Exploring the Relationship Between Plant Provenance and Insect-Flower Interactions in Southern Ontario, Canada Seed Production Areas

by

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A Thesis
presented to
The University of Guelph

In partial fulfilment of requirements
for the degree of
Master of Landscape Architecture
in
Landscape Architecture

Guelph, Ontario, Canada

Abstract

Exploring the Relationship Between Plant Provenance and Insect-Flower Interactions in Southern Ontario, Canada Seed Production Areas

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Southern Ontario landscape architects infrequently consider plant provenance, and nursery-supplied plants often originate far from installation sites. However, recent research suggests provenance may affect plant-pollinator interactions. I explored whether the frequency of insect-inflorescence interactions differ with respect to translocation distance, microclimatic factors, floral characteristics, or landscape context. In July and August of 2024, I monitored insect visitation of *Monarda fistulosa* and *Rudbeckia hirta* inflorescences at three seed production areas in Southern Ontario. My findings did not indicate a relationship between translocation distance and insect-inflorescence interactions. Air temperature and wind speed were the only variables to exhibit significant relationships (positive and negative, respectively) with visitation, but these relationships were not evident across all insect taxa. For translocations of less than 200 km, adaptation and genetic considerations should be prioritized over translocation distance. To aid future research and inform planting decisions, seed collectors and plant growers should develop detailed plant provenance tracking.

Dedication

This research is dedicated to the life and memory of Melissa Spearing, whose influence created the opportunity for me to immerse myself in the world of seed production and whose absence will continue to be felt by those working on and advocating for improvements in plant procurement.

Acknowledgements

I have received a tremendous amount of technical and emotional support throughout this process. I would like to express my heartfelt thanks to the following people and organizations in particular, listed by thematic groupings rather than in hierarchical order:

Rob Corry, my advisor, for being a steadying presence throughout my time in the program and for turning around revisions quicker than you can say “seed production area.”

Karen Landman for offering ongoing mentorship and always being ready to lend support, even at odd hours.

Jane Mah Hutton for inviting me to join her journey down this rabbit hole and for sticking with me as I’ve continued to venture downward.

Jonas Spring for being the one to step up and bring people together and for figuring out how to fund work that I love.

Karen May and Ben Watt-Meyer for their camaraderie and shared passion.

Ryan Godfrey for his role in the creation of so many innovative seed production operations that made this research possible.

Samm Reynolds, Andrew Young, and Peter Kevan for sharing their time, their insights, and their entomological expertise.

Stefan Weber for warning me about the pitfalls of this research, even if I blundered into them anyway under the guise of first-hand learning.

All the wonderful folks at Kayanase but especially Renai Kloetstra and Dan Werner for their interest and timely correspondence.

The faculty, staff, and students of Hillfield Strathallan College for hosting this research and especially John Hannah for his passion and commitment to innovation and learning.

The good folks at NVK for having the initiative to host the Toronto Seed Orchard and always being ready to share their experiences.

Alex Sheinbaum for continually reminding me what I’m capable of and simultaneously tempering my oftentimes burdensome self-expectations.

Harrison Doyle and Kate Kearney for encouraging me to take breaks, laugh, and kick barrels.

The members of my MLA cohort for struggling and suffering and persevering alongside me.

The Landscape Architecture Canada Foundation, Pollination Guelph, and the Oakville Horticultural Society for generously funding this research.

So many others who have supported me and my research directly or indirectly and who have shared time, passion, insights, curiosity, companionship, or just a good bowl of soup.

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Acknowledgements

Finally, I would like to thank the plants and pollinators for being unwitting participants in my research but also, and even more so, for being generous teachers.

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1. Introduction

The ecological function of a designed landscape may be substantially related to the sourcing of plants, or provenances. That is, the geographic origins, and associated genetic lineages, of individual plants may have some bearing on their interactions with animals. This represents a more nuanced consideration than the simple categorization of plant species as native or introduced. That these geographically linked evolutionary relationships between plants and the non-human animals that depend on them differ between plant species is somewhat commonly understood (e.g., Tallamy, 2009). The idea that intraspecific plant provenance may also have implications for these relationships seems to have been largely overlooked by landscape professionals and scholars. Southern Ontario designers seldom consider plant provenance (Lawson-Canning, 2023). Additionally, there is a paucity of provenance-related landscape scholarship from an ecological standpoint (but see Hutton, 2020). In the absence of external pressure or encouragement, landscape praxis, broadly speaking, seems ambivalent or resistant to adopt these considerations.

Impetus for change is emerging in Southern Ontario, in the form of municipal legislation. The Toronto Green Standard (TGS) outlines requirements for new public and private developments within Ontario's most populous municipality (City of Toronto, 2024b). The current iteration of the TGS (v4), which came into effect on May 1, 2022, mandates the use of plants from a "regionally appropriate seed source" in some contexts (City of Toronto, 2023, 2024a). Those contexts include only landscaped areas within the Ravine and Natural Feature Protected area and the Natural Heritage System (City of Toronto, 2023). Within those areas, 50% of plants must be from seed sourced from the following ecodistricts: Toronto (7E-4), Oak Ridges (6E-7), Essex (7E-1), St Thomas (7E-2), Grimsby (7E-3), and Niagara (7E-5; City of Toronto, 2023; Figure 1.1). This is a fairly modest provision. However, it sets an important precedent in Ontario, and other municipalities may follow suit with respect to their own natural heritage systems.

It merits consideration whether landscape professionals who strive to be leaders in addressing ecological crises ought to advocate for and practice this level of ecological rigour uniformly, across all project contexts. This would mean specifying and installing only native plants of known and reasonably local provenance. Specifying these plants would require involving growers and making planting decisions earlier in the design process than is conventionally the case to allow sufficient time for acquisition and growing of plants (May et al., 2024). Otherwise, last minute substitutions are likely (May et al., 2024). Plant growers would have to adapt their procurement strategies to account for the increased demand in source-identified plants. In the absence of municipal oversight, the onus of determining suitable seed sources would fall on the landscape professional. To ensure emerging professionals had the ecological literacy to make such determinations, the Canadian Society of Landscape Architects' (CSLA) accreditation standards for undergraduate and graduate programs would have to reflect this required expertise. Alternatively, professional bodies, such as the CSLA and Ontario Association of Landscape Architects, might produce or fund the production of comprehensive seed source guidelines for practitioners. Another possibility is that those bodies might lobby provincial or municipal governments to deliver this guidance. Considerable effort would be associated with these and other factors in adopting locally-sourced plants uniformly across landscape project contexts.

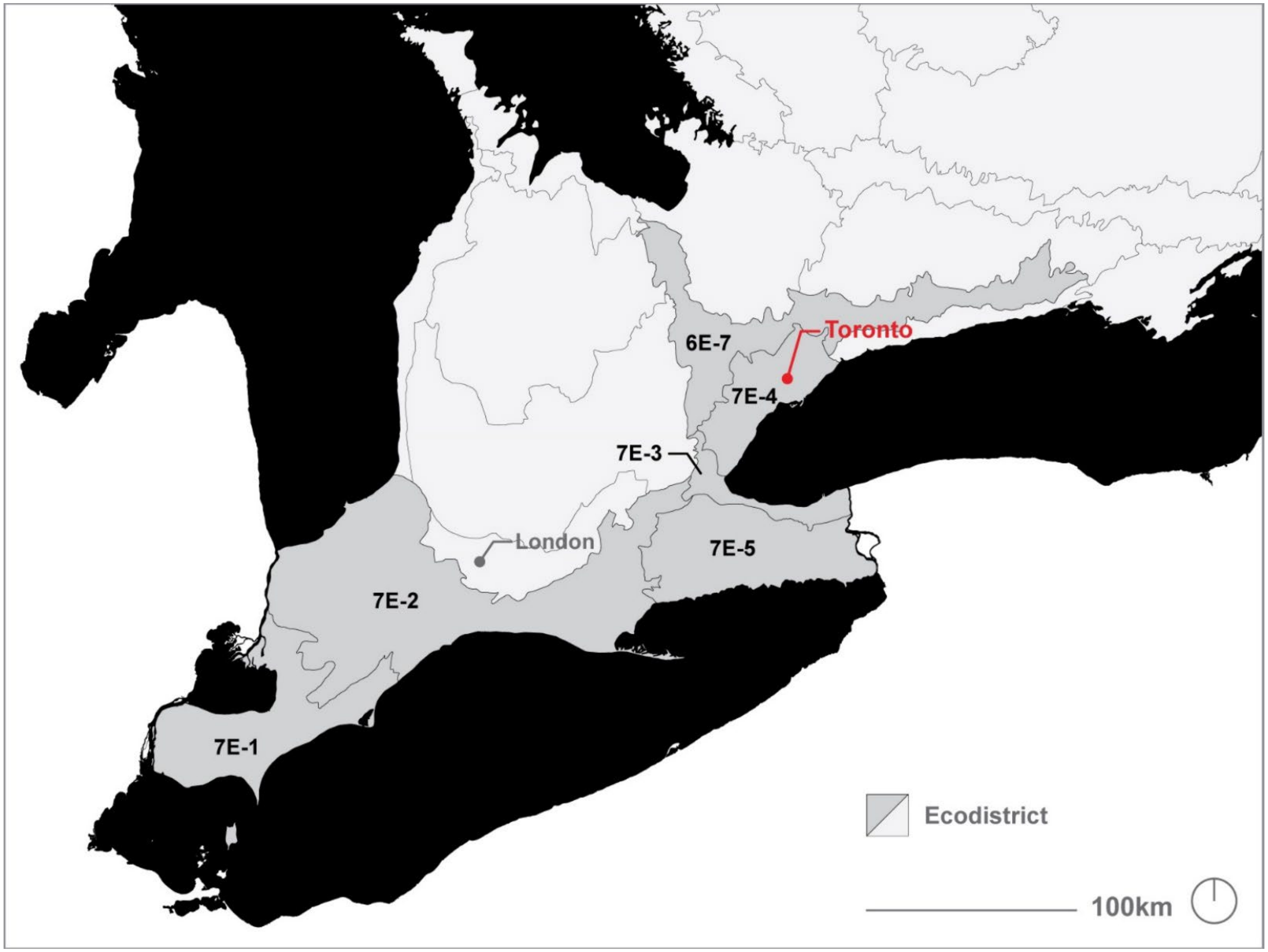

Figure 1.1: The Toronto Green Standard v4 requires new public and private developments to source 50% of plants installed within the Ravine and Natural Feature Protected area and the Natural Heritage System to be sourced from one of six ecodistricts: Toronto (7E-4), Oak Ridges (6E-7), Essex (7E-1), St Thomas (7E-2), Grimsby (7E-3), and Niagara (7E-5).

Some have formally argued, in line with the provision of the TGS, that provenance considerations ought to be context dependent. Kramer et al. (2019) suggest that provenance need only be seriously considered in particular project contexts – large, undisturbed sites with possibility for gene flow into natural remnant populations. In more typical landscape project contexts – small, disturbed sites with no gene flow into natural remnant populations – aesthetic considerations, they say, ought to be prioritized over provenance-based ones. The authors seem to suggest that cultivated varieties are suitable in these latter sites, provided they are not so substantially altered from their natural state that they fail to provide desired ecosystem functions. Their reasoning, thus, hinges on plants' ecological functions not being inherently tied to their genetic lineages and, consequently, geographic origins. However, Bucharova et al. (2016, 2022) have demonstrated that biotic interactions, between plants and insects, are associated with plant provenance. There have been few studies, however, into these relationships. A more robust understanding of the link(s) between plant provenance and ecological function would help resolve the landscape professional's ethical responsibility in this regard.

Whether landscape professionals ought to consider plant provenance uniformly across projects or only in ecologically focused work, as prescribed in Toronto, should not be considered lightly. There are substantial barriers to broader-scale use of locally-sourced seed. At present, the supply of source-identified seed is insufficient to meet the existing demands. Canada's seed supply is insufficient to meet the needs of planned ecological restoration and reclamation projects (Spearing et al., 2023). With respect to restoration projects, the demands of landscape projects ought to be comparatively small, given that the geographic scale of the latter may be orders of magnitude smaller. However, uniform use of wild-sourced, seed-grown plants across landscape projects would further burden an already inadequate supply of seeds. Increasing the seed supply is no simple matter, particularly because it cannot happen in isolation from the design and construction process.

The barriers to increasing seed supply are complex. Barriers faced in Southern Ontario can be coarsely categorized into issues of knowledge and risk. Documented knowledge of Southern Ontario's local plant populations is severely lacking. Composition of local genotypes and adaptation to local environmental conditions in these populations is largely unknown (Toronto Seed Strategy Working Group [TSSWG], 2021a, 2021b, 2021c, 2022). There is also a substantial knowledge gap regarding plant species' suitability for commercial seed production and species-specific propagation practices (TSSWG, 2021a, 2021b, 2021c, 2022).

Economic risks associated with increasing seed supply are borne disproportionately by plant growers. Southern Ontario growers lack the infrastructure (skilled labourers; storage and propagation facilities; seed forecasting, harvesting, and processing technologies, for example) to produce plants from seed at the scale needed (May et al., 2024). Developing this infrastructure represents a substantial investment of resources. That investment may not pay off for growers. Interannual variability in demand can result in growers struggling to fulfill large contracts in high-demand years but being unable to sell excess seed in low-demand years (Jones, 2019). Additionally, conventional construction contracts and administration can leave growers to absorb plant storage and maintenance costs associated with project delays (May et al., 2024). In the United States, knowledge and risk barriers have been addressed largely through decades-long public-private partnerships (Jones, 2019; White et al., 2018). Government agencies have researched plant species and funded growers, providing the information and economic stability necessary for large-scale seed production (Jones, 2019). Lack of comparable government support in Southern Ontario has been repeatedly identified as a key issue (May et al., 2024; TSSWG, 2021a, 2021b, 2021c, 2022). Extension services at land grant universities in the United States, a system that has no direct analogue in Canada, also conduct and publicize research into source-identified seed production. Given the complexity involved in increasing seed supply, which I've only sparingly described here, it is worth considering whether uniform use of source-identified seed for landscape projects is worth the effort involved in addressing these challenges.

My goal is to help develop our understanding of the association between a plant's provenance and its interactions with other biota. Specifically, I'm interested in the relative strength of the relationship between a plant's translocation distance (seed source to planting site) and its interactions with insect pollinators. Toward that end, my specific research questions are: (1) does the frequency of insect-inflorescence interactions differ with respect to translocation distance, and (2) does the frequency of insect-inflorescence interactions differ with respect to microclimatic factors, floral characteristics, or landscape context and, if so, what are the relative strengths of those relationships? Resolving these questions will help landscape professionals understand the relative prioritization of factors in plant selection decisions.

In the second chapter of this work, I review the existing state of knowledge in the literature pertaining to plant provenance and plant-pollinator relationships. In the third chapter, I detail the methods that I used to derive an answer to my research questions. In the fourth chapter, I present the results of this research and my analysis of those results. In the fifth and final chapter, I discuss possible explanations of my findings with respect to the literature and the implications of those findings for policymakers and for landscape and horticultural professionals.

2. Literature Review

2.1 Theoretical Framework

In this section, I attend to the fundamental scientific concepts that inform my development and contextualization of a research question. Four disciplines substantially form the basis of my research: evolutionary biology, biogeography, phenology, and conservation biology. Evolutionary biology is foundational to any discussion of genetic variation between or within species and establishes many assumptions of the other three disciplines. Biogeography establishes that intraspecific phenotypic variation exists over geographic distance and ecological differentiation. Phenology is concerned with the seasonal timing of biological events and the role of timing in mediating relationships between species. Conservation biology describes, among other things, genetic risks faced by small populations. In laying out some of the constituent concepts of each of these disciplines, I hope to help the reader follow my line of scientific inquiry.

2.1.1 Evolutionary biology

Evolutionary biology, concerned with the development of biodiversity through speciation, establishes many of the foundational assumptions of this research. The field was established by Charles Darwin, with the publication of *On the Origin of Species by Means of Natural Selection* in 1859, and substantially developed by him and his contemporaries. In his seminal works, Darwin laid out many foundational concepts that are still broadly accepted. The most immediately relevant to my research are natural and artificial selection and coevolution and specialization.

2.1.1.1 Natural and artificial selection

Understanding natural and artificial selection is essential in any consideration of plant procurement methods. Darwin (1859) first described natural selection as the process by which traits that lend themselves to the survival and reproduction (fitness) of individuals tend to be preserved in the population. Artificial selection, by contrast, results from the direct intervention of humans (Darwin, 1859). This process can be either methodological or unconscious (Darwin, 1868). Methodological (intentional) selection is the systematic modification of a breed to produce and retain desirable traits (Darwin, 1868). Unconscious (unintentional) selection is the inadvertent result of preserving the most valued or destroying the least valued individuals (Darwin, 1868). This latter definition is insufficient for two reasons. First, Darwin described only the resultant selection of this process of preservation or destruction as unconscious. However, the acts of preservation or destruction themselves may also be unconscious if value is ascribed to an individual as a consequence of the process of preservation or destruction rather than as the intention behind it. For example, plant propagules with traits that improve ease of collection or propagation by a specific method are more likely to be incidentally preserved through these operations. Second, Darwin's definition pertains only to managed populations. If humans harvest the most robust, well-adapted individuals from an unmanaged population, it represents the loss (destruction) of the most valued individuals from the population. This process was unaccounted for in Darwin's writing, but it clearly constitutes an artificial selective pressure (resulting from direct human intervention) on such a population. Darwin also asserted that natural and artificial selection are not mutually exclusive and may simultaneously act on a population. Natural selection, in particular, is complicated by the dynamic nature of evolving species' interdependence on one another.

2.1.1.2 Coevolution and specialization

Darwin (1859) also described what he called coadaptation, the apparently perfect suitability of some species to benefit from others through, for example, predation, seed dispersal, and parasitism. One illustrative case is specialization in plants whose flowers are only pollinated by one particular type of insect (Darwin, 1859). Coevolution refers to the process by which these specialized relationships have come to exist. The term was coined by Ehrlich and Raven (1964) more than a century after the publication of *On the Origin of Species*. Those authors describe coevolution as the process of reciprocal evolutionary changes in two species resulting from the selective pressures exerted by each on the other. Ehrlich and Raven (1964) described, specifically, the process in which a random mutation causes plants to produce secondary metabolites that decrease palatability to herbivorous insects, and some insects, in turn, evolve a capacity to feed on those plants. The authors suggest that the degree of genetic specialization involved in this process would limit the insect's ability to feed on other plants. These insects can be called specialists. Specialized relationships, resulting from coevolution of species, also occur between plants and pollinators, as Darwin (1859) observed.

2.1.2 Biogeography

Biogeography is the study of the geographical distribution of plants and animals (Michaux, 2008). Michaux (2008) attributes its formation and development largely, though not exclusively, to Alfred Russel Wallace's work between 1853 and 1880. Two important developments of biogeography occurring after Wallace's death, however, were the creation of the concepts of ecotypes and clines. Each of these concepts describes spatial patterns of intraspecific differentiation between or within populations.

2.1.2.1 Ecotype

An effective but somewhat limited understanding of spatial patterns of variation within species is encapsulated in the ecotype. Ecotypes are phenotypically differentiated populations of the same species resulting from differential selective pressures. The term was coined by Turesson (1922, as cited in Gregor, 1944), who described an ecotype as "the product arising as a result of the genotypical response of an ecospecies to a particular habitat." The concept of ecospecies has since fallen into disuse, but the general principle of Turesson's argument remains intact. Ecotypes have been more recently and comprehensively described by Hufford and Mazer (2003, p. 147) as "distinct genotypes (or populations) within a species, resulting from adaptation to local environmental conditions; capable of interbreeding with other ecotypes… of the same species." One illustrative example is the case of Common Ragweed (*Ambrosia artemisiifolia*). Dickerson and Sweet (1971) grew plants from 12 different ragweed populations, from different regions of the United States, in a common garden. The populations (ecotypes) exhibited different developmental timing in flowers and vegetative growth. The authors observed that the developmental differences between ecotypes were positively related to latitude, such that plants at higher latitudes developed quicker in the common garden. The ecotypic model, however, fails to account for gradients of environmental change. Within this model, differentiation in response to a climatic gradient, for example, is not continuous across that gradient and results instead in distinct populations (Gregor, 1944). A more nuanced concept was required to deal with gradients of change.

2.1.2.2 Cline

A similar but more comprehensive understanding of intraspecific phenotypic variation is captured in the cline. A cline is a geographic gradient in the phenotypic character of a species (Huxley, 1938). The term was coined and elaborated by Huxley (1938), who named and described various patterns of continuous and discontinuous clines. A continuous cline, according to Huxley (1938, p. 494), exists when the "whole population considered constitutes a single, inter-breeding unit." A discontinuous cline exists when that condition is not met but when phenotypic characters differ between geographically isolated groups. Dickerson' and Sweet's (1971) series of ragweed populations may better have been described as a cline than a collection of ecotypes, given that they reflected a gradient of change related to latitude and, presumably, climate. As with the ecotype, the cline describes a pattern of phenotypic differentiation across geographic distance and ecological change.

2.1.3 Phenology

Phenology is the study of successive occurrences of biological phenomena and their timing in relation to the environment (Demarée & Rutishauser, 2009). It entered the scientific lexicon in the mid-1800s. The term was first used by Morren in 1849 to describe his work on the history of plant phenomena (Demarée & Rutishauser, 2009). Morren (1849), however, advocated for the consideration of phenology as its own scientific discipline, rather than a facet of botany or any other field (as cited in Demarée & Rutishauser, 2009, p. 291). He used the term broadly to address the timing of recurrent natural phenomena in relation to the environment (Demarée & Rutishauser, 2009). Other scientists have appropriated the term to describe a subfield within their respective disciplines. Clark (1923, p. 49), for example, describes phenology as, "that *branch of meteorological science* which has as its object the studied effect of weather conditions upon the seasonal development of animal and plant life" [emphasis added]. Whether viewed as its own discipline or as a component of others, phenology touches many fields, including evolutionary biology.

Despite Morren having coined the term phenology a decade before Darwin published *On the Origin of Species*, consideration of the genetic underpinnings of phenological observations lagged behind Darwin's research by several decades. That internal biological factors were at least partially responsible for periodicity in plants seems not to have been demonstrated until 1876 (de Candolle, 1876, as cited in Salisbury, 1921, p. 252). Prior to these findings, phenological studies appear to have attributed recurrent biological phenomena entirely to external, meteorological factors (Salisbury, 1921). The heritability of phenological traits in plants appears to have been first described in 1918, when Raunkaier (1918, as cited in Salisbury, 1921) demonstrated in plants a heritable propensity towards being exceptionally "early" or "late." Thus, when Robertson (1890, as cited in Robertson, 1927), decades earlier, demonstrated a relationship between timing of blooming and the types of insect visitors a flower received, he gave no consideration to the possibility of underlying coevolutionary forces. These ideas would be developed later.

2.1.3.1 Phenological mismatch

The role of phenology in mediating interactions between organisms became more robustly understood when the concept of phenological mismatch was introduced. Mismatches in seasonal timing between species was first described in marine ecosystems (Hjort, 1914, as cited in Stenseth & Mysterud, 2002). The term phenological mismatch, however, may not have appeared in the literature until the 1980s. Nothnagle and Schultz (1987) used the term to describe spring insect emergence misaligning with the optimal food quality window.

Much of the recent discourse, since the early 2000s, around phenological mismatches has related to climate change. Walther et al. (2002, p. 389) recognized phenology as “perhaps the simplest process in which to track changes in the ecology of species in response to climate change.” Those authors report differential effects of climate change on the seasonal timing of individual species, creating asynchrony between, for example, insect emergence and peak breeding bird food demand. These changes may be attributed to differential seasonal warming effects of climate change between birds’ breeding grounds and their wintering grounds and migratory paths, or to differential effects of warming on the seasonal timing of birds and their insect prey (Stenseth & Mysterud, 2002; Walther et al., 2002). Whether caused by climate change or other factors, mismatches in the timing of seasonal phenomena between species may substantially impact those species.

2.1.4 Conservation biology

Conservation biology is a scientific discipline that deals with human-disturbed species, communities, and ecosystems, toward the preservation of biological diversity (Soulé, 1985). Michael Soulé and his contemporaries are credited with substantially developing the field of conservation biology through their work in the 1970s and 80s (Caughley, 1994; Simberloff, 1988). Soulé, along with Otto Frankel, is credited with having recognized genetic factors in conservation biology (Simberloff, 1988). This early work in conservation biology fell within what Caughley (1994) would later coin the small-population paradigm, a school of work oriented around extinction risks faced by populations with few individuals and capped growth. Through this work, three discrete concepts (along with many others) were developed that inform my research: genetic drift, inbreeding depression, and outbreeding depression.

2.1.4.1 Genetic drift

Genetic drift is the tendency, in the absence of immigration and mutation, for the number of alleles at any locus in a population to decrease (Caughley, 1994). This loss of alleles results in a decrease in heterozygosity, the incidence of heterozygotes (individuals possessing multiple different alleles of a particular gene) within the population (Caughley, 1994). Decrease in heterozygosity is strongly associated with decreased population-level fitness (elaborated in section 2.1.4.2; Caughley, 1994). The risk from genetic drift is inversely related to population size, such that smaller populations are at greater risk (Caughley, 1994). Genetic drift is a substantial risk to small populations, but certainly not the only factor that can cause loss of heterozygosity and consequent loss of fitness.

2.1.4.2 Inbreeding depression

As with genetic drift, inbreeding, the mating of closely related individuals, can cause a loss of heterozygosity (Caughley, 1994). The negative impacts of this loss are referred to as inbreeding depression. Inbreeding depression can be specifically considered expression of deleterious recessive traits from inbreeding-related homozygosity and the consequent decrease in fitness (Caughley, 1994). In simpler terms, the mating of closely related individuals, which are more likely than unrelated individuals to carry identical alleles for any given gene, is more likely to produce offspring that carry two identical copies of that gene. If that gene is recessive, it is less likely to have been selected against, and so more likely to be deleterious (Caughley, 1994). That is, its expression is more likely to reduce the fitness of the individual. The incidence of inbreeding is higher in smaller populations (Caughley, 1994). Consequently, smaller populations are more likely than larger ones to suffer from inbreeding depression.

2.1.4.3 Outbreeding depression

Unlike in inbreeding, the impact of outbreeding, mating between individuals from genetically distinct populations, is variable. Outbreeding effects may be negative, as in the case of inbreeding, or they may be positive (Lynch, 1991). Positive impacts of outbreeding are surmised to be the result of counteracting the deleterious effects of inbreeding (Lynch, 1991). Negative impacts of outbreeding are referred to as outbreeding depression. Specifically, outbreeding depression is the lowered fitness of offspring, or subsequent generations, resulting from crosses between genetically different sources (Rhymer & Simberloff, 1996). Where that genetic differentiation is great, outbreeding depression will be stronger (Frankham, 1995). Outbreeding depression is partially associated with local adaptation (see section 2.2.2 for a detailed discussion of local adaptation), in that crosses between individuals adapted to different environmental conditions may result in offspring less adapted to the conditions to which they are subject (Waser & Price, 1989). Whether the impact of outbreeding on a population is positive or negative seems to depend on the degree of outbreeding (Lynch, 1991). Some level of outbreeding is, thus, theoretically optimal to counteract the effects of inbreeding by introducing new and diverse genetic material to replace that which has been previously lost from a population (Lynch, 1991). Despite the potential benefits of outbreeding, outbreeding depression still represents a genetic risk to small populations.

2.2 Plant Provenance

Restoration ecologists conduct research on the influence of plants' geographic origins on restoration project success. However, they disagree about the most appropriate provenancing strategy. Common approaches include local, regional, regional admixture, climate-adjusted, predictive, composite, and admixture provenancing (Bucharova et al., 2019). Admixture provenancing supposes that plants originating from multiple, geographically distant locations will maximize genetic diversity and adaptive potential at the planting site (Bucharova et al., 2019). Predictive provenancing supposes that plants originating from a place whose current climate matches the planting site's projected future climate will survive best (Bucharova et al., 2019). Local provenancing (often called "local is best") supposes that plants originating in close proximity to a planting site will be, on average, and in all respects, optimal (Bucharova et al., 2019). Between those three extremes, regional, regional admixture, climate adjusted, and composite provenancing strategies balance, with varying biases, three chief considerations: genetic conservation, plant fitness, and biotic interactions. These considerations are the cornerstones of the provenance discourse. Detailed examination of the evidence for provenance effects on each of those three items will help to inform plant sourcing decisions by landscape professionals.

2.2.1 Genetic conservation

Restoration ecologists are substantially concerned with the possibility of compromising native plant genetic diversity. An important factor is the degree of genetic differentiation between natural and restored populations, because of the possibility of outbreeding depression in the former. It is intuitive that locally sourced plants will be the least differentiated from natural populations. However, Höfner et al. (2022) recently reported that populations restored using regionally (as opposed to locally) sourced seed are not dramatically differentiated from natural populations. They found that the degree of genetic differentiation between natural plant populations and restored populations was similar to the degree of differentiation amongst natural populations. Those restored populations, just 20 years after establishment, had also begun to resemble adjacent natural populations, which is evidence of gene flow from natural to restored populations. In contrast, a conventional seed mixture of unknown provenance was strongly differentiated from natural populations. These researchers' findings support regional provenance, with respect to genetic differentiation, in situations where remnant populations' genetic diversity is already diminished. Differentiation between populations is only one consideration for genetic conservation.

Another critical consideration for conservation is genetic diversity. Diversity is a crucial functional consideration. Genetically diverse populations are suspected to have greater capacity to adapt to changing environmental pressures resulting from, for example, anthropogenic climate change (Jump et al., 2008). However, evidence of the relationship between provenance and diversity is mixed. Reviewing global restoration projects, Jordan et al. (2019) found that genetic diversity of restored populations was greater than that of natural populations about half the time, and many reported differences were marginal or insignificant. Populations established with seed from multiple sources, however, tended to be more genetically diverse than natural populations. These authors, however, did not consider the effect of source proximity on relative genetic diversity.

Aavik et al. (2012) report higher inbreeding in populations restored using regional seed than in natural populations, but they suggest this may be due to propagation practices. With respect to genetic diversity, there seems to be no clear support for one provenance strategy over another, except that sourcing from multiple populations appears preferable to sourcing from a single population. However, absolute genetic diversity must be balanced against other considerations, and concern for future adaptability should be weighed against adaptation to existing environmental conditions.

2.2.2 Plant fitness

Local adaptation of plants to their environments may be a substantial point in favour of local plant provenance. Plants adapted to the local environmental conditions of their installation site will, by definition, exhibit greater survival than plants that are not locally adapted. Within the provenance discourse, researchers have dedicated much time to understanding the nature and degree of local adaptation. Evidence of local adaptation is mixed, but some general trends are apparent. The geographic proximity that constitutes “local” appears to depend on the environmental variable acting as a selective agent, with some studies evaluating the relative fitness of local and non-local plants over translocation distances as little as 3 m (Leimu & Fischer, 2008). In some studies, local plants exhibit greater fitness than non-local plants, but the opposite is also true, and these instances vary between species and ecotypes (Bischoff et al, 2010; Bucharova et al., 2017a, 2017b; Leimu & Fischer, 2008). However, Bucharova et al. (2017a) found that the commonly used “local vs foreign” (local vs. non-local) approach to evaluating results of reciprocal transplant experiments can mask the effect of local adaptation. Under this approach, demonstrating that local plants are best adapted to their environment requires the local ecotype to outperform all non-local ecotypes, whereas rejecting that idea requires only one of the non-local ecotypes to outperform the local ecotype (Bucharova et al., 2017a). Thus, it may be that the effect of local adaptation is greater than reported. Additionally, Leimu and Fischer (2008) report substantial variety in fitness metrics within the literature, but those authors don’t suggest any hierarchy in suitability of those metrics. Some metrics, like biomass, plant height, and leaf size, however, fail to capture the critical aspects of survival and reproductive success that characterize fitness. In contrast to the confused state of local adaptation, there is clear and substantial evidence against local maladaptation (Bucharova et al., 2017b; Leimu & Fischer, 2008). That is, in a reciprocal transplant experiment considering paired sites, lower fitness tends not to be observed in both of the local ecotypes at their respective sites (Bucharova et al., 2017b; Leimu et al., 2008). The potential for local adaptation, and unlikely scenario of local maladaptation, suggests that local provenance may result in plants that are best suited to local environmental conditions and is unlikely to result in plants that are more poorly suited to local environmental conditions, compared to non-local plants. A more nuanced review of the factors involved is necessary to understand the relationship between provenance and fitness.

The effect of provenance on plant fitness is complex and has many interacting factors. Interactions with fitness have been found in competition, source population size, and translocation distance. Bischoff et al. (2006, 2010) found that competition between plant species can mask or exaggerate the effect of provenance on fitness. These findings reinforce the complexity of studying provenance-fitness relationships. Leimu and Fischer (2008), however, clarify these relationships. These researchers, in a review of reciprocal transplant experiments, found that source population size is the greatest determinant of local adaptation. Populations with more than 1000 individuals are typically locally adapted and populations with fewer than 1000 individuals are typically not, likely due to smaller populations having insufficient genetic diversity to adapt to local environmental conditions (Leimu & Fischer, 2008).

Further complicating matters, apparent relationships between fitness and geographic distance appear to be mediated by degree of ecological and climatic differentiation between sites, fitness decreasing with increasing differentiation (Bucharova et al., 2017b; Leimu & Fischer, 2008). There is little research into the relative fitness of local plants and nonlocal plants from climates that match a planting site's projected climate (Bucharova, 2017). With firmer evidence of local adaptation confidence to embrace local provenance might increase. The risks associated with source population size and ecological differentiation between source and installation sites warrant caution. Additional factors must be considered, alongside plant fitness, to inform a provenancing strategy.

2.2.3 Biotic interaction

The potential influence of provenance on biotic interaction has been studied, and is clarified, in the relationships between plants and their insect pollinators and herbivores. Researchers have only recently begun exploring the influence of plant provenance on these relationships, but well-established theory based on the concept of coevolution supports this work. There is clear evidence of geographically linked relationships between insects and their plant hosts. A plant species' pollinators change throughout the plant's geographic range (Espíndola et al., 2011). In pollinator-specialist plants, this means different primary pollinators in different regions (Espíndola et al., 2011). This suggests plants may express geographically linked phenotypic differences, related to local pollinators.

Specialist pollinators are theorized to exert selective pressure on plant floral traits (Willmer, 2011). In at least one pollinator-generalist plant, though, whole pollinator communities have been found to collectively exert selection pressure on some floral traits (Gómez et al., 2015). Different communities, then, may exert different pressures on the same plant species. For example, Parker et al. (2018) discovered that differences between plant ecotypes in pollen timing and total pollen production are related to morphological and behavioural differences in locally dominant pollinators. Similar effects in plant-herbivore interactions seem to exist, too. For example, Lehndal and Ågren (2015) found a negative relationship between plant populations' latitude and their insect herbivore tolerance and resistance, which the authors attribute to decreased selective pressure (resulting from fewer insect herbivore species) at more northern latitudes. That is, the authors surmise that geographic variation in insect herbivore communities results in differential selection pressures between plant populations, causing phenotypic differences in those populations. This effect, they report, may be mediated by plant growth phenology. These spatially linked evolutionary relationships between insects and their plant hosts suggests potential behavioural mismatches between local insect populations and nonlocal plants. This theoretical basis grounds research on the effect of provenance on biotic interactions.

A clearer understanding of plant provenance's effect on plant-animal interactions is necessary to evaluate the impacts of various provenance strategies. Early research shows an impact of provenance on pollinator flower visitation, which seems to be mediated by flower phenology. Bucharova et al. (2022) observed pollinators differentiating between plant provenances, the insects' visitation rates at various trial plantings differing significantly from what would be expected of random visitation. However, they did not observe the highest visitation in local provenance. The difference in visitation seems to be mediated by flower diversity in multispecies plantings, which is a function of individual plants' flower phenology (Bucharova et al., 2022). Plant phenology traits differ more, in relation to provenance, than do fitness traits, but the relative effects on phenology vary substantially between species

(Bucharova et al., 2017b). In some species, the effect of provenance on phenology is related to geographic distance or climatic difference between seed source and installation site (Bucharova et al., 2017b). Although these studies are few, the results suggest provenance-related differences in flower phenology, which have implications for local pollinators and, consequently, for their plant hosts. This early evidence of a link between plant provenance and biotic interactions warrants consideration in seed sourcing strategies.

The effect of provenance on plant development is interesting in its own right, but a principal concern is the implication of those changes for the biotic community. Provenance-related differences in plant phenology may be detrimental to local insect populations, and these effects may cascade between trophic levels. Provenance affects plant phenology dramatically enough to create temporal mismatch and deprive native pollinators of floral resources. Bucharova et al. (2017b) found that differences in flower onset between provenances – up to 23 days in one species – can be great enough to detrimentally impact pollinators. Adults of most Ontario native bees are only active for 2-6 weeks (Holm, 2023). Phenological mismatch may also impact multiple trophic levels. Bucharova et al. (2017b) also report that provenance-related differences in flower phenology affect flowerhead herbivores and their parasitoids. These results may support local provenance, but more research is required to clarify the potentially detrimental impacts of provenance on native pollinators in order to inform plant selection that support local fauna.

Failure to consider the complexity of the organisms comprising plant-animal relationships risks inadvertently compromising those relationships. These organisms' behaviour is malleable, and their responses may differ from what theory predicts. Phenotypic plasticity and insect learning, in particular, have implications for provenance relationships. Phenotypic plasticity is "the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions" (West-Eberhard, 1989, p. 249). Learning, in this context, is the process in which an "individual's behavior changes in a repeatable way as a consequence of experience" (Papaj & Prokopy, 1989, p. 316). Plant phenology traits exhibit greater plasticity than fitness traits (Bucharova et al., 2017b). This plasticity could make biotic interactions less susceptible than plant fitness to provenance effects. However, there is insufficient evidence to conclude this with confidence. It is also possible that the phenology-mediated impacts of provenance may be mitigated by insect learning. There is ample evidence of bee, butterfly, and moth learning (Jones & Agrawal, 2017). However, none of it seems to indicate temporal learning (Jones & Agrawal, 2017). Pollinators may lack the capacity to understand and adapt their behaviour to temporal changes in resource availability, or the research may simply not yet exist. Capacity for learning has also been associated with insect socialization (Jones & Agrawal, 2017). Most bees native to Ontario, however, are solitary (Holm, 2023). It is possible that pollinator learning might mitigate the impact of phenological mismatch, but this lacks evidence. In seeking to understand the relationship between plant provenance and biotic interactions, the complexity of these dynamics, and dearth of targeted research, may obscure the true effects.

2.2.4 Summary

The relative qualities of various provenance approaches can only be understood by carefully considering the effects of provenance on genetic conservation, plant fitness, and biotic interactions. The evidence of these relationships drafts only a coarse image, but this is hardly surprising, given the complexity of ecological relationships. Regional seed, from multiple populations, seems to harbour substantial genetic diversity without compromising local remnant diversity. Where remnant genetic diversity is sufficient for local adaptation, local plants tend to exhibit greater fitness than nonlocal plants. Nonlocal plants, in theory, may fail to maintain evolved relationships with local fauna. However, the advantage of local plants to local pollinators has yet to be demonstrated experimentally. The existing literature is mixed. Given the contrasting evidence, landscape architects ought to approach plant provenance cautiously. The prudent practitioner might adopt an approach like regional admixture provenance, which balances genetic conservation, plant fitness, and biotic interactions by sourcing seed from several near-local populations with ecological conditions similar to the planting site. Additional research, particularly into the relationship between provenance and biotic interaction, will add confidence to the selection of a provenance approach.

2.3 Native Plant Procurement

Having considered the evidence supporting where plants ought to come from, I now turn to where plants do come from. I will focus on the local context of Southern Ontario and the genetic implications of various procurement strategies. Plant procurement practices vary between regions. Fortunately, a comprehensive survey of Southern Ontario native plant nurseries has recently been conducted. Lawson-Canning (2023) surveyed 51 native plant producers and identified trends in plant procurement practices. The majority of Ontario producers, Lawson-Canning found, rarely or never import native plants from outside the province. For forbs (herbs) and graminoids (grasses, sedges, and rushes), producers are more likely to use collection than other procurement methods and more likely to use seed than other propagule types. For forbs and graminoids, producers collect seeds from natural and managed populations at similar rates. The former practice, collection from natural populations, is commonly called wild harvest. Lawson-Canning did not define the term “natural population” in their survey. In some instances, natural populations are managed to promote seed production (Meissen et al., 2015). Lawson-Canning, however, describes managed populations as being intentionally established by humans. Human-established populations that are used for seed collection are commonly called Seed Production Areas (SPAs; Greening Australia Capital Region, n.d.), and I will refer to them this way to distinguish them from managed natural populations. Collection from natural populations and SPAs each have genetic and ecological implications, and each approach warrants detailed consideration.

2.3.1 Wild harvest

Wild seed harvest involves risks of extinction and demographic changes to harvested plant populations. The likelihood and degree of impact seem to be contingent on harvesting regime and plant population characteristics. Menges et al. (2004) modeled the impact of seed collection on 100-year population viability in 22 perennial plant species. They sought to understand the effects of harvest frequency and intensity, population size, and plant life history traits on population viability. They defined a safe harvest as one that increased a population’s probability of extinction by no more than 5%. The authors found different effects between species and categorized each species as Extinction-prone, Sensitive Type I, Sensitive Type II, or Insensitive. Extinction-prone species exhibited 100% extinction risk in the absence of seed harvest. Sensitive Type I species had high initial extinction risk, which increased with increasing harvest frequency and intensity. Sensitive Type II species had low initial extinction risk, which increased with increasing harvest frequency and intensity. Insensitive species exhibited no extinction risk under any treatment except frequent (9/10 years) *and* intense (100% seed collected) harvest or at very small population size (10 individuals).

Despite the species-specific differences, Menges et al. (2004) found some consistent trends across species. Even in sensitive species, infrequent (1/10 years) and low intensity (10% seed collected) harvest did not substantially increase extinction risk. Conversely, moderate harvest frequency (5/10 years) and intensity (50% seed collected) was unsafe except in populations larger than 500 individuals. Population viability substantially depended on initial population size, with smaller populations exhibiting higher extinction risk than larger ones under the same harvest regime. Extinction risk was also more sensitive to harvest intensity than harvest frequency, such that infrequent, high-intensity collection increased extinction risk more than frequent, low-intensity collection. These theoretical findings have since been corroborated by field research.

Harvested plant communities can exhibit changes in composition, related to differing harvest sensitivities of their constituent species. Meissen et al. (2015) conducted a retrospective study of tallgrass prairies in Minnesota, U.S.A. to clarify the impact of wild harvest on remnant ecosystems and the role of plant life history traits in individual species' responses. These authors found that plant species composition of frequently (every year) combine-harvested prairies differed significantly from those of infrequently (2/10 – 3/10 years) harvested and unharvested prairies. In addressing species-specific effects, the authors refer to Menges et al.'s (2004) classification system. Generally, they found that short-lived and non-clonal species were likely to be Sensitive to seed harvest, and long-lived and clonal species were likely to be Insensitive. Forty-one of 59 total species were found to be Insensitive to harvest, occurring as often in frequently harvested prairies as in unharvested prairies. Fourteen species were found to be Sensitive, being significantly less abundant in frequently harvested prairies than unharvested prairies. Three of those species were also significantly less abundant in infrequently harvested prairies than unharvested prairies, which the authors suggest constitutes Sensitive Type I. One Sensitive species, *Fragaria virginiana*, was likely too short for its seeds to have been harvested by the combine. The authors suggest that this species' apparent harvest response may actually be associated with burning in harvested prairies, a management practice to improve seed yields. This finding indicates that harvest-associated management practices, irrespective of direct seed removal, may impact plant populations. The potential for direct impact of wild harvest on remnant plant populations is well established and seems to be based on harvesting regime, species' life history traits, and plant population size. The authors advocate for caution especially in the absence of regulation concerning coordination of harvest between collectors.

Despite possible impacts on remnant plant populations, wild harvest may still be favoured for genetic considerations. Using seed from natural populations instead of SPAs theoretically provides a more direct representation of genetic diversity of those populations. However, poor collection, cleaning, storage, and production practices can compromise genetic diversity and source population representation. Basey et al. (2017) reviewed the potential loss of genetic diversity at each step of the plant production process. During seed collection, they report that the following practices compromise genetic diversity in harvested seed:

- collecting from smaller (<1000 plants, but especially <100 plants) populations
- collecting from too few (<50) plants, collecting from adjacent plants
- collecting different numbers of seeds from each plant
- avoiding plants that look different from others in the population
- avoiding plants growing at the edge of a population or in unique microhabitats
- collecting only once during the season

- varying collection protocols between populations

During seed cleaning and storage, they report that the following practices may similarly compromise genetic diversity:

- cleaning multiple populations' seeds together
- applying identical cleaning protocols to different populations
- failing to recover seeds inadvertently culled based on size or weight
- storing seeds under non-ideal temperature and moisture regimes

During germination, in instances where seed is used to produce nursery stock, the authors report that sowing different populations together and favouring fast-germinating seeds or seeds that germinate under certain conditions may also compromise genetic diversity in harvested seed. Thus, wild-harvested seed is not necessarily genetically diverse or representative of the source population. There are many instances in which plant producers can lose genetic diversity throughout collection, cleaning, storage, and production. This process is further complicated in SPAs, because that style of procurement involves repetition of several of the steps outlined previously and introduction of additional steps with novel risk.

2.3.2 Seed production areas

SPAs allow producers to harvest more seed without increasing the collection pressure on remnant ecosystems. However, these areas introduce additional risk of genetic differentiation from source populations, related to establishment, maintenance, and collection practices. SPAs are established from wild-harvested seed. Accordingly, they are subject to the same genetic risks summarized in section 2.3.1 associated with collection, cleaning, storage, and production. Many of those risks are duplicated in subsequent collection, processing, storage, and production practices at the SPA.

Espeland et al. (2017) reviewed potential impacts of natural and artificial selection in SPAs on restored population viability and ecological function. These authors report that cultivation practices, such as harvest timing, may favour certain traits over others, culling some genetic material from managed populations. A single, annual harvest, they report, may not capture the genetics of individuals that readily shatter seed. Seed retention, advantageous in cultivation because seeds remain on the plant until harvest, may, thus, be unconsciously selected for. Rapid seed germination and rapid growth could be similarly selected for under cultivation (Espeland et al., 2017).

These ideas are consistent with Dyer et al. (2016), who studied genetic differentiation between natural and cultivated populations of two grasses with contrasting breeding systems, one predominantly selfing and one predominantly outcrossing. For each species, the authors collected seed from 50 plants across four populations, grew the plants row-crop style, and mechanically harvested seed once during the plants' second growing season. They found significant genetic differences between seed harvested from the SPA and seed harvested from the natural source populations. They attribute these findings to significant differences in mortality, total seed production, seed maturation timing (relative to harvest timing), and seed retention between plants in the SPA. The authors attribute the high rate of mortality they observed to infection by a rust (*Puccinia* sp.). To counteract the effects of mortality, they advocate for frequent replenishment of SPAs with wild-harvested seed, but they don't indicate how often this replenishment should occur.

Nagel et al. (2019) found differential genetic effects of cultivation related to life history traits. Those authors evaluated phenotypic and genetic differences between five generations of cultivated seed in five herbaceous species. Original collections were from at least 50 individuals at each of several large (>1000 individuals) populations in Germany. The authors detected significant phenotypic changes in two species and significant genetic changes in three species, but they detected no change in overall genetic diversity. They report that differences were minor, except in a short-lived and predominantly selfing species, *Medicago lupulina*. In this species, the authors suggest that its tendency toward selfing, rather than outcrossing, maintained short-lived and longer-lived phenotypes separately, and that a single harvest of each generation captured only the seed from particularly long-lived individuals.

Spatial organization of SPAs also seems to impact preservation of source population genetics. St. Clair et al. (2020) tracked changes in the plant genetic diversity through the process of wild harvest, SPA cultivation, and restoration site installation. The authors established two SPAs, each with different spatial organization, to evaluate the effects of each on genetic differentiation of seeds from the source population. They found that genetic representation of source populations was greatest when plants from different source populations were row-segregated in the production area and their seed was mixed immediately prior to direct seeding or growing into nursery stock. SPAs introduce many opportunities for genetic differentiation of nursery stock from source populations, in addition to those risks associated with the initial collection.

2.3.3 Summary

Most Southern Ontario producers of native forbs and graminoids rely on in-province seed collection from natural or managed populations. In either case, production practices impact the genetic representation of source populations in nursery stock. Wild harvest introduces fewer opportunities for genetic changes but can detrimentally impact remnant populations. This risk to remnants is exacerbated in Southern Ontario, in the absence of regulation concerning coordination of harvest between producers. Impacts to wild populations are more likely if producers independently increase wild harvest to meet the outstanding demand. Spearing et al. (2023) surveyed Canadian organizations involved in native tree seed production and found that current production is inadequate to meet Canada’s reclamation and restoration goals. A similar study does not seem to have been conducted of Canada’s herbaceous seed supply chains. However, increased wild harvest may pose greater risk to natural herbaceous populations than to natural tree populations, given the former’s higher rate of harvest sensitivity. SPAs allow producers to increase seed harvest without placing additional collection pressure on natural remnants. However, SPAs also introduce more opportunities for genetic differentiation of plants from their source populations. The degree of genetic change seems to be related to species’ life history traits, but also, substantially, to cultivation practices. Thus, several SPA populations of the same species may differ in degree of genetic resemblance to their respective source populations based on differences in collection, establishment, and maintenance regimes and, potentially, the degree of environmental difference between source and site. It is possible, then, that, in cultivated plants, these factors may impact presumed relationships between plant provenance and biotic interactions.

3. Methods

3.1 Site Selection

Monitoring sites constitute a non-random sample of Southern Ontario SPAs. Sites were selected from a subset of all Ontario SPAs, those funded by WWF-Canada between 2021 and 2022 (Figure 3.1). I assumed that these sites, relative to more conventional plant production operations, would have high spatial accuracy plant provenance information. Additionally, the plants in these recently established sites were unlikely to exhibit substantial genetic differentiation from their source populations, having had few or no generations produced under cultivation (see section 2.3.2). I screened the WWF-Canada-funded SPAs for availability of data and access. Geographic proximity of sites to one another, and consequent convenience of access, was also a consideration. Sites that may have been otherwise suitable but were prohibitively far from one another were not selected.

3.1.1 Hillfield Strathallan College

The Hillfield Strathallan College SPA (HSC) was established in 2021 by the faculty, staff, and students. Plants were installed as plugs. The total planted area is 1,000 m^2. The SPA, at the time of installation, was comprised of 11 unique monospecific (Table 3.1) blocks, each 90 m^2. Since installation, maintenance has been discontinued (the intensity of maintenance not having been anticipated), and the site has become substantially dominated by spontaneously occurring goldenrods, thistles, and other vegetation. Installed plant species occur sporadically, and persistence varies between species. Many planted species are now totally absent. The primary goal of this SPA is education.

3.1.2 Kayanase Greenhouse

The Kayanase Greenhouse SPA (KAY) was established in the fall of 2023. Eleven species were installed (Table 3.1), some of these planted as plugs and some seeded directly. The total planted area is 250 m^2. The site is hand weeded, mulched, and watered. The site is divided into three multispecies planting beds. At the time of this study, plant emergence was sporadic, with few total plants and substantial bare (mulched) ground between most of them. This goal of this SPA is commercial seed production.

3.1.3 Toronto Seed Orchard

The Toronto Seed Orchard (NVK), hosted by NVK Nurseries, was established in June of 2022. Additional species were installed in the springs of 2023 and 2024 (Table 3.1). Plants were installed as plugs. The site is comprised of multispecies rows, 170 m long and spaced 2 m on centre, themselves comprised of monospecific strips ranging from 4 m to 70 m long. The total planted area is 2,430 m^2. The site is weeded (mechanically cultivated between rows and hand weeded within) and fertilized to encourage vegetative growth, and newly installed plants are watered regularly. Early inflorescences of some species are cut back to encourage development of a greater number of inflorescences throughout the season. The goal of this SPA is commercial seed production.

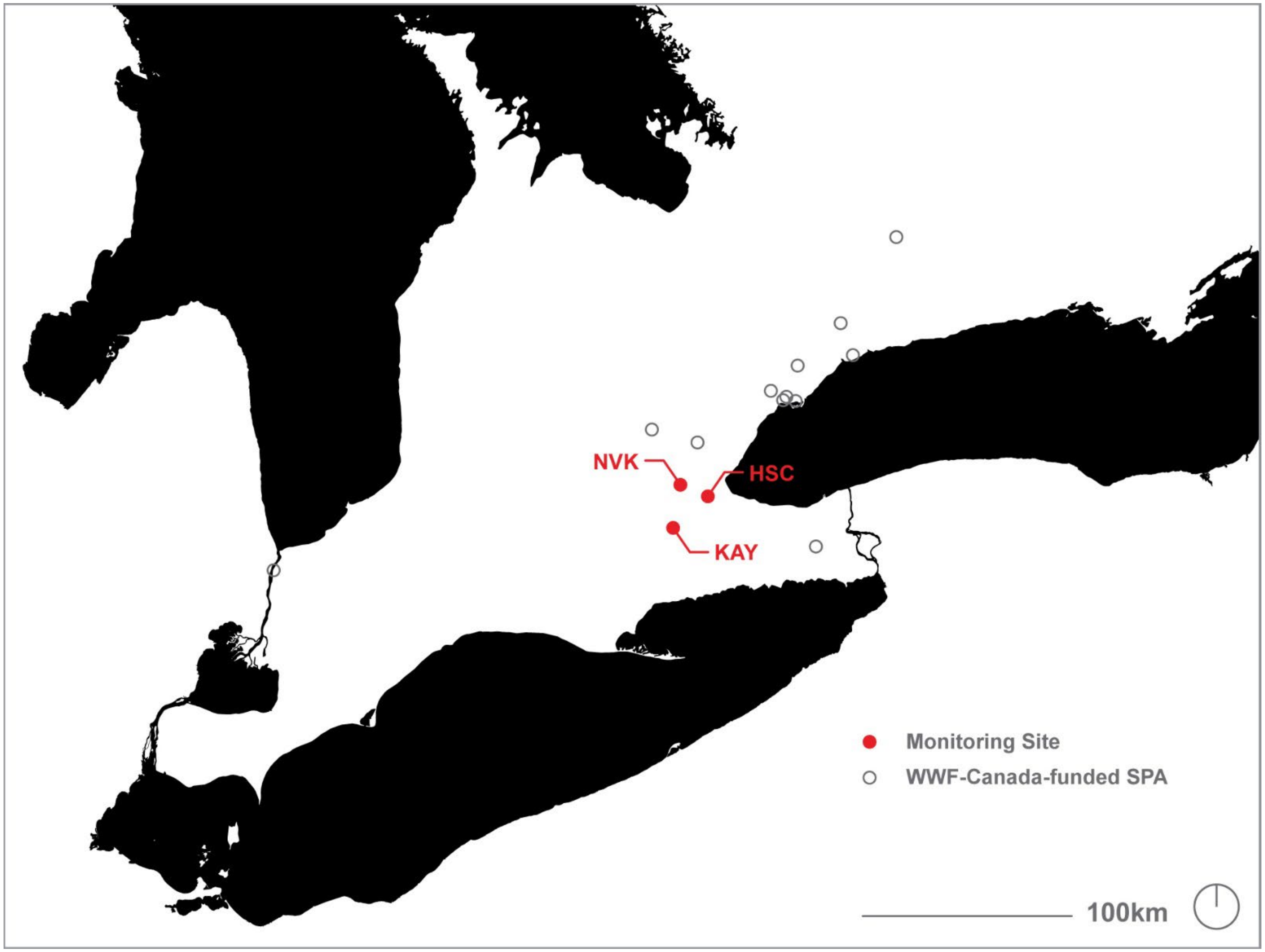

Figure 3.1: Between 2021 and 2022, WWF-Canada funded 17 SPAs across Southern Ontario. Monitoring sites were selected by screening that subset for data availability and access.

Table 3.1: Species installed at each SPA, denoted by an X. Not all species were observed on site at the time of monitoring.

Species	HSC	KAY	NVK
Achillea millefolium			X
Agastache nepetoides			X
Agastache scrophulariifolia			
Allium cernuum			X
Anaphalis margaritacea	X		
Andropogon gerardii	X	X	X
Anemone virginiana			X
Apocynum cannabinum			X
Aquilegia canadense			X
Asclepias incarnata	X		X
Asclepias syriaca			X
Asclepias tuberosa	X	X	X
Calamagrostis canadensis			X
Chelone glabra			X
Coreopsis tripteris			X
Desmodium canadense			X
Doellingeria umbellata			X
Echinacea pallida		X	X
Elymus canadensis			X
Elymus hystrix			X
Erigeron pulchellus			X
Euphorbia corollata			X
Eurybia macrophylla			X
Euthamia graminifolia			X
Eutrochium purpureum			X
Geum canadense			X
Geum triflorum			X
Helianthus strumosus			X
Heliopsis helianthoides	X	X	X
Lespedeza capitata			X
Lespedeza hirta			X
Liatris cylindracea			X
Liatris spicata			X
Lilium michiganense			X
Lobelia inflata			X

Lobelia kalmii			X
Monarda didyma		X	
Monarda fistulosa	X	X	X
Monarda punctata			X
Oenothera biennis			X
Oenothera gaura			X
Panicum virgatum	X	X	X
Penstemon digitalis		X	X
Penstemon hirsutus	X	X	X
Physostegia virginiana	X		
Potentilla arguta			X
Pycnanthemum tenuifolium			X
Pycnanthemum virginianum	X	X	X
Ratibita pinnata	X		
Rudbeckia hirta	X	X	X
Silphium laciniatum			X
Silphium terebinthinaceum			X
Sisyrinchium montanum			X
Solidago juncea			X
Solidago nemoralis			X
Solidago ohioensis			X
Solidago ptarmicoides			X
Solidago riddellii			X
Solidago rigida			X
Sorghastrum nutans	X	X	X
Sporobolus cryptandrus			X
Sporobolus heterolepis	X		
Symphyotrichum laeve	X		X
Symphyotrichum novae-angliae	X		
Symphyotrichum shortii	X		
Symphyotrichum urophyllum			X
Verbena hastata			X
Vernonia missurica			X
Veronicastrum virginicum			X
Zizia aurea			X

3.2 Species of Focus

I selected two herbaceous species, *Monarda fistulosa* (Wild Bergamot) and *Rudbeckia hirta* (Black-eyed Susan), as the subjects of my research. These were two of the few species in common between the three sites. Additionally, the species' flowering periods substantially overlap. Species with substantially different flowering periods would have necessitated more site visits over a longer duration, which would have been cost- and time-prohibitive.

3.2.1 *Monarda fistulosa*

Monarda fistulosa (Figure 3.2) is a perennial herbaceous plant native to much of Canada and the continental United States (Anderson, 2007). *M. fistulosa* is partially self-compatible but predominantly outcrossing, with seed set and germination rates higher under open pollination conditions (Anderson, 2007; Cruden et al., 1984).

Figure 3.2: *Monarda fistulosa* in bloom (source: author)

Flowers of *M. fistulosa* are visited by bees, flies, clearwing moths, wasps, butterflies, and hummingbirds (Johnson & Colla, 2022). The plant is a host for two species of pollen specialist bee (*Dufourea monardae*, *Protandrena abdominalis*) and larval host for ten species of moth (*Pyrausta orphisalis, P. signatalis, Coleophora monardae, C. heinrichella, Xenotemn pallorana, Acleris curvalana, Papaipema nebris, Aphelia alleniana, Anterastria teratophora, and Lintneria eremitus*; Johnson & Colla, 2022).

3.2.2 *Rudbeckia hirta*

Rudbeckia hirta (Figure 3.3) is a short-lived herbaceous plant native to North America (Harkess & Lyons, 1994). Within Canada, the plant is native to parts of Ontario, Manitoba, and Saskatchewan but is introduced in all other provinces (Canadensys Biodiversity Centre, n.d.) *R. hirta* may behave as an annual, biennial, or perennial, depending on location and genotype (Harkess & Lyons, 1994). It is self-incompatible: seeds produced from self-fertilization are non-viable (Abrahamson & McRae, 1977; East, 1940; Palmer et al., 2007). Achenes are long-lived. Toole and Brown (1946) buried achenes of *R. hirta* under eight inches of soil and found that more than 30 % survived at least 20 years and more than 10 % survived at least 30 years. The species also reproduces vegetatively, forming distinct “bunches” (Nuzzo, 1978).

Figure 3.3: *Rudbeckia hirta* in bloom (source: author)

Flowers of *R. hirta* are visited by bees, flies, moths, butterflies, and beetles (Foote, 2002; Johnson & Colla, 2022). The plant is host for 16 species of pollen specialist bee (*Andrena aliciae, Pseudopanurgus albitarsis, P. andrenoides, P. compositarium, Melissodes agilis, M. boltoniae, M. druriellus, M. illatus, M. subillatus, M. trinodis, Svastra obliqua, Paranthidium jugatorium, Megachile inimica, M. pugnata, Colletes americanus,* and *C. compactus*), and larval host for two species of butterfly (*Chlosyne nycteis* and *C. gorgone*) and ten species of moth (*Synchlora aerate, Chlorochlamys chloroleucaria, Lithophane unimoda, Papaipema cataphracta, P. nebris, P. nelita, P. unimoda, Epiblema carolinana, Orthotaenia undulana,* and Eupithecia miserulata; Johnson & Colla, 2022).

3.3 Data Collection and Processing

3.3.1 Field data collection

Each site was visited twice between July and August, 2024, to monitor insect pollinator flower visitation. The first monitoring visit to each site occurred 2-3 weeks after the onset of flowering in both *R. hirta* and *M. fistulosa*. The second visit to each site occurred 2-3 weeks after the first. Data collection was only conducted on clear or lightly overcast days with local air temperature equal to or greater than 15 ^{o}C. Visits began midmorning and lasted approximately two hours.

During the first visit, three inflorescences of each of the two species were randomly selected in a two-stage process. First, a cluster of inflorescences was selected. At each of HSC and KAY, discrete groupings of target species were assigned sequential numbers. At NVK, distance (m) along a row was used instead. A number, corresponding to a cluster, was generated using a random number generator. Second, an individual inflorescence was selected from within the cluster. Inflorescences within the cluster were assigned sequential numbers. A number, corresponding to a single inflorescence, was generated using a random number generator. This process was conducted three times for each species at each site. This did not result in a simple random sample because clusters contained different numbers of inflorescences. Inflorescences in lower density clusters had a greater likelihood of being selected than inflorescences in higher density clusters. Selected inflorescences were marked with a piece of sisal twine. Video of each marked inflorescence was recorded, using the integrated camera of an iPhone 15 Pro, during a five-minute observation period. The camera was mounted on a tripod and positioned 15-30 cm from the inflorescence. Recordings were collected between 10:30 AM and 12:15 PM.

During each observation period, microclimatic variables (instantaneous air temperature, relative humidity, and maximum wind speed) were measured using a Kestrel 4000 Weather and Environmental Meter. Measurements were taken 1.2 m above the ground, in light shade, adjacent to the inflorescence being recorded. Instantaneous air temperature and relative humidity were recorded once measures appeared to have stabilized, after 3-4 minutes. Maximum air speed observed during the same period was recorded.

Following the conclusion of all observation periods on a site, aerial photographs were taken using the integrated camera of an Autel Evo Nano drone. Photographs, centred on each marked inflorescence, were taken at each of several heights, between 4 m and 11 m altitude.

Each operation was repeated on the second visit to each site. In instances where the marked inflorescence was no longer flowering, the nearest flowering inflorescence of the same species was selected as a replacement.

3.3.2 Insect identification

Insect flower visitors were identified from recordings by Samm Reynolds, PhD candidate in Environmental Science at the University of Guelph, to the taxonomic level discernable for each based on insect size, video resolution, and visibility of distinguishing characteristics.

3.3.3 Floral characteristics

Using the drone photos, I calculated floral density and diversity in the area immediately surrounding (1.5 m radius) each inflorescence. This radius was a pragmatic limit, given the time-intensive nature of counting inflorescences and the exponential rate of increase in area with respect to radius. Prior to counting, photos were corrected for lens distortion using Adobe Lightroom v7.5 (Figure 3.4).

Figure 3.4: Example of uncorrected (left) and corrected (right) aerial photo used in calculation of floral characteristics. Distortion was mild and predominantly near the edges, outside the 1.5 m radius for calculation of floral metrics.

Floral density was calculated as number of inflorescences of all species per unit area. Measures of floral diversity included richness, evenness (Equation 3.1), and the Shannon-Wiener index (Shannon, 1948; Equation 3.2). The latter two metrics were calculated from the number of inflorescences, rather than the number of individuals, of each species. Inflorescences obscured from view by overlying vegetation were not counted or included in the calculation of these metrics.

E = H / ln(k)

Equation 3.1: Floral evenness. Where E = evenness; H = Shannon-Wiener index; and k = # of species

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

Equation 3.2: Shannon-Wiener index.

3.3.4 Landscape context analysis

I calculated proportion of natural and semi-natural land cover as a metric of sites' geographic context. Contextual analyses were conducted in ArcGIS Pro v3.2.2 using the Southern Ontario Land Information System (SOLRIS) 3.0 dataset, produced by Land Information Ontario (2019), which has a 15 m pixel resolution.

I calculated proportion of natural and semi-natural cover within eight radial distances around each site: 250 m, 500 m, 750 m, 1000 m, 1500 m, 2000 m, 2500 m, and 3000 m. This is consistent with the protocol used by Steffan-Dewenter et al. (2002). Those authors found correlations between proportion of semi-natural habitat and wild bee species richness and abundance at various spatial scales. The authors did not provide a rationale for not considering natural cover. Refer to Table 3.2 for land cover type classification.

Table 3.2. Categorization of SOLRIS land cover classes for the calculation of the proportion of natural and semi-natural cover.

Natural	**Semi-Natural**	**Other**
Forest	Plantations - Tree Cultivated	Open Water
Coniferous Forest	Hedge Rows	Tilled
Mixed Forest	Undifferentiated	Transportation
Deciduous Forest		Built-up Area - Pervious
Treed Swamp		Built-up Area - Impervious
Thicket Swamp		
Marsh		

Note: Undifferentiated includes orchards, vineyards, perennial crops, idle (>10 years) agricultural lands, urban brown fields, hydro and transportation right-of-ways, upland thicket, and openings within forests.

3.3.5 Translocation distance

For each plant species I measured straight-line distances between each SPA and its seed source. Precise seed collection locations were not available from SPA operators. Instead, I used a centroid value for the seed collection zone or ecodistrict from which each species' seeds were obtained. In instances where a given species in a given SPA had multiple provenances, the mean centroid-to-site distance was taken. Centroid values were calculated and measurements taken in ArcGIS Pro v.3.2.2.

3.4 Statistical Analysis

All statistical tests were conducted using RStudio v4.3.2.

A Scheirer-Ray-Hare test (SRH) was conducted to determine whether there were significant differences in mean total insect visitors between different sites and between different plant species, and to determine whether there was any interaction effect between site and species on total insect visitation. A Kruskal-Wallis test was conducted to determine whether there were significant differences in mean total insect visitors between observation dates. The Kruskal-Wallis test is a nonparametric test used to evaluate whether samples originate from the same distribution (Ostertagová et al., 2014). It is a suitable alternative to the one-way analysis of variance (ANOVA) when the assumptions for the latter test (e.g., normality) are not met (Ostertagová et al., 2014). The SRH is an extension of the Kruskal-Wallis test (Scheirer et al., 1976). The SRH is used to evaluate the effects of multiple independent factors, and the interactions between them, on a single dependent variable (A. Bazrgar, personal communication, October 29, 2024). It is a suitable alternative to the two-way ANOVA when the assumptions for the latter test are not met (A. Bazrgar, personal communication, October 29, 2024). The Kruskal-Wallis test and SRH are suitable for zero-inflated datasets, whose distributions depart markedly from normality. The Kruskal-Wallis test and SRH assume:

1. The observations in each group come from populations with identical (except medians) distributions.
2. Samples are random and independent of one another (Ostertagová et al., 2014).

Spearman Rank Correlation tests (SRC) were conducted to evaluate the strengths and directions of relationships between each of (a) microclimatic variables, floral characteristics, and proportion of natural and semi-natural cover and (b) total insect visitors and insect visitors of each taxon. Microclimatic variables include air temperature, wind speed, and relative humidity. Floral characteristics include inflorescence density, richness, evenness, and Shannon-Wiener index. The SRC is used to evaluate the strength of association between two variables (Spearman, 1904). The SRC is less sensitive than the Pearson Correlation, a common alternative, to extreme values (Caruso & Cliff, 1997). Thus, SRC is the more appropriate test for zero-inflated datasets.

The methods detailed in this chapter are the basis for analysis of relationships between frequency of insect-inflorescence visitation and each of translocation distance, microclimatic factors, floral characteristics, and landscape context. In combination, these methods fulfill the research purpose of clarifying the relationship between plant provenance and insect visitation. Results are reported in the next section and analyzed to answer the research question.

4. Results and Analysis

In total, I observed 24 insect-inflorescence interactions, representing five identified insect orders (Coleoptera, Diptera, Hymenoptera, Lepidoptera) and ten identified taxa (two identified to order, five identified to family, and three identified to genus). One taxon (referred to as *Unknown*) could not be identified from the recordings. The minimum number of visitors of any individual taxon was one (Lepidoptera, Aleyrodidae, Syriphidae, Chrysomalidae, Formicidae, Stratiomyidae, *Xylocopa*, and *Bombus*; 4% of total interactions each) and the maximum was seven (*Unknown*; 29% of total interactions). Twenty-two (69%) observation periods had no insect visitors, resulting in a zero-inflated dataset.

4.1 Translocation Distance and Plant Species

Provenance information was available for each plant species at each site except for *R. hirta* at HSC. At HSC, *M. fistulosa* originated from two seed collection areas. At KAY, *M. fistulosa* and *R. hirta* originated from the same seed collection area. At NVK, *M. fistulosa* and *R. hirta* also originated from the same seed collection area. Consequently, translocation distance and site were treated interchangeably, each site being associated with a single translocation distance or single average translocation distance (Table 4.1; Figure 4.2).

Table 4.1: Translocation distances between seed collection area centroids and sites vary substantially. For each site except HSC, *M. fistulosa* and *R. hirta* shared a single seed source.

Site	Seed Source	Distance (km)
HSC	Z34 / Z37	87*
KAY	Z37	40
NVK	7E-2	116

*Mean distance given for HSC
Note: Provenance information unavailable for *R. hirta* at HSC.

I observed seven (29%; $\bar{x} = 0.78$; s.d. = 1.4; Min = 0; Max = 4) total insect-inflorescence interactions at HSC, six (25%; $\bar{x} = 0.5$; s.d. = 0.80; Min = 0; Max = 2) interactions at KAY, and eleven (46%; $\bar{x} = 1$; s.d. = 1.9; Min = 0; Max = 6) interactions at NVK. I conducted nine observation periods at HSC, twelve at KAY, and eleven at NVK.

I observed 10 (42%; $\bar{x} = 0.67$; min = 0, max = 4) total insect-inflorescence interactions on *M. fistulosa* and 14 (58%; $\bar{x} = 0.82$; min = 0, max = 6) interactions on *R. hirta*. However, I conducted two fewer observation periods of *M. fistulosa* (15) than of *R. hirta* (17).

Discrepancies in observation periods between sites and species were a consequence of adapting my monitoring protocol in the field to accommodate the unanticipated cessation of flowering in marked inflorescences.

The assumptions of a two-way analysis of variance (ANOVA) were not met by the data. The results of a Shapiro-Wilk test indicate that the distribution of residuals departs significantly ($p = 0.002$) from a normal distribution, violating the assumption of normality of residuals. Thus, the results of an ANOVA conducted on these data would be invalid. A SRH test was conducted instead.

No significant relationship was found between translocation distance and total insect visitors, with the mean number of total insect visitors not significantly different between translocation distances (p = 0.93; Table 4.2; Figure 4.1A). Similarly, no significant relationship was found between plant species and total insect visitors, with the mean number of total insect visitors not significantly different between plant species (p = 0.60; Table 4.2; Figure 4.1B). No significant interaction effect was found between translocation distance and plant species on total insect visitation (p = 0.61; Table 4.2). That is, the effect of neither translocation distance nor plant species on total insect visitors differed with respect to the other.

Table 4.2: Results of the Scheirer-Ray-Hare test indicate no significant difference in mean total insect visitors between different sites (translocation distances) or plant species and no significant interaction effect between site and species.

	df	**Sum Sq**	**H**	**p**
Site	2	4.46	0.15	0.93
Species	1	8.00	0.27	0.60
Site x Species	1	7.66	0.26	0.61

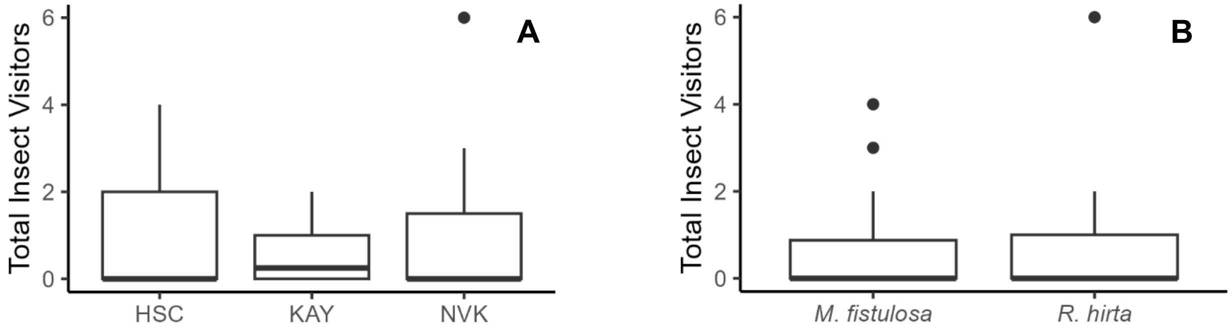

Figure 4.1: Boxplots of total insect visitors by site (A) and by plant species (B). Boxes reflect Q1 – Q3 interquartile range, median values. Outliers are shown. Data are substantially skewed.

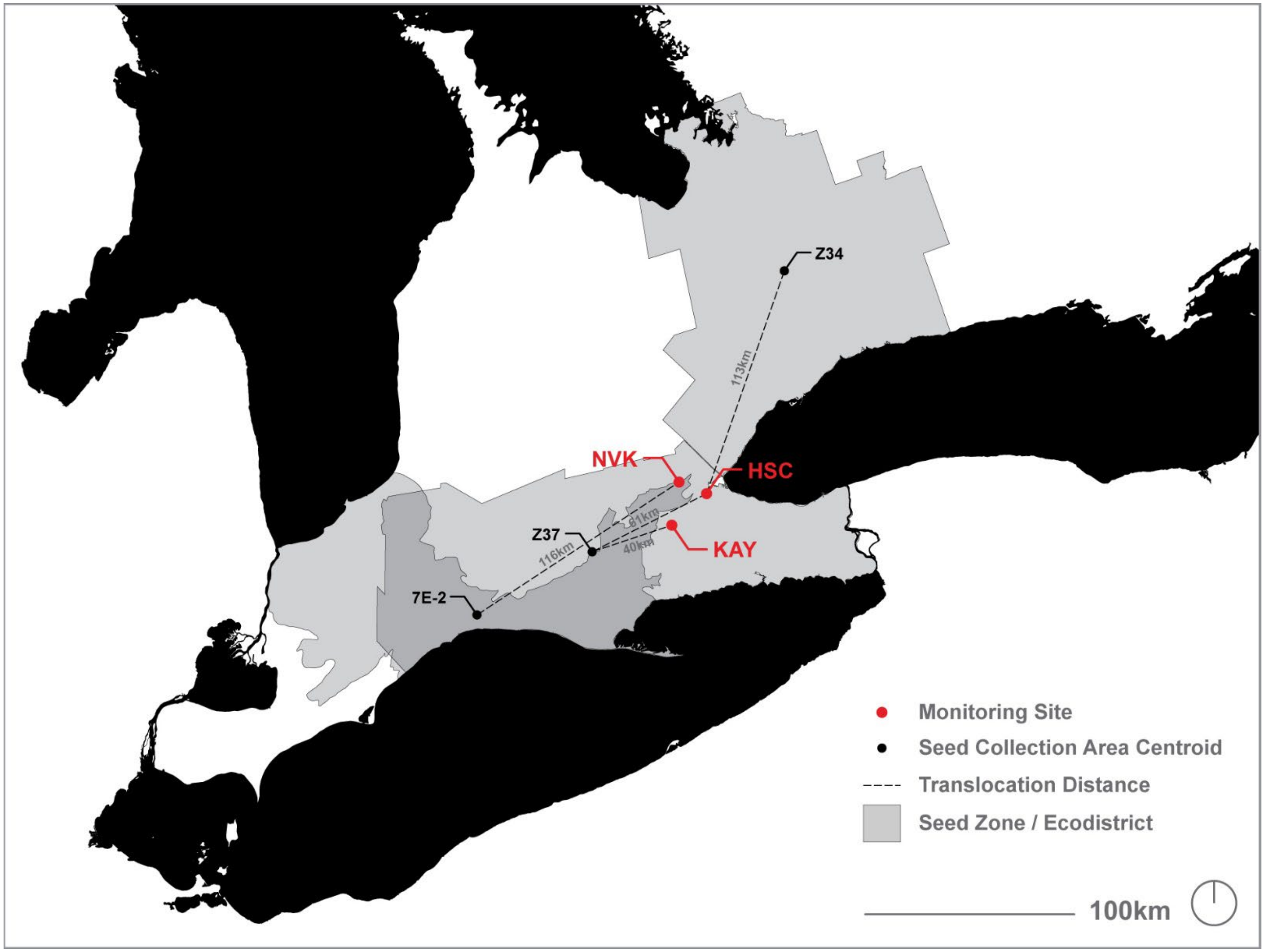

Figure 4.2: Reported seed sources for each site are within Southern Ontario and were reported as either seed zone or ecodistrict.

4.2 Date

Mean visitors per observation period ranged from 0 to 2.2. Two observation dates (33%) had no insect-inflorescence interactions. These dates (2024-07-18 and 2024-08-07) notably had the lowest observed temperatures (respectively, x̄ = 22.3 °C, 22.4 °C; Min: 19.5, 21.7; Max: 24.7, 23.0). Additionally, 2024-08-07 had the greatest wind speed of any monitoring date (x̄ = 6.4 m/s; Min = 5.7; Max = 7.2).

The two dates with greatest average visitation, 2024-07-19 (x̄ = 1) and 2024-08-01 (x̄ = 2.2), had low wind speed (respectively, x̄ = 1.02, 1.04 m/s; Min = 0.7, 0.5; Max = 1.5, 1.7) relative to most other dates. However, these wind speeds did not substantially differ from 2024-07-31 (x̄ = 1.02, 1.00 m/s; Min = 0.7, 0.5; Max = 1.3, 1.7). The dates with the greatest visitation did not differ substantially from other dates with respect to air temperature or relative humidity.

The assumptions of a one-way ANOVA were not met by these data. The results of a Shapiro-Wilk test indicate that the distribution of residuals departs significantly ($p = 0.002$) from a normal distribution, violating the assumption of normality of residuals. Thus, the results of an ANOVA conducted on these data would be invalid. A Kruskal-Wallis test was conducted instead.

No significant relationship was found between date and total insect visitors, with the mean number of total insect visitors not significantly different between dates at a 95% confidence level ($p = 0.07$; Figure 4.3).

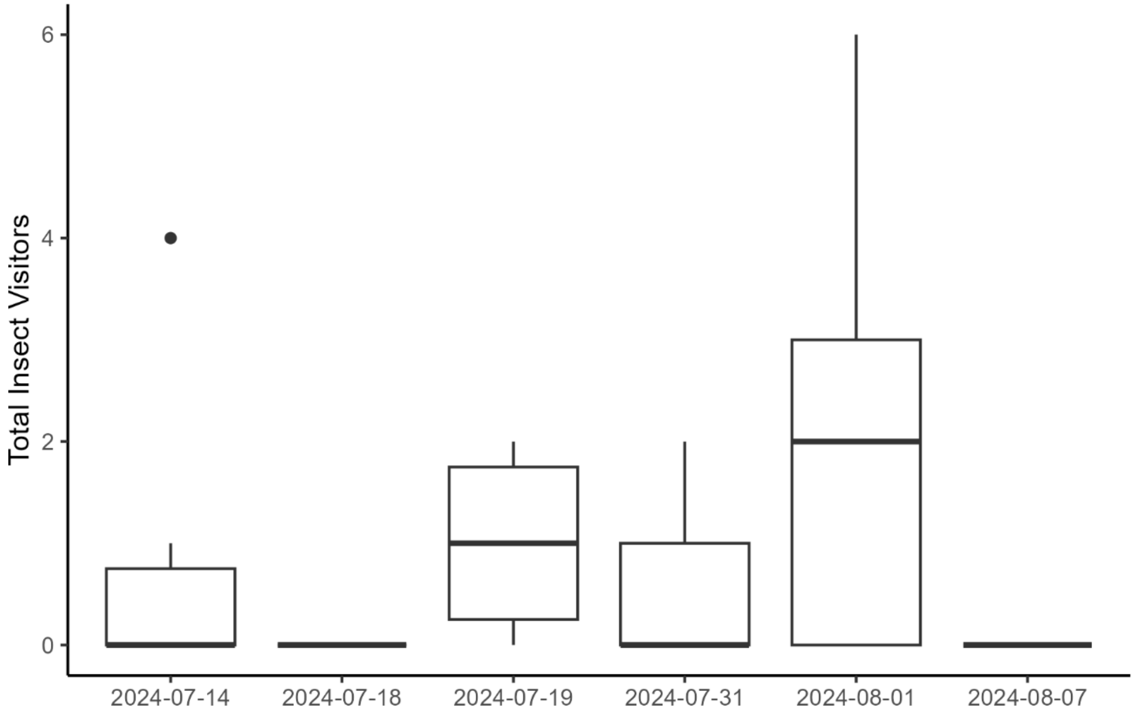

Figure 4.3: Boxplots of total insect visitors by date. Boxes reflect Q1 – Q3 interquartile range, median values. Outliers are shown. Data are substantially skewed.

4.3 Microclimate, Floral Characteristics, and Context

4.3.1 Microclimate

Microclimatic factors varied substantially between observation periods (Table 4.3). Air temperature during observation periods ranged from 19.5 ^oC to 33.7 ^oC ($\bar{x}$ = 26.3 ^oC; s.d. = 3.7). Wind speed ranged from 0.5 m/s to 7.2 m/s ($\bar{x}$ = 2.7 m/s; s.d. = 2.1). Relative humidity ranged from 53.8 % to 80.9 % ($\bar{x}$ = 69.8 %; s.d. = 7.8). Significant correlations were found between several microclimatic variables and total insect visitors or visitors of a particular taxon (Table 4.4).

Correlations between air temperature and visitation were mostly positive, and negative correlations were very weak. A significant, moderate, positive correlation was found between air temperature and total insect visitors (r_s = 0.45, p = 0.01; Figure 4.4A). A significant, weak, positive correlation was found between air temperature and *Unknown* visitors (r_s = 0.37, p = 0.04; Figure 4.4B). No significant correlation was found between air temperature and visitors of any other taxon.

Table 4.3: Summary of microclimatic variables across observation periods.

	Mean	**Median**	**SD**	**Min**	**Max**
Air temperature (C)	26.3	26.1	3.7	19.5	33.7
Wind Speed (m/s)	2.7	1.7	2.1	0.5	7.2
Relative Humidity (%)	69.8	71.0	7.8	53.8	80.9

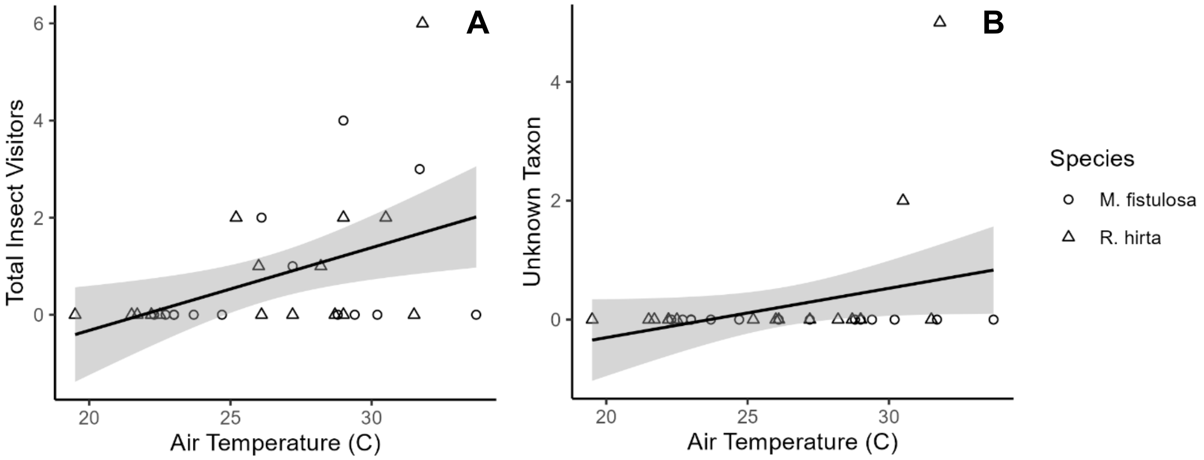

Figure 4.4: The relationships between air temperature and total insect visitors (A) and between air temperature and *Unknown* visitors (B) are both significant and, respectively, moderate and weak.

Correlations between wind speed and visitation were mostly negative, and positive correlations were very weak. Significant, moderate, negative correlations were found between wind speed and each of total insect visitors (r_s = -0.50, p = 0.04; Figure 4.5A), Hymenoptera visitors (r_s = -0.45, p = 0.01; Figure 4.5B), and *Lasioglossum* visitors (r_s = -0.41, p = 0.02; Figure 4.5C). No significant correlation was found between wind speed and visitors of any other individual taxon.

Correlations between relative humidity and visitation were substantially a mix of positive and negative. No significant correlation was found between relative humidity and total insect visitors or visitors of any individual taxon.

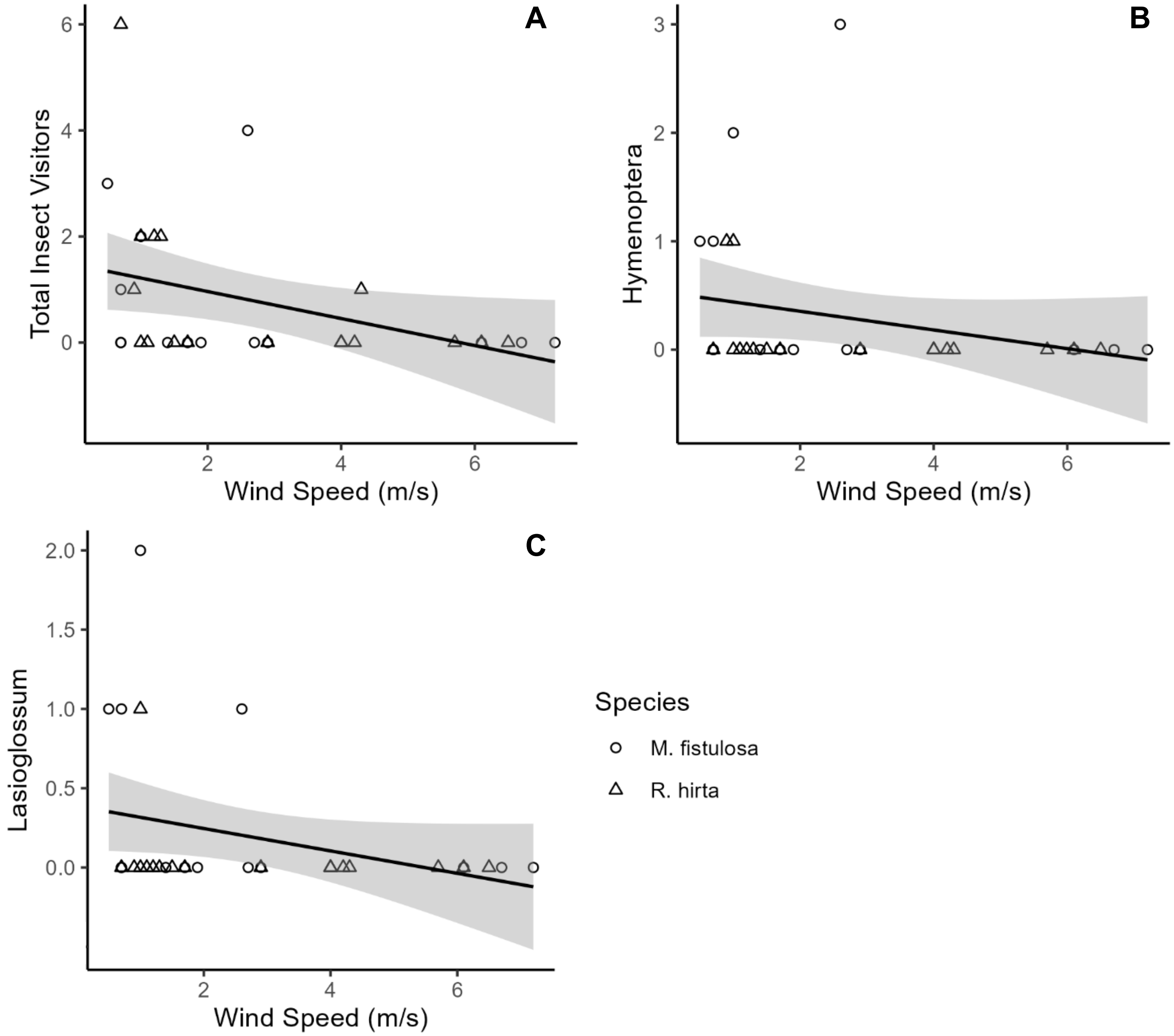

Figure 4.5: The relationships between wind speed and total insect visitors (A), wind speed and Hymenoptera visitors (B), and wind speed and Lasioglossum visitors are all significant and moderate.

Table 4.4: Spearman correlation coefficients show significant relationships between air temperature, wind speed, and various types of insect visitors. No significant relationships were observed in other variables.

	Air Temp	Wind Speed	Relative Humidity	Floral Density	Floral Richness	Floral Evenness	Floral - Shannon	Context 250m	Context 500m	Context 750m	Context 1000m	Context 1500m	Context 2000m	Context 2500m	Context 3000m
Total Visitors	0.45*	-0.50*	0.05	0.05	0.14	0.16	0.15	-0.01	-0.01	-0.01	-0.01	-0.01	-0.03	-0.03	-0.03
Coleoptera	0.15	0.04	0.30	0.23	0.31	0.10	0.27	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Diptera	0.34	-0.30	0.21	0.07	-0.04	-0.06	-0.05	-0.03	-0.03	-0.03	-0.03	-0.03	-0.16	-0.16	-0.11
Hymenoptera	0.17	-0.45*	-0.23	-0.11	0.02	0.13	0.08	-0.07	-0.07	-0.07	-0.07	-0.07	0.22	0.22	0.09
Lepidoptera	0.29	-0.28	0.27	0.04	0.06	0.00	0.05	-0.01	-0.01	-0.01	-0.01	-0.01	-0.19	-0.19	-0.13
Aleyrodidae	0.26	-0.31	0.15	0.04	-0.17	-0.16	-0.16	0.22	0.22	0.22	0.22	0.22	-0.03	-0.03	0.11
Apidae	0.15	0.04	0.30	0.23	0.31	0.10	0.27	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Chrysomelidae	0.15	0.04	0.30	0.23	0.31	0.10	0.27	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Formicidae	-0.03	-0.20	-0.24	-0.14	-0.17	-0.16	-0.16	-0.02	-0.02	-0.02	-0.02	-0.02	0.21	0.21	0.11
Halictidae	0.18	-0.41*	-0.17	-0.08	0.07	0.21	0.14	-0.04	-0.04	-0.04	-0.04	-0.04	0.18	0.18	0.08
Stratiomyidae	-0.05	-0.16	-0.20	-0.02	-0.17	-0.16	-0.16	-0.02	-0.02	-0.02	-0.02	-0.02	0.21	0.21	0.11
Syrphidae	0.07	0.18	0.23	-0.05	0.18	0.21	0.16	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Bombus	0.15	0.04	0.30	0.23	0.31	0.10	0.27	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Lasioglossum	0.18	-0.41*	-0.17	-0.08	0.07	0.21	0.14	-0.04	-0.04	-0.04	-0.04	-0.04	0.18	0.18	0.08
Xylocopa	0.15	0.04	0.30	0.23	0.31	0.10	0.27	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	-0.29
Unknown	0.37*	-0.26	0.06	0.19	0.00	-0.03	-0.05	0.31	0.31	0.31	0.31	0.31	-0.04	-0.04	0.16

* denotes significant correlation at 95% confidence level.

4.3.2 Floral characteristics

Floral characteristics varied substantially between sites and plant species (Table 4.5), likely due to differences in time since establishment, site layout, maintenance practices (see section 3.1 for detailed site descriptions), and species' natural growth habits. Densities ranged from 1.1 inflorescences / m^2 to 116 inflorescences / m^2 ($\bar{x}$ = 26; s.d. = 28). Richness ranged from 1 to 5 ($\bar{x}$ = 2; *Mdn* = 1; s.d. = 1.4). Evenness ranged from 0 to 0.996 ($\bar{x}$ = 0.27; *Mdn* = 0; s.d. = 0.34). Shannon-Wiener index values ranged from 0 to 1.27 ($\bar{x}$ = 0.31; *Mdn* = 0; s.d. = 0.40).

Correlations between floral characteristics and insect visitation were all weak or very weak. Floral density (all r_s = 0.23), floral richness (all r_s = 0.31), and Shannon-Wiener index (all r_s = 0.27) all exhibited the strongest correlations with the family Chrysomelidae and the genera *Bombus* and *Xylocopa*. Floral evenness exhibited the strongest correlations with the family Syrphidae and the genus *Lasioglossum* (both r_s = 0.21).

No significant correlation was found between any floral characteristic and total insect visitors or visitors of any individual taxon.

Table 4.5: Floral characteristics within 1.5 m of recorded inflorescences varied substantially between sites and species. Diversity metrics, irrespective of species, were highest at HSC. Density, with respect to species, was highest at NVK.

	Density				**Richness**				**Evenness**				**Shannon-Wiener index**			
	x̄	**SD**	**Min**	**Max**	**x̄**	**SD**	**Min**	**Max**	**x̄**	**SD**	**Min**	**Max**	**x̄**	**SD**	**Min**	**Max**
HSC																
M. fisulosa	42.6	11.5	29.3	49.2	4.7	0.6	4	5	0.6	0.2	0.5	0.8	0.9	0.2	0.8	1.2
R. hirta	18.7	4.9	15.6	27.3	3.8	0.8	3	5	0.6	0.1	0.5	0.8	0.8	0.1	0.7	1.3
KAY																
M. fisulosa	2.7	1.5	1.4	5.5	1.5	0.5	1	2	0.4	0.5	0	1.0	0.3	0.5	0.0	0.7
R. hirta	6.9	7.2	1.1	16.8	1.0	0.0	1	1	0	0	0	0	0	0	0	0
NVK																
M. fisulosa	65.1	44.8	17.7	116.0	1.4	0.5	1	2	0.1	0.1	0.0	0.3	0.1	0.1	0.0	0.2
R. hirta	34.5	11.8	15.4	46.1	1.5	0.8	1	3	0.1	0.2	0.0	0.5	0.1	0.2	0.0	0.6

Note: calculation of floral characteristics was based inflorescence counts from aerial photographs. Visual occlusion of some inflorescences by overlying vegetation makes these counts approximate.

4.3.3 Context

Proportion of natural and semi-natural land cover varied substantially between sites but was relatively similar between radial distances for each site (Table 4.6; Figure 4.6). Proportion of natural and semi-natural land cover ranged from 0 (250 m radius) to 0.10 (1000 m) at HSC, 0.35 (750 m) to 0.55 (2000 m) at KAY, and 0.51 (3000 m) to 0.76 (250 m) at NVK.

Table 4.6: Proportion of natural and semi-natural land cover was consistently lowest at HSC at all radial distances. This proportion was highest for NVK at smaller radial distances but became substantially similar in NVK and KAY as distance increased.

	Radius							
Site	**250m**	**500m**	**750m**	**1000m**	**1500m**	**2000m**	**2500m**	**3000m**
HSC	0	0.003	0.03	0.10	0.09	0.08	0.08	0.09
KAY	0.52	0.37	0.35	0.42	0.51	0.55	0.52	0.51
NVK	0.76	0.75	0.76	0.72	0.59	0.53	0.51	0.51

Note: Refer to Table 3.1 for categorization of natural and semi-natural cover.

Correlations between total visitation and proportion of natural and semi-natural cover and between visitation of individual taxa and proportion of natural and semi-natural cover were weak or very weak at all radial distances. However, the direction of the relationships varied between taxa and, for some taxa, between radial distances. No significant correlation was found between proportion of natural and semi-natural cover at any radius and total insect visitors or visitors of any individual taxon (Table 4.4).

Figure 4.6: Proportion of natural and semi-natural land cover (black) ranged from 0 (250 m radius) to 0.10 (1000 m) at HSC, 0.35 (750 m) to 0.55 (2000 m) at KAY, and 0.51 (3000 m) to 0.76 (250 m) at NVK.

5. Discussion and Conclusion

I evaluated the relationships between insect flower visitation and each of plant translocation distance, microclimatic factors, floral characteristics, and landscape context. Microclimatic factors (air temperature and wind speed) were the only variables able to account for differences in pollinator visitation between observation periods. I found no significant relationship between visitation and any of translocation distance, floral characteristics, or landscape context.

5.1 Translocation Distance

Pollinator visitation was not significantly different between the three sites. Site and translocation distance were interchangeable in this study, each site having a single associated distance from its seed source (or average distance from its seed sources, if multiple), irrespective of plant species. This lack of significant relationship may indicate a true absence of relationship between translocation distance and pollinator visitation. Or it may reflect a true absence of relationship at this geographic scale (translocation less than 200 km). Bucharova et al. (2022) found that pollinators differentiated between plant provenances when translocation distances of up to 450 km were involved.

Alternatively, a true relationship may have been missed due to constraints in the research. One such constraint was a lack of geographic specificity in plant source. Sources were reported as seed zone or ecodistrict, polygons up to 240 km across. The centroid values of these polygons, used in the analysis, may have differed from actual seed collection locations by up to 140 km. It’s possible that actual translocation distances did not differ between sites. In that case, a true relationship between translocation distance and pollinator visitation would not have been reflected in the plants used in this study.

Lack of information regarding seed collection sites introduces other possibilities. It could be that the collection site for some or all of the plants in the study does not reflect their genetic provenance, if the plants were recent immigrants to those sites. Additionally, if seeds were collected from a small, genetically constrained remnant population, the plants may fail to exhibit geographically linked phenotypic behaviour. Leimu and Fischer (2008) report that local adaptation in plants is substantially contingent on population size, with large populations tending to be locally adapted and small populations tending not to be. I assumed that any relationship between translocation distance and visitation would be rooted in geographically differentiated phenotypic traits, such as flower phenology, for example, as Bucharova et al. (2022) demonstrated. It would be plausible, then, for these traits to be lost in small populations, in similar fashion to the presumed loss of local adaptation by genetic drift or other genetic risks faced by small, capped populations.

Another possibility is that my limited monitoring window missed temporal variation in a true relationship between translocation distance and visitation. If the effect of provenance on pollinator visitation is mediated by flower phenology, as Bucharova et al. (2022) found, that effect may be more pronounced or may only exist during certain seasonal periods, possibly near the onset flowering. I may have missed such an effect by starting to monitor visitation after both plant species had begun to flower at all sites.

It is also possible that some other variable, differing between sites, which I failed to capture, had a contrasting effect that obscured a true effect of translocation distance on visitation. Possible occluding factors include site layout (e.g., size, shape, proximity to neighbouring habitat patches), cultural landscape context (e.g., pesticide use at neighbouring sites), and habitat patch connectivity surrounding the site.

Finally, it may simply be that the limited number of observations in this study lacked the statistical power to elucidate a true relationship between translocation distance and visitation. Bucharova et al. (2022), for example, had 737 total observations of insect-inflorescence interactions. I had just 24. This possibility would be supported by a lack of other significant relationships, which prior research suggests I ought to have found, amongst the data.

This last possibility is not mutually exclusive with other factors that may have obscured a true relationship between translocation distance and visitation. It is possible, for example, that some contrasting, occluding variable between sites masked a relationship and that, had I captured that variable in my study, my small dataset may still have lacked the power to demonstrate a relationship between translocation distance and visitation.

Further studies into the relationship between plant provenance and pollinator visitation may grapple with similar challenges. Recommendations to this effect are given in section 5.5.

5.2 Microclimate

Air temperature, which ranged from 19.5 ^{o}C – 33.7 ^{o}C, and wind speed, which ranged from 0.5 m/s to 7.2 m/s, were the only variables to show a significant relationship with total visitation or with visitation of any individual taxon. Relative humidity, which ranged from 53.8 % to 80.9 %, showed no significant relationship with visitation.

5.2.1 Air temperature

Total insect visitation and visitation of *Unknown* were positively and moderately correlated with air temperature. These findings align with those of others, demonstrating positive relationships between air temperature and total insect flower visitation across ecologically distinct sites (Goodwin et al., 2021; McCall & Primack, 1992). However, I would have expected to see stronger and significant relationships between temperature and some other taxa, given reports in the literature.

Goodwin et al. (2021) found a positive correlation between Hymenoptera visitation and air temperature. Totland (1994) found a positive correlation between Diptera visitation and air temperature. These were two of the most numerous taxa I observed. While the direction (positive) of the correlations I found in those taxa aligns with the literature, the lack of significance in these relationships supports the possibility that my dataset was too small to demonstrate true relationships that may exist. Another explanation, however, is that the range of temperatures I observed (19.5 ^{o}C – 33.7 ^{o}C) was too high for these taxa to exhibit similar relationships to those reported in the literature. Goodwin et al. (2021) reported temperatures between 6 ^{o}C and 28.2 ^{o}C, and Totland (1994) reported temperature between 5.4 ^{o}C and 25 ^{o}C.

I also would have expected to see differences in the relative strengths of the relationships between air temperature and each of the three bee genera I observed. None of these correlations were significant, but they were nearly identical in strength. Bishop and Armbruster (1999) found different thermoregulatory ability between bee species related substantially to body size. Thermoregulatory ability is the ability of an insect to maintain relatively constant thoracic temperature over a wide range of environmental temperature plus the ability to elevate thoracic temperature above environmental temperature when environmental temperature is relatively low (Bishop & Armbruster, 1999). Minimum environmental temperatures observed by Bishop and Armbruster (1999) during flights of small-bodied bees (including Halictidae, the family to which *Lasioglossum* belongs) were within the range of temperatures I observed. Thus, temperatures during observation periods may have been above some threshold value for even the smaller-bodied *Lasioglossum* spp.

5.2.2 Wind speed

Wind speed showed a moderate, negative correlation with total insect visitors and with visitors of Hymenoptera and *Lasioglossum* spp. These findings agree generally with the trend of others, demonstrating negative relationships between visitation and wind speed.

Correlations between wind speed and visitation by Hymenoptera other than *Lasioglossum* spp. (Formicidae, *Bombus* sp., *Xylocopa* sp.) were weak or very weak and non-significant. Thus, *Lasioglossum* spp. visitation seems to account predominantly for the correlation observed at the order level.

Winged insect taxa other than *Lasioglossum* spp. were observed in relatively low numbers. Diptera, the only winged taxon aside from *Lasioglossum* to have occurred more than once, was nearly significantly correlated with wind speed. It is, thus, plausible that too few observations were collected of winged taxa other than *Lasioglossum* spp. to reflect true relationships between wind speed and visitation, if any exist. However, prior findings of relationships between wind speed and visitation amongst various insect taxa do not suggest a uniform, easily-discernable pattern.

Reported findings suggest that relationships vary between taxa and between ecological contexts. Goodwin et al. (2021) found that total insect visitation was negatively correlated with wind speed, in agreement with my findings. However, those authors did not find a significant correlation between Hymenoptera visitors and wind speed. Goodwin et al. (2021) report that Diptera was the only order whose visitation was significantly correlated with wind speed. Di Trani et al. (2022) found visitation frequency was significantly related to wind speed in all bee taxa they reviewed. However, they also found differences between taxa; one bee taxon exhibited peak visitation at low wind speed, but the rest exhibited peak visitation at moderate wind speed. In addition to differences between taxa, McCall and Primack (1992) report that the relationship between wind speed and insect flower visitation varies between ecological communities. However, those authors found that visitation was not related to wind speed in a New England deciduous woodland-meadow, the site most ecologically similar to mine.

Relationships between wind speed and insect visitation appear complex and warrant caution in their interpretation. Thus, a lack of alignment between my findings and those of others (in Diptera visitation, for example) does not necessarily support the possibility that my dataset was too small to have revealed other relationships.

5.2.3 Relative humidity

I found no significant relationships between relative humidity and total insect visitors or visitors of any individual taxon. Such relationships seem less studied than those of air temperature or wind speed.

Goodwin et al. (2021) report total insect visitation and Hymenoptera visitation negatively correlated with humidity. I also found a (nonsignificant) negative correlation between Hymenoptera visitation and wind speed. As with wind speed, McCall and Primack (1992) found that the relationship between total insect visitation and relative humidity varied between ecological communities. Again, however, they found no relationship between relative humidity and total visitation at the site most ecologically similar to mine. Di Trani et al. (2022) report that *Lasioglossum* spp. were the only one of five bee taxa whose visitation frequency was not significantly related to relative humidity. Given that *Lasioglossum* spp. account for the majority of bee observations in my study, and that the genus did not exhibit a significant correlation with humidity, this finding seems to agree with my own.

My results seem generally, if not uniformly, to agree with prior findings. As with wind speed, relationships between visitation and humidity seem characterized by complexity.

5.3 Floral Characteristics

Pollinator visitation did not significantly differ with respect to any floral characteristic. Constraints in data collection may have influenced these results. Layering of vegetation presumably obscured underlying inflorescences in some aerial photos, decreasing the accuracy of inflorescence counts. Additionally, consideration of floral characteristics within a single radial distance, rather than at several distances, may have failed to capture the scale at which differences in floral characteristics become meaningful to various insect pollinators.

5.3.1 Floral density

Floral density was not significantly correlated with total insect visitation or visitation of any individual taxon. This seems, generally, unaligned with the literature, where increased total density of inflorescences has been correlated with increased visitation.

Relationships between floral density and insect visitation have been repeatedly demonstrated by others at various scales (Lázaro et al., 2013; Real & Rathcke, 1991; Shao et al., 2008; Thompson, 1981; Totland, 1994). However, findings seem to depend substantially on whether conspecific (species of focus), heterospecific (other species), or combined (species of focus + others) floral densities are considered. Barley et al. (2022), for example, found no relationship between conspecific floral density in *M. fistulosa* and insect flower visitation. Results of studies on combined floral density seem generally to indicate a positive relationship with visitation, while heterospecific densities remain below some threshold (Thompson, 1981; Totland, 1994). That my data displayed no relationship between combined (total) floral density and visitation is, thus, somewhat unexpected.

One possible explanation is the size of my experimental unit (individual inflorescence) relative to others in the literature (typically a quadrat). It’s possible that total floral density is positively related to visitation within a patch but unrelated to visitation of individual inflorescences. The ratio of pollinators to inflorescences (and consequent likelihood of visitation at any inflorescence) may not differ between high- and low-density patches.

5.3.2 Floral diversity

No metric of floral diversity was significantly correlated with total insect visitation or visitation of any individual taxon. These results contrast the literature.

Others have found significant relationships between various floral diversity metrics and pollinator visitation or related measures. Bucharova et al. (2022), found that pollinator visitation was significantly and positively related to floral diversity (Shannon-Weiner index). They report that the relationship they observed between visitation and provenance was, in fact, mediated by floral diversity in experimental communities. Similarly, Ghazoul (2006) found that insect flower visitation increased with flowering species richness, the number of flowering plant species within the experimental unit. Though they did not measure visitation, Bihaly et al. (2024) found that wild bee and butterfly abundance were positively related to flowering species richness.

Given that the findings of others consistently indicate a relationship between insect visitation (or at least insect abundance) and floral characteristics, it is surprising that neither floral density nor any metric of floral diversity had significant explanatory power over insect visitation. This discrepancy may be associated with differences in pollinator behaviour between geographic or ecological contexts. However, it also seems to support the conclusion that true relationships between some variables may simply have failed to manifest in such a small dataset.

5.4 Landscape Context

Pollinator visitation did not substantially differ with respect to the proportion of natural and semi-natural cover surrounding the site at any spatial extent. These findings seem to disagree with the findings of others. However, prior research has predominantly considered pollinator abundance, rather than visitation, in relation to proportion of natural and semi-natural land cover. Abundance refers to the total number of individual insects observed in the study unit, rather than the total number of insect-inflorescence interactions. Higher abundance does not necessarily correspond to higher flower visitation because individuals may exhibit differences in visitation behaviour. Thus, differences between abundance and visitation may explain a lack of alignment between my findings and findings reported in the literature.

Steffan-Dewenter et al. (2002) found significant positive relationships between semi-natural land cover, at radial distances of 250 m, 500 m, and 750 m, and insect abundance in solitary bees but not in social bees (*Bombus* spp.). All of the bee genera I observed were social (*Bombus* spp.), predominantly social (*Lasioglossum* spp.), or facultatively social (*Xylocopa* spp.; Danforth et al., 2003; Prager et al., 2014), suggesting I might expect to see similar results to those of Steffan-Dewenter et al. (2002). However, those authors did not report the range of values they observed at each of those radial distances, limiting direct comparison. Watson et al. (2011) found significant positive relationships between total native bee abundance and proportion of forest cover at radial distances of 500 m, 750 m, 1000 m, and 2,000 m. Kremen et al. (2004) similarly found significant positive relationships between native bee abundance and proportion of natural land cover at radial distances of 1200 m, 1800 m, 2400 m, 4800 m.

Research into the effects of landscape context on pollinators seems to be overwhelmingly focused on bees. This may be because bees, representing some of the larger-bodied insect pollinator taxa, are expected to have the greatest foraging distances and, thus, are expected to exhibit relationships with landscape context at spatial extents in which coarse measures of land cover become meaningful. It may also be attributable to bees' relative notoriety as pollinators, compared to other insects. Regardless, highly mobile taxa other than bees occurred in relatively small numbers in my study. So, the apparent lack of consideration for these other taxa in the literature is not a substantial constraint in interpreting my results. The discrepancy in bee taxa between my findings and those of others supports the possibility that my dataset may be too small to reflect some true relationships.

There is no evidence, in my research, that translocation distance, at this geographic extent, affects pollinator visitation. Other factors, namely air temperature and wind speed, are more clearly associated with visitation. Those relationships were evident even in this small dataset. However, those microclimatic variables exhibited only weak or moderate correlation strength with visitation and only for total visitation and a small number of taxa. Air temperature and wind speed failed to explain the variation in visitation of most taxa, including some of the more frequently observed ones. Furthermore, neither proportion of natural and semi-natural land cover nor any floral characteristic exhibited a significant relationship with visitation. Some of those potential relationships would not be supported by existing literature and so were not expected. Other relationships, however, are commonly reported in prior studies. The relative lack of significant findings from this study suggests that further investigation may be worthwhile.

5.5 Recommendations

The relatively weak explanatory power of variables other than translocation distance on visitation suggests that this topic warrants more detailed consideration. Further research into this relationship might consider a greater range translocation distance, geographic contexts other than Southern Ontario, site contexts other than SPAs, or flower phenology as a mediating factor of provenance effects. My study design was a product of substantial time, resource, and informational constraints. Accordingly, I recommend others not replicate this exact design but instead improve upon it. Researchers undertaking similar studies would benefit from:

- Conducting the study over multiple years and seasons to capture interannual and interseasonal variation in pollinator populations and mitigate the impacts of plant establishment and maternal effects on flower phenology.
- Working with local seed collectors directly to specify/understand source population conditions and maintain strict provenance tracking.
- Using a larger experimental unit than a single inflorescence to provide sufficient observations and, consequently, statistical power.
- Ensuring visitation monitoring participants are capable of field-identifying local insects to avoid possible impacts of recording equipment on pollinator behaviour. To capture video of insect visitors in adequate detail for identification, the camera in this study was positioned close to the inflorescence being recorded. The presence of this unfamiliar device may have dissuaded pollinators from visiting recorded inflorescences. I have seen no evidence in the literature of such an impact, however.
- Employing drone-captured aerial photography to efficiently count inflorescences. Processing efficiency could be improved by using image classification algorithms (Underwood et al., 2016). More sophisticated sensors such as LiDAR are also subject to occlusion, as from overlying vegetation, but these could be used in some instances (Underwood et al., 2016). In row-crop style SPAs, using a LiDAR sensor from multiple angles, following the methods of Underwood et al. (2016), may yield more accurate

inflorescence counts. However, this technique is unsuitable for study contexts in which plants are obscured from most angles. If a higher degree of accuracy is required in these contexts, manual counting may be the most appropriate approach.

- Focusing on factors (e.g., flower phenology) likely mediating a relationship between plant provenance and flower visitation.

Despite the need for clarification, the results of this research, taken as they are, bear some relevance to policymakers, plant growers, and designers in Southern Ontario. These results support a "local enough" approach to plant provenance (e.g., regional admixture). With respect to local pollinator populations and outside of strict restoration contexts:

- *Policymakers* need not be overly prescriptive in mandating local plant provenance; sources within 200 km of a planting site seem to be equally suitable based on my findings. This generally aligns with the plant source provisions set out in the TGS v4. However, as our understanding of provenance-linked biotic interactions develops, distances may need to be adjusted to reflect emerging evidence. Policymakers should devise plant provenance regulations or incentives that are easily modified. Effects of provenance may differ between insect taxa or guilds. Policy may need to stipulate conservative values (i.e., err on the side of caution) to account for this possible variation, such that taxa or guilds more sensitive to plant provenance are not detrimentally impacted by policy based on coarse patterns of observation.

- *Plant growers* should develop provenance tracking practices for wild-harvested seed, whether installed in a SPA or grown and sold directly. Poor spatial accuracy in tracking severely limits the knowledge that can be gleaned from these operations. Additionally, pre-emptively implementing better source tracking will ease the transition for growers if legislation mandating source tracking is introduced, as has been done in Ontario, in the case of crown reforestation, and in countries, such as the United States and Germany. Growers should look to these precedents in the absence of guidance from local governments.

- *Designers* ought to prioritize other plant provenance considerations (namely: genetic diversity and adaptation for existing / future site conditions) above strict geographic proximity. A precautionary approach would be to follow a provenancing strategy like regional admixture, which balances genetic conservation, plant fitness, and potential biotic interactions by sourcing seed from several near-local populations with ecological conditions similar to the planting site. Designers can also advocate for improvements from plant growers in source tracking, including spatial accuracy and source population characteristics. There is little economic incentive for Southern Ontario growers to implement these changes, but such changes are important to inform planting decisions and aid knowledge acquisition. Designers can support growers through this transition by advocating for government financial support and guidance, reimagining plant procurement specifications, and involving growers earlier in the design process, especially in species selection.

Landscape designers are aware of the need to safeguard and enhance biodiversity (Canadian Society of Landscape Architects, n.d.). However, they may be less versed the genetic aspects of biodiversity stewardship. Native plants are commonly (though, certainly not ubiquitously) used in designed landscapes. Source-identified native plants are sometimes, but not commonly, specified (Lawson-Canning, 2023). Achieving intended ecological outcomes requires greater understanding and application of emerging and established knowledge through the design-implementation process. These aims can be advanced through integration of research and practice, toward the provision of better landscape experience for human and non-human members of the ecological community.

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