

Pollinator communities in saltmarshes and dykes: comparing habitat value in agroecosystems

by

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ABSTRACT

Pollinators that visit croplands rely on adjacent ecosystems to provide essential resources such as pollen, nectar and nesting habitat. However, the relative amount of pollination services associated with different types of habitat bordering farms in coastal environments is poorly understood. This study compared insect pollinator assemblages on saltmarshes and dykes, two habitats in coastal dykelands proximal to cropland. It was hypothesized that dykes would have a greater abundance and diversity of pollinators compared to saltmarshes due to greater showy floral abundance and diversity, and availability of nesting habitat. Pollinators from dyke and saltmarsh sites in the Bay of Fundy dykelands in Nova Scotia Canada were sampled using pan traps. Floral resources were measured using an abundance index, and flowering species were recorded. Average pollinator abundance was similar between the two habitats with dykes having slightly higher counts than saltmarsh. Average pollinator taxon richness, and standard deviation in richness was greater on dykes, compared to lower richness, and a smaller range on saltmarshes.. Floral abundance and taxon richness were significantly higher in dyke habitats. These results seem to contradict other studies that indicate a tight relationship between floral and pollinator abundance. One explanation is an underestimation of floral resources in saltmarshes. This is validated by a field observation of *Bombus* and *Megachilidae* bees visiting flowers of *Spartina pectinata*, a wind-pollinated saltmarsh grass that was not included in my measures of floral abundance. Further research is needed to understand how pollinators use saltmarshes and dykes (i.e. potentially visiting wind-pollinated species, and availability of nesting habitat) to conserve these wild pollinators and maximize their ecological and economic benefits.

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Table of Contents

1. INTRODUCTION.....	1
1.1 Insect Pollinators.....	1
1.1.1 Insect pollinator importance	1
1.1.2 Pollinator-plant interaction	2
1.1.3 Insect pollinator decline and global climate change	5
1.1.4 Native insect pollinators in Nova Scotia.....	7
1.2 Bay of Fundy dykelands	9
1.2.1 Dykeland communities	9
1.2.2 Saltmarsh versus dyke.....	11
1.3 Objectives	12
2. METHODS	13
2.1 Study sites	13
Table 1. List of the study sites.	15
Figure 1. Map of study sites.....	16
2.2 Pollinator and floral surveying.....	17
2.2.1 Pan traps and sampling regime	17
2.2.2 Transect placement	17
Figure 2. Transect map.	18
2.2.3 Floral survey	18

2.3 Specimen preparation and identification	19
2.4 Statistical analysis.....	20
3. RESULTS	21
3.1 Pollinator assemblages.....	21
3.1.1 Pollinator abundance.....	21
Figure 3. Pollinator assemblage.....	22
Table 2. Pollinator abundance.....	22
Figure 4. Mean pollinator abundance.	23
Figure 5. Temporal pollinator abundance.....	24
3.1.2 Pollinator field observations	24
3.1.3 Bee taxa.....	25
Table 3. Bee taxa.....	26
Figure 6. Bee nesting biology.	28
3.1.4 Pollinator richness.....	28
Table 4. Pollinator richness.....	28
Figure 7. Mean pollinator taxon richness.	29
3.1.5 Bray-Curtis dissimilarity.....	30
Figure 8. Bray-Curtis site dendrogram.	31
Figure 9. NMDS site plot.....	31
Figure 10. NMDS habitat by date plot.....	32

3.2 Floral resources	33
3.2.1 Floral abundance	33
Table 5. Floral abundance.....	34
Figure 11. Mean floral abundance.	35
Figure 12. Temporal floral abundance.....	36
3.2.2 Floral richness	36
Table 6. Floral richness.....	37
Figure 13. Mean floral taxon richness.	38
Table 7. Flowering species.	39
3.3 Pollinator-plant relationship.....	41
Figure 14. Pollinator and floral abundance.....	41
Figure 15. Pollinator and floral richness.....	42
4. DISSCUSION	42
4.1 Dyke versus saltmarsh habitat	42
4.1.1 Pollinator community.....	42
4.1.2 Plant community	44
4.1.3 Nesting habitat	45
4.2 Landscape and site context	47
4.2.1 Landscape context.....	47
4.2.2 Saltmarsh sites	48

4.2.3 Dyke sites	51
4.3 Pollination services and disservices	54
4.3.1 Crop pollination	54
4.3.2 Dyke management and re-alignment/breach	56
4.4 Limitations	58
5. CONCLUSION	60
6. WORK CITED.....	62
7. APPENDIX.....	77
7.1 Satellite imagery of each site	77
Appendix 2 Satellite image of Starr’s Point North.	78
Appendix 3 Satellite image of Starr’s Point South.	79
Appendix 4 Satellite image of Belcher Street Restoration and Reference.	80
Appendix 5 Satellite image of Elderkin Creek Dyke.....	81
Appendix 6 Satellite image of Newport Dyke and Newport Marsh South.....	82
Appendix 7 Satellite image of Newport Marsh North.	83
Appendix 8 Satellite image of Cogmangun Restoration and Cogmangun Other.	84
Appendix 9 Satellite image of Cogmangun Reference.....	85
Appendix 10 Satellite image of Bramber.....	86
Appendix 11 Satellite image of Noel West.....	87
Appendix 12 Satellite image of Noel Northeast.	88

Appendix 13 Satellite image of Noel Southeast.	89
7.2 Supplementary statistics.....	89
Appendix 14 Temporal pollinator abundance type-II ANOVA.	89
Appendix 15 Temporal floral abundance type-I ANOVA.	90
Appendix 16 Pollinator – plant abundance type-I ANOVA.....	90
Appendix 17 Pollinator – plant richness type-I ANOVA.....	90

Note from the author: *Spartina pectinata*, *Spartina alterniflora*, and *Spartina patens* have been recently reclassified as *Sporobolus michauxianus*, *Sporobolus alterniflorus*, and *Sporobolus pumilus* respectively.

1. INTRODUCTION

1.1 Insect Pollinators

1.1.1 Insect pollinator importance

Insect pollinators such as bees, wasps, hover flies and beetles provide an essential ecosystem service by pollinating insect-pollinated flowering plant species (henceforth referred to as flowering plant species) in both agricultural and natural ecosystems. Globally, flowering plant species' dependence on animal pollinators for successful reproduction is estimated at 78% in temperate ecosystems and 94% in tropical ecosystems, and without these pollinators the majority of the world's flora would be at risk (Ollerton et al., 2011). Additionally, pollinators have enormous agricultural value as their pollination services globally are worth an estimated \$315-773 billion (CAD) annually, or 9.5% of the world's agricultural economic output in 2005 (Ollerton et al., 2011; Potts et al., 2016). The total volume of global food production that is dependent on pollinators is estimated at 35% (van der Sluijs and Vaage, 2016). In Canada alone the value of pollination services of honey bees (*Apis mellifera*) for direct harvested agriculture (e.g. blueberry, squash, apple crops) has an estimated worth of \$2.57 billion (CAD) annually, and when production of hybrid canola seed (and products derived from canola) is included this value increases to between \$4.0 to \$5.5 billion (Agriculture and Agri-Food Canada, 2018).

The majority of studies researching crop pollination and pollination value have focused primarily on domesticated managed bee species such as the European Honey Bees (*Apis mellifera*) (Garibaldi et al., 2014; Goulson, 2003), and undervalue the contributions of wild pollinators. *A. mellifera* are native to Europe, Western Asia, and Africa, however they have been exported globally for use in agricultural crops (Garibaldi et al., 2014). Currently <11 species of the 20000 –30000 bee species worldwide are managed for use in crop pollination (Kremen, et

al., 2002). The total value of pollinator (especially native pollinator) ecosystem services, both cultural and economic, is grossly understudied, which has implications on conservation management (Goulson, 2003; Klein et al., 2007; Potts et al., 2016). Some research has shown that native pollinators worldwide such as bumble bees are more effective as crop pollinators than the non-native honey bees (Garibaldi et al., 2014). Empirical evidence of wild/native pollinators increasing crop yields is growing, which support crop yields globally would increase if managed bees such as *A. mellifera* were used to supplement wild pollinators instead of replace them (Garibaldi et al., 2014; Goulson, 2003; Isaacs and Kirk, 2010; Kremen, et al., 2002; Rader et al., 2016; Winfree et al., 2008). This combined with the unexplained rapid decline of *Apis mellifera* colonies globally, known as colony collapse disorder (CCD), warrant more reliance on and better management of native pollinators (Watson and Stallins, 2016). Additionally there is evidence to say that the presence of non-native honey bees may be detrimental to the structure and functionality of native pollinator-plant systems (Do Carmo et al., 2004; Valido et al., 2019). Research into the contributions native pollinator provide in agriculture is gaining momentum, however, more is needed at the agroecosystem level to understand dynamics of wild pollinators surrounding cropland (Klein et al., 2007).

1.1.2 Pollinator-plant interaction

The symbiotic mutualistic relationship of insect pollinators and flowering plant species may be the most widely known example of co-evolution. Flowering plant species rely on pollinators to collect and spread pollen for sexual reproduction (Thomann et al., 2013). Pollen contains the male microgametophytes that produce sperm. In the case of cross-pollination the pollen is collected (or otherwise transferred) from the anther (male reproductive organ) of one individual plant and transferred to the stigma (female reproductive organ) of a different individual, resulting

in the male sperm fusing with the female ovule and completing fertilization (Abrol, 2011). Cross-pollination combines gametes of different individuals therefore increasing genetic diversity, and also increases fruit set compared to self-pollination ('selfing') (Hudewenz et al., 2014). Flowering plants have evolved to attract (e.g. ultraviolet showy corollas, fragrances (sweet scents to vile odors), etc.) pollinators to facilitate this fertilization (Peñalver et al., 2012), in contrast to more wind-pollinated plant species such as gymnosperms and graminoids that rely on air currents and chance to achieve successful fertilization (Abrol, 2011). In return for pollinators facilitating cross-pollination flowering plants offer nectar (sugar), which is essential for sustaining adult pollinators. Moreover, these flowers provide protein/lipid rich pollen to pollinators that include essential nutrients for larval development (Moquet et al., 2017). In addition to these nutrients, there are other resources specific to different insects and their life histories that these plants provide. Examples of this are the phytotoxins (cardenolide) that Monarch butterflies (*Danaus plexippus*) receive from milkweed (*Asclepias* spp.) (Kephart, 1983), or leaves used to construct nests by Megachilidae bees (Cane et al., 2007).

The insect pollinator-plant relationship has been evolving for >100 million years, with the first known example appearing in Mesozoic thrips (*Gymnopollisthrips* spp.) and gymnosperm form-genus *Cycadopites* (Peñalver et al., 2012). Today the majority of pollination services rely on bees (*Hymenoptera: Apoidea*). Bees have several anatomical (corbicula, scopa, etc.) and behavioral adaptations (diapause emergence with co-plant species) to enable their pollination and are dependent on flowering plants. Bee species have great phenological variability ranging from generalists capable of pollinating several plant genera (polylectic pollination) to specialists only able to pollinate a single genus and in some cases a single plant species (oligolectic pollination). Other orders such as *Coleoptera* (beetles and weevils), *Diptera* (flies, particularly

Syrphidae), *Lepidoptera* (butterflies and moths), and non-bee *Hymenopterans* (wasp, and ants) also contain large numbers of pollinator species, with other insect orders containing minor amounts (Kevan and Baker, 1983). Non-bee pollinators are not as effective at pollination, as they deposit less pollen on a flower per visit. Nevertheless, their contribution to pollination services cannot be ignored due to their high abundance and visitation frequency (Rader et al., 2016). For example, Rader et al. (2016) found that 39% of insect flower visitations globally were non-bee pollinators, with other works also stressing the importance of non-bee pollinators (Abrol, 2011; Rader et al., 2016). In some cases, the primary (or only) pollinator of a plant may be a non-bee species. An example of this is *Catocheilus* wasps and warty hammer orchids, *Drakaea livida* (Bohman et al., 2012). It is important to remember that focusing on only bees may not be appropriate for all landscapes, as these non-bee insects also must be considered when developing management and adaptation plans for conservation or agricultural applications.

The composition of a pollinator assemblage is highly dependent on which flowering plant species are present within the ecosystem, with population richness typically being skewed by a handful of dominant pollinator species and many rare species within a given landscape (Potts et al., 2003). The two greatest positive predictors of pollinator population size and richness are floral abundance and floral species richness (Potts et al., 2003; Roulston and Goodell, 2011). It is also important to consider the temporal floral distribution, or how much flowering ‘overlap’ there is within a given habitat over time. If there are not enough flowers over an entire growing season then the pollinator populations cannot be sustained (Roulston and Goodell, 2011). This is because the summer months are important for foraging and building up overwinter food reserves and fat bodies, and without sufficient pollen and nectar resources local pollinator populations will collapse (Lonsdorf et al., 2009; Roulston and Goodell, 2011). This is particularly relevant in

an agricultural context; for example, lowbush blueberry (*Vaccinium angustifolium*) in Nova Scotia which rely on pollinators for fruit set, only flower for a limited time (e.g. early June in blueberry) (Kinsman, 1993) leaving pollinators to find other foraging patches during the off-crop period (Roulston and Goodell, 2011). Research on the effectiveness of agro-ecological management practices, such as managing floral resources or planting of mass flowering crops (MFCs) along margins of agricultural crops are promising methods for facilitating and conserving native pollinators and the services they provide (Dicks et al., 2016; Goulson, 2003; Hanley et al., 2011). Given this, pollinator-plant interactions must be evaluated at a landscape specific level, meaning management practices that work in one region may not work in another.

1.1.3 Insect pollinator decline and global climate change

A shift in agricultural and land management practices may be needed in face of declines in managed pollinator stocks. Many questions have been raised about the future availability of European Honey Bees (*A. mellifera*), as their populations are on the decline due to a number of abiotic (e.g. pesticides) and biotic (e.g. parasitism), and social factors (fewer apiculturists) (Goulson, 2003; Watson and Stallins, 2016). In the United States (US) the number of managed *A. mellifera* hives being lost annually due to these stressors is 50-90% since 2006 (Kulhanek et al., 2017; Steinhauer et al., 2014; VanEngelsdorp et al., 2010) and other records show that naturally occurring colonies of *A. mellifera* are practically non-existent today (Requier et al., 2020). One such stressor, an invasive ectoparasitic mite, *Varroa destructor*, affects honey bee colonies by sucking significant amounts of hemolymph from adults as well as larval brood, and are known to carry additional synergistic pathogens which cause secondary infection (Rosenkranz et al., 2010). Two of these synergistic pathogens are Deformed Wing Virus (DWV) and the closely related *Varroa destructor* virus-1 (VDV1). A report published by Ryabov et al.

(2017) showed an increase in VDV1 present in apiaries from 2% in 2010 (n=75) to 66.0% in 2016 (n=240), which has been linked directly to colony loss. This along with other reports of VDV1 and DWV in other parts of the US and Europe suggest these pathogens are rapidly spreading (Ryabov et al., 2017). Today, *V. destructor* are found in honey bee colonies globally with exception to Australia. Two ectoparasitoid resistant *Varroa* subspecies (rVMf and rVMc) are known to exist and both have been documented in Canada (Rosenkranz et al, 2010; Nova Scotia Regulations, 2012). In Nova Scotia the number of registered honey bee colonies increased from 19000 in 2012 to 25000 in 2016 (Agri-food Canada, 2018). In an effort to protect managed pollinator populations policy surrounding apiculture in Nova Scotia has become stricter. In 2019, an outright ban of importation of honey bees from other provinces was enacted by the Nova Scotia Department of Agriculture citing concerns over diseases and pests such as European foulbrood (*Melissococcus plutonius*), Honey bee tracheal mite (*Acarapis woodi*), and the aforementioned *Varroa* mite. Poor management practices, such as the global spread of *Varroa* mite through poor exportation/importation regulation is thought to be at the root of many colonies suffering colony collapse disorder (Watson and Stallins, 2016).

Native pollinators are also being threatened world wide (van der Sluijs and Vaage, 2016). One species of bumble bee, the Rusty Patched Bumble Bee (*Bombus affinis*) native in range to Southern Ontario has now become virtually extinct and is listed as an endangered species in both the US and Canada (Colla and Packer, 2008; Lambe, 2018). Other bumble bee populations are being threatened as well, which will have cascading effects on flora and fauna alike (Colla and Packer, 2008; Goulson, 2003; Kerr et al., 2012). A number of factors are contributing to the decline of wild native pollinators. The rampant use of pesticides, such as neonicotinoids, globally in a multitude of contexts including agriculture has threatened native pollinators

(Goulson, 2003; Morandin et al., 2005; Watson and Stallins, 2016). Insecticides can cause pollinator mortality directly with intoxication (Morandin et al., 2005), and herbicides affect pollinator populations indirectly by decreasing floral resource availability (Gabriel and Tschardt, 2007; Holzschuh et al., 2008), as well other sublethal effects of pesticides are known (Morandin et al., 2005). Additionally, ground nesting pollinators within agroecosystems are threatened by tilling or other such disturbances, which is alarming as 70% of bee species nest in the ground (Roulston and Goodell, 2011). Currently how these disturbances affect population dynamics are not well studied, but some research has shown that just providing floral resources is not enough to sustain these pollinators (Sardiñas et al., 2016; Sardiñas et al., 2016)

These risks, combined with changes in habitable range due to global climate change as well as changes in land use such as urbanization are threatening wild pollinator populations worldwide, particularly in North America and Europe (Kerr et al., 2012; Kremen et al., 2002). Global climate change also has indirect negative effects on wild pollinator populations due to changes in plant communities (Roulston and Goodell, 2011). There is an urgent need for research of native pollinators globally as the decline in plant species is directly linked to decline in pollinators, and vice versa (Thomann et al., 2013). Plant species will need a rapid evolutionary response of new reproductive strategies less reliant on pollination services in order to cope with declines of pollinator diversity (Thomann et al., 2013).

1.1.4 Native insect pollinators in Nova Scotia

A review by Sheffield et al. (2003) compiled all documented species of *Apidae* in Nova Scotia (NS). They found 157 indigenous bee species (and two additional recent arrivals), from 26 different genera of six families. Many of these species are known to exhibit polylectic and several oligolectic relationships with plant species. This review also identified a lack of research

on the reproduction of native plant communities within NS, including the relationships with Nova Scotian indigenous bees. Solitary bees in NS spend the majority of the year in an overwintering stage (diapause), some overwinter in adult stages, while some overwinter as pupae (matured larvae). In temperate climates the majority of bees overwinter as pupae (Stephen et al., 1969). In contrast, Sheffield et al. (2003) reported that 73% of NS bee species overwinter as adults. Emergence from diapause typically occurs in early spring (when daily temperatures reach >14 °C) with flight periods of bees spanning from June into the summer and autumn – however, this varies by species. Other non-bee pollinators can have very different life histories, and their emergence and pollination periods can vary greatly (Abrol, 2011). However, in general these pollinators' flight periods in temperate regions closely reflect those of their bee counterparts (Abrol, 2011).

Only a handful of pollinator studies have been completed in Nova Scotia. Population surveys of native pollinator does not exist for many parts of Nova Scotia. There is some population data for managed bees (*Apis mellifera*, Agriculture and Agri-food Canada, 2018), and anecdotal reports of *A. mellifera* population decline have been made in NS. Potts et al. (2010) criticize the value of such reports for informing status of honey bee populations, as the number of bee keepers globally (and in Canada) has declined as well (Potts et al., 2010). It is important to note that previous research completed in the Annapolis Valley, and Nova Scotia in general has focused primarily on bees, so little is known about non-bee pollinators, despite their importance.

When examining the number of bee species that pollinate two staple agricultural crops in NS it is clear that it is inappropriate to only consider *Apis mellifera* as pollinators of these crops; 42 species pollinate apples (*Malus domestica*) and 78 species (40 shared with apple) pollinate lowbush blueberry (*V. angustifolium*) (Sheffield et al., 2003). Many other fruit and vegetable

crops are also grown within the Annapolis Valley which include pears, plums, cherries, bramble, peaches, strawberries, grapes, highbush blueberry, and squash (Sheffield et al., 2003). Research into the contribution of native pollinators of blueberry crops has shown that native bumble bees are typically more abundant and effective pollinators of these crops compared to *A. mellifera* (Garibaldi et al., 2014; Isaacs and Kirk, 2010; Winfree et al., 2008), which is important to consider as Nova Scotia is the second largest global producer of lowbush blueberries (Kinsman, 1993). Unfortunately high pesticide use and poor management practices has led to native pollinator population decline and an increased reliance on managed pollinators which is likely limiting crop yields (Goulson, 2003; Isaacs and Kirk, 2010). The value of these native pollinators and their services in Nova Scotia has been overlooked, and studies in agroecosystems such as the Bay of Fundy dykelands are needed.

1.2 Bay of Fundy dykelands

1.2.1 Dykeland communities

The Bay of Fundy dykelands are spread along coastal regions of the Bay of Fundy in Nova Scotia and New Brunswick (Figure 1). These dykes were originally made by the Acadians (early French settlers) starting in the late 16th century to protect their crops from saltwater intrusion (Landscape of Grand Pré, n.d.). The creation of these dykes drastically changed the landscape behind the dykes and allowed for more agricultural land; as well the dykes provided irrigation systems for the fields and crops (Desplanque, 1982). Tidal saltmarsh reclamation continued to convert saltmarshes around the Bay of Fundy to agricultural land into the mid-twentieth century, and today approximately 77% of Nova Scotia's natural tidal saltmarsh has been lost due to dyking (MacDonald et al., 2010; Wollenberg et al., 2018). Tidal saltmarshes are unique but stressful intertidal wetland habitat characterized by predictable periodic inundation of salt (or

brackish) waters, which connects the marsh to the water body (Broome and Craft, 2015; Pennings and Bertness, 2001). These marshes are highly productive ecosystems that support a number of species and provide a number of water quality and hydrological functions (Pennings and Bertness, 2001). The Bay of Fundy dykelands remain a region of high agricultural activity, with the majority of agriculture taking place in the Annapolis Valley in Nova Scotia, which has a regional economy largely dependent on the success of its agriculture (Van Proosdij et al., 2018; Sheffield et al., 2003). The dykes also protect land important for other agricultural activities such as hay fields that are producing feed for cattle and other livestock, or even grazing areas for this livestock. These Nova Scotian dykes are now regulated under the Agricultural Marshland Conservation Act 2000, c. 22, s. 1 (Nova Scotia Legislature, 2000). The Nova Scotia Department of Agriculture (NSDA), Land Protection Section is responsible for maintaining 241 km of dykes along Nova Scotia's coasts and waterways, protecting 16,139 Ha of agricultural marshland behind them (van Proosdij et al., 2018) . In addition to protecting agricultural land these dykes protect a number of coastal communities and infrastructure.

Unfortunately, the sustainability of the Bay of Fundy dykelands is now being called into question due to increasing rates of sea level rise (SLR), as well as the possibility of increased storm severity due to effects of climate change on the region. Policy makers and other stakeholders have begun to reconsider the long-term cost effectiveness associated with maintaining dykes (Wollenberg et al., 2018). Additionally these dykes are vulnerable to overtopping events under current and future sea level rise and storm scenarios; 2100 SLR scenarios show that dyke tracts in Annapolis, Digby, Hants, and Kings counties are at extreme risk of dyke overtopping and erosion (Van Proosdij et al., 2018). In response to the rising costs and questions of dyke sustainability, coastal managers and researchers have turned to the

potential managed realignment of these dykes. The managed realignment process is a nature-based adaptation which includes breaching, removal, and/or realignment of the dyke further inland (French et al., 2000). This process allows for the natural intertidal habitat including tidal saltmarsh to be restored (Bowron et al., 2011; French et al., 2000; Garbutt et al., 2006). Tidal saltmarshes have been shown to provide a number of ecosystem services including climate regulation services such as wave action attenuation, protection against storm surge, and carbon sequestration (Gallant et al., 2020; McKinley et al., 2018). Additionally, saltmarshes benefits wild species (particularly bird and fish) diversity and other cultural services (Bowron et al. 2011; McKinley et al., 2018). Today there are several ongoing managed realignment and coastal restoration projects in the Bay of Fundy region (van Proosdij et al., 2018; Wollenberg et al., 2018; Fisheries and Oceans Canada, 2019).

1.2.2 Saltmarsh versus dyke

Although the restoration of tidal saltmarsh has great potential as a nature-based adaptation to protect coasts and provide ecosystem services along the Bay of Fundy, there are potential negative trade-offs for removing or disturbing dykes. Restoration of saltmarsh will require that valuable agricultural land be forfeited, which has implications for policy makers and stakeholders alike. Additionally, managed realignment has the potential to negatively affect native pollinator populations. The dykes as well as the land behind the dyke provide freshwater habitat for many flowering plants species, which cannot tolerate seawater; <0.25% of angiosperms are salt tolerant (Bromham, 2015). Many of the flowers on dykes are non-native naturalized species such as *Medicago sativa*, *Sonchus oleraceus*, *Daucus carota*, *Trifolium* spp. and *Taraxacum* spp. Nevertheless, there are some native species such as *Solidago* spp., and *Symphyotrichum novi-belgii*. The dykes also may be providing nesting habitat for ground nesting

bees and other insects both behind the dyke as well as on the dyke itself (Sardiñas and Kremen, 2014). By comparison tidal saltmarshes are composed of primarily wind pollinated graminoids (e.g. *Carex palacea*, *Juncus gerardii*, *Spartina patens* and *Spartina alterniflora*), with a low abundance and diversity of insect pollinated species (e.g. *Solidago sempervirens*, *Limonium* spp, and *Tripolium pannonicum*) compared to those on dykes (Bowron et al., 2011). Additionally, there is little to no viable nesting habitat in saltmarsh, due to wave intrusion during high tide causing the marsh to become flooded periodically. There is a limited amount of research and literature investigating pollinators on saltmarsh. Davidson et al. (2020) in the United Kingdom did complete a study that showed that pollinators (mainly *A. mellifera*, and *Bombus* spp.) are accessing these habitats. They also found that grazing of saltmarsh meadows negatively affects pollinator abundance and diversity by reducing the flower cover of *Tripolium pannonicum* and *Limonium* spp. However, more research is needed to properly understand how pollinators may be utilizing saltmarshes to better predict how dykeland restoration will affect agriculture in the Bay of Fundy.

1.3 Objectives

This study is a novel comparison of pollinator assemblages (abundance and diversity) found on tidal saltmarsh and dykes. Additionally, surveying of pollinators in either habitat not been done in the Bay of Fundy dykelands. This research aimed to understand differences in these habitats for supporting pollinators, in part to inform their relative value for pollination services to proximal crops. This work also began addressing a gap in the literature surrounding how pollinators access saltmarsh. This work will inform potential ecosystem service trade-offs between saltmarsh and dykes, which will help stakeholders make informed agro-ecological land management decisions. For example, this study may provide insight into how dyke realignment

and/or breach may negatively impact pollinators – by potentially disrupting ground nesting bees and the floral resources dykes offer.

As little work has been done on surveying of wild native pollinators in the Annapolis Valley as well as Atlantic Canada, this study will be used in future studies to track pollinator population changes. Most importantly, this research will further our understanding of what insect pollinator species are present on saltmarshes and dykes and potentially assist managers making species-specific conservation decisions/tools within the Bay of Fundy dykelands agroecological landscape.

I predicted that dykes will support greater abundance and diversity of pollinators compared to saltmarsh, as dykes typically have greater insect pollinated floral diversity and abundance, as well dykes have greater amounts of potential ground nesting habitat.

2. METHODS

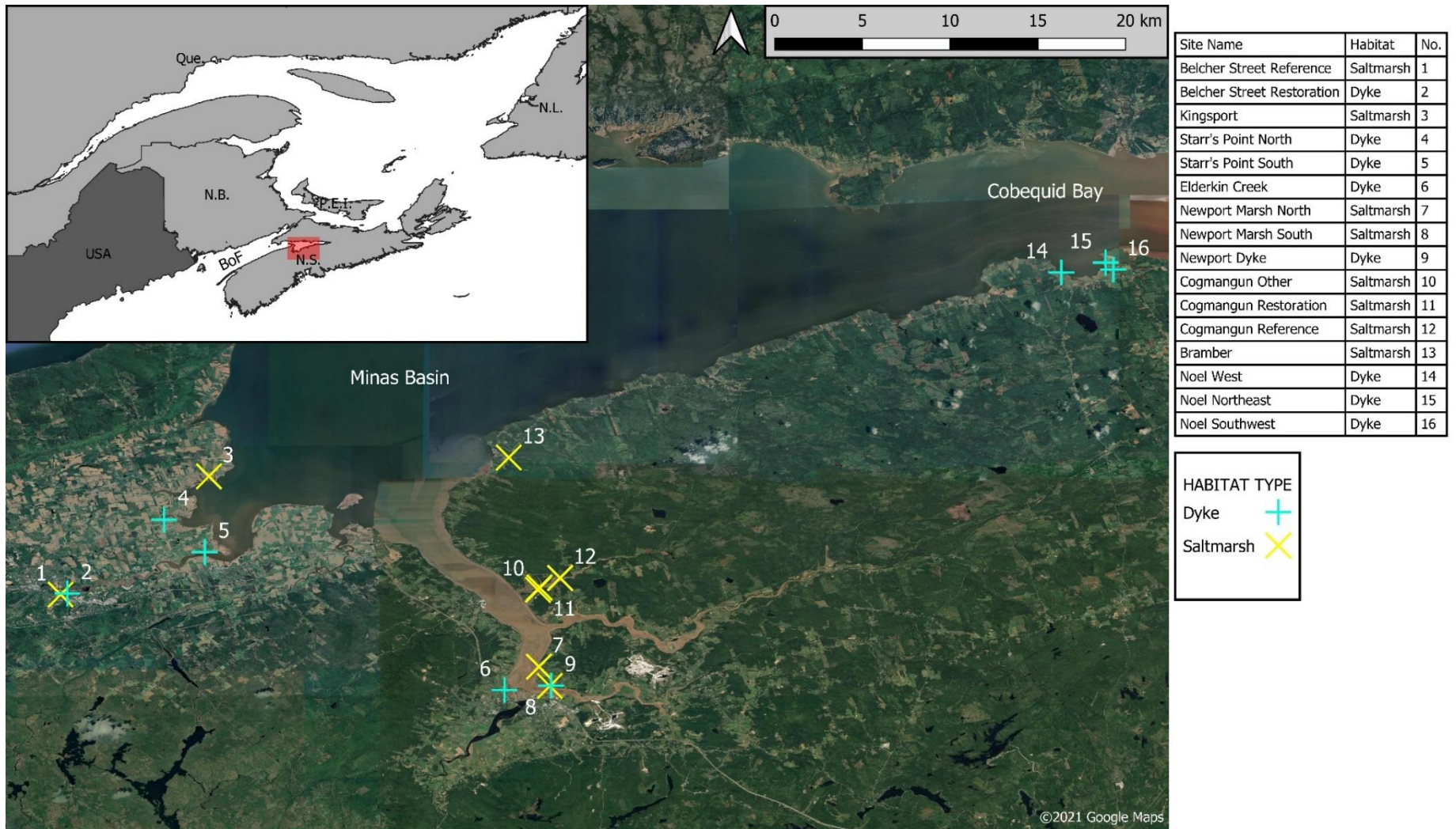
2.1 Study sites

Insect pollinators were sampled from eight saltmarshes and eight dykes in the Annapolis Valley (Figure 1, Table 1, Appendix 1-13). The Annapolis Valley is in western Nova Scotia and is characterized by two mountains that form a valley parallel to the Bay of Fundy. The valley facilitates a microclimate which produces relatively mild temperatures compared to the rest of mainland Nova Scotia. This paired with fertile glacial sedimentary soils makes the area suitable for agriculture. Average monthly high temperatures range from the -1.3 °C in January to 24.9 °C in July (Environment Canada, 2020). The Annapolis Valley has an average annual precipitation of 1181 mm (Environment Canada, 2020). The highest temperature during the study period was 37 °C (July 21st, 29th and 31st), and the lowest was 17 °C (July 9th).

Saltmarsh and dyke sites were initially selected using satellite images and were confirmed to be appropriate upon initial visits. All sites were located near agricultural land (< 1 kilometres), with crop and management type varying. Saltmarsh sites were selected to include high (upper), middle, and lower marsh vegetation zones to ensure sites were representative of natural ecosystems (Foster et al., 2013; Porter et al., 2015). However, due to logistical limitations, the Newport Marsh South and Belcher Street Marsh sites were included but did not include have any high marsh vegetation. Dyke sites were chosen based off proximity to agricultural land, as well as ease of access from near by roadways. Most dyke sites had some fringe saltmarsh on the foreshore side of the dyke, however, these zones did not exceed > 15 metres, with the exception of the Newport Dyke site which had approximately 100 metres of saltmarsh on the foreshore side of the dyke. Experimental sites varied in their position in the tidal frame, with some sites being located in or near the Minas Basin (e.g. Kingsport Marsh, Noel Dykes) and other sites located further up the tidal frame (e.g. Belcher Street Marsh and Dyke).

Table 1. List of the study sites.

No.	Site Name	Coordinates (DD)	Habitat
1	Belcher Street Reference	N45 04.390' W064 28.626'	Saltmarsh
2	Belcher Street Restoration	N45 04.430' W064 28.338'	Dyke
3	Kingsport	N45 09.508' W064 22.202'	Saltmarsh
4	Starr's Point North	N45 07.629' W064 24.143'	Dyke
5	Starr's Point South	N45 06.231' W064 22.384'	Dyke
6	Elderkin Creek Dyke	N45 00.252' W064 09.399'	Dyke
7	Newport Marsh North	N45 01.264' W064 07.904'	Saltmarsh
8	Newport Marsh South	N45 00.429' W064 07.432'	Saltmarsh
9	Newport Dyke	N45 00.445' W064 07.380'	Dyke
10	Cogmangun Other	N45 04.595' W064 07.946'	Saltmarsh
11	Cogmangun Restoration	N45 04.692' W064 07.879'	Saltmarsh
12	Cogmangun Reference	N45 05.107' W064 06.987'	Saltmarsh
13	Bramber	N45 10.323' W064 09.211'	Saltmarsh
14	Noel West	N45 18.342' W063 45.273'	Dyke
15	Noel Northeast	N45 18.765' W063 43.357'	Dyke
16	Noel Southeast	N45 18.464' W063 43.021'	Dyke



Sources: Provincial boundary data Statistics Canada (<https://www12.statcan.gc.ca/census-recensement/2011/geo/bound-limit/bound-limit-eng.cfm>); USA boundary data United States Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.html>); satellite imagery ©2021 Google Maps (<https://www.google.com/maps>)

Figure 1. Map of study sites. See Table 1 for site coordinates. BoF = Bay of Fundy.

2.2 Pollinator and floral surveying

2.2.1 Pan traps and sampling regime

Sampling of insect pollinators began on June 26th, 2020 and continued until October 5th, 2020. To capture temporal changes in the pollinator assemblages, each site was sampled approximately every ten days (minimum seven days, maximum fourteen days). An exception to this condition was sampling completed between October 1st and October 5th which occurred thirty days after the previous sampling event. Several sites were visited on each day and all sites were sampled within five days of each other to flowering plant species were consistent. Sampling only went ahead on sunny days when maximum temperatures reached or were above 15 °C, to ensure pollinators had suitable flight conditions.

Pollinators were sampled using passive pan traps placed at ground level on all saltmarsh and dyke sites. Pan traps were UV-bright blue, yellow and white plastic bowls (15 cm diameter, 12 oz; Polar PartyWare) – the three colours known to be commonly attractive to a range of pollinators (Saunders and Luck, 2013). On each site these traps were laid between 08:00 and 10:00 hr and were collected after a six-hour period. All specimens were stored in 95% ethanol at room temperature until pinning.

2.2.2 Transect placement

On each site, three parallel transects spaced 30 metres apart were laid perpendicular to the waterway (Figure 2). Pans were placed in alternating colours (e.g. blue, white, yellow, blue, etc.) in transects of 10 pans each spaced ~ 3 metres apart. Once placed, bowls were filled $\frac{3}{4}$ full of soapy water to ensure the surface tension was broken. Soapy water was made by adding three-to-six drops of Blue Original Dawn soap to 5 litres of water. Coordinates for the ends of each transect were taken using a handheld GPS to ensure location of transects were consistent during

the study. On saltmarsh sites transects were placed in the mid marsh zone, between the low/mid marsh edge and the high marsh vegetation. One exception to this was Cogmangun Restoration where 1-2 traps per transect were placed in the high marsh zone in order to maintain transect spacing. No pan traps were laid in low marsh areas as tidal inundation would have disrupted the traps over the surveying period. On dyke sites transects were laid between the foreshore base of the dyke footprint – up and over the dyke-proper – stopping before the landward dyke footprint. Due to area constraints transects at Noel Northwest, Noel Southwest, Starr’s Point North, and Starr’s Point South had 1-2 traps were placed in the fringe marsh. Again, this was done to maintain transect spacing.

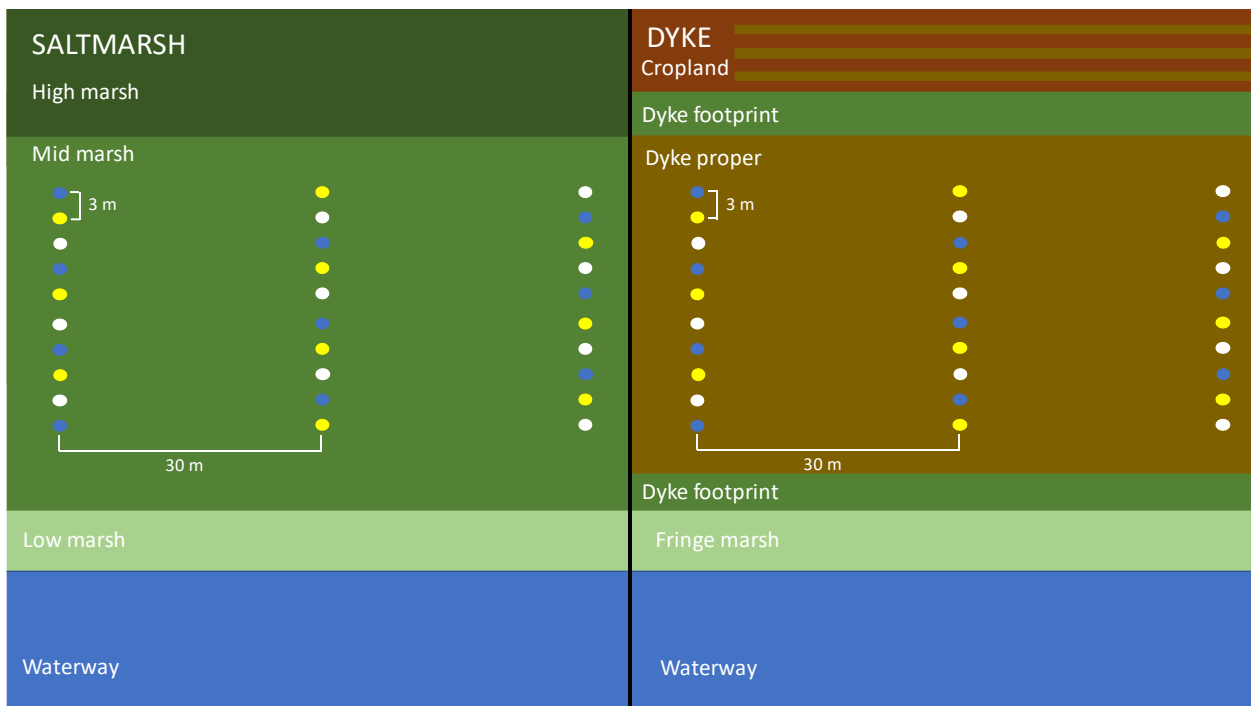


Figure 2. Transect map. Example of pan trap transects on saltmarsh (left) and dyke (right) sites. To maintain transect spacing, the range of trap placement varied (see text above) from site-to-site due to area constraints. Diagram not to scale.

2.2.3 Floral survey

During each visit to a site the abundance of floral resources was estimated using a visual index ranging from 0-to-3. Grasses and other wind-pollinated species were excluded from floral

surveys – only showy flowers were included. A score of 0 represented no floral resources (no flowering individuals), 1 represented very low to low abundance of resources (~ 1-10 individual plants), 2 represented low to intermediate abundance of resources (~ 11-20 individual plants), and 3 represented high to very high abundance (~ 21+ individual plants). Flowering species were noted on each site to measure floral species richness.

2.3 Specimen preparation and identification

All specimens were cleaned and prepared before being pinned. Cleaning involved removing vegetation and other debris from all samples before segregating bees and wasps (Superfamily Apoidea), syrphids (Family Syrphidae), (Order Coleoptera), and butterflies (Order Lepidoptera) from other non-pollinator invertebrate by-catch. Insects in by-catch were classified to order, and other invertebrate by-catch was classified by phylum before being disposed. The remaining pollinator specimens were lightly rinsed and transferred to soapy water bath, where they were swirled for 60 seconds to removed dirt and other debris. The specimens were gently rinsed again and replaced into a clean water bath and swirled for another 60 seconds to remove any soap residue. Specimens and small pieces of dry paper towel were then placed into a plastic vial with mesh covering both ends. A hair dryer (Conair 1875 Watt Full Size Tourmaline Ceramic Hair Dryer) was then used to dry the specimens. Following cleaning, specimens were pinned using BioQuip No. 0, 1, and 2 gauge insect pins and stored at room temperature in collection boxes until identification.

All bee specimens were identified to genus with the exception of a several easily identifiable species (e.g. *Apis mellifera*, *Agapostemon virescens*, and *Halictus ligatus*) Bee specimens were identified using Discover Life keys by Polistes Foundation, Inc. (2020), and

“The Bee Genera of Eastern Canada” by Laurence Parker et al. (2007). Syrphids, lepidopterans, and wasps were recorded to morphospecies.

2.4 Statistical analysis

All statistical tests were performed in R v 3.5.1 (The R Project for Statistical Computing, <http://www.rproject.org/>), using RStudio interface v 1.2.5033. Bee richness were calculated as the total number of genera or species. Syrphid, lepidoptera, and wasp richness was left as each respective morphospecies. Pollinator abundance was the total number of specimens collected in each habitat for each respective taxon. Means (rounded to nearest whole number) and standard errors were calculated for pollinator abundance and richness. Statistically significant results were considered $\alpha = 0.05$. A Welch’s two-sample t-test were used to compare mean pollinator abundance and richness between habitats, using the base R function ‘t.test’. Homoscedasticity of residuals was verified before continuing analysis. A generalized mixed linear effects model with Poisson fit and site random effect was used to model pollinator abundance between habitats over the sampling period. This was then analysed using a Type II ANOVA (Wald chisquare test). Bray-Curtis dissimilarity coefficients (quantifies differences in assemblages between sites, considering abundance and richness) from pollinator abundance data was calculated using the ‘vegan’ package function ‘vegdist(method=”bary”)’. This data was then used in a Non-metric multidimensional scaling (NMDS) ordination to visualize variation in bee community composition across site types, using the ‘NMDS’ function in the ‘vegan’ package. Means (rounded to nearest whole number) and standard deviations were calculated for floral abundance and standard errors richness. A Welch’s two-sample t-test were used to compare mean floral abundance and richness between habitats, using the base R function ‘t.test’. A linear model was used to measure floral abundance scores over the sampling period. This was then analysed using

a Type I ANOVA (F test). A linear regression (base R, 'lm') was used to explore the relationship between pollinator abundance by mean floral abundance, and pollinator richness by floral richness, which was then analysed using a Type I ANOVA (F test). Other supplementary packages 'dplyr', 'ggplot2', 'ggdendro', 'ggsignif' and 'esmeans' were used for data manipulation and visualization.

3. RESULTS

3.1 Pollinator assemblages

3.1.1 Pollinator abundance

A total of 2386 pollinator specimens were collected across both habitats, with the total dyke catches equalling 1355, and total saltmarsh catches equalling 1031. Of pollinators sampled on dyke sites there were 1070 bees, 233 wasps, 26 syrphids, and 26 Lepidopterans, and on saltmarsh sites there were 756 bees, 200 wasp, 58 syrphids, and 17 Lepidopterans (Figure 3). The dyke sites Starr's Point South and Belcher Restoration had the two greatest total counts with the next greatest being a saltmarsh site, Cogmangun Reference (Table 2). The least total count was on dyke site, Noel West, with Kingsport (saltmarsh) and Noel Southeast (dyke) having the next least (Table 2). The mean abundance of pollinators was greater for dyke sites (169 ± 34.01 SE) than the saltmarsh sites (129 ± 14.11 SE) (Figure 4, Table 2). However, a Welch's two-sample t-test reported this result was non-significant ($t(9.34) = 1.11$, $p = .2989$). The number of pollinators captured in both habitats slightly increased later into the sampling period, with the five greatest single day catches occurring between Aug 20th and September 5th 2020 (Figure 5). The type II ANOVA (Wald chi-square test) reported a strong effect of time ($\chi^2(28) = 613.606$, $p < < 0.001$), and a significant interaction between habitat and date ($\chi^2(14) = 436.258$, $p < < 0.001$). However,

habitat alone did not affect pollinator abundances over the study period ($p=0.3075$) (Appendix 14).

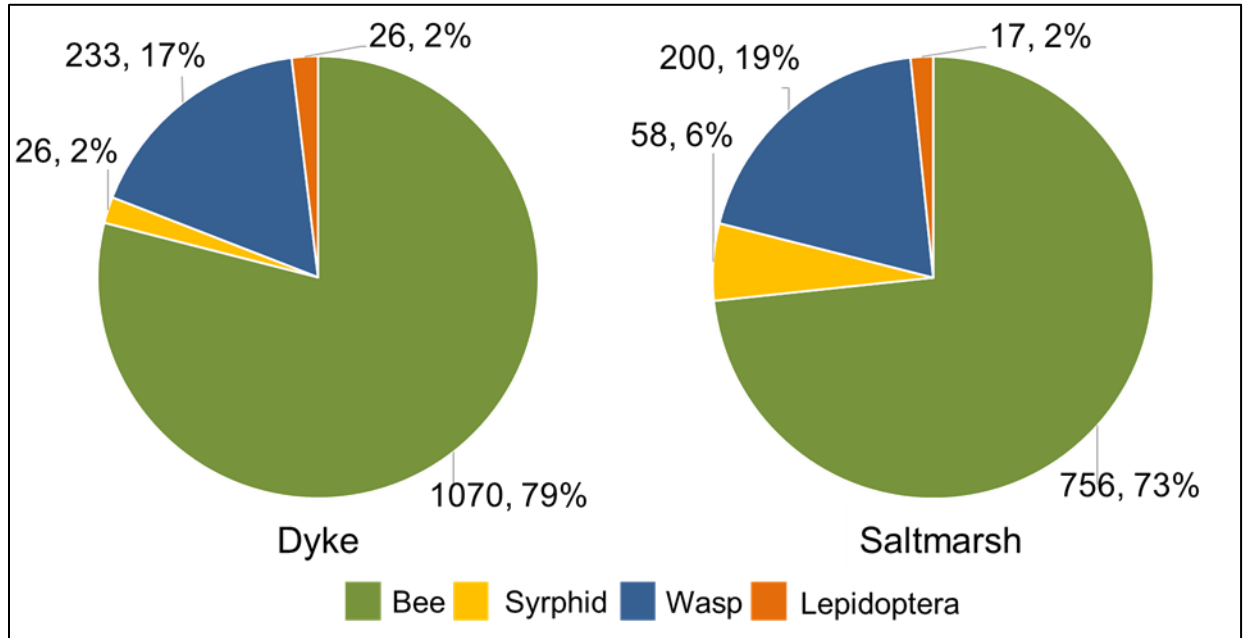


Figure 3. Pollinator assemblage. Total proportion of pollinator groups found in both dyke and saltmarsh sites. Pollinators were sampled using pan traps laid at ground level, see Figure 2 for example of sampling transects.

Table 2. Pollinator abundance. Total count of pollinator catches by site. Total catches were greater in dykes however, both habitats did have a few outlying samples. ‘SE’ = standard error.

Site	Dyke Abundance	Saltmarsh Abundance
Belch Restoration	253	
Starr's Point North	143	
Starr's Point South	361	
Elderkin Dyke	110	
Newport Dyke	176	
Noel Northeast	153	
Noel Southeast	93	
Noel West	66	
Belch Reference		110
Kingsport		81
Newport Marsh North		122
Newport Marsh South		132
Cogmangun Other		219

Cogmangun Reference	117
Cogmangun Restoration	134
Bramber	116
Mean ± SE	169 ± 34.01
	129 ± 14.11

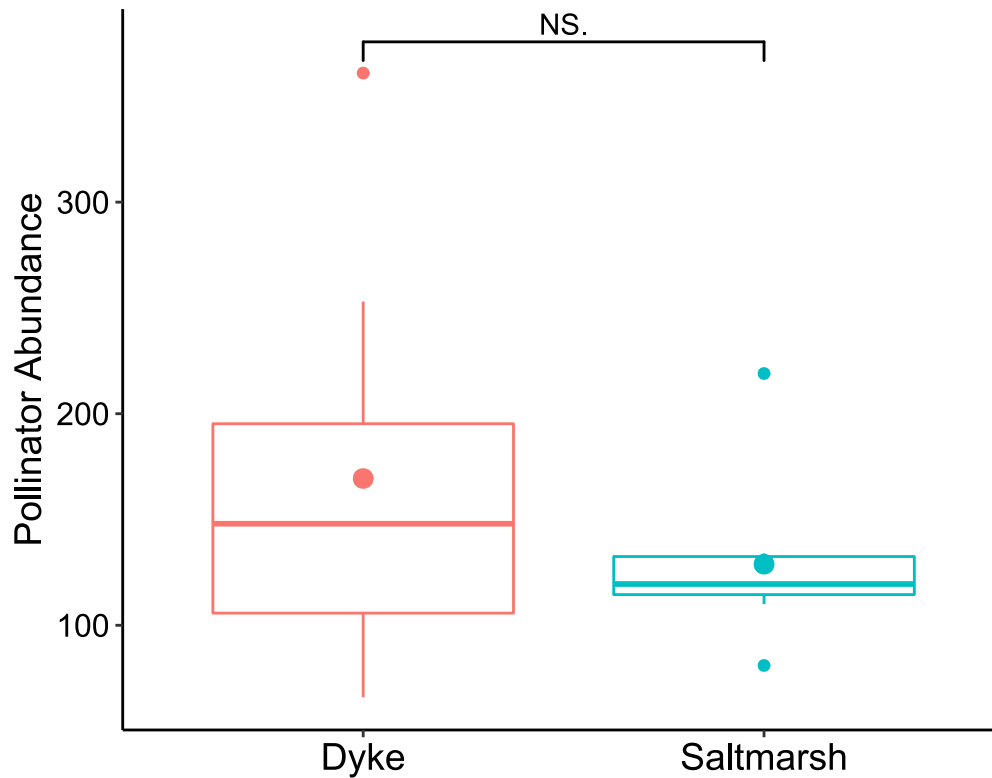


Figure 4. Mean pollinator abundance. Dyke sites had a greater mean (169 ± 34.01) abundance of pollinators than saltmarsh (129 ± 14.11). Specific site abundances values can see in Table 2. Large dot represents the means, the lower and upper hinges correspond to the first and third quartiles, the upper and lower whiskers extend to the largest/smallest value no further than 1.5 interquartile range (IQR) beyond the hinges, dots are outliers that values that fall outside of this range. Welch's two sample t-test: $t(9.34) = 1.11$, $p = 0.2989$. 'NS.' = non-significant.

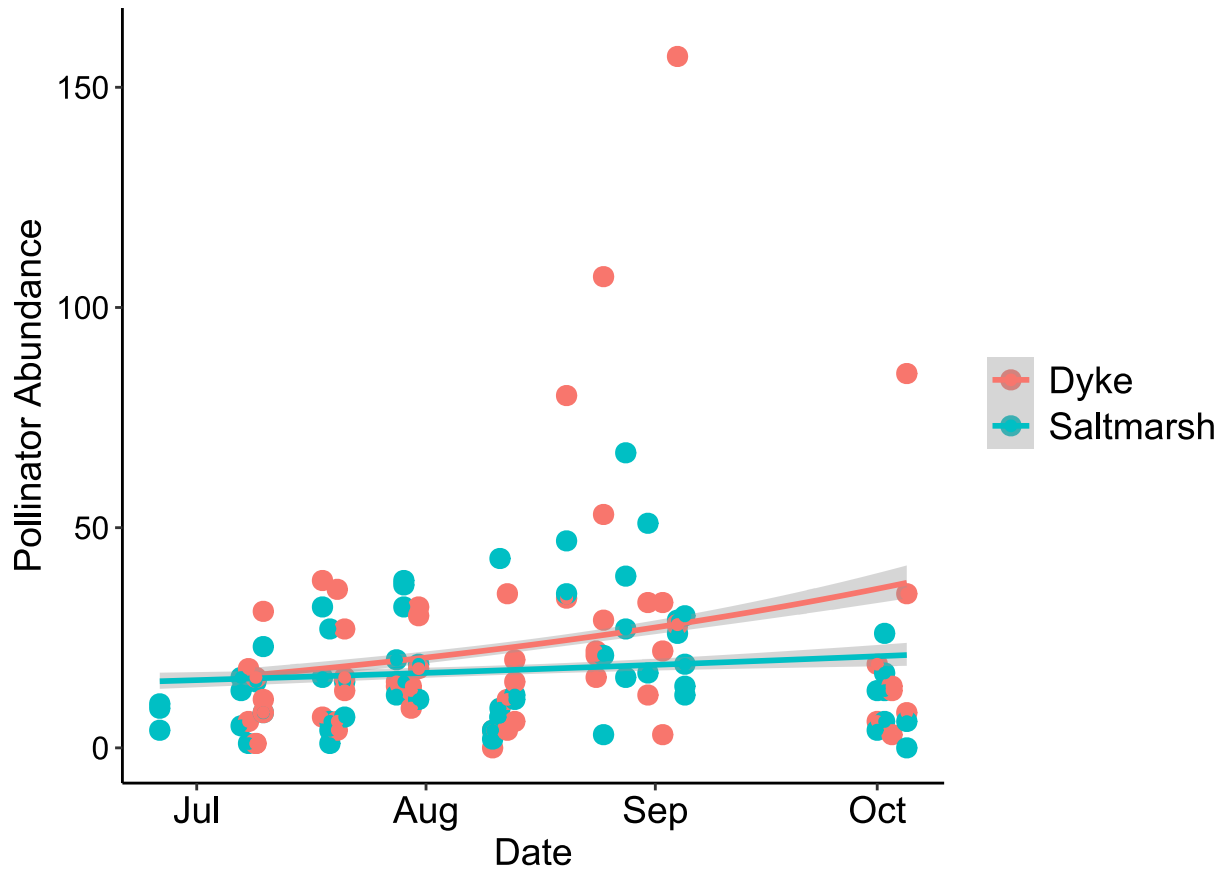


Figure 5. Temporal pollinator abundance. Pollinator abundances increased slightly in both habitats starting in August and continued into September. Regression (\pm) shown is a generalized mixed linear effects model with logistic Poisson fit and site random effect (deviance = 1123.6). A type II ANOVA reported significant interaction between habitat and time ($\chi^2(14) = 436.258$, $p < 0.001$) and indicated a significant time effect on pollinator abundance ($\chi^2(28) = 613.606$, $p < 0.001$), but no effect of habitat on pollinator abundance ($\chi^2(1) = 1.042$, $p = 0.3075$) (Appendix 14).

3.1.2 Pollinator field observations

At all sites bees and other pollinators were seen visiting showy flowers within the area's of the transects. No observations of bees nesting on or within either habitat were made however it should be noted that several dyke sites had suitable ground nesting soils (exposed, sunny, sloped) in addition to vegetation (such as cone flowers) and dead wood suitable for cavity nesting bees. On saltmarsh sites lepidopterans were found commonly resting on *Spartina patens* in July and August. Paper wasp (Family: Vespidae) nests were found on the Elderkin Creek and Noel West

dyke sites. Most notably, bees believed to be *Bombus* spp. and Family: Megachilidae were seen visiting a wind-pollinated saltmarsh grass, *Spartina pectinata*. This was observed at Bramber and Cogmangun Restoration sites on several occasions. It appeared *Bombus* bees were pollinating *S. pectinata*, by hanging onto the flowering stem. Additionally, Megachilidae were specifically observed removing sections of *S. pectinata* leaves and flying away with them. Although not directly measured in this study, *S. pectinata* can be found on all saltmarsh sites, as well as several dykes sites (Personal observations, T. T. Roulston and Evan McNamara – MSc. student).

3.1.3 Bee taxa

The majority (92.4%) of bee catches were wild native Nova Scotian species, with the remaining proportion (7.6%) of catches including 58 *Apis mellifera* (non-native; managed), three *Anthidium manicatum* and six *Anthidium oblongatum* (both non-native; wild) 72 *Bombus impatiens* (non-native; wild/managed). The most abundant bee taxa in both habitats was genus was *Lassioglossum*, with 325 and 460 sampled in saltmarshes and dykes, respectively. The next most abundant genera were *Bombus* with 97 on saltmarsh and 126 on dyke, and *Agapostemon* with 72 on saltmarsh and 111 on dyke sites. Rare taxa (≤ 10 total individuals) included: *Anthidium*, *Coelioxys*, *Heriades*, *Hoplitis*, and *Osmia*. See Table 2 for a complete list of all bee taxa.

Bee nesting biology was found to be similar in both habitats (Table 3, Figure 6). Cavity nesting bee taxon composed 36% and 35% in dykes and saltmarshes respectively. Ground nesting pollinators were found in similar portions of 33% and 31%, again respectively. Two genera of nest parasites were found, *Sphecodes* and *Coelioxys* on both habitats, however a greater abundance was found on dykes.

Table 3. Bee taxa. Bee specimens were identified to genus, and species depending on difficulty of identification. Note that rows with ‘—’ indicates those specimens were not identified to species. **Sphecodes* species parasitize mainly Family:Halictinae; along with some *Andrena*; *Calliopsis*; *Perdita*; and *Collets*. Nesting biology described by (Packer et al., 2007)¹, (Colla et al., 2012)², (Sheffield et al., 2011a)³, (Sheffield et al., 2011b)⁴, (Sheffield et al. 2003)⁵.

Family	Genus	Species	Nesting biology	Dyke abundance	Saltmarsh abundance	Total abundance	
Megachilidae	<i>Anthidium</i>	<i>manicatum</i>	Cavity ¹	2	1	3	
		<i>oblongatum</i>	Cavity ¹	4	2	6	
		<i>psoraleae</i>	Cavity ¹	1		1	
	<i>Coelioxys</i>	<i>modestus</i>	<i>Megachile</i> nest parasite ¹	1		1	
		<i>moestus</i>	<i>Megachile</i> nest parasite ¹		1	1	
		<i>octodentatus</i>	<i>Megachile</i> nest parasite ¹	2		2	
		<i>rufitarsis</i>	<i>Megachile</i> nest parasite ¹	1		1	
		<i>sayi</i>	<i>Megachile</i> nest parasite ¹	1		1	
		<i>Heriades</i>	<i>carinatus</i>	Cavity ¹	2		2
		<i>Hoplitis</i>	<i>producta</i>	Cavity ¹	2		2
	<i>Megachile</i>	<i>centuncularis</i>	Cavity/ground	3		3	
		<i>frigida</i>	Cavity/rotten logs ⁴	1	2	3	
		<i>inermis</i>	Cavity/rotten logs ⁴	4	1	5	
		<i>latimanus</i>	Ground ⁴	2		2	
		<i>melanophaea</i>	Ground ⁴	3		3	
		<i>relativa</i>	Cavity/rotten logs ⁴		1	1	
		—	?Cavity/ground ⁴		1	1	
		<i>Osmia</i>	—	Cavity ¹	4	2	6
	Apidae	<i>Apis</i>	<i>mellifera</i>	Colony hive ¹	19	39	58
			<i>Bombus</i>	<i>impatiens</i>	Colony underground ²	40	32
		<i>borealis</i>	Colony underground ²	20	12	32	
			Colony ²				
		<i>vagans</i>	Underground/surface ²	11	13	24	
	<i>fervidus</i>	Colony surface ²	7	6	13		

		<i>rufocinctus</i>	Colony underground/surface ²	18	3	21
		<i>ternarius</i>	Colony underground ²	29	30	59
		<i>perplexus</i>	Colony surface/trees & logs ²		1	1
		<i>terricola</i>	Colony underground ²	1		1
	<i>Ceratina</i>	<i>dupla</i>	Cavity ¹	20	5	25
		<i>mikmaqi</i>	Cavity ¹	34	2	36
		<i>calcarata</i>	Cavity ¹	11	4	15
		—	Cavity ¹	4		4
	<i>Melissodes</i>	—	Ground ¹	62	61	123
Andrenidae	<i>Calliopsis</i>	<i>adreniformis</i>	Ground ¹	20	2	22
	<i>Perdita</i>	—	Ground ¹	24	14	38
Halictidae	<i>Agapostemon</i>	<i>virescens</i>	Ground ¹	111	72	183
	<i>Augochlorella</i>	<i>aurata</i>	Ground ¹	53	19	72
	<i>Halictus</i>	<i>ligatus</i>	Ground ¹	8	29	37
		<i>rubicundus</i>	Ground ¹	3	1	4
		<i>confusus</i>	Ground ¹	1		1
		—	Ground ¹	33	51	84
	<i>Lasioglossum</i>	—	Ground ¹	460	325	785
	<i>Sphecodes</i>	—	Ground nest parasite* ⁵	13	1	14
Colletidae	<i>Colletes</i>	—	Ground ¹	28	16	44
	<i>Hylaeus</i>	—	Cavity ³	7	7	14
Total				1070	756	1826

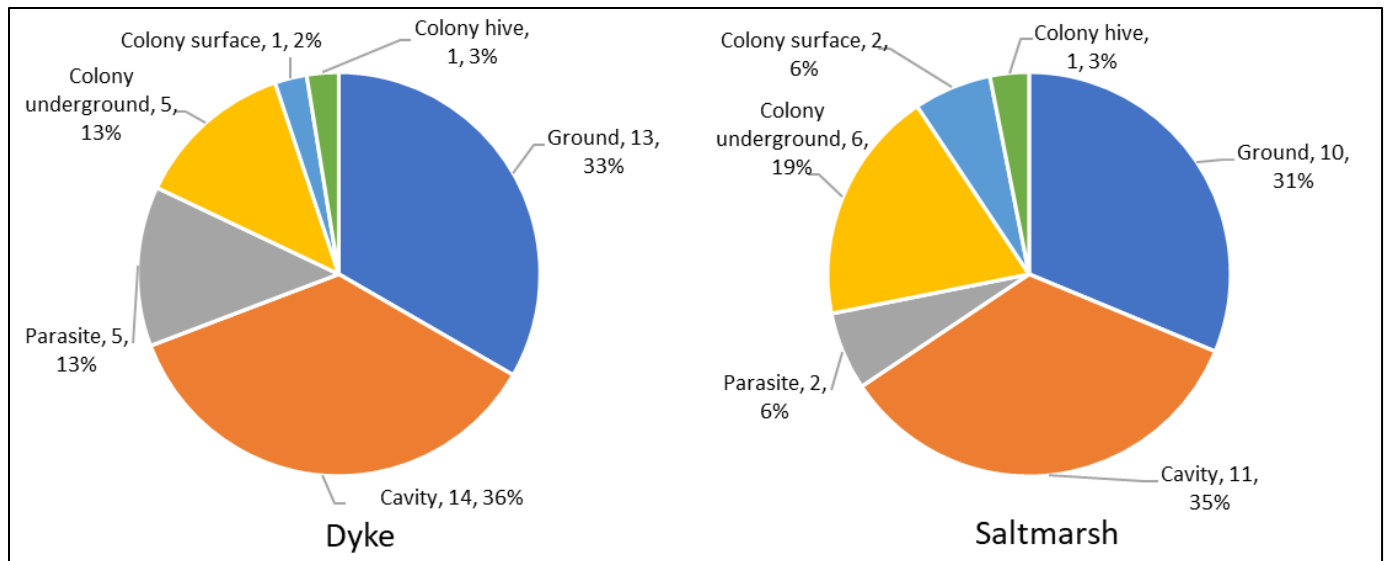


Figure 6. Bee nesting biology. Proportion bee taxa with respective nesting biology by habitat. Specific taxa preferences reported in Table 3.

3.1.4 Pollinator richness

In total 47 different taxa were collected across both sites, with 43 taxa found on dyke sites and 34 taxa found on saltmarsh sites. Between the two habitats 30 taxa were shared – including all bee genera sampled in this study. Dyke sites, Belcher Restoration and Starr’s Point South were tied for the greatest richness across both habitats, with another dyke site Starr’s Point North having the third greatest taxa richness (Table 4). The lowest richness was found on Kingsport, with another saltmarsh site Cogmangun Other and dyke site Noel West tied for second lowest taxa richness (Table 4). Mean pollinator richness on dyke sites (22 ± 1.51 SE) was significantly greater compared to saltmarsh sites (16 ± 0.86) (Figure 6). A Welch’s two sample t-test reported mean pollinator richness significantly differed between habitats ($t(11.99)=2.78, p=0.0166$).

Table 4. Pollinator richness. Total taxa richness per site – bees identified to genera/species, and wasps, lepidopterans, and syrphids identified to morphospecies. ‘SE’ = standard error.

Site	Dyke Richness	Saltmarsh Richness
Belch Restoration	26	
Starr’s Point North	25	

Starr's Point South	26	
Elderkin Dyke	22	
Newport Dyke	17	
Noel Northeast	24	
Noel Southeast	19	
Noel West	15	
Belch Reference	17	
Kingsport	11	
Newport Marsh North	18	
Newport Marsh South	19	
Cogmangun Other	15	
Cogmangun Reference	17	
Cogmangun Restoration	17	
Bramber	17	
Mean ± SE	22 ± 1.51	16 ± 0.86

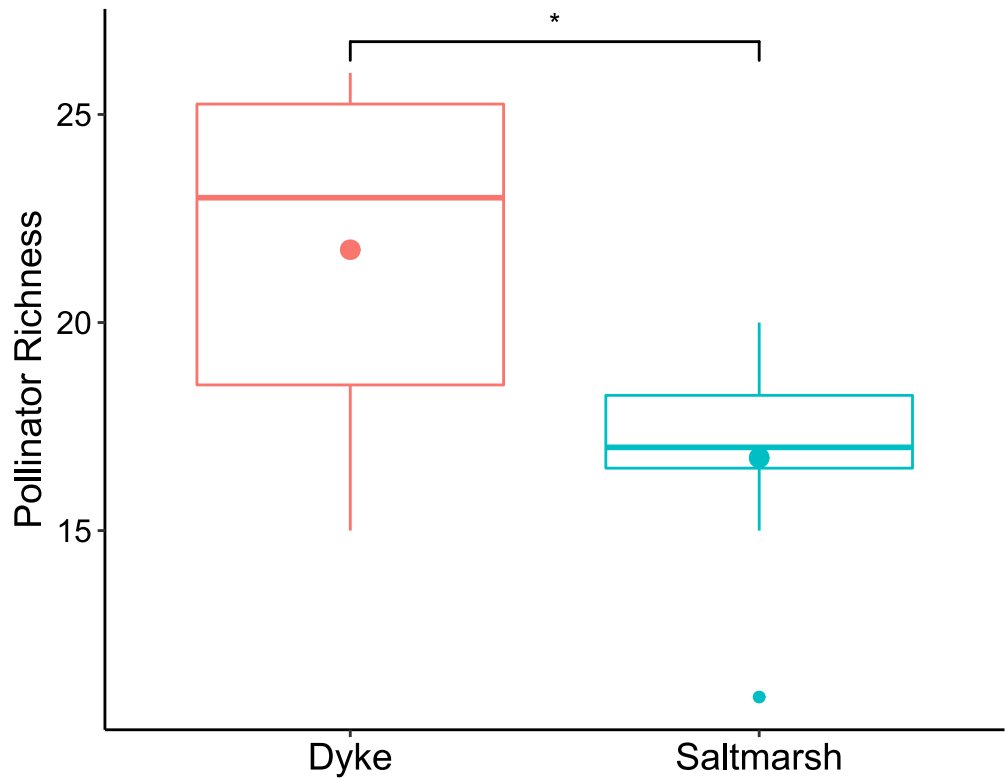
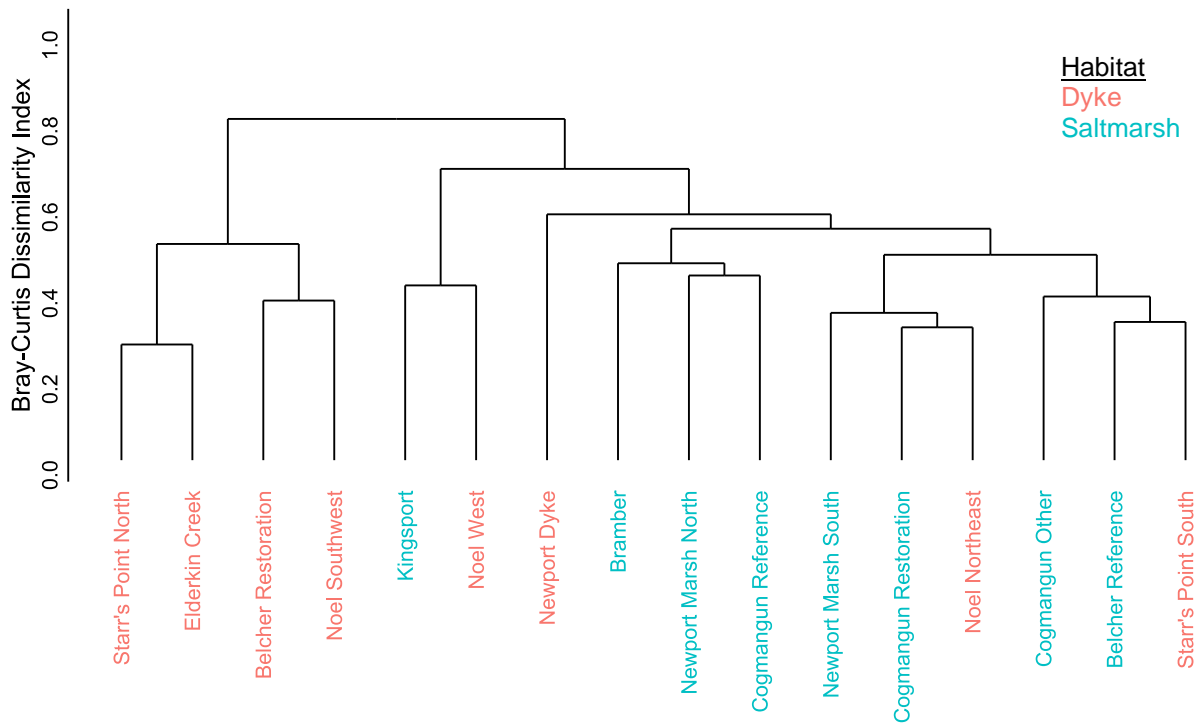


Figure 7. Mean pollinator taxon richness. Dyke sites had a greater mean richness, as well as a larger range in richness than the saltmarsh sites. Specific site richness values are specified in Table 4. Welch’s two sample t-test: $t(11.99)=2.78$, $p=0.0166$. ‘*’ = $p \leq 0.05$.

3.1.5 Bray-Curtis dissimilarity

Pairwise Bray-Curtis (B_c) dissimilarity values among sites ranged from 0.79 – 0.27, with mean B_c value of 0.49. Sites showed no predictable patterns of hierarchical clustering based on the B_c index, and sites of classified of the two habitats often were grouped with sites of the different habitat type (Figure 7). NMDS ordination of site B_c indexes showed no apparent clustering of habitats or genera/species ($k=2$, stress=0.169), indicating similar differences in pollinator assemblages (abundance and richness) across all sites and habitats (Figure 8A/B). NMDS ordination repeated for site by date B_c indexes showed some clustering of habitat ($k=2$, 0.269) – indicating pollinator assemblages on both habitats similar for a given time. Overall, no apparent clustering is observed, meaning pollinator assemblages were different in both habitats on any given sampling day (Figure 9A). Some clustering of species within a given genera was seen, meaning genera accessing these habitats were similar for a given day (Figure 9B.).



indicates greater dissimilarity. A) Temporal habitat scores. B) Temporal species scores Some temporal clustering of habitats was observed – indicating pollinator assemblages within a both were similar at a given time. Overall, no apparent clustering is observed for habitats. Some cluster of genera is seen, indicating species within a genera are accessing these habitats at similar times.

3.2 Floral resources

3.2.1 Floral abundance

Floral abundance index scores were much higher on dyke sites compared to saltmarsh sites (Table 5). Over the sampling period floral abundance on dykes were consistently scoring 2 or 3 with a few outliers (0 or 1) due to the tops of dykes being mowed (Figure 11). Dykes were mowed on 21 Jul, Starr's Point South and Starr's Point North; 28 Jul, Newport Dyke; 13 Aug, Starr's Point South; 24 Aug, Noel Northeast and Noel West; 02 Sep, Noel Southeast. Floral abundance on saltmarsh sites was low at the beginning of the study and increased later into the season (Figure 11). However, the majority of scores were 0, with only two sampling events reaching a score of 3 (Bramber; 09 Jul and 02 Oct) (Figure 11). This increase of floral abundance which began in mid August is explained by the flowering of Seaside goldenrod (*Solidago sempervirens*) which continued to flower into October. Mean floral abundance was greater on dykes compared to saltmarshes, with means of 1.982 and 0.569 respectively (Figure 10, Table 5). A Welch's two sample t-test reported significant differences in average abundance between habitats ($t(108.52) = 9.57, p \ll 0.001$). The standard deviations of floral abundance were similar between habitats (Table 5). A type I ANOVA on a linear model of indexed abundance by date (Multi $R^2 = 0.451$), reported a significant effect of habitat over time ($F(1) = 92.08, p \ll 0.001$) (Figure 11, Appendix 15).

Table 5. Floral abundance. Floral abundance index scores ranged from 0-3 (see methods). Floral abundance was greater on dyke sites then saltmarsh. ‘SD’ = standard deviation.

Site	Dyke Mean	Dyke SD	Saltmarsh Mean	Saltmarsh SD
Belch Restoration	2.286	0.756		
Starr's North	2.286	0.756		
Starr's South	1.571	0.535		
Elderkin Dyke	2.857	0.378		
Newport Dyke	1.143	0.690		
Noel Northeast	1.857	0.690		
Noel Southeast	1.714	1.113		
Noel West	2.143	0.690		
Belch Reference			0.571	0.535
Kingsport			0.429	0.535
Newport Marsh North			0.286	0.488
Newport Marsh South			0.500	0.837
Cog Other			0.571	0.535
Cog Reference			0.222	0.441
Cog Restoration			0.375	0.518
Bramber			1.714	0.951
Total	1.982	0.842	0.569	0.728

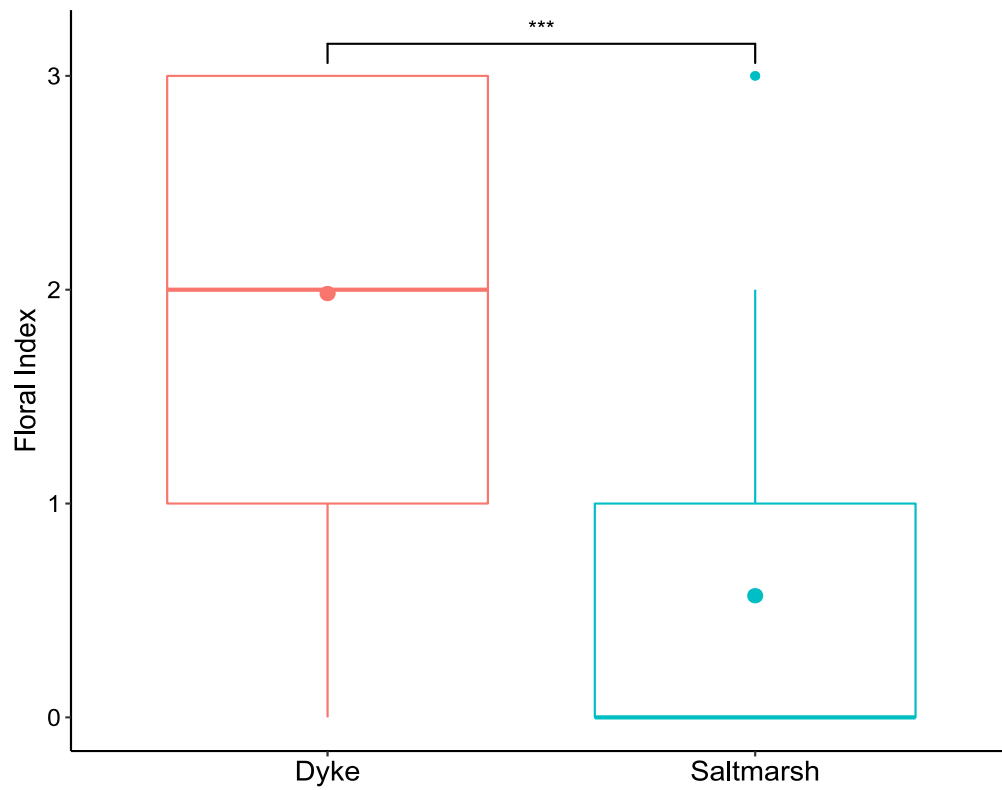


Figure 11. Mean floral abundance. Floral index was used to measure floral abundance (see methods). Dyke sites had a greater mean abundance, as well as a larger range in abundance than the saltmarsh sites. Each site's average (\pm SD) values are specified in Table 5. Welch's two sample t-test: $t(108.52) = 9.57$, $p \ll 0.001$. '***' = $p \leq 0.001$.

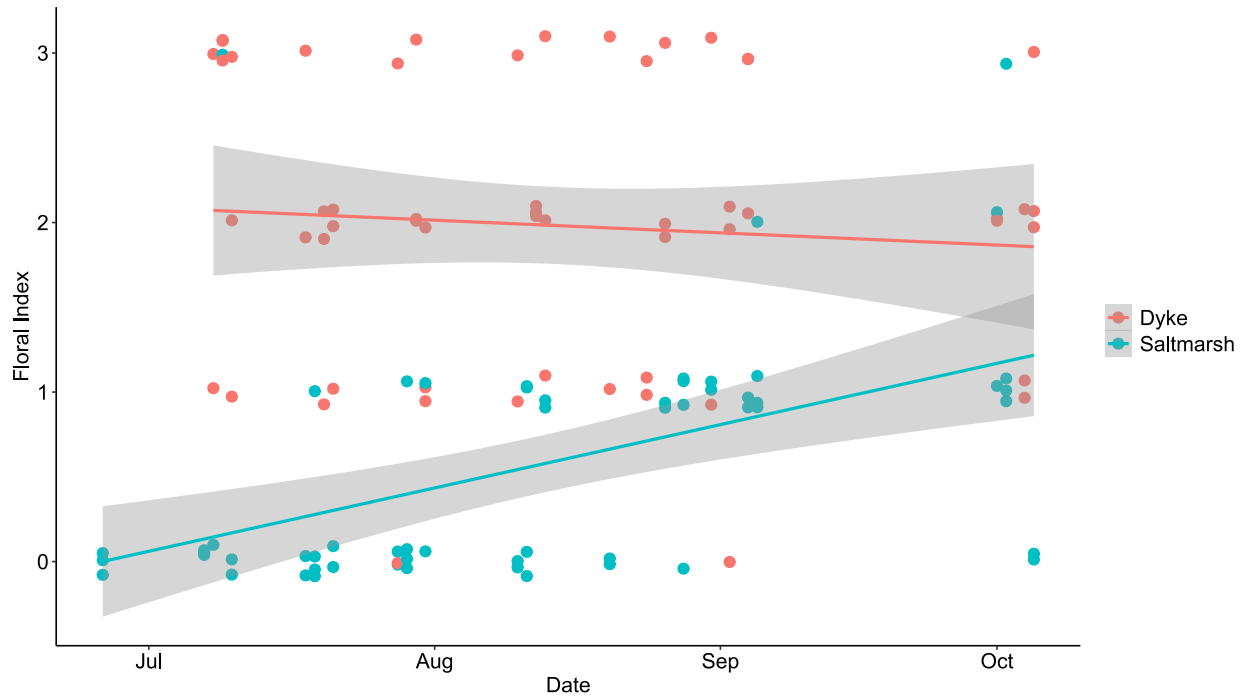


Figure 12. Temporal floral abundance. Floral abundance measured using index, ranging from 0-3 (see methods). Floral abundance was greater on dykes during the entire study. Floral abundance on saltmarshes increased as time went on, associated mainly to flowering of *Solidago sempervirens*. Regression (\pm SD) shown is a linear model (Multi $R^2 = 0.451$). A type I ANOVA reported significant effect of habitat ($F(1) = 92.08$, $p < 0.001$) (Appendix 15). Note points are jittered to prevent data overlap.

3.2.2 Floral richness

In total 38 flowering (morpho)species were recorded in this study (Table 7). Most flowering individuals observed in this study were herbaceous perennial species, apart from *Rosa* spp. Floral richness was much greater on dykes, ranging from 10-21 unique species observed on a given site (Table 6). This is contrasted by much lower floral richness on saltmarshes, which ranged from 1-10 for a given site, with 10 unique species being an outlier from the Bramber site (Table 6).

Three flowering species were seen on all dyke sites, *Daucus carota*, *Sonchus* spp.

(morphospecies), and *Trifolium pratense*. Other genera *Trifolium*, *Taraxacum officinale* and *Vicia cracca* were common on dyke sites. *Solidago sempervirens* was common across most sites in both habitats, as it was only absent from Noel Southeast, Noel West, and Kingsport sites. On

dyke sites *S. sempervirens* was always found on the waterway side of the dyke footprint along the fringe marsh. Not including Bramber, only six unique species were observed across all saltmarsh sites. *Limonium carolinianum* was the second most common taxon found in saltmarshes, with occurrences in Kingsport, Newport Marsh South, Cogmangun Other, and Cogmangun Restoration. *Limonium carolinianum* was only found on a single dyke site, Newport Dyke. Like *S. sempervirens*, *Limonium carolinianum* was located on the dyke footprint/fringe marsh boundary. The mean floral richness on dykes was greater than saltmarshes (Figure 12, Table 6). A Welch's two sample t-test reported significant differences in mean richness between habitats ($t(12.15) = 6.37, p << 0.001$).

Table 6. Floral richness. Floral taxon richness measures as the total unique flowering species (or genera) observed on each site. See table 7 for list species found on each site.

Site	Dyke Richness	Saltmarsh Richness
Belch Restoration	18	
Starr's North	20	
Starr's South	12	
Elderkin Dyke	21	
Newport Dyke	10	
Noel Northeast	11	
Noel Southeast	14	
Noel West	12	
Belch Reference		3
Kingsport		1
Newport Marsh North		2
Newport Marsh South		2
Cog Other		3
Cog Reference		2
Cog Restoration		2
Bramber		10
Mean ± SE	15 ± 1.52	3 ± 1.01

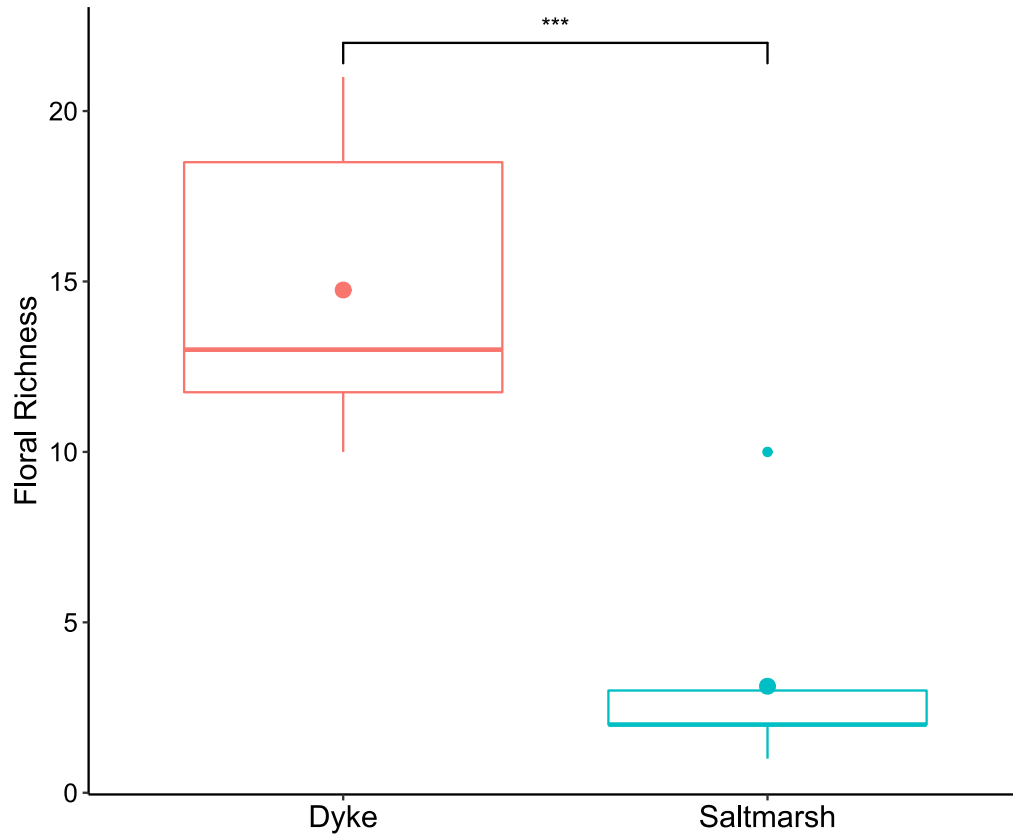


Figure 13. Mean floral taxon richness. Mean richness is the total mean of unique species across all sites for a given habitat. Dyke sites had a greater mean richness, as well as a larger range in richness than the saltmarsh sites. Each site's mean (\pm SE) values are specified in Table 6, and flowering species are listed in Table 7. Welch's two sample t-test: $t(12.15) = 6.37$, $p << 0.001$. '***' = $p \leq 0.001$.

Table 7. Flowering species. All showy flowering taxon found within the area of the transects were identified in the field or later using photos taken. Some photos were unable to be identified to species and were left to genus level. ‘BS’ = Belcher Restoration, ‘SN’ = Starr’s Point North, ‘SS’ = Starr’s Point South, ‘ED’ = Elderkin Creek Dyke, ‘ND’ = Newport Dyke, ‘NNE’ = Noel Northeast, ‘NSE’ = Noel Southeast, ‘NW’ = Noel West, ‘BF’ = Belcher Reference, ‘KS’ = Kingsport, ‘NMN’ = Newport Marsh North, ‘NMS’ = Newport Marsh South, ‘CO’ = Cogmangun Other, ‘CF’ = Cogmangun Reference, ‘CS’, Cogmangun Restoration, ‘BM’ = Bramber.

Flowering Species	Dyke site								Saltmarsh site							
	BS	SN	SS	ED	ND	NNE	NSE	NW	BF	KS	NMN	NMS	CO	CF	CS	BM
<i>Agalinis maritima</i>													x			
<i>Chamaenerion angustifolium</i>		x														
<i>Cichorium intybus</i>	x			x												x
<i>Cirsium arvense</i>	x	x	x	x												
<i>Convolvulus arvensis</i>		x	x			x										x
<i>Daucus carota</i>	x	x	x	x	x	x	x	x	x							x
<i>Dianthus armeria</i>							x									
<i>Epilobium spp.</i>			x					x								
<i>Erigeron annuus</i>				x				x								
<i>Hieracium spp.</i>							x									
<i>Hypericum perforatum</i>			x	x		x	x	x								
<i>Leucanthemum vulgare</i>				x			x									
<i>Limonium carolinianum</i>					x					x		x	x		x	
<i>Linaria vulgaris</i>		x			x											
<i>Lotus corniculatus</i>	x	x		x		x	x	x								
<i>Medicago sativa</i>	x	x														
<i>Melilotus albus</i>				x		x	x									
<i>Oenothera biennis</i>	x	x														
<i>Persicaria sagittata</i>		x														
<i>Rosa spp.</i>				x												x
<i>Solidago canadensis</i>	x	x		x				x								x
<i>Solidago sempervirens</i>	x	x	x	x	x	x			x		x	x	x	x	x	x
<i>Solidago spp.</i>	x			x			x									

<i>Sonchus canadensis</i>	x	x										
<i>Sonchus spp.</i>	x	x	x	x	x	x	x	x	x			x
<i>Spiraea alba</i>		x										
<i>Spiraea tomentosa</i>				x								
<i>Symphotrichum novi-belgii</i>	x			x	x		x	x		x		x
<i>Symphotrichum spp.</i>	x											
<i>Tanacetum vulgare</i>		x	x									
<i>Taraxacum officinale</i>	x	x	x	x		x		x				
<i>Trifolium aureum</i>									x			
<i>Trifolium hybridum</i>				x								
<i>Trifolium pratense</i>	x	x	x	x	x	x	x	x				x
<i>Trifolium repens</i>	x	x		x	x							
<i>Trifolium spp.</i>		x	x		x		x					
<i>Vicia cracca</i>	x	x		x	x	x	x	x				x
<i>Vicia spp.</i>	x		x	x		x	x					

3.3 Pollinator-plant relationship

Combined habitat data showed pollinator abundance increased slightly with mean floral abundance (Figure 14, Appendix 16). However, this result was weak and not statistically significant ($F(1,14) = 0.1854$, $p = 0.6733$). Combined pollinator richness increased with floral richness, with floral richness having a significant positive effect ($F(1,14) = 12.88$, $p = 0.00296$) (Figure 15, Appendix 17).

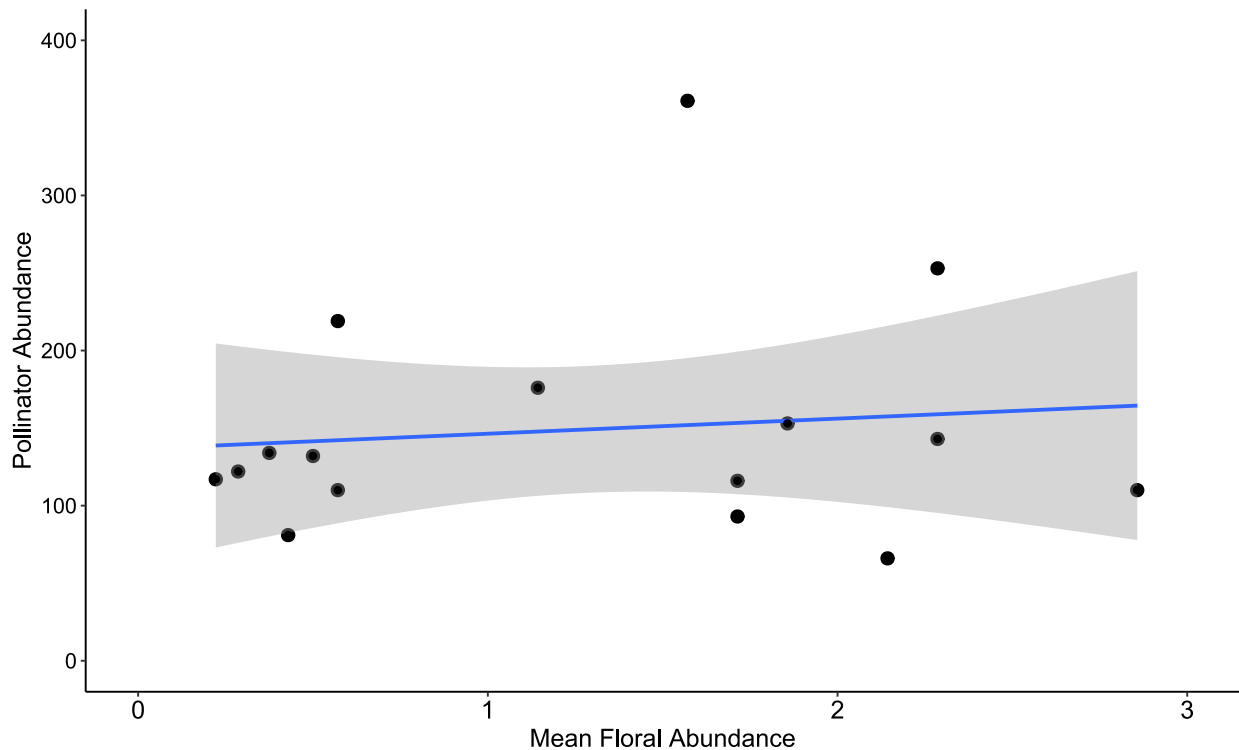


Figure 14. Pollinator and floral abundance. Linear regression of pollinator abundance (n=16) by mean showy floral abundance (n=16). Multiple $R^2 = 0.01307$. Shaded area = +/- standard deviation of regression.

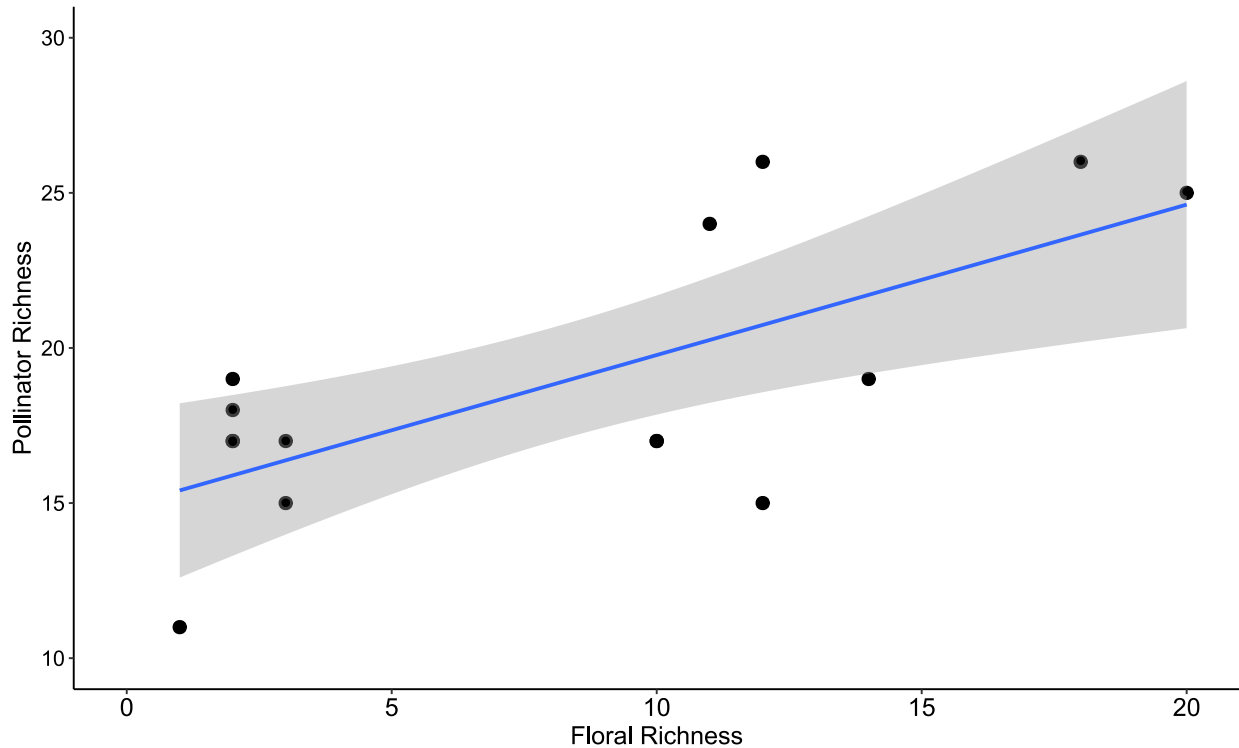


Figure 15. Pollinator and floral richness. Linear regression of pollinator richness (n=16) by mean showy floral abundance (n=16). Multiple $R^2 = 0.4792$. Shaded area = +/- standard deviation of regression.

4. DISSCUSSION

4.1 Dyke versus saltmarsh habitat

4.1.1 Pollinator community

As predicted dykes supported a greater mean abundance of pollinators compared to saltmarshes (Figure 4). Although, the result of the abundance comparison was not statistically significant, the signal of a great abundance was clear. This non-significant result can be explained by the low sample size, as well needing to use a nonparametric test t-test, both factors in reducing statistical power. Given that, the abundance of pollinators found on saltmarshes was surprising. This is because the amount of showy floral resources in comparison is low on saltmarshes, and thus I expected the number of pollinators to reflect this difference (Dicks et al., 2015; Roulston & Goodell, 2011). However, the relationship between floral abundance and

pollinator abundance was weak (Figure 14). The differences in abundance in this study rather may be explained by some other factor than floral abundance (further discussion in next section). Results of temporal abundance also show that pollinators are accessing these habitats simultaneously (Figure 5) – which eliminates any temporal access differences over the season. This result is still interesting as pollinators are not changing foraging strategies as the season goes on – which can inform the habitat management regimes.

However, the observations of *Bombus* spp. and Family: Megachilidae bees visiting *Spartina pectinata* does suggest I may have underestimated the relative value of saltmarshes to pollinators. A review by Saunders (2018) reported a number of pollinators visit wind pollinated plant taxa, as well it is known that Megachilidae bees use sections of leaves to build nests as well protect food stocks for immatures (Cane et al., 2007). Although no reports of bees visiting *S. pectinata* could be found in the literature, one previous study has noted *Bombus* spp. visiting wind pollinated saltmarsh graminoids in Western Canada (Pojar, 2008). Pojar (2008) argued that the relationship between these pollinators and plants was opportunistic. Notably high rainfall made for poor conditions wind pollination on the studied saltmarsh, and pollen was thus available to be distributed by pollinators, and these bees chose to pollinate these flowers due to their high abundance. Pollinators typically visit a nearer flowering patch of less nutritional quality than a further patch of greater quality, however these depends on specific life histories, sex and age of pollinator (Harder, 2001; Motro & Shmida, 1995; Ne'eman et al., 2006). Bees and other pollinators may be visiting saltmarsh graminoids due to opportunity or may be accessing specific resources on this habitat (e.g. nesting material, nesting habitat, immature life stage, etc.) (Abrol, 2011; Mader, 1972). Further research into pollinators visiting wind pollinated taxa,

particular within the Bay of Fundy system due to its unique local conditions (intense water intrusion) is needed to understand the ecology of pollinators in these habitats.

Pollinator richness was greater on dykes than saltmarshes, which follows the original prediction. The positive relationship between pollinator richness and floral richness is well understood, and the results of this study is no different (Potts et al., 2003; Roulston and Goodell, 2011) (Figure 15). However, it is important to not overlook the makeup of a given community – as some mono/oligophilic plant-pollinator relationships may exist. Specialist bee taxa were rare in this study, and were found both on habitats, and thus no clear relationship between a given habitat's ability to support these specialist taxa could be made. The Bray Curtis dissimilarity allowed some insight (or rather lack thereof) into the community composition pollinators between habitats. No clear clustering of sites by habitat were seen (Figure 8 and 9A). Similarly, no clustering of genera for species scores summed for the entire study was seen indicating again that these communities are vastly different locally (Figure 9B). This information tells us that these pollinator communities are most likely specific to site – the potential reasons for these differences will be discussed below in section 4.2. No clear changes in pollinator assemblages on each site was seen over the study period (Figure 10A). Interestingly though, when looking at species scores as a function of time some groupings of species within a given genera are seen (Figure 10B) – indicating these species are accessing both habitats at the same time. However, this result is not very clear as overall no clustering was seen, and the stress level of the NMDS is rather weak to be making such claims.

4.1.2 Plant community

Plant communities are vastly different between these two habitats. The dykes offer freshwater habitat, suitable to many graminoids and ruderal showy flowering species (Table 7). This is

contrasted by the saltmarsh where the majority of plants are wind pollinated graminoids (e.g. *Spartina* spp., *Juncus* spp., etc.) with only a handful of flowering species (Table 7). This study showed that mean floral abundance is much higher on dykes compared to saltmarshes (Figure 11), otherwise greater availability of floral resources which pollinators need to sustain themselves (Roulston & Goodell, 2011). As well results showed that floral abundance on dykes was stable across the growing season, whereas floral abundance only increased on saltmarshes into the fall (Figure 12). This has important implications for conservation of wild bees, as dykes are offering not only greater amounts of flowers to pollinators but also more sustained resources. In agroecosystems providing sustained off crop floral resources is important for sustaining healthy pollinator populations for crop pollination (Dicks et al., 2016, 2010; Roulston and Goodell, 2011).

Floral richness was also found to be higher on dykes than saltmarshes (Figure 13). This is an important result as more diverse floral communities are known to support more diverse pollinator communities (Dicks et al., 2015; Potts et al., 2003). A number of different weedy non-native weedy species such as clover and alfalfa were seen on the dykes. There may be some influence of cover crops blowing onto the surrounding dykes. Only a handful of flowering species were seen on saltmarshes, with only a single species seen on all saltmarsh sites except Kingsport, *Solidago sempervirens* (Table 7).

4.1.3 Nesting habitat

Although I did not directly quantify nesting habitat in this study I can make some anecdotal statements on the relative value of each habitat for nesting resources. Ground nesting bee species typically prefer small grain densely compacted soils, with majority of species preferring exposed soils while some prefer surrounding ground cover (Sardiñas and Kremen, 2014). One notable

characteristic of a number of dykes in this study (as well as dykes in general in the Bay of Fundy) is many are made of sandy soils – which pollinators are known to nest in (Sardiñas and Kremen, 2014). Additionally the bank of the dyke is most suitable to ground nesting bees, as bees are known to prefer slopes (particularly those south facing) (Mader, 1972). Given this, I believe dykes are offering significant amount of nesting habitat to bee ground nesters. This is contrasted by the saltmarshes where the sediment (mud and clay) is typically unsuitable for most ground nesters, however some *Megachile* spp. prefer muddy soils which they then line with leaves (Buschini, 2006). However it should be noted that the majority of a saltmarsh is periodically inundated with water (Foster et al., 2013; McKinley et al., 2018), and as such nests would be destroyed during flooding which would severely disrupt pollinators (Roulston and Goodell, 2011). However, it is possible pollinators are nesting in the furthest upper reaches of the saltmarsh in the high marsh zone. More research is needed into both habitats ability to support nesting habitat, with dyke habitats in particular likely to reveal the most potential to support pollinators.

Cavity nesting habitat within both habitats is rather limited in comparison to hedgerow or forest edges. However, several Asteraceae species were seen on the dyke which a handful of bee species nest in (Potts et al., 2003). Other pollinators nest in vegetation found on dykes as well, with many wasp species nesting in paper nests built in amongst dense grass (Steffan-Dewenter, 2003). Overall dykes are more likely to support a greater amount of nesting habitat in comparison to saltmarshes.

4.2 Landscape and site context

4.2.1 Landscape context

As any ecological study, landscape characteristics and site locations are likely to have an effect on the pollinator assemblages found between habitats and also have effects at the site level (Herrera, 1995; Edwards et al., 2019). This is exemplified by the results of the Bray Curtis dissimilarity, which showed no apparent clustering of sites by proximity of site or habitat type (Figure 7 and 8). A multitude of biotic and abiotic influences makes it difficult to tease apart themes at a site level, however trends can appear on a macro-landscape scale such as focused in this work (Goulson et al., 2015). It is important to note that saltmarsh and dyke habitats in Nova Scotia (specifically in Annapolis, Kings, Hants, Colchester, and Cumberland counties) and are natural and semi-natural habitat respectively, which both occur in close proximity to intensely managed crops which can (dependent on crop area, and quality of adjacent habitat) fragment bee populations (Gabriel & Tschardt, 2007; Goulson, 2003). Crop intensification has threatened native bees globally (Kremen et al., 2002), and also threatened other pollinators (Abrol, 2011). These farms have adverse effects on pollinators not only from fragmentation, but also through incidental risks such as pesticide exposure, increase pest and parasites, and tillage (Dicks et al., 2015; Goulson, 2003; Klein et al., 2007; Roulston and Goodell, 2011). These adjacent natural and semi-natural habitats are known to be important for supporting wild pollinators that offer their services to crops (Garibaldi et al., 2014; Goulson, 2003; Roulston and Goodell, 2011).

In the case of saltmarshes, these habitats are largely fragmented in the province. Today approximately 77% of Nova Scotia's natural tidal saltmarsh has been lost due to dyking (MacDonald et al., 2010; Wollenberg et al., 2018). In Nova Scotia > 241 km of dykes along run along coasts and waterways, protecting 16,139 Ha (161 km²) of agricultural marshland behind

them (van Proosdij et al., 2018). All dyke sites in this studied are owned, monitored and maintained by the Nova Scotia Department of Agriculture. Maintenance regimes of dykes often include frequent mowing of dyke tops, as will be discussed later. Alternatively, in some cases agreements have been made so the tops of dykes will be hayed by the landowner adjacent to the dyke. As will be discussed later this has implications on potential management strategies which may support wild pollinators in these habitats. In regards to saltmarsh numbers, no estimates of private landownership can be found, however it is known that 86% of Nova Scotia's coastline is privately owned (Soomai et al., 2011).

4.2.2 Saltmarsh sites

All Cogmangun sites were proximal (<100 m for Cogmangun Other and Restoration; ~600 m for Reference) to a no-spray organic farm – therefore the influence of pesticide exposure can largely be ignored on these sites. However, it is likely that pollinators visiting these sites may also be visiting the flowering crops, which may influence pollinator abundance by offering floral resources. This farm grows a multitude of diverse crops which may be attracting the diverse pollinator assemblages seen on these sites as greater diversity of floral resources is known to attract more diverse pollinator communities (Roulston and Goodell, 2011). However previous research has shown that the small scale and mixture of crop to semi-natural habitat (spatial heterogeneity in vegetation and intensity of management) is what drives pollinator diversity within these organic farms, and not crop diversity (Hass et al., 2018). These sites also had dense woodland within 100 meters of the sampling transects, which is important to consider as it is known woodland habitats support pollinators by offering diverse niches for a range of pollinators (Mallinger et al., 2016). These saltmarshes are found further from the coast of the Minas Basin, along the Cogmangun River. As such the wind as well as exposure to salinity influences (less

frequent tidal inundation, lower soil salt content) are lesser compared to the coast, which could potentially stress pollinators (Roulston & Goodell, 2011). These factors may help explain why abundance of pollinators captured on the Cogmangun Restoration and Reference sites were relatively higher than saltmarsh sites without these influences. However, it is unclear why Cogmangun Other had a much greater abundance than all saltmarsh sites given that the other Cogmangun Restoration was only a few hundred meters away, and shared the mentioned environmental features. Differences in floral abundance between Cogmangun Other (Index score = 0.571, Table 5) and Cogmangun Restoration (Index score = 0.375, Table 5) may explain the discrepancy in pollinator abundance. However, floral index scores similar to Cogmangun Other at other saltmarsh sites like Belcher Reference did not translate to the same abundance as Cogmangun Other – leading back to some other unmeasured site influence. Although not the focus of this work, it is interesting to note the pollinator abundance and richness were comparable between the Restoration site (restoration completed in 2010) and Reference site.

Both Newport saltmarsh sites were located within 300 m of intensively managed and pesticide spray crops (hay and corn). There is potential of pesticide drift onto these habitats which would influence pollinator assemblages (Kremen et al., 2002; Roulston and Goodell, 2011). That being said we see comparable pollinator abundances to Cogmangun sites. These sites are located along the Saint Croix river, and like Cogmangun sites are further from the coast and thus have lower coastal stressors.

Belcher Reference and Bramber saltmarsh sites are the unique among the saltmarsh sites, as these two are the highest in elevation and consequently more brackish-fresh water communities exist nearby and to some extent on the sites themselves – making these sites more . This difference is reflected in the higher floral abundance scores seen on these two sites (Table

5), as well as a higher plant taxon richness at Bramber (Table 6). Belcher Reference is the only saltmarsh site which had heavy urbanization within its proximity (~200 m). The effects of urbanization on pollinators varies greatly depending on life histories and location, however overall pollination services are not disrupted (Wenzel et al., 2020).

Kingsport was certainly the most coastal of all saltmarsh sites, as it is located in a inter tidal zone along the Minas Basin. Wind conditions were often more extreme on this site, which may negatively affect pollinator visitations (Crall et al., 2019). Wind directly effects pollinators increased flight costs (Kevan and Baker, 1983), as well indirectly by disrupting scent plumes from flowers that attracts pollinators (Murlis and Jones, 1981). This may explain why this site had the lowest pollinator abundance and taxon richness as conditions on this are unfavorable to pollinators. This site is very frequently inundated by tidal flow, and even the upland reaches of this marsh experience high water stress. The vegetation on this site was frequently flattened or broken after tidal events. This may explain why the floral resources were so low, as Kingsport also scored lowest in the floral index (Table 5) and only a single showy plant species was recorded (Table 6). Of course the low availability may be the driving factor of the low pollinator abundance and richness (Roulston and Goodell, 2011). Some buildup of drift wood, and other dead vegetation was seen on the upper region of this marsh which may offer potential nesting habitat (Sheffield et al., 2003). There are several crop types located within 500 m of this site, with both organic no-spray and conventional (spraying of pesticides) managed fields proximal. This again may have some influence on the pollinators seen on this site. In this case it appears these farms are more attractive, and or possibly too far away for pollinators to frequent this site.

4.2.3 Dyke sites

The Noel dyke sites were the farthest East of all study sites, and were the only sites located in the Cobequid Bay, specifically in the Noel Bay inlet. Wind on all three of these sites was typically greater compared to other dykes due to the proximity to the open bay, which as discussed above can have adverse effects on pollinators. All other these dykes are relatively narrow with a steep grade (slope incline). Noel West was the only in this study to not have any foreshore fringe marsh, as the dyke was directly in front of the bay. The landward side of this site was dense hedgerow which transitions into forest. A conversation with a nearby landowner revealed this dyke had been directly sprayed with herbicide the year prior, to eliminate a poison hemlock (*Conium maculatum*) infestation. This may have negatively affected the pollinator population the year prior, and thus may explain why pollinator abundance was less compared to other Noel sites (Haines et al., 2019). This claim however cannot be substantiated by this study; rather is a potential hypothesis. The two remaining Noel sites had intensely managed agricultural corn crops, but no pollinator facilitated crops were proximal. Given these conventionally managed fields it is possible that these sites may have a negative pesticide influence (Klein et al., 2007; Roulston and Goodell, 2011). Additionally, the Noel Northeast site had substantial buildup of drift wood and other dead vegetation which may offer some nesting habitat (Cory S. Sheffield et al., 2003). Overall, there are no clear non-vegetative discrepancies between these sites to explain why pollinator abundance was so much lower on the Noel West sites compared to the other two Noel sites.

The two Starr's Point sites are located on the Wellington Dyke, which is one of the longest dykes in the province, protecting approximately 3,000 acres (12 km²) of farmland (Whitelaw, 1997). This dyke follows the Canard River, which is fed by the Minas Basin. The

Starr's Point South pollinator counts were more than double that of the Starr's Point North site. It is somewhat unclear why this is the case. An apiculture (honey bee) farm is located ~1.5 km from the South site, and ~5 km from the North site and thus may have some potential influence as this is well within the foraging range of *Apis mellifera* (Beekman and Ratnieks, 2000). However, these sites did not see greater numbers of *A. mellifera* compared to other sites. Honey bees can disrupt wild bee pollination networks, and can damage native plant ecosystems through inadequate pollination (Do Carmo et al., 2004; Valido et al., 2019). This is seemingly counterintuitive as Starr's Point South site had the greatest pollinator abundance in this study. The effects of honey bees on wild pollinators in these agroecosystems is still poorly understood, and likely there are landscape specific circumstances (Do Carmo et al., 2004; Lonsdorf et al., 2009). The main difference between these two sites were their proximity to adjacent crops. Starr's Point North was immediately flanked by a legume crop and other surrounding fields included corn crops likely being sprayed with pesticides. The South site was surrounded by fallow fields and hay fields. Also there is a U-Pick farm (conventionally managed) with apple, pumpkin, squash, and other berry crops located <1 km from the site. These crops may be helping to attract more pollinators in comparison to the North site, however further research is needed to understand the movement of pollinators between crops and these habitats.

Elderkin Creek and Newport Dyke sites were located on opposite sides on the Saint Croix River which implies they should have almost perfectly similar local weather conditions. When comparing pollinator abundances between these two sites they are similar, however Elderkin Creek did have slightly fewer counts. The Elderkin Creek site is flanked by foraging crops, for cattle. Whereas the Newport Dyke is surrounded by hay fields, with a number of hedgerows as well as nearby forest that may offer more resources for pollinators (Dicks et al., 2015; Roulston

and Goodell, 2011). These dykes also differ in that the Newport Dyke has approximately 100 m of foreshore marsh, compared to only 5-10 m of fringe marsh at the Elderkin Creek site. This potentially implies that pollinators visiting the Newport Dyke are also attracted being attracted to the nearby expansive marsh body, indicating this site supports more pollinators locally (Roulston and Goodell, 2011). This claim is supported by the flowering of *Solidago sempervirens* on Newport Marsh South (located immediately next to the Newport Dyke site) in mid-August into the fall, as well potential of pollinators visiting wind pollinated grasses. Pollinators moving between dyke and fringe marsh, and other nearby saltmarsh will be discussed in more detail in another section below.

Belcher Restoration is unique among the dyke sites, as it was recently realigned in May 2018 when the previous dyke was breached and tidal flow was reintroduced to the current day foreshore fringe marsh. This dyke is also wider and has a shallow grade (slope of bank) in comparison to other dyke sites. This dyke is also particularly different for the amount of exposed soil it has, as it is not currently being hayed like a number of dyke sites, and weedy ruderals seem to have not completely colonized. This bare soil may offer more nesting habitat to ground nesters, as some ground nesters only nest in exposed soils without vegetation (Cane et al., 2007; Sardiñas and Kremen, 2014). Given that this dyke was realigned in 2018, it is possible ground nesters could return as at least one undisturbed foraging season had passed (2019 season) prior to sampling in this study (Tonietto and Larkin, 2018). However, the effects on pollinator communities, (particularly ground nesters as they are most at risk) of dyke realignment are not currently well understood.

4.3 Pollination services and disservices

4.3.1 Crop pollination

Wild pollinators globally are believed to be on decline (Potts, Biesmeijer, et al., 2010). This is worrying, as diverse bee communities are needed to support sufficient pollination of crops, and reliance on honey bees is a dangerous gamble (Klein et al., 2007). Pollinators are essential in the global food security equation (van der Sluijs and Vaage, 2016), and without these pollinators approximately a third of global food production would be lost (Ollerton et al., 2011). Additionally research has shown wild pollinators increase crop yields in comparison to honey bees, and heavier utilization on wild pollinators for crop should be favoured (Dicks et al., 2016; Winfree et al., 2008). It is essential to understand how pollinators access adjacent natural and semi-natural habitat to ensure their health for pollination services (Dicks et al., 2016, 2010; Winfree et al., 2008).

The results of this study showed that the majority of pollinators visiting saltmarsh and dykes were in native species, and only three unmanaged (wild) non-native species. This shows that these habitats are valuable to wild Nova Scotian species, and should be considered when accounting ecosystem services of these spaces. Bees made up the majority of pollinator catches in both habitats in this study, however it is important to consider the pollination services of the non-bee taxa as well. In some cases these non-bee taxa are in fact more efficient pollinators of some plant species (Rader et al., 2016). A study looking at nocturnal *Vaccinium angustifolium* (lowbush blueberry) pollination found a high abundance Dipteran and Lepidopteran taxa visiting these flowers, suggesting these insects contribute significantly to *V. angustifolium* pollination (Cutler et al., 2012). This is relevant locally, as Nova Scotia's largest agricultural productivity comes from blueberry production, with the annual 2010 production reported as \$22,278,000

(CAD) (NS Agri, 2010). Of course bee pollinators typically contribute the most to overall pollination services (Garibaldi et al., 2014; Goulson, 2003), which has also been seen in Nova Scotian lowbush blueberry fields (Cutler et al., 2015). As low bush blueberry is native to Nova Scotia, it is most likely that Nova Scotian native pollinators are the most effective pollinators due to co-evolution of these taxa (Potts et al., 2003), with previous work in the province indicating wild bees are the most effective (Javorek et al., 2002).

Bee taxa are particularly important for apple pollination, which in Nova Scotia makes up the second most crop productivity (after blueberry) with a value of \$12,178,000 (NS Agri, 2010). *Osmia* spp. are among the most efficient pollinators of apples, and in some cases as few as 100 females per Ha are needed (Porter et al., 2015), compared to 10-15 colonies (10000-15000 bees per colony) of *Apis mellifera* over that same area (Colwell et al., 2017). Already *Osmia tersula* and *O. lignaria* have been proven as a viable option for apple pollination in the province however their commercial adoption has yet to be tested (Sheffield et al., 2008; Sheffield, 2014). Prior to the introduction of honeybees in the province, wild bee *Andrena* spp. and *Halictus* spp. were among the most common wild pollinators of apple orchards, and were thought to offer adequate services (Gooderham, 1933). However, it is not known if current wild pollinator stocks are enough to support crop pollination without supplementary honeybee colonies in the province. In total there are 42 species of bees known to visit apples in Nova Scotia compared to 78 bee species which visit lowbush blueberry (40 shared species) (Sheffield et al., 2003). Given this, apple pollination in the province is more vulnerable to pollinator decline compared to lowbush blueberry (Goulson, 2003; van der Sluijs & Vaage, 2016). It should also be noted that only apple, blueberry, and haskap (*Lonicera caerulea*) crop pollination has been

studied in Nova Scotia, and surveys of other crop's pollinators are desperately needed to understand crop vulnerability in the province.

Conservation of wild pollinators in agroecosystems such as the Bay of Fundy dykelands offers a two-sided benefit, offering a biocultural approach to their conservation (Hill et al., 2019; van der Sluijs and Vaage, 2016). First conserving these species are a service to farmers and their crops, as well to the surrounding terrestrial ecosystems that rely on these pollinators (Klein et al., 2007; Ollerton et al., 2011). In addition to the above-mentioned benefit of potential increases in crop yields, using wild pollinators can decrease crop production cost if fewer *A. mellifera* and *B. impatiens* (increasing use in NS) colonies need to be rented. A increase in crop profitability (in crop yield) despite costs (loss of productive land) of setting aside land for floral crops or natural habitat in order to support pollinators, is seen compared to crops with no set aside land (greater comparable productive land) (Albrecht et al., 2020; Dicks et al., 2015; Morandin & Winston, 2006). In tandem these benefits increase crop profitability (Goulsons, 2003). Secondly many pollinator species are on decline, and are in imminent need of conservation efforts (Potts, Biesmeijer, et al., 2010). It is believe intervention in agroecosystems offer a great opportunity to conserve wild pollinator species, and has already shown promise in the United Kingdom (Dicks et al., 2016, 2010). Although its not always clear if conservation of species for ecosystem services (ES) is the same as conservation of biodiversity as focus on ES can oversimplify and ignore key ecosystem relationships (Mace et al., 2012); it is at least a starting point for the conservations of wild pollinators (van der Sluijs & Vaage, 2016).

4.3.2 Dyke management and re-alignment/breach

Although not directly researched in this study a few predictions can be made regarding the potential disservices dyke realignment and or breach will have on pollinator communities

accessing this habitat. Pollinator abundance was seen to be greater on dykes, so if dyke habitat is completely removed during salt marsh restoration pollinator abundance may be adversely affected. Saltmarsh restoration will take away more abundant and diverse showy plant communities, which are valuable for supporting pollinators (Roulston and Goodell, 2011). The relationship between plant community and pollinator community is mutualistic, and if one is changed then the other will follow suit (Potts et al., 2003; Thomann et al., 2013). However, more research is needed to understand how pollinators are accessing these saltmarsh before this habitat is deemed poor pollinator habitat. As seen in this study saltmarsh may offer other benefits (discussed above) to pollinators (Saunders, 2018), and the benefits of this habitat for pollinators may be currently overlooked in the literature (Davidson et al., 2020). Although it is possible that pollinators are visiting these saltmarshes simply because they are available and are not preferable foraging habitat of pollinators (in cited study bumble bees) (Pojar, 2008). A likely negative effect to pollinators during dyke disturbance will be to ground nesting pollinators (Sardiñas and Kremen, 2014), as many bee species' broods are located near the surface (<30 cm deep) (Roulston and Goodell, 2011). This is perturbing, as many bee species in Nova Scotia are known to be ground nesters (Cory S. Sheffield et al., 2003). Even realignment of a dyke will in short term disrupt ground nesters, if present, before they are to re-establish themselves in the new dyke. Additionally, floral resource, valuable particularly during off-bloom of crops, may be disrupted. However, given that many of the flowering species seen on dykes were non-native weedy species, floral resources are likely to return quickly (possibly within first year) after dyke breach. More research is needed to understand how pollinators access this habitat. Specifically, studies quantifying nesting habitat these dykes will prove valuable to stakeholders weighting the cost-benefit of dyke re-alignment.

I believe dykes offer an opportunity to provide management intervention for wild pollinators. These interventions will help conserve these pollinators which have the above-mentioned benefits. Currently the tops of dykes are frequently mowed by NSDA to prevent pest species from establishing. Although understandable, often the floral resources were destroyed on these events, and subsequent pollinator abundances (catches) were affected soon after these mowing events. Sowing of showy flowering species on tops of dykes after realignment will provide valuable floral resources (Dicks et al., 2015; Hanley et al., 2011; Roulston and Goodell, 2011). This practice would be similar to planting of flowering crops in fields, or hedgerows (Albrecht et al., 2020; Sardiñas, Tom, et al., 2016) which have shown to increase crop pollination, and limit pollinator habitat fragmentation (Gabriel & Tschardtke, 2007; Holzschuh et al., 2008). It may be beneficial to use of native showy flower species (such as Asteraceae species), or if not available non-native naturalized species (*Trifolium* spp., *Medicago sativa*, *Lotus corniculatus*, etc.) or allow dyke tops to grow fallow (Hanley et al., 2011; Mallinger et al., 2016; Cory S. Sheffield et al., 2013). This flowering species would also offer nesting habitat to cavity nesters who nest in pithy stems (Requier et al., 2020; Cory S. Sheffield et al., 2008). In fact the density of the grass monoculture vegetation often seen on dykes is likely a disservice to many ground nesting pollinators who require exposed soil (Cane et al., 2007; Williams et al., 2010). Nesting habitat could also be facilitated by removing colonizing plants within a set aside section of bare substrate, however this would likely prove tedious. Other artificial nests could be implemented on these dykes, however these nests can be costly (Mader, 1972).

4.4 Limitations

Unfortunately, due to COVID-19, this study was delayed and sampling begin after the desired start of late-April/early-May. A review by Sheffield et al., (2003) reported 73% of bee

species in Nova Scotia emerge in early spring (mid April). As such this study failed to capture pollinator assemblages that emerge in early spring, into May and June. Depending on individual bee (and other pollinator) life histories species may only forage for a short period after emergence, and abundances may decrease drastically as summer goes on (Kevan & Baker, 1983). This study may have failed to capture temporal changes in pollinator assemblages over the entire foraging season as a result.

Sampling was also limited by the time of day which pollinators were sampled, as pollinators particularly those that fly at (or before) dawn are missed (Drummond, 2016). Having several collection periods scattered at times throughout the day could provide a better representation of the pollinator communities in each of these habitats. Additionally, pollinators were only sampled using a single method, pan trapping. Although generally effective at sampling a wide range of pollinators, these traps typically underestimate abundance of larger pollinators who can more easily escape the traps (Grundel et al., 2011; Prendergast et al., 2020; Saunders & Luck, 2013).

This study is also limited in that not all pollinators were identified to species. This leaves information ‘on the table’ regarding potential assemblage differences between these two habitats. For non-bee taxa in-particular this study is somewhat flawed, as potential specimens included as pollinators may in fact be non-pollinators which were caught as non-targeted by-catch, as groups such as wasps have a range in ecological specializations. Further identification may change relative pollinator taxon richness between the two habitats, which to some degree may change some conclusions from this work. For example, hover fly taxa were identified further it is likely given the greater abundance, that species richness of hover flies is greater on dykes compared to saltmarsh. This is because as abundance of a particular group of pollinators increases, their

species richness also tends to increase (Herrera, 1995; Potts et al., 2003). Further identification is also important in the context of crop pollination, to identify what pollinators (especially specialists species) accessing these habitats may also be visiting crops (Garibaldi et al., 2014; Klein et al., 2007).

Despite these several limitations the results obtained in this study were still important for accessing the relative value of each habitat for supporting wild pollinators, particularly in the context of agroecosystems.

5. CONCLUSION

This study is the first to examine pollinator assemblages on saltmarshes and dykes in the Bay of Fundy dykelands. This research aimed to understand differences in these habitats for supporting pollinators, in part to inform their relative value for pollination services to proximal crops. This work also began addressing a gap in the literature surrounding how pollinators access saltmarsh.

The results of this study indicate that dykes support a greater abundance and richness of pollinators compared to saltmarshes. However, abundance of pollinators caught on saltmarshes was higher than expected. Bees were the most abundant group of pollinators on both habitats, with wasps being the second most. This study supports previous work that shows bees are typically the most dominant pollinator in a landscape. However, it is important to consider other non-bee taxa. Of the bee taxa *Lassioglossum* spp. were most abundant, with *Bombus* spp. being the second most abundant on both habitats. No patterns of community differences (measured as Bray Curtis dissimilarity) were seen consistently between these two habitats, likely due to two factors a) that pollinators observed in this study are probably moving between these two systems and b) several taxa were only encountered on certain sites leading to considerable community

difference among sites within a habitat type. Additionally, no strong temporal trends in abundance or dissimilarity were seen, again supporting that these pollinators are accessing these habitats simultaneously during this study.

Differences in pollinator abundance and richness are likely driven by differences in floral resources (Potts et al., 2003; Roulston and Goodell, 2011), as dykes were shown to have a greater abundance and richness of showy floral species. Interestingly, and perhaps one of the most important results of this study, *Bombus* and Family: Megachilidae bees were seen visiting a saltmarsh wind-pollinated species *Spartina pectinata*. Although no reports of bees visiting *Spartina pectinata* could be found in the literature, similar reports on *Bombus* spp. visiting other saltmarsh graminoids have been published from Western Canada (Pojar, 2008). Additionally, Megachilidae bees were seen removing sections of *S. pectinata* leaves which this family uses to build nests and keep immatures food moist. Further research is needed on pollinators on saltmarshes is needed to understand how they access this habitat. These observations at least suggest that saltmarsh does provide resources for bees.

Dyke realignment/breach in order to restore saltmarsh may be an ecosystem disservice to pollinators and local crop pollination. Disturbance of the dyke is likely to disrupt ground nesting pollinators, which will have effects of on populations if progeny are destroyed. Sowing of showy floral species could be used on dykes after realignment in order to support wild pollinators. Additionally, nesting habitat could be facilitated on dykes to help facilitate pollinators. Conservation of these wild pollinators is important in the face of their (trending) global decline, as well to crop yield and profitability and support local/global food security. Stakeholder's may use this study to weight cost-benefits of dyke realignment and saltmarsh restoration in the region.

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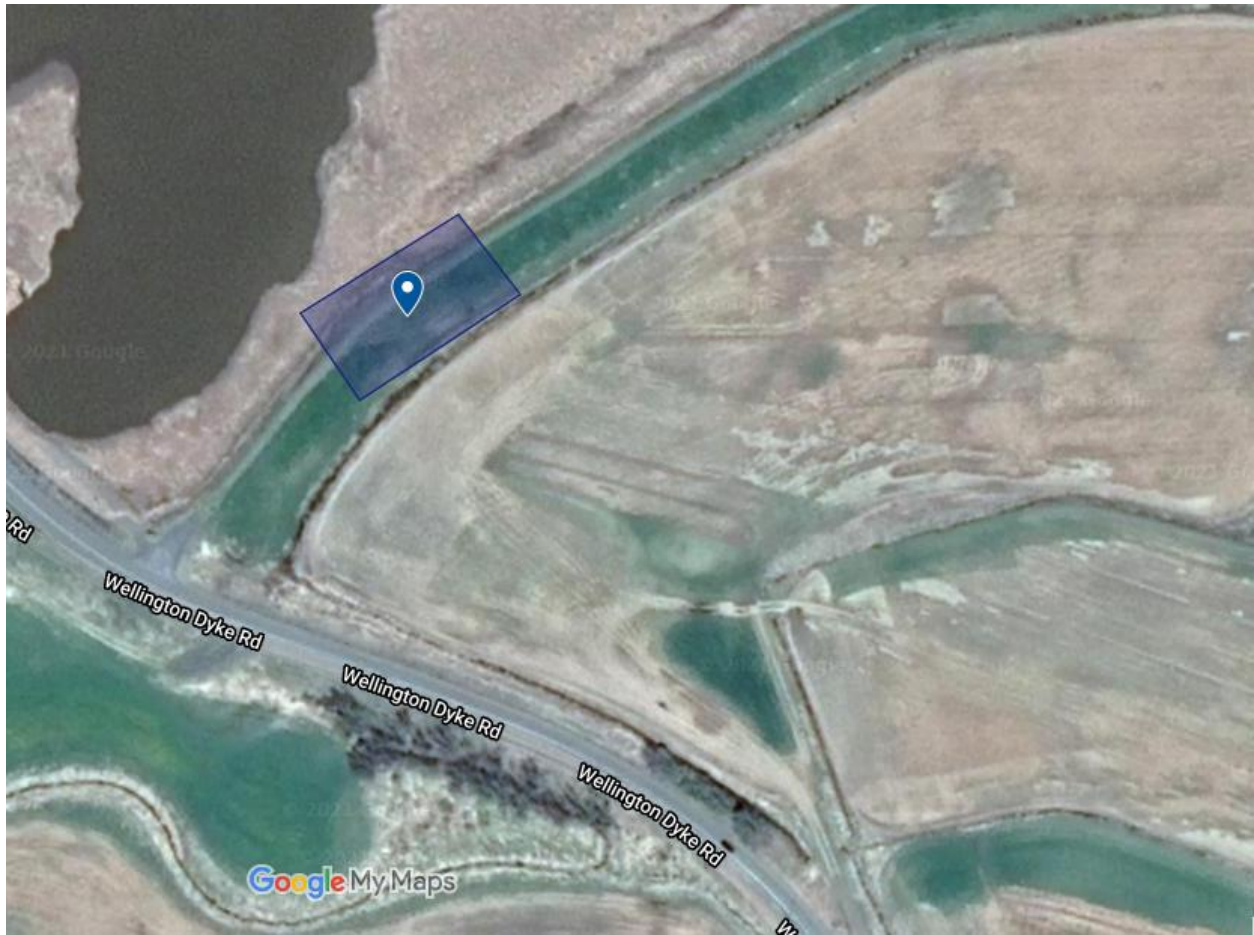
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7. APPENDIX

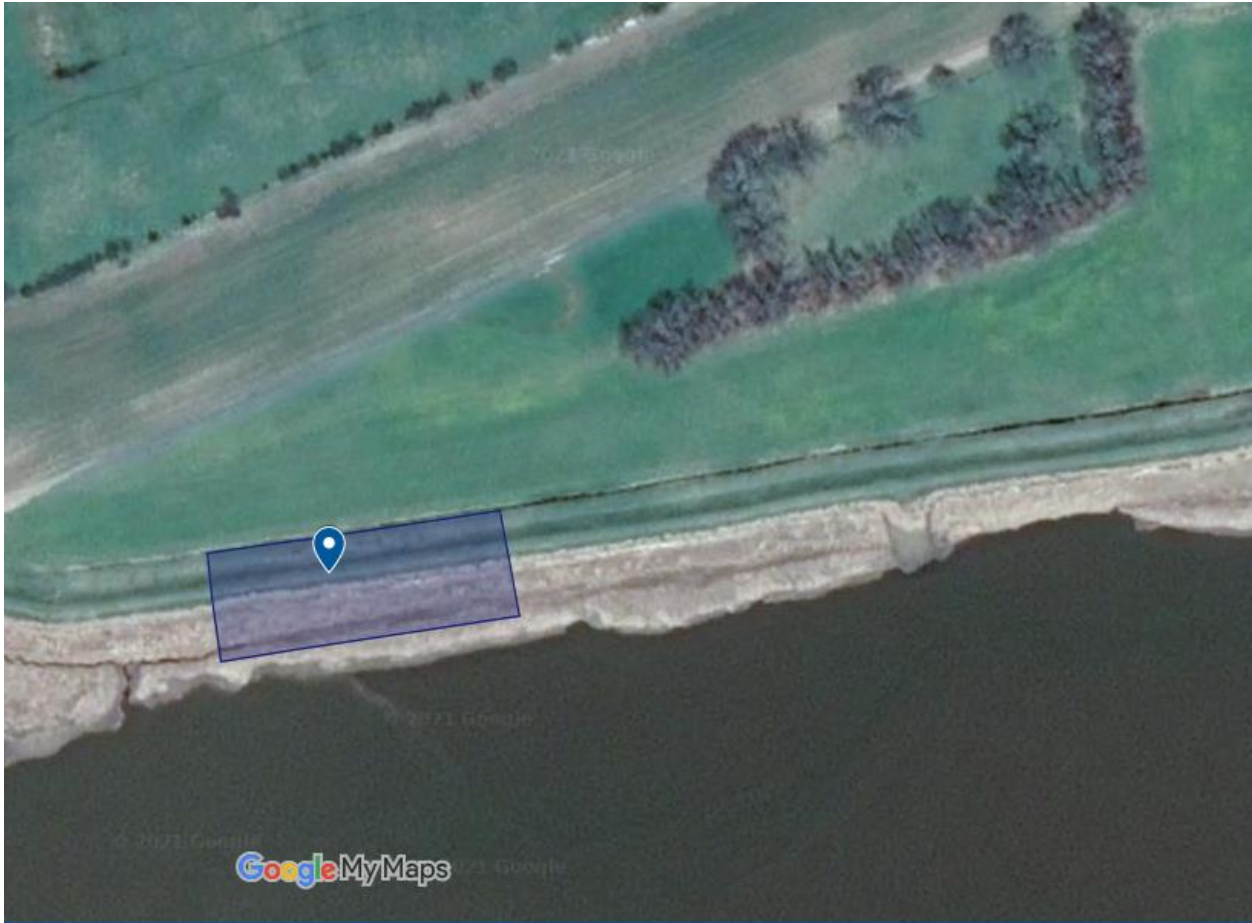
7.1 Satellite imagery of each site



Appendix 1 Satellite image of Kingsport. The blue highlight is the approximate sampling area.



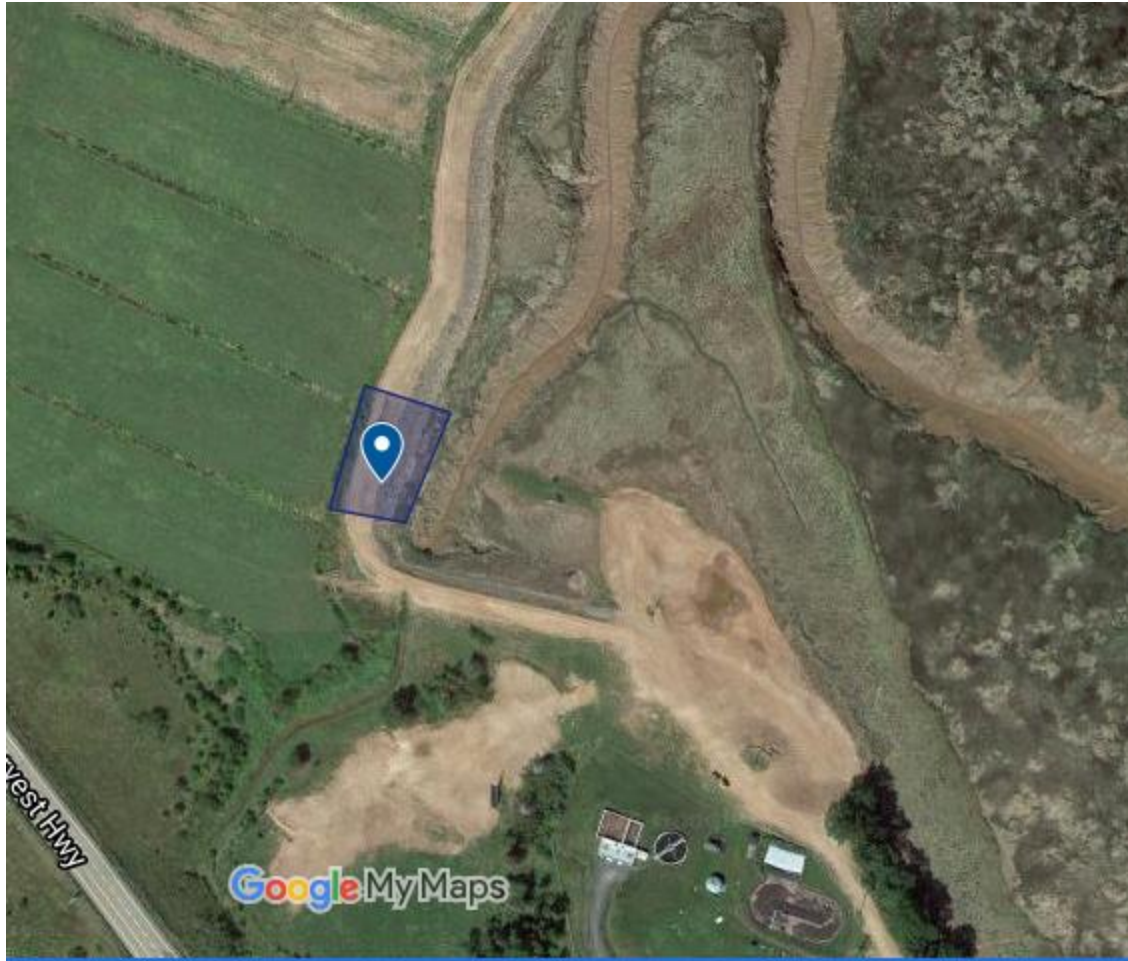
Appendix 2 Satellite image of Starr's Point North. The blue highlight is the approximate sampling area.



Appendix 3 Satellite image of Starr's Point South. The blue highlight is the approximate sampling area.



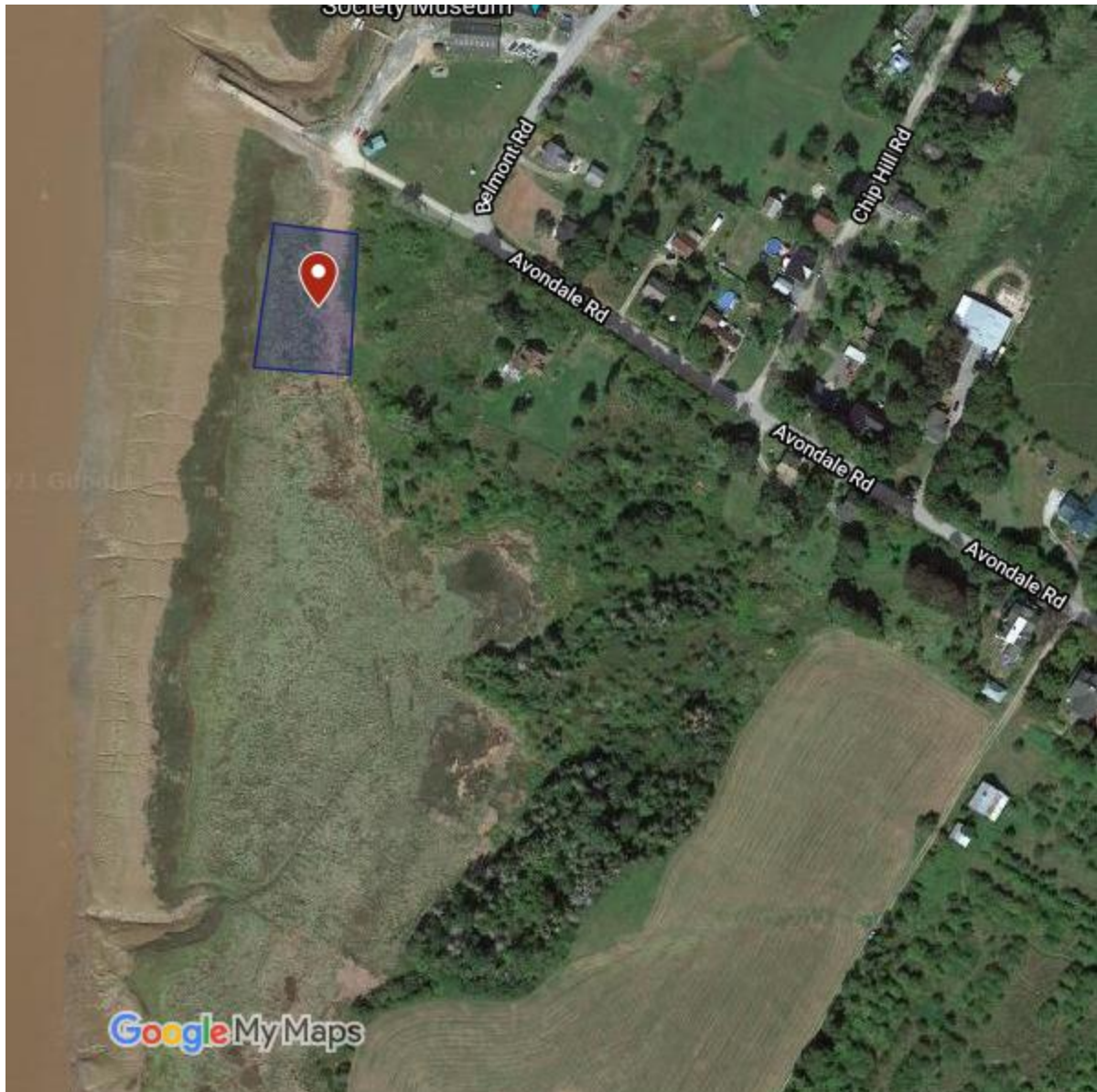
Appendix 4 Satellite image of Belcher Street Restoration and Reference. The blue highlight is the approximate sampling area.



Appendix 5 Satellite image of Elderkin Creek Dyke. The blue highlight is the approximate sampling area.



Appendix 6 Satellite image of Newport Dyke and Newport Marsh South. The blue highlight is the approximate sampling area.



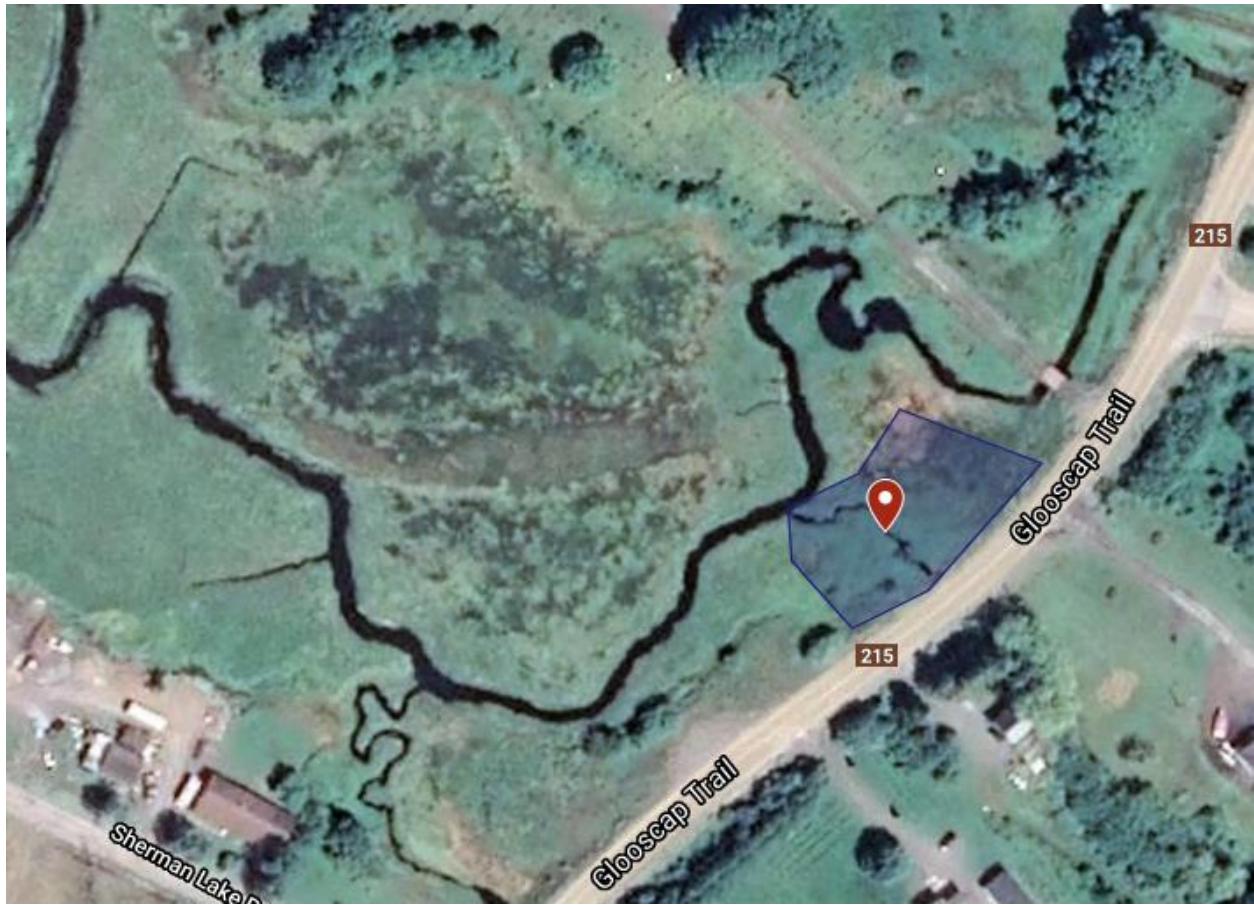
Appendix 7 Satellite image of Newport Marsh North. The blue highlight is the approximate sampling area.



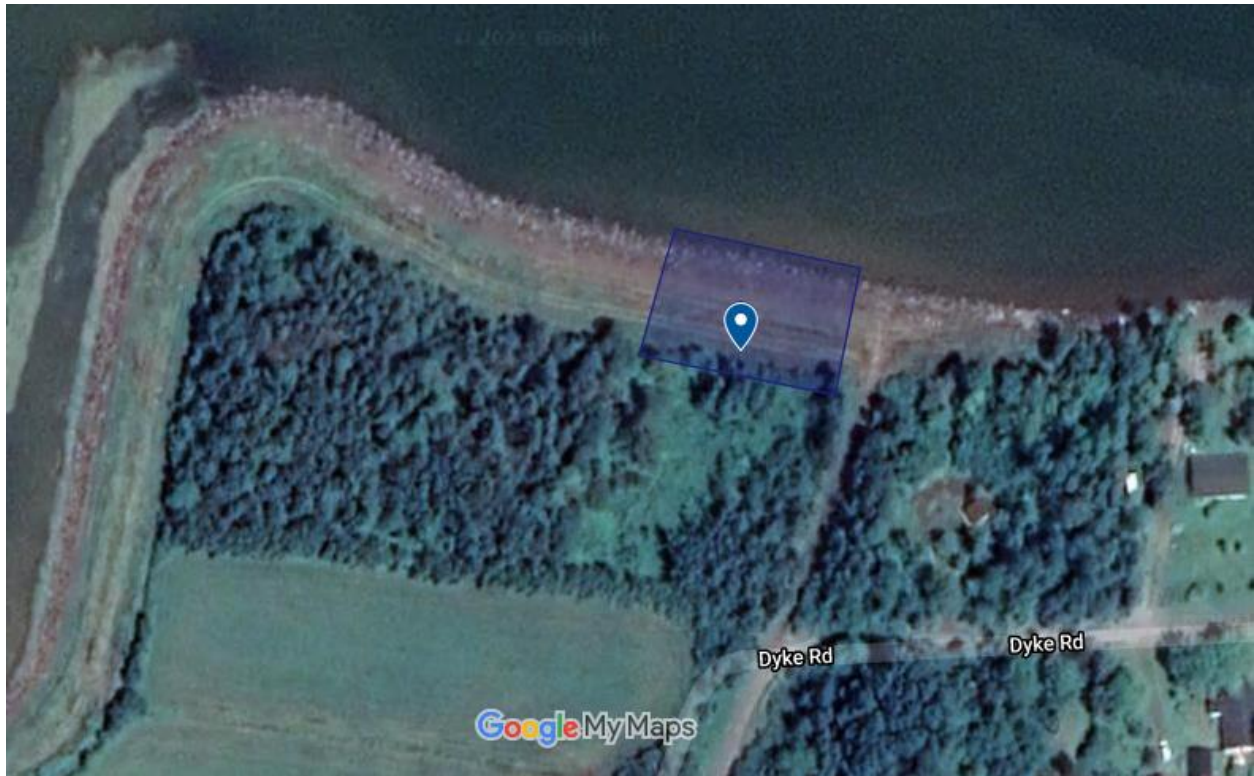
Appendix 8 Satellite image of Cogmagun Restoration and Cogmagun Other. The blue highlight is the approximate sampling area.



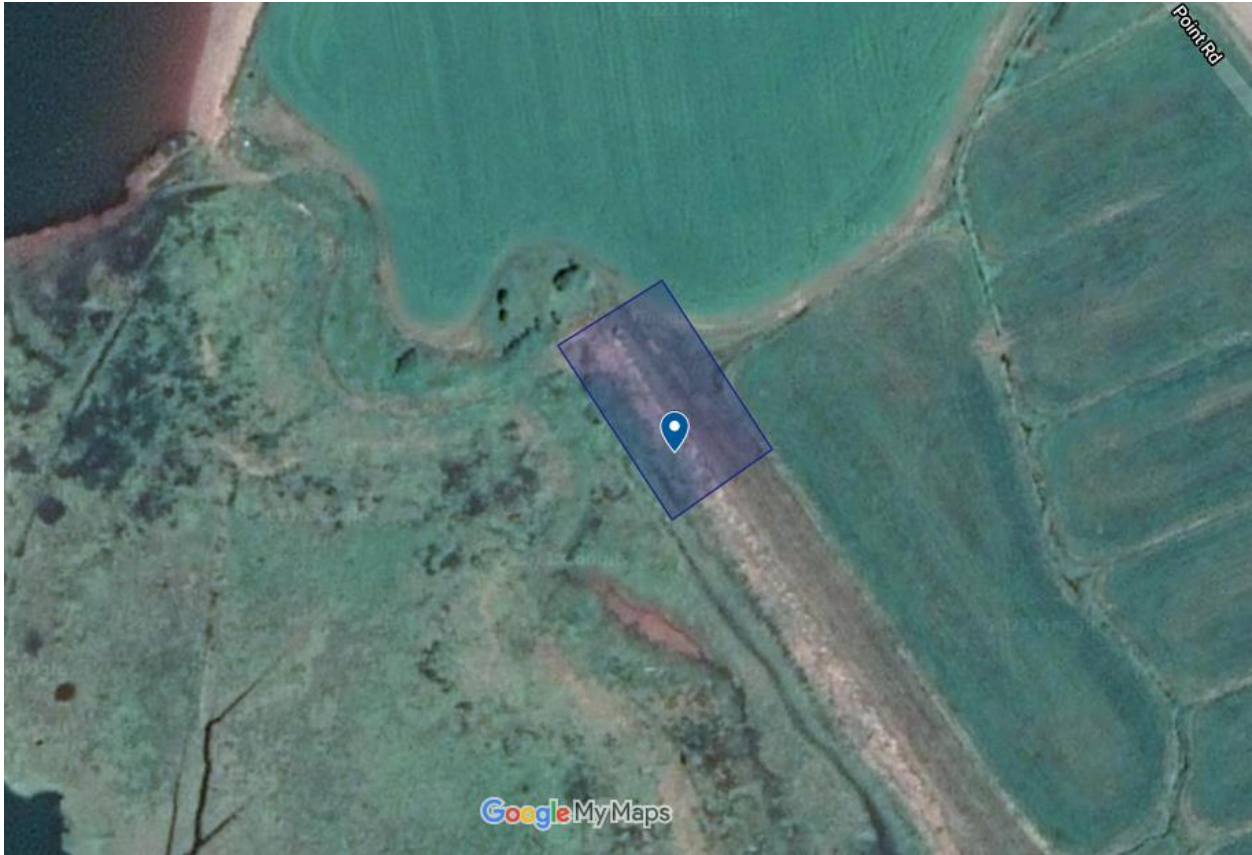
Appendix 9 Satellite image of **Cogmagun Reference**. The blue highlight is the approximate sampling area.



Appendix 10 Satellite image of Bramber. The blue highlight is the approximate sampling area.



Appendix 11 Satellite image of Noel West. The blue highlight is the approximate sampling area.



Appendix 12 Satellite image of Noel Northeast. The blue highlight is the approximate sampling area.



Appendix 13 Satellite image of Noel Southeast. The blue highlight is the approximate sampling area.

7.2 Supplementary statistics

Appendix 14 Temporal pollinator abundance type-II ANOVA. GLMER model with Poisson distribution, Wald Chi Square test was used to measure significance. Significant p-values ($p < 0.05$) are bolded.

	Chisq	Type-II SS	
		Df	Pr(>Chisq)
Habitat	1.0415	1	0.3075
Date	613.606	28	0.0001
Habitat:Date	436.258	14	0.0001

Appendix 15 Temporal floral abundance type-I ANOVA. LM model with a Gaussian

distribution, F-test was used to measure significance. Significant p-values ($p < 0.05$) are bolded.

		Type-I SS			
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Habitat	1	56.90	56.90	92.08	0.0001
Residuals	112	69.21	0.62		

Appendix 16 Pollinator – plant abundance type-I ANOVA. LM model with a Gaussian

distribution, F-test was used to measure significance. Significant p-values ($p < 0.05$) are bolded.

		Type-I SS			
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Floral					
Abundance	1	1078.00	1078.20	0.1854	0.6733
Residuals	14	81410	5815		

Appendix 17 Pollinator – plant richness type-I ANOVA. LM model with a Gaussian

distribution, F-test was used to measure significance. Significant p-values ($p < 0.05$) are bolded.

		Type-I SS			
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Floral Richness	1	136.55	136.55	12.883	0.003
Residuals	14	148.39	10.599		
