	Dry.arg	(Pursh) Rydberg	6
Erigeron glabellus	Eri.gla	Nuttall	41
Erigeron pulchellus	Eri.pul	Michaux	4
Erigeron strigosus	Eri.str	Muhlenberg	15
Euthamia graminifolia	Eut.gra	(Linnaeus) Nuttall	100
Gaillardia aristata	Gai.ari	Pursh	11
Galium boreale	Gal.bor	Linnaeus	26
Gentianopsis crinita	Gen.cri	(Froelich) Ma	1
Grindelia squarrosa	Gri.squ	(Pursh) Dunal	56
Helianthus maximiliani	Hel.max	Schrader	45
Helianthus pauciflorus	Hel.pau	Nuttall	1
Heuchera richardsonii	Heu.ric	R. Brown	1
Hieracium umbellatum	Hie.umb	Linnaeus	133

Hypoxis hirsuta	Hyp.hir	(Linnaeus) Coville	2
Mulgedium pulchellum	Lac.tat	(Pursh) G. Don	39
Lathyrus palustris	Lat.pal	Linnaeus	7
Leucanthemum vulgare	Leu.vul	Lamarck	72
0	Lia.lig	(A. Nelson) K.	
Liatris ligulistylis		Schumann	20
Linum lewisii	Lin.lew	Pursh	4
Lobelia spicata	Lob.spi	Lamarck	4
Lotus corniculatus	Lot.cor	Linnaeus	14
Lysimachia ciliata	Lys.cil	Linnaeus	19
Medicago sativa	Med.sat	Linnaeus	25
Melilotus albus	Mel.alb	Medikus	306
Melilotus officinalis	Mel.off	(Linnaeus) Lamarck	33
Mentha canadensis	Men.can	Linnaeus	74
Monarda fistulosa	Mon.fis	Linnaeus	48
Nabalus albus	Nab.alb	(Linnaeus) Hooker	6
	Pac.pau	(Michaux) A. Löve & D.	
Packera paupercula		Löve	23
Pedicularis lanceolata	Ped.lan	Michaux	1
Polygala senega	Pol.sen	Linnaeus	3
Potentilla anserina	Arg.ans	Linnaeus	4
Prunella vulgaris	Pru.vul	Linnaeus	93
Rosa woodsii	Ros.woo	Lindley	30
Rudbeckia hirta	Rud.hir	Linnaeus	81
Sanicula marilandica	San.mar	Linnaeus	19
Solidago canadensis	Sol.can	Linnaeus	206
Solidago gigantea	Sol.gig	Aiton	135
Solidago hispida	Sol.his	Muhlenberg	72
Solidago juncea	Sol.jun	Aiton	12
Solidago nemoralis	Sol.nem	Aiton	215
-	Sol.pta	(Torrey & A. Gray) B.	
Solidago ptarmicoides		Bovin	102
Solidago rigida	Sol.rig	Linnaeus	167
Solidago sp. x	Sol.sp.		35
Sonchus arvensis	Son.arv	Linnaeus	472
Spiraea alba	Spi.alb	Du Roi	13
Stachys palustris	Sta.pal	Linnaeus	14
Symphoricarpos occidentalis	Sym.occ	Hooker	107
	Sym.cil	(Lindley) A. Löve & D.	
Symphyotrichum ciliolatum		Löve	9
Symphyotrichum ericoides	Sym.eri	(Linnaeus) G. L. Neson	132
	Sym.lae	(Linnaeus) A. Löve &	
Symphyotrichum laeve		D. Löve	163

	Sum.lan	(Willdenow) G. L.	
Symphyotrichum lanceolatum		Neson	94
	Sym.lat	(Linnaeus) A. Löve &	
Symphyotrichum lateriflorum		D. Löve	5
Taraxacum officinale	Tar.off	F. H. Wiggers	6
Trifolium hybridum	Tri.hyb	Linnaeus	41
Trifolium pratense	Tri.prat	Linnaeus	36
Trifolium repens	Tri.rep	Linnaeus	1
Vicia americana	Vic.ame	Muhlenberg	2
Vicia villosa	Vic.vil	Roth	3
Zizia aptera	Ziz.apt	(A. Gray) Fernald	19
-	Ziz.aur	(Linnaeus) W. D. J	
Zizia aurea		Koch	53
Total			4958

Table S6. Study site coordinates, ecoclimatic region, and management category.

Site	Latitude	Longitude	Ecoclimatic region	Management
BP 1	50.258	-97.694	GT	grazed
BP 2	50.314	-97.786	GT	IVM
BP 3	50.419	-97.883	GT	mowed
BP 4	50.474	-97.923	GT	IVM
BP 5	50.552	-97.977	GT	pasture fallow
BP 6	51.205	-98.397	LBs	pasture fallow
BP 7	51.421	-98.571	LBs	pasture fallow
BP 8	51.479	-98.619	LBs	IVM
BP 9	51.565	-98.694	LBs	grazed
BP 10	51.652	-98.715	LBs	pasture fallow
BP 11	52.355	-98.888	MBs	IVM
BP 12	52.456	-98.889	MBs	IVM
BP 13	52.516	-98.892	MBs	IVM
BP 14	52.596	-98.895	MBs	IVM
BP 15	52.751	-98.96	MBs	IVM



Figure S1. Site 1 pollination network. Grazed site. Network size = 57 species. Green = plants, yellow = insects.



Figure S2. Site 2 pollination network. IVM site. Network size = 87 species.



Figure S3. Site 3 pollination network. Mowed site. Network size = 78 species.



Figure S4. Site 4 pollination network. IVM site. Network size = 112 species.



Figure S5. Site 5 pollination network. Pasture fallow site. Network size = 81 species.


Figure S6. Site 6 pollination network. Pasture fallow site. Network size = 85 species.



Figure S7. Site 7 pollination network. Pasture fallow site. Network size = 64 species.



Figure S8. Site 8 pollination network. IVM site. Network size = 82 species.



Figure S9. Site 9 pollination network. Grazed site. Network size = 55 species.



Figure S10. Site 10 pollination network. Pasture fallow site. Network size = 87 species.



Figure S11. Site 11 pollination network. IVM site. Network size = 96 species.



Figure S12. Site 12 pollination network. IVM site. Network size = 113 species.



Figure S13. Site 13 pollination network. IVM site. Network size = 93 species.



Figure S14. Site 14 pollination network. IVM site. Network size = 105 species.



Figure S15. Site 15 pollination network. IVM site. Network size = 114 species.

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CHAPTER 4. CONCLUSIONS AND IMPLICATIONS

Thesis Summary

In this study, I explored the biodiversity of pollinators within roadside verges (Chapter 2) as well as the structure and stability of plant-pollinator interaction networks in a major powerline easement (Chapter 3) in sub-taiga Manitoba. My objectives throughout this study were: (i) document the diversity of flower-visiting bees, flies, and wasps within the roadside verges and powerline easement corridor, (ii) determine what environmental variables (local and landscape-scale) are affecting pollinator biodiversity and network structure and stability, and (iii) gather insights from my findings and from previous research to provide informed suggestions for ROW vegetation management for pollinator conservation.

I met my first objective by recording 319 pollinator species out of the 9,190 individuals sampled throughout the two research projects. The 154 bee species I observed within the road and powerline ROWs account for almost 42% of the total fauna recorded from Manitoba (Gibbs et al. unpublished). I added four new bee species to the provincial record, as well as a previously undescribed bee species that represents a new national record for Canada. I also recorded many rare or uncommon bee species including several kleptoparasites, which are considered indicator species (Sheffield et al. 2013). The surveyed ROWs also provided habitat resources to a diverse flower-visiting fly community, with 100 species recorded. Many fly species in the Syrphidae family were frequent floral visitors. Finally, I recorded 65 species of wasps visiting flowers in the ROWs. My results revealed that the surveyed road verges and powerline easement were harbouring a significant portion of Manitoba's insect pollinator species, highlighting their high conservation value. I also found that the ROWs, particularly the road verges, harboured abundant populations of invasive plant and insect species such as sweet white clover and the alfalfa leafcutter bee.

I met my second objective by showing that both pollinator biodiversity and plant-pollinator interaction networks in the ROWs were significantly affected by environmental variables. Pollinator communities in the powerline easement responded positively to local blooming plant richness and abundance. This relationship however did not occur in the roadside verges, possibly due to the weedy and invasive nature of the most dominant plant species. I also found contrasting effects of landscape diversity, which had positive effects on roadside and negative effects on powerline biodiversity. However, the effect of landscape diversity on the powerline pollinator communities was region-dependent, probably due to a difference in dominant land-cover types between ecoclimatic regions. Pollinator communities were in general positively affected by the amount of natural and semi-natural habitat in the landscape. However, pollinators should benefit more from ROWs within highly disturbed landscapes, where the corridors might represent much of the remaining early-successional habitat (Phillips et al. 2020). I found that plant-pollinator interaction networks responded positively to integrated vegetation management. IVM sites in the powerline hosted larger networks that were more specialized and modular. Despite also having a lower connectance, IVM networks were the most robust to simulations of random sequential plant species extinctions. Furthermore, I have shown that flowering plant cover has a strong effect on pollination networks within the ROWs, increasing specialization and modularity, which in turn boost robustness.

I used the results from my study in combination with reports from previous research to make recommendations for ROW management practices, meeting my third objective. I found that the habitat quality of roadside verges and powerline easements in Manitoba could be enhanced for insect pollinators by increasing the richness and abundance of flowering plants, as well as the amount of exposed ground. Restoring the plant communities with native forbs, flowering shrubs and grasses would benefit a larger diversity of native specialist pollinators, who are particularly susceptible to anthropogenic disturbance (Spiesman and Inouye 2013). However, since many invasive plant species seem to play keystone roles in the interaction networks, efforts to remove them should also focus on replacing them with equivalent native species) are recommended since they are less disturbing to the habitat and therefore allow ROWs to harbour larger pollination networks that are more modular, specialized, and robust. In conclusion, I recommend using these management practices in ROWs situated within disturbed landscapes with low patch diversity and a low proportion of natural and semi-natural habitats. These are the areas where insect pollinator populations would be struggling the most, and where conservation efforts should be targeted.

This study fills in some of the deficits in the ROW biodiversity literature. My results corroborate that roadside verges and powerline easements in North America act as habitats for significant bee biodiversity, including rare species. However, rather than being limited to a single pollinator taxon, my study shows that ROWs provide valuable habitat resources to a substantial portion of the pollinator community (bees, flies, and wasps). Besides showing that ROWs can host

biodiverse pollinator assemblages, this study also demonstrates that the pollinators within these narrow habitats can form specialized interaction networks with flowering plants that are stable and robust to species loss. My study, therefore, shows that ROWs can harbour plant-pollinator communities which are highly diverse and resilient. This greatly increases our appreciation of ROWs as pollinator habitats and refugia for biodiversity and ecosystem conservation in disturbed landscapes. Additionally, I have shown that two local environmental factors – flowering plant richness and cover, and integrated vegetation management practices – can have strong positive effects on both pollinator biodiversity and the structure and stability of networks. This is encouraging because it shows that ROWs within highly disturbed or homogeneous landscapes can still host biodiverse and stable plant-pollinator communities if managed accordingly.

My study has shown that ROWs may serve as refugia for diverse and stable plant-pollinator communities in disturbed and/or homogeneous areas. However, much still needs to be done to properly evaluate the value of these corridors for pollinators at the landscape scale. Research on pollinator movement along these conduits would allow us to determine how ROWs might be connecting insect metapopulations and meta-networks across fragmented landscapes, and whether this might benefit landscape-level pollinator biodiversity and community stability. Additionally, more needs to be done to investigate whether ROWs act as sources of pollinator populations in the landscape. There is a need to ascertain that ROWs aren't simply attracting insects from the surrounding land via plentiful floral resources. Therefore, future studies should investigate the presence of bee and wasp nests, as well as that of butterfly and fly larvae, to give a better idea of the reproductive success of various pollinator species within these linear habitats. Finally, my study design failed to incorporate pollen transport/deposition data into the pollination networks, which should therefore only be considered visitation networks and treated as such. My visitation networks offer a good indication of which species are critical for maintaining web stability within the ROW, however visitation-level data should be incorporated to fully appreciate the impact of various species. Pollen transport and deposition data could allow future studies to investigate the impact of the dominance of eusocial generalist pollinator species as well as invasive generalist plant species on native and/or specialist species, and on entire networks in the ROWs.

Rights-of-Way as Pollinator Habitat

In Canada, roads and powerlines extend for one million and 160,000 kilometres respectively, with the associated verges and easements occupying a vast area of land rivalling that of many national parks (Wojcik and Buchmann 2012). This land needs to be continuously managed to prevent tall-growing vegetation from interfering with the infrastructure. These corridors therefore occupy a large area of land that is maintained at various early-successional stages, and which is precluded from further development. This land is uniquely influential because it is widespread and connects and intersects a huge variety of habitats across the landscape. ROWs are corridor habitats with a high edge-to-area ratio, the creation of which may cause drastic variations in microclimate, plant and animal community composition, and biotic interactions including predation, parasitism, competition, herbivory, and seed dispersal (Willyard et al. 2004). ROWs may have detrimental effects on wildlife, acting as filters or barriers to animal movement across them, or acting as population sinks when animals move into the corridor from surrounding habitats and die because of the increased predation, parasitism or competition (Jalkotzy et al. 1997). Concurrently, however, ROWs may have beneficial effects, acting as habitats for wildlife and plants, conduits for animal and plant movement/dispersion along them, or population sources when wildlife or plant reproduction is boosted in the corridor and individuals move out into the surrounding habitats (Jalkotzy et al. 1997). Whether a ROW is detrimental or beneficial to wildlife highly depends on the type of corridor, how it is managed, the surrounding habitat and landscape, and the traits of the species in question. For insect pollinators, ROWs may represent a continuous, extensive source of foraging and nesting resources (Russell et al. 2018), and may therefore have a strong conservation value. This may be particularly relevant within landscapes lacking quality natural and semi-natural habitats, where pollinator populations are highly dependent on marginal habitats (Jalkotzy et al. 1997; Michener 2007). In these landscapes, ROWs have the potential to act as refugia for insect pollinator communities and ecological interactions, and may provide connectivity among habitat patches.

Network Theory for Conservation Management

The global decline of insect pollinators is an urgent call towards conservation action. As human activity keeps degrading ecosystems, ecological restoration becomes increasingly important in recovering biodiversity and ecosystem functions. Standard conservation assessments that involve listing species diversity and the presence of endangered taxa in given localities are essential but lack important ecological information. Species exist in a framework of interactions, which are also in need of conservation (Tylianakis et al. 2010). Conserving interaction networks within an ecosystem helps conserve the species within it and the ecosystem services arising from such interactions (Tylianakis et al. 2010). Species should thus not be considered as mere lists but should also be viewed in the context of their interactions. Network analyses are useful for monitoring the functioning and stability of an ecosystem, as well as its sensitivity to invasion and extinction (Harvey et al. 2017). Several network metrics can be used to determine environmental quality (Soares et al. 2017). For instance, since rare species and specialist-specialist interactions are most vulnerable to disturbance and habitat loss, networks within degraded ecosystems tend to experience a concentration of interactions among generalists. Therefore, network-level specialization (H2') can be very useful to determine habitat quality. Network robustness analyses are very useful to determine the stability of the ecosystem towards perturbation. Extinction simulations may be performed to determine the sensitivity of the network towards the loss of certain species. Species could be removed sequentially based on specific criteria such as vulnerability to grazing activity, or to climate change, or could be removed randomly. Robustness analyses can be very helpful in determining the effects that different management strategies have on ecosystem structure. Finally, network theory can aid restoration by helping the identification of those species which are likely to produce the highest benefit to the restored community, based on how they connect species and modules (module hubs, connectors and network hubs). Managing for the conservation of keystone species and interactions benefits the whole network and is critical for ecosystem preservation (Harvey et al. 2017).

Conclusion

ROWs tend to be considered an ecologically-negative feature of anthropogenic activity, however, we have seen that in certain conditions they may contribute to biodiversity conservation. ROWs are already actively managed to keep a low-stature vegetation community and given the large amount of land occupied by these green belts in North America, policy makers should take these landscape elements into consideration in pollinator (and other) biodiversity conservation strategies. The little natural land that remains in North America should be spared and designated as protected area for biodiversity conservation. However, given global declines in biodiversity, the

conservation potential of land within anthropogenic systems must also be considered, such that we may work towards cohabitating with nature rather than supplanting it.

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