# Myrmecophily and habitat use of the European Common Blue (*Polyommatus icarus:* (Lycaenidae Rottemburg, 1775)) in Quebec, North America

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# ABSTRACT

Myrmecophily and habitat use of the European Common Blue (*Polyommatus icarus:*
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Eric Dexheimer

Invasive species have become a growing ecological concern caused by the increase in frequency of global human transportation. An important step in studying biological invasions is identifying the ecological niche a new species will occupy in its environment. in an effort to predict its expansion and its effect on native ecosystems. The effective range of a species consists of habitats in which a species is able to complete its life cycle, to sustain its population. The European Common Blue (*Polyommatus icarus*) is a non-native species established in Quebec since 2005, its only known distribution in North America to date and its first occurrence outside of its native range. As a species that forms mutualistic interactions with ants, i.e., a myrmecophilous species, this butterfly represents an opportunity to study the role of mutualistic interactions in the role of invasion success. The following research questions were investigated:

1. Whether myrmecophilous interactions persist in the new range of *P. icarus*.
2. Which factors drive adult abundance and oviposition decision, among host preference, plant structures and habitat structure?

Myrmecophilous interactions, adults and oviposition were surveyed through a field study in the area of Montreal, Quebec. A novel myrmecophilous interaction between the native ant species *Lasius neoniger* and *P. icarus* was documented in the summer 2019. Adult presence was positively correlated with the abundance of *Lotus corniculatus*, *Trifolium pratense and Medicago lupulina*. More adults and eggs were found in sites with shorter vegetation. *T. pratense* and *M. lupulina*. Eggs were laid as a function of host availability, without any significant preference for a particular species, and preferably in shorter vegetation. This field study gives support for the importance of vegetation structure in habitat selection in *P. icarus*, and suggests that this species will likely occupy disturbed or artificial habitats in North America.

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## Contribution of authors

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# 1. Introduction and context

## 1.1. Literature review

### *1.1.1. Invasion biology*

Biological invasions may occur naturally, and at least one record of a natural mass biological invasion has been recorded, the Great American Biotic Interchange (Leigh et al., 2014). Such a large and relatively sudden event has led to extinctions, e.g. due to ecological naiveté of the native fauna to arriving mammalian predators (Leigh et al., 2014). However, species introduction events have become more frequent with the development of human transportation and globalization (Hulme, 2009). Humans have developed transportation means to cover large distances and cross obstacles, which would otherwise be difficult or impossible to traverse for other species. Thus, obstacles such as distance and physical barriers such as oceans are potentially removed because of these means and may act as dispersal vectors for non-native species.

While the field of invasion biology has received increasing attention over the years, the terminology used in invasion biology has been inconsistent across publications (Colautti & MacIsaac, 2004). For this reason, authors have reviewed the terms based on the different stages of invasion of a non-native species (Blackburn et al., 2011; Colautti & MacIsaac, 2004). Throughout this thesis, the species of interest, *Polyommatus icarus* Lepidoptera (presented in section 1.1.4) will be referred to as "introduced", as it is not native to North America. The term "invasive" may not be appropriate as the term applies to species that have overcome all barriers to species establishment (Figure 1) and cause some adverse effects on recipient ecosystems. While the species can be prolific and has expanded its distribution in North America since its arrival (*EButterfly*, 2020), it has not caused any detectable adverse effects to date.

With the increasing number of recorded invasive species, authors have aimed to find common traits that facilitated establishment in the new ranges these species colonized. In their meta-analysis, Hayes & Barry (2008) identified climate or habitat matching, past invasion success and the number of individuals introduced as common factors in successfully established non-native species.

### *1.1.2. Barriers to establishment*

Despite the large increase in introduction events, it is unlikely that a newly arriving species will establish in its new range, due to several barriers impeding this process, as summarized in Figure 1 (Blackburn et al., 2011; Colautti & MacIsaac, 2004; Kennedy et al., 2002). Physical barriers such as geological obstacles or distance are the ones bypassed by human transportation. For a non-native species to establish, its new range must have suitable conditions for its survival. For this reason, the receiving habitat and the time of year in which a species arrives are crucial factors determining the likelihood of successful establishment. The time period during which conditions are suitable for a species' survival represents the "window of opportunity" for said species in a given region and climate.

It is worth noting that not all introduced species become invasive upon establishing a sustainable population (Zenni & Nuñez, 2013). Some may become naturalized as a part of the trophic system they colonized (Schlaepfer, 2018; Thomas & Palmer, 2015). Conversely, an invasive species may be a native species, that has become much more prolific due to a drastic change in its ecosystem, either from the removal of a top-down control or a surge in limiting resources (Valéry et al., 2009).

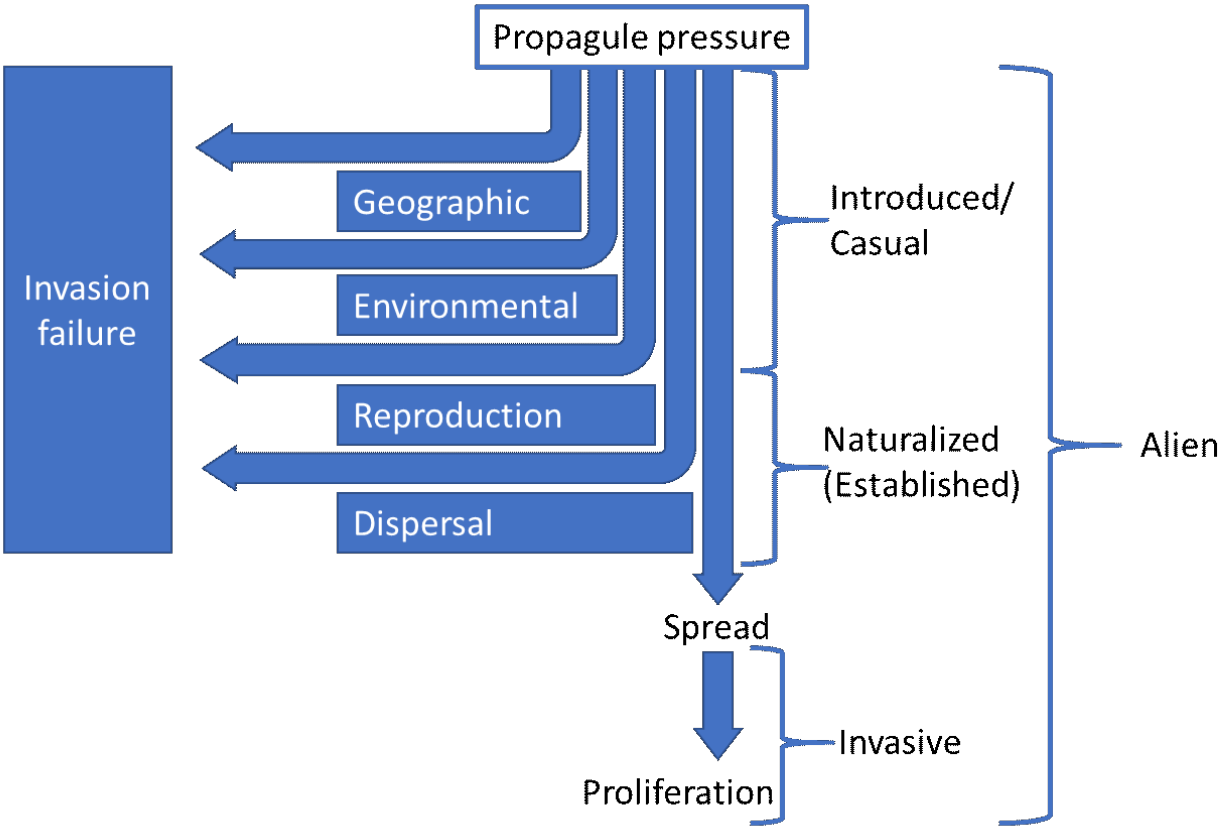

Figure 1. Barriers to biological invasion, adapted from Kennedy et al. (2002); Colautti & MacIsaac (2004); Blackburn et al. (2011).

In order to colonize and persist in a new range, a species must be able to overcome these barriers. Propagule pressure is an important contributing factor in establishing new populations (Lockwood et al., 2005, 2009). Propagule pressure can be broken down in two components: propagule size, and the frequency of propagule introduction events (Lockwood et al., 2009; Wittmann et al., 2014), which correspond to the number of arriving individuals and the frequency of introduction events respectively.

Native species in the recipient ecosystem may impede or prevent an introduced species from establishing, either through competitive exclusion or exploitation, a phenomenon known as biotic resistance (Alofs & Jackson, 2014; Byers & Noonburg, 2003; deRivera et al., 2005; Kimbro et al., 2013; Levine et al., 2004; Maron & Vilà, 2001; Parker & Hay, 2005).

### *1.1.3. Habitat definition*

An early concept of habitat described a habitat as a homogenous patch surrounded by a matrix of unsuitable environment (Hanski, 1999; Seymour et al., 2003; Skórka et al., 2013). Moreover, habitats were characterized using vegetation assemblages and biotope. The term "biotope" designates a homogenous space characterized by both its environmental conditions and the assemblage of species residing within (Udvardy, 1959). However, there is a discrepancy between the two, as biotope does not always match a species' habitat. Although species distributions may be entirely contained within biotopes, they may also exceed the boundaries of said biotopes, meaning that biotope and a species' ecological niche aren't intrinsically linked, but often co-occur (Dennis et al., 2014). In that regard, biotope designates the "community habitat", hereby merging the niches of all species within.

The resource – based habitat model was thus developed as an alternative to the patch/matrix habitat model. It bases the habitat of a species on the necessary elements it requires to sustain a viable population, and was initially introduced in studies of butterfly life history (Wiklund, 1977; Wiklund & Åhrberg, 1978). While said resources frequently co-occur in a given vegetation assemblage, the two are not intrinsically linked, and may spatially exceed or encompass one another (Dennis, 2012; Dennis et al., 2014). This applies similarly to the different life stages of a butterfly's life cycle, as each life stage uses different resources, which may themselves overlap or exclude one another (Figure 2). This approach provides accurate information when restoring butterfly habitat. As insects, the different life stages of butterflies use different resources, and thus require all of them within reach in order to sustain themselves. Butterfly conservation efforts should use this definition to restore habitat and create areas that allow the completion of their life cycles. By extension, a non-native species arriving in a new region would require all of these resources in order to establish a new population.

This approach was welcomed by butterfly conservationists, as it accounted for these life stages in restoring or creating butterfly habitats (Dennis, 2012; Turlure et al., 2019; Vanreusel & Van Dyck, 2007). In order for an insect population to persist, it needs resources for each of its life stages.

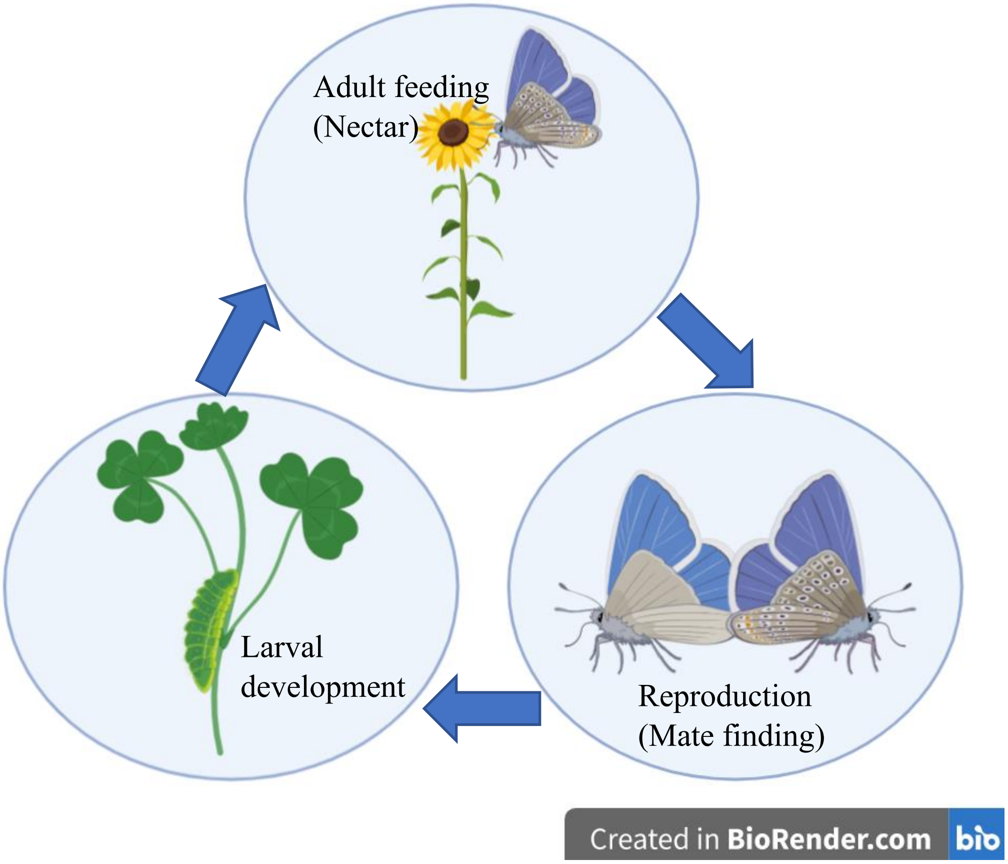

Figure 2. Life cycle of the European common blue, and the resources used at each life stage (from C. Wiklund, 1977).

### *1.1.4. Study system*

The species of interest in this project, the European Common Blue (*Polyommatus icarus*, Rottemburg 1775) is a butterfly species (Lepidoptera) belonging to the Lycaenidae family. This family of butterflies is comprised of relatively small-sized species, further classified into subfamilies, the most well-known being the Coppers (Lycaeninae), the Blues (Polyommatinae) and the Hairstreaks (Theclinae). *P. icarus* is one of the most widespread of this family as it is found to inhabit multiple habitats in its native distribution as a generalist species (Hughes, 2000). *P. icarus* is multivoltine and overwinters as a late instar larva. Colautti & MacIsaac (2004). *P icarus* appears to have established successfully in Quebec, since it is consistently observed in large numbers by the public every year (*EButterfly*, 2020). However, like many non-native species, it is most frequently observed in managed areas such as urban parks and gardens or disturbed habitats (*EButterfly*, 2020). Indeed, urban environments are characterized by frequent disturbances, which are a main contributor of establishment success by creating openings for space and resources free of competition (Gaertner et al., 2017; Hobbs & Huenneke, 1992; Lear et al., 2020).

The ecology of *P. icarus* in its new range remains to be investigated. *P. icarus* mostly feed on Legumes (Fabaceae) as larvae, although there are records of other plant families being used as hosts (Robinson et al., 2010). In herbivorous insects, the most essential resource needed to sustain a population are host plants, as a source of nutrition. In butterflies, the larval stage is crucial, since it is less mobile than the adult and is the growing stage of a butterfly's life cycle. Thus, host plant selection during oviposition is a crucial step in the life history of herbivorous insects, since larvae need to feed immediately after hatching. Migrating early from a host plant is risky due to predation and low chances of finding a suitable host. Herbivorous insects mainly use the chemoreceptors on their antennae to assess host quality, but butterflies also possess tarsal chemoreceptors that aid them in determining host suitability (Chun & Schoonhoven, 1973; Lund et al., 2019). Therefore, the presence of suitable host plants, native or non-native, is essential for the successful establishment of non-native herbivorous insects.

### *1.1.5. Myrmecophily in Lycaenidae*

Lycaenidae are distinguished from other Lepidoptera families by their unique biology. Nearly all species are myrmecophilous, meaning they associate with ants during their larval stage. This association is similar to that between aphids and ants, whereby the larvae secrete a carbohydrate-rich substance as a reward to attract and keep ants nearby, and in return the ants guard the larva from predators.

Three specialized organs have evolved in Lycaenidae as adaptations to their myrmecophilous lifestyle, allowing them to interact with their ant partners:

- Tentacle organs: their function is generally associated with communication and alerting ants when disturbed (Axén et al., 1996; Fiedler et al., 1996; Henning Stephen F., 1983; Hojo et al., 2015), but no secretory structures have been found, and their precise function remains unclear (Gnatzy et al., 2017).
- Dorsal Nectar Organ (DNO). This is a specialized gland located dorsally on the 7th abdominal segment, used to secrete the carbohydrate-rich substance as a reward to maintain ant presence.
- Pore cupolas – paired organs present on each segment, have been shown to play a role in recruiting ants (Malicky, 1970). It has since been posited that these organs secrete allomones to attract ants, but the exact chemical function of these organs remains unexplored to date.

The intensity of myrmecophily in Lycaenidae is wide ranging in intensity, going from non-obligate associations to parasitism. The majority of Lycaenidae, including *P. icarus,* are facultative myrmecophiles, meaning that the association is beneficial, but not vital to the completion of their life cycle. By contrast, parasitic species (e.g. the genus *Maculinea*) feed on the host ant's offspring for nutrition in order to complete their development (Als et al., 2001).

Because many myrmecophilous Lycaenidae also use Fabaceae as host plants, this plant family was thought to be optimal hosts to compensate for the nutritional costs associated with maintaining ant presence. However, only one third of obligately myrmecophilous Lycaenidae are specialists of Fabaceae, which undermines the hypothesis that Fabaceae play a vital role in Lycaenidae myrmecophily (Fiedler, 1995).

### *1.1.6. Host plant selection and oviposition*

Host selection is crucial in butterflies, since the quality of the selected host will determine larval performance, survival and ultimately the individual's fitness. Thus, butterflies need to accurately recognize suitable hosts and make the decision to oviposit on said host. Herbivorous insects face a trade-off when laying eggs, between maximising the number of eggs laid and taking the time to make optimal decision about where to lay eggs (Jaenike, 1978; Janz, 2003; Jones et al., 2019; Rosenheim et al., 2008; Wiklund, 1975). Some butterfly species are generalist herbivores, but even in these cases, populations can display specialist patterns of herbivory (Wiklund, 1981; Wiklund et al., 2018). Host plant nutritional content and defensive chemistry are main drivers of host selection in herbivorous insects, however predation and parasitism are also shown to shape preference among hosts, expressed as the "enemy-free space" hypothesis (E. Bernays, 1989; E. A. Bernays & Chapman, 2007).

Nearly all recorded hosts plants used by *P. icarus* in its native range are Fabaceae, mainly *Lotus corniculatus*, *Medicago spp* and *Trifolium repens* (Robinson et al., 2010; Wolfgang, 2021). Additionally, this butterfly has been observed to oviposit shortly after consuming nectar from the flowers host plants, indicating that nectar sources play a role in oviposition decision (Janz et al., 2005). In the case of parasitic Lycaenidae species, which are obligate myrmecophiles, ants or nearby ant nests are used as cues to oviposit on host plants (Dyck et al., 2000; Fürst & Nash, 2010), since the former are vital to the completion of the life cycle of the butterfly (but see Musche et al., 2006).

### 1.2. Research questions and rationale

Since its discovery near Mirabel in 2005, *P. icarus* has received little attention as a non-native species (Hall, 2007). To date, at least one study has modelled the future range of the species as it disperses in North America (Al-Rewashdy et al., 2010), and a more recent study investigated its dispersal capacity and the role of disturbances in creating suitable habitats (Rivest & Kharouba, 2021). The model successfully predicted the native distribution of *P. icarus*, using important environmental factors, thus estimating its future distribution in Canada. This project will aim to define the resource-based niche in the invasion range l(see previous section) by examining trophic relationships with native and non-native local ants and host plants.

The first chapter of this master's project studied myrmecophily in *P. icarus* larvae in its new range, and its possible role in the establishment of the species. This aspect of *P. icarus* biology has been well studied in its native range (Burghardt & Fiedler, 1996; Fiedler, 1990, 2006; Fiedler & Maschwitz, 1989; Fiedler & Saam, 1995), but it has not been examined in the context of invasion biology, despite the fact the establishing novel symbioses has been shown to be important in the establishment of other non-native myrmecophilous insects (Feng et al., 2015).

*P. icarus* larvae couldn't be observed *in situ* in large enough numbers to allow a quantitative analysis of myrmecophilous interactions, so the second chapter switched the focus of the project to habitat use of the species of interest, another important aspect of invasion biology. Specifically, the chapter aimed to identify predictors of the species' distribution at based on adult habitat use and host plant choice. In particular, this work further investigated the results of León-Cortés *et al.* (1999), who found that vegetation height may drive habitat selection in *P. icarus* in Great Britain. A preference for short vegetation could contribute to limiting *P icarus* to disturbed habitats within its invasion range and hence to mitigating its impact on native ecosystems.

## 2. Chapter I: Novel mutualisms between native ants and *P. icarus* larvae

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### 2.1. Introduction

Mutualist species from different geographic ranges that come into contact may form novel relationships via ecological fitting. Ecological fitting is defined as the matching of a species with a novel situation or species for which it already possesses traits that benefit its fitness or allows it to interact with said species (Janzen, 1985; Roux et al., 2017). This is more likely to occur if both form associations with species with similar traits in their respective native distributions (Traveset & Richardson, 2014). Lycaenidae is a family of Lepidoptera that often maintain mutualistic or parasitic relationships with ants, an interaction known as myrmecophily (Fiedler & Hölldobler, 1992; Pierce & Mead, 1981). Symbiotic relationships occur mostly in the larval or pupal phase and may be obligatory or optional (Jordano & Thomas, 1992). Myrmecophily has proven to be the insect-insect relationship with the greatest ecological impact in these groups, directly influencing the relationships between lepidopteran larvae and both their host plants (Fiedler, 1990) and other insects (Pierce & Mead, 1981), as well as even inducing a selective pressure for the development of specialized bodies (Fiedler, 1990; Pierce et al., 2002). In this type of interaction, the larvae generally have morphological adaptations (dorsal nectary organ) whose function is to appease ants and attract them by offering a nutritious reward (Malicky, 1970). In return, the ants protect the larvae against natural enemies (Fiedler, 2012; Kaminski & Rodrigues, 2011; Pierce et al., 2002).

The European common blue *Polyommatus icarus* (Rottemburg) (Lepidoptera: Lycaenidae) was first observed in the Montreal region (Quebec) in 2005 (Layberry & Jones, 2008) and has since become prolific (*EButterfly*, 2020). The host plants of *P. icarus*, ruderal herbs in the family Fabaceae, were also introduced in North America generations ago, and are now common urban plants in Montreal (Marie-Victorin et al., 2002). *Polyommatus icarus* belongs to the family that includes the blue, copper, and hairstreak butterflies, all generally small species that typically inhabit open habitats. They are represented in most parts of the world. *P. icarus* is one of the most widespread species in its native range, which spans most of Europe, North Africa and parts of Western Asia. The species is multivoltine, having two to four generations per year depending on the local climate. Like most Lycaenidae of the subfamily Polyommatinae, *P. icarus* forms myrmecophilous associations in the late larval instars, as described above.

The adaptive advantage of myrmecophily in lycaenid caterpillars in North America is the same as in European species; most are attacked by parasitoids, such as Braconidae (Hymenoptera) and Tachinidae (Diptera) (Fiedler et al., 1992; Pierce & Mead, 1981). Exclusion of ants results in higher parasitization rates in larvae, which no longer benefit from ant protection (Pierce & Mead, 1981). The secretions the larvae produce to maintain ant presence are rich in carbohydrates (Daniels et al., 2005). Since *P. icarus* is facultatively myrmecophilous, we investigated whether ant-larva interactions were maintained in the introduced population in the area of Montreal and if so, which ant species were involved.

## 2.2. Materials and methods

### *2.2.1. Study sites*

Two distinct sites on the Island of Montreal containing introduced Fabaceae were surveyed for lycaenid larvae from June to August 2019. Adult *P. icarus* observations at both sites are documented in the e-Butterfly citizen science database (*EButterfly*, 2020). The first site is an unmowed 2.8 ha old-field next to the visitor's parking area of McGill University's Morgan Arboretum (45°25'47.7"N; 73°56'34.3"W). The site is an open habitat with mostly tall grass vegetation. The second site is the City Farm School on Concordia's Loyola campus (45°27'34.0"N; 73°38'33.0"W), which contains a permaculture garden (150 m2) in a matrix of urban parkland. The permaculture is used to grow ornamental flowers, including nectariferous species that attract pollinators.

### *2.2.2. Data collection*

Butterflies were identified in the field when at rest. *P. icarus* is distinguishable from native lycaenid species by the presence of distinct orange spots on the underside of both pairs of wings in both males and females. Collected ant specimens were identified in the lab with the help of a dissecting microscope and a field guide to ants of New England (Ellison et al., 2012).

To test for temporal niche overlap in these two co-occurring lycaenid species, citizen-science data from the e-Butterfly database was queried for observations of adult *P. icarus* and *Glaucopsyche lygdamus* (Doubleday) (Lycaenidae) between 2014 and 2019 in a quadrat centered on Montreal (46°N; 73°W – 46°N; 76°W by 44°N; 73°W – 44°N; 76°W).

## 2.3. Results

*P. icarus* early instar (<5 mm) caterpillars (N = 10) were observed in the City Farm School on 29 August 2019, feeding on *M. lupulina* Linnaeus (Fabaceae) and *Lotus corniculatus* Linnaeus (Fabaceae), both introduced from Europe. Two of the ten larvae were tended by a native ant, *Lasius neoniger* Emery (Hymenoptera: Formicidae) on *M. lupulina* (Figure 3). The ant's behavior corresponded to the description of groping by Malicky (1970), whereby the ants touch the larva with their antennae at an obtuse angle when the ants are not excited. The ants were also tending aphids present on the host plant. Late instar (>5 mm) *G. lygdamus* (N = 6) larvae were observed on 3 July 2019 at the Morgan arboretum feeding on *Vicia cracca* Linnaeus (Fabaceae), a plant species also introduced from Europe (Figure 4). The caterpillars were also tended by *L. neoniger* ants.

Figure 3. *Lasius neoniger* ant tending a young instar of *P. icarus* larva found among *Medicago lupulina* fruit in the City Farm at Loyola campus of Concordia University. Photo: Eric Dexheimer.

Figure 4. *Lasius neoniger* ants tending a *Glaucopsyche lygdamus* larva feeding on *Vicia cracca* flowers at the Morgan Arboretum (McGill University). Photo: Eric Dexheimer.

During subsequent fieldwork done in July 2020, five more larvae were spotted in Parc de la Cité in Longueuil feeding on white sweet clover (*Melilotus alba* Medik. (Fabaceae)) (45°29'21.8"N; 73°24'27.6"W), three of them tended by *L. neoniger* (see Supplementary Material: https://doi.org/10.6084/m9.figshare.14096828). Ant specimens collected in the summer of 2020 have been submitted to the Ouellet-Robert collection at Montreal University (*P. icarus* collection numbers: 56609, 56610, 56611, 56612; *L. neoniger* collection number: 56608). Adult *P. icarus* were also observed near the Arboretum in highway margins outside the park, and no other lycaenids, adults or larvae, were observed at either site.

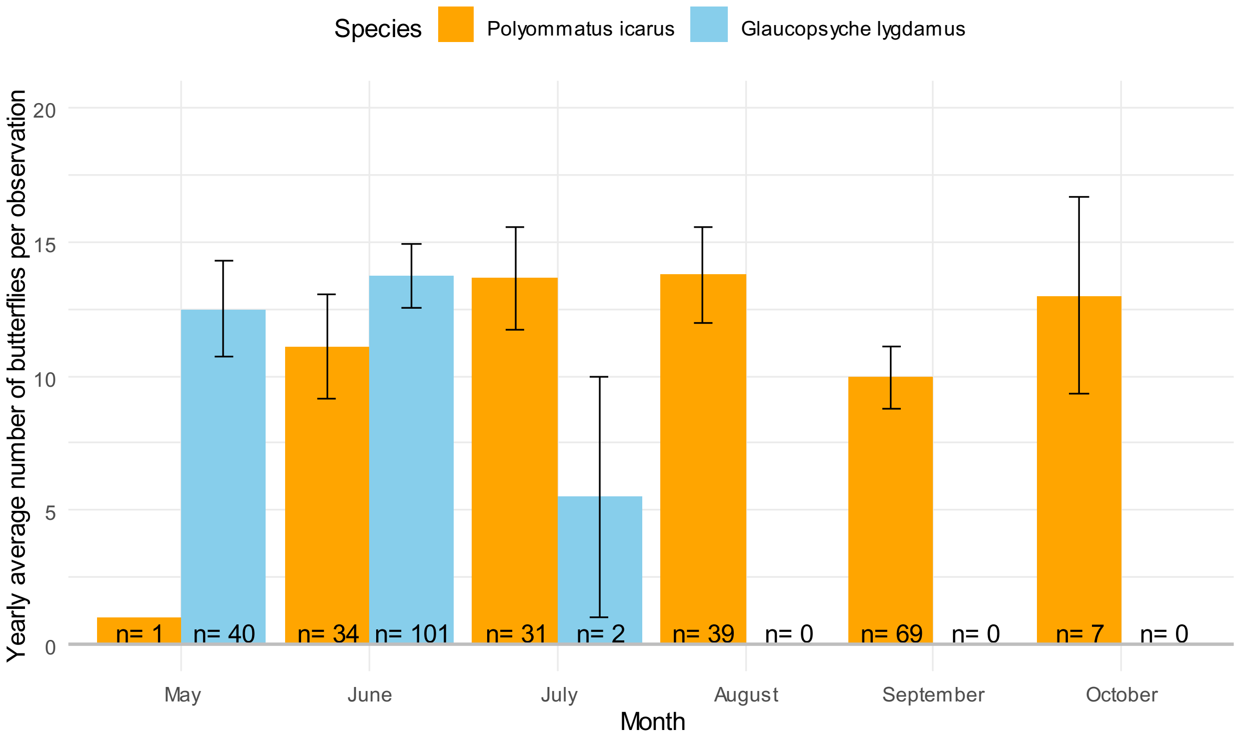

Figure 5. Yearly average observations (an observation is a submitted report of one or more individuals) of *P. icarus* and *G. lygdamus* submitted to e-Butterfly between 2014 and 2017. “n” indicates the sample size of observations across the four years.

The flight periods of both butterfly species showed significantly different phenological patterns (Fig. 2, Pearson’s chi-squared test, $\chi25 = 898753$, $P < 0.0001$). Indeed, *G. lygdamus* is known to be univoltine and to hibernate as a pupa (ITIS 2020), whereas *P. icarus* is multivoltine, exhibiting two to four generations per year in different parts of its native range, and overwintering as a larva (Eeles, 2019).

### 2.4. Discussion

*L. neoniger* is ecologically dominant in urban habitats in Montreal (Lessard & Buddle, 2005). It is thus both abundant in habitats occupied by *P. icarus* larvae and an opportunistic species that does well in novel community contexts. The discovery of this novel association adds the first North American ant to the list of species known to interact with *P. icarus* (Handfield, 1999). This supports previous research showing that facultatively myrmecophilous lycaenids can associate with a broader range of ant species compared with parasitic lycaenids (Fiedler, 2001; Pierce et al., 2002). Parasitic lycaenids associate more closely with ants in that they feed on ant larvae within their ant host's nest, and associate with fewer ant species as a result of their specialized life cycle (Als et al., 2001; Dierks & Fischer, 2009).

This has led to further research in the role of host plant quality in secretion composition, attractiveness to ants, and the intensity of myrmecophilous relationships in lycaenids (Burghardt & Fiedler, 1996; Fiedler, 1990, 1995, 1996a; Fiedler & Maschwitz, 1989; Fraser et al., 2001). Naomi E. Pierce & Elgar (1985) suggested that Lycaenidae preferred Fabaceae host plants due to their high concentration of nitrogen, but (Fiedler, 1995, 1996b) found that only twenty percent of all obligate myrmecophilous lycaenids use them as hosts. This suggests Fabaceae are not vital to the larvae for maintaining ant presence through nutrient-rich secretions.

*Lasius neoniger* and *G. lygdamus* have been shown to partake in myrmecophily (see Appendix 1 and Appendix 2), and the latter has been consistently used as a study system as it is a common species (Fraser et al., 2001; Pierce & Easteal, 1986; Pierce & Mead, 1981). Thus, this ant species has evolutionary experience with at least one native lycaenid species with similar anatomical traits to *P. icarus* (production of nutritious secretions from a dorsal nectary organ upon mechanical stimulation) but different phenologies. The different phenology of *P. icarus* and *G. lygdamus* suggest that competition between them will be limited and furthermore, that the *P. icarus* - *L. neoniger* interaction is truly novel.

Disruption of mutualisms is increasingly common under global change, as a consequence of species introductions but also global warming and habitat disturbance (Brambilla et al., 2020; Memmott et al., 2007; Morales et al., 2017; Rogers et al., 2017; Telfer et al., 2005; Tylianakis et al., 2010). Our results support the emerging generalization that species can establish mutualisms with novel partners (Traveset & Richardson, 2014). In this instance, the pre-adaptations of a myrmecophilous species allowed it to integrate a novel species in its interaction network.

### 2.5. Acknowledgements

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## 2.7. Connecting statement

Since larvae were found in too small numbers to effectively complete statistical analyses on myrmecophilous interactions, the second chapter focused instead on another aspect of invasion biology: habitat use, with particular focus on vegetation structure and host preference.

# 3. Chapter II: Habitat structure and host plant use

## 3.1. Introduction

Species introduction events have become much more frequent with the development of human transportation. An introduced species is unlikely to become invasive upon arriving in a new range, as it has to pass a series of biotic and abiotic barriers in order to sustain its population. However, successful species may become prolific to a degree that they cause drastic alterations that compromise the current ecosystem, which can in turn lead to the exclusion of some of the native species. Others become pest species and go on to cause economic losses or decrease ecosystem services. Thus, despite being unlikely, biological invasions are an important environmental concern.

A key aspect of invasion biology is determining the niche a species will occupy in its new range. This is used to predict its range expansion, or contain it if it has been detected early since its introduction. Most case studies use stepwise models that predict range expansion over time at the regional or landscape level (Kadoya & Washitani, 2010; Lyons & Scheibling, 2009; Morrison et al., 2005; Phillips et al., 2008; Snow et al., 2017). At these scales, habitat is defined as patches of varying quality, and is more broadly used in metapopulation studies and minimum habitat requirements (Brown, 1988; Girvetz & Greco, 2007; Hanski, 1999; Hodgson et al., 2009; McCoy & Mushinsky, 2007; Moilanen, 1999; Seymour et al., 2003). So far, a single study has modelled the spread and future distribution of *P. icarus* in Northa America using this concept (Al-Rewashdy et al., 2010).

However, while abiotic factors tend to drive large-scale patterns of species distribution, biotic interactions are often more important at the local scale and can count as resources for defining habitat. Moreover, butterfly conservationists have emphasized that there is a distinction between biotope and habitat (see Habitat definition). Since the resources used by a species may exceed or be encompassed by biotope, it is more accurate to use the resource-based habitat definition for predicting a species' distribution and ecological niche at the local scale.

While *P. icarus* butterflies are able to use flowers of several other species as sources of nectar, it can only be expected to persist in areas in which it can complete its life cycle, i.e., where larval host plants are present. Thus, predicting the species habitat use is based on larval resource-based habitat definition. *P. icarus* in its native range feeds on open-area ruderal Fabaceae plants and is more abundant in zones with shorter vegetation (León-Cortés et al., 1999). The larvae can feed on several different plants in the family, many of which have been naturalized across North America, including the Montreal region (Turkington & Franko, 1980). However, in the British isles, caterpillars are most abundant on *L. corniculatus*, and the presence of trefoil is the best predictor of patch use of *P. icarus* (León-Cortés et al., 1999). *L. corniculatus* is abundant on roadsides and disturbed areas in Eastern Canada (Turkinton & Franko 1980). It is very tolerant of dry, infertile and acidic soils and of salt contamination and is used in land reclamation. Based on these larval feeding preferences, we can predict that this butterfly will be more abundant in urban settings and other periodically disturbed areas in North America. This implies limited biotic interactions with native biota beyond myrmecophilous partners and predators within these disturbed areas, and hence limited effects on native ecosystems. It is worth mentioning that because this host plant thrives on the edges of large roads and highways, *P. icarus* may be able to expand its range in North America using these areas as corridors, which seems to be reflected by recent observations (*EButterfly*, 2020; *GBIF Secretariat: GBIF Backbone Taxonomy*, 2021).

Establishment success in herbivorous insects has been linked to several traits, namely wide host plant ranges, phenological plasticity and rapid development (Ward & Masters, 2007) but their potential distribution is often limited by their thermal tolerance (Jarošík et al., 2015). These invasible ranges are likely to expand as climate change leads to warmer average temperatures (Ward & Masters, 2007). In addition, non-native insects arriving in regions with marked seasonality are subject to strong selection pressure in the winter, meaning that species with effective overwintering strategies are more likely to successfully establish.

In addition to biological traits, disturbances are an important contributing factor to the establishment success of an invasive species (Cadotte et al., 2017; Calderon-Aguilera et al., 2012; Hobbs & Huenneke, 1992; Lear et al., 2020; Marvier et al., 2004), as they act to negate the effects of biotic resistance through the removal of competition or exploitation (see Barriers to establishment). In particular, the alteration of resource availability is the primary factor facilitating biological invasion by introduced species (Davis et al., 2000; Davis & Pelsor, 2001; Pearson et al., 2018; Walker et al., 2005). While natural disturbance regimes were found to play a role in regulating biodiversity (Chesson & Huntly, 1997), anthropogenic disturbances tend to be more frequent and stochastic, which reduces biodiversity overall in favor of species capable of rapid colonization. Because of these factors, invasive species are more common in areas affected by human activity (Gaertner et al., 2017; Hobbs & Huenneke, 1992; Lear et al., 2020; Marvier et al., 2004; Pearson et al., 2018). As an introduced species, *P. icarus* seems to benefit from the aforementioned factors in its range in North America, as it is mainly found in disturbed semi-natural habitats and is a generalist herbivore.

Lastly, evolutionary history with host plants found in a novel region has been identified as a contributing factor to the successful establishment of invasive herbivorous insects, more so than the insect's traits (Mech et al., 2019). The host plants used by *P. icarus* in North America have all been introduced from its original range in the Palearctic, likely explaining its predisposition to use these hosts through ecological fitting. More generally, because co-introduced species aren't likely to have coevolved, non-native flora is more likely to be used by generalist herbivores (Rodríguez et al., 2019).

The present chapter investigates habitat use by *P. icarus* in the Montreal area in sites where the butterfly has been observed by citizen scientists. In these sites, adult butterfly abundance was examined with respect to host plant cover and vegetation structure. Oviposition behavior was linked to individual plant traits, namely height, species and plant structure. This field study tested the prediction that *P. icarus* associates with any of the Fabaceae hosts and to habitats with short vegetation structure. These associations are further investigated with regards to oviposition behavior, namely whether eggs are laid predominantly on shorter hosts, at which height on the plant they are laid and on which species.

## 3.2. Methods

### *3.2.1. Field sites*

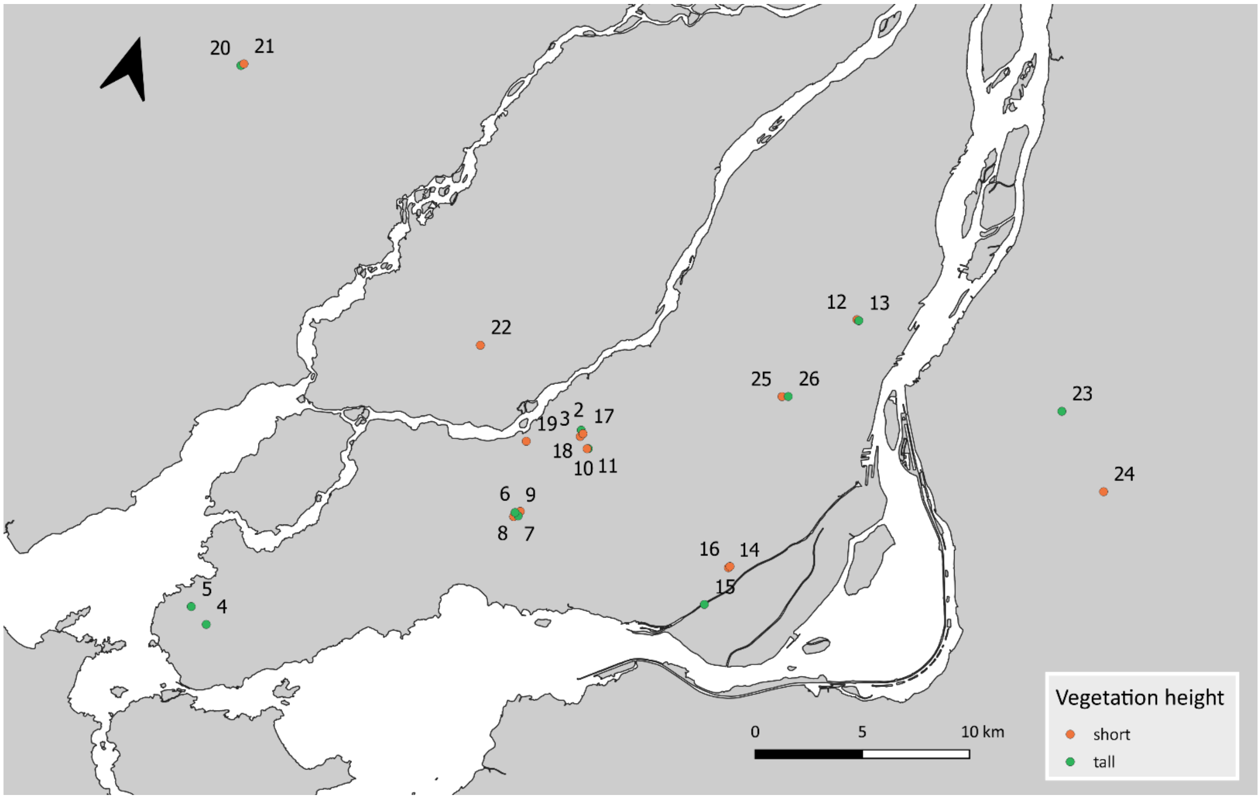

Figure 6. Field sites used throughout the summer 2020 (listed in Table 1).

| Site number | Site | Latitude | Longitude | Vegetation height |
|---|---|---|---|---|
| 1 | Cavendish-Henri Bourassa | 45.51342 | -73.72 | tall |
| 2 | Outardes-Construction Site | 45.51077 | -73.7206 | short |
| 3 | McGill Arboretum (near Parking) | 45.42981 | -73.9423 | tall |
| 4 | McGill Arboretum (Champ des Erables) | 45.43721 | -73.9514 | tall |
| 5 | Alexander Fleming (Short) | 45.47902 | -73.7559 | short |
| 6 | Alfred Nobel | 45.47678 | -73.7599 | short |
| 7 | Alfred Nobel Run Path | 45.47708 | -73.7572 | tall |
| 8 | Alexander Fleming (Tall) | 45.4785 | -73.759 | tall |
| 9 | Raymond-Lesnier (Tall) | 45.50568 | -73.7157 | tall |
| 10 | Raymond-Lesnier (Short) | 45.50564 | -73.7165 | short |
| 11 | Botanical Gardens (Short) | 45.56099 | -73.556 | short |
| 12 | Botanical Gardens (Tall) | 45.56055 | -73.5548 | tall |
| 13 | StJacques-Helen-Rochester | 45.45636 | -73.6313 | short |
| 14 | Canal Lachine | 45.44082 | -73.6455 | tall |
| 15 | Lily-Simon x Saint Jacques | 45.45686 | -73.6304 | short |
| 16 | Cavendish Sidewalk (Tall) | 45.51192 | -73.719 | tall |
| 17 | Cavendish Sidewalk (Short) | 45.51196 | -73.719 | short |
| 18 | Bois de Liesse | 45.50846 | -73.7528 | short |
| 19 | Mirabel-Path | 45.66469 | -73.9265 | tall |
| 20 | Mirabel-Clearing | 45.6654 | -73.9247 | short |
| 21 | Laval 2050 Condo | 45.54856 | -73.7809 | short |
| 22 | Vauquelin Boulevard | 45.52315 | -73.4331 | tall |
| 23 | Parc de la cité | 45.48955 | -73.4078 | short |
| 24 | Champ des Possibles (Short) | 45.52838 | -73.6003 | short |
| 25 | Champ des Possibles (Tall) | 45.52846 | -73.5966 | tall |

Table 1. Summer 2020 field sites and center coordinates (Web Mercator WGS 84 projection system).

Field sites were defined as having host plants present, from the list of known host species used by *P. icarus* (HOSTS). Two types of sites were defined, categorizing the overall vegetation height of the site: “Tall” sites were areas where overall vegetation reached more than 50cm of height, and “Short” sites are areas where vegetation did not exceed 50cm.

Vegetation height was used as a proxy for anthropogenic disturbance levels to investigate the effect of vegetation height on habitat selection following the findings of (León-Cortés et al., 1999).

Each site was visited once per month between 9:30AM and 6:00PM from June 16th to August 31st of 2020, for a total of two or three visits to each site in total.

### *3.2.2. Adult survey*

Adult abundance was estimated across 100m transects walked at the pace of ~ 50cm per second, such that each transect took about 5 minutes to complete. The transect were done twice per site visit, the first in one direction, and the second in reverse. The transects were entirely encompassed within the defined area of each field site. If a field site was too small or irregular to contain a linear 100m transect, the transect would instead follow the edge of the site. Surfaces that clearly aren't usable by the study species, such as forests or canals would be excluded from the site area. The number of butterflies of each sex within a 5m radius was recorded.

### *3.2.3. Plant survey*

The abundance of all host plants used by *P. icarus* listed in Table 2 was estimated in each site.

| **Family** | **Scientific name** | **Vernacular name** |
|---|---|---|
| Fabaceae | *Lotus corniculatus* | Bird's foot trefoil |
| | *Medicago lupulina* | Black medick |
| | *Medicago sativa* | Alfalfa |
| | *Melilotus alba* | Sweet white clover |
| | *Trifolium pratense* | Red clover |
| | *Trifolium repens* | White clover |
| | *Vicia cracca* | Cow vetch |

Table 2. Host species used by *P. icarus* in Quebec.

Ten quadrats of 50cm by 50cm in size were drawn along the same linear transect used to estimate butterfly abundance and spaced by 10m. The percentage of surface area occupied by each host plant species was visually estimated to the nearest 5% within each quadrat. The maximum height reached by any host plants present within each quadrat was measured, rounded to the nearest 5cm. Finally, the average height of the herbaceous stratum as a whole (referred thereafter as "canopy") and the maximum height reached by any of the plants present were measured to the nearest 5cm.

### *3.2.4. Egg survey*

Upon each visit, the whole site was searched for *P. icarus* eggs on every host plant species present. The search area extended beyond the transect used for estimating plant and butterfly abundance. Hatched eggs were also counted. All host plant species present were searched to avoid biasing the results. For each egg found, the following variables were measured:

- the host plant species on which the egg was laid
- the height of the plant in cm
- the height above ground at which the egg was laid in cm
- the structure of the plant serving as receptacle for the egg (young leaf, mature leaf, or flower)
- whether flowers or flower buds were present at the apex of the stem on which the egg was laid

No other Lycaenid species were observed as adults in the field sites, so Lycaenid eggs found on host plants were assumed to belong to *P. icarus*. When possible, female *P. icarus* were followed to observe oviposition events directly, after which the measurements for the egg were made immediately. Eggs were sampled throughout the site and without time controls, between one and three hours, to ensure statistical power for the analysis.

### *3.2.5. Spatial analysis*

The surface proportion of each land use type defined by section 3.1 of the Scheme of urban development of the Montreal administration (Schéma d'aménagement et de dévelopement de l'agglomération de Montréal, Section 3.1), was measured within 1km buffer areas of the field sites. Data was obtained at GeoIndex via access by Concordia University. The layer named "grandes affectations 2019" (main affectations 2019) was used. The proportion cover of each land use type was extracted using QGIS (v3.10.5).

### *3.2.6. Statistical analyses*

The replication units used for the analyses of adult and egg abundance were sites per dates. Butterfly and egg count per site were used as dependent variables for this study, whereas measures of host cover and both vegetation and host plant height were used as independent variables. Values for both dependent variables were grouped by site and by sampling date prior to computing statistics and hypothesis testing. "Voltinism" is an independent numerical variable. This was done to account for different amounts of variation in adult abundance in these periods of the Summer 2020, and does not carry the true meaning of the term, which is defined as "regime of the annual number of generations of a species". Three periods were defined as having differing amounts of variation in adult densities. "Voltinism" was assigned a value of 1 between the first day of sampling and Julian day 193, 2 for the time period between Julian days 193 and 218 and 3 for the period after Julian day 218 (Appendix 3). Site is a true replication unit and date is a pseudoreplication unit, since each site was sampled more than once over the field season. Both site and date were included as mixed effects in all statistical models.

A correlation matrix was used to identify which of the measured variables were linearly correlated with adult abundance. A generalized linear mixed model (GLMM) was then implemented, since the data obtained for the response variable was in counts. Because the abundance of each host plant was recorded as a separate variable, each host species was tested independently in the model. Adult counts per site were averaged over both walking transects and rounded to the nearest integer to allow a Generalized Linear Mixed Model analysis on a Poisson distribution using R (v. 3.6.2).

Effects of host species, flower presence and vegetation height on oviposition choice were analyzed separately. All analyses on egg data were done using Generalized Linear Mixed Models (GLMM) following a Poisson distribution to find correlations between the independent variables and egg abundance. Eggs were recorded individually, and so the data was summarized by grouping eggs per host plant species and plant structure prior to the analysis. The analysis evaluated correlations between egg abundance and the following independent factors: vegetation height, the interaction between host species and host cover, the interaction between host species and plant structure and finally the interaction between host choice and flower presence.

## 3.3. Results:

An estimated 365 butterflies were observed, and 213 eggs were counted across 13 field sites over the course of the field season. Hatched eggs were counted in the egg survey. Since it is unknown how much time has elapsed after an egg has hatched, there is a possibility that the leaf it was laid on has matured during that time, and was thus recorded as "mature" instead of "young". Since practical knowledge of the study systems is scarce, priority was given to data amount vs observation control.

### *3.3.1. Spatial analysis*

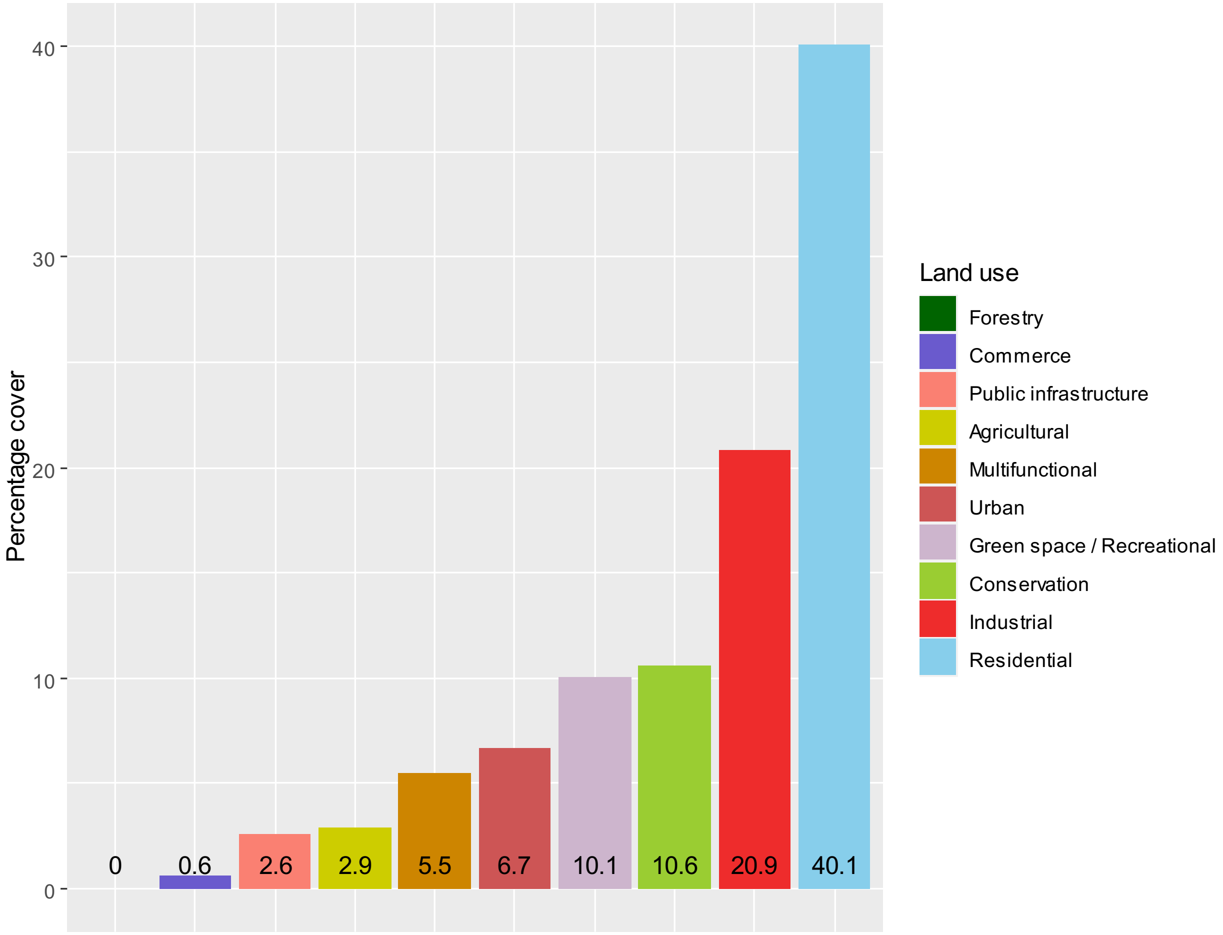

Figure 7. Relative percentage cover of land use types within 1 kilometer of all summer 2020 field sites. (Data from: Québec (Province). Ministère des Affaires municipales et Occupation du

territoire (accessed on GeoIndex, through Concordia University), Ville de Laval and Ville de Longueuil (accessed through https://www.donneesquebec.ca)).

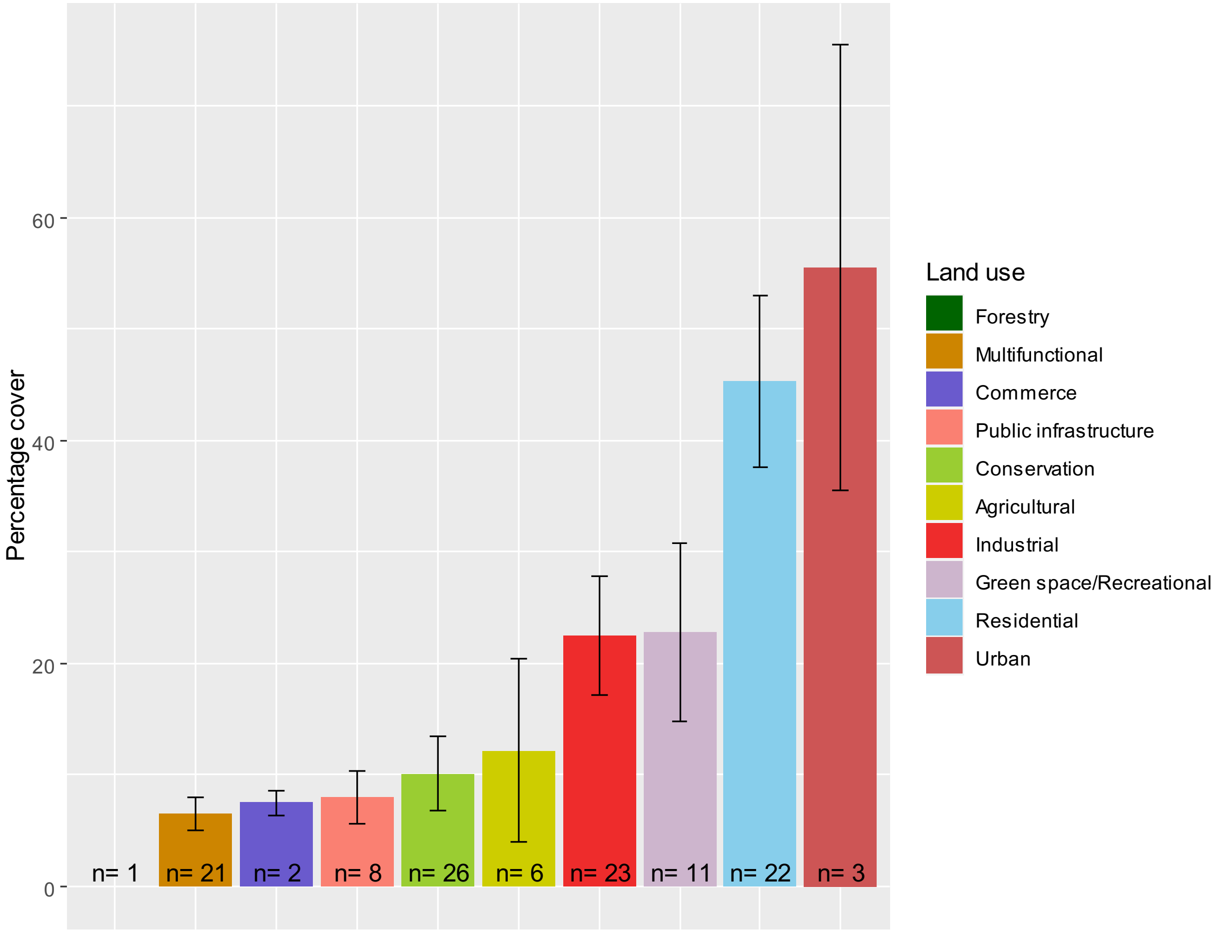

Figure 8. Average values of surface cover for each land use per site within 1 kilometer of all summer 2020 field sites. (Data from: Québec (Province). Ministère des Affaires municipales et Occupation du territoire, 2020 (accessed on GeoIndex, through Concordia University), Ville de Laval, 2020 and Ville de Longueuil, 2020 (accessed through https://www.donneesquebec.ca)).

Industrial as well as residential areas were dominant around the selected field sites, accounting for 21% and 40% of the total surface of the buffer areas respectively. These correspond to city streets with commercial or recreational activities and suburban neighborhoods, respectively, as defined by chapter 3 of the urban development scheme for Montreal (Ville de Montréal, 2015).

### *3.3.2. Adult presence*

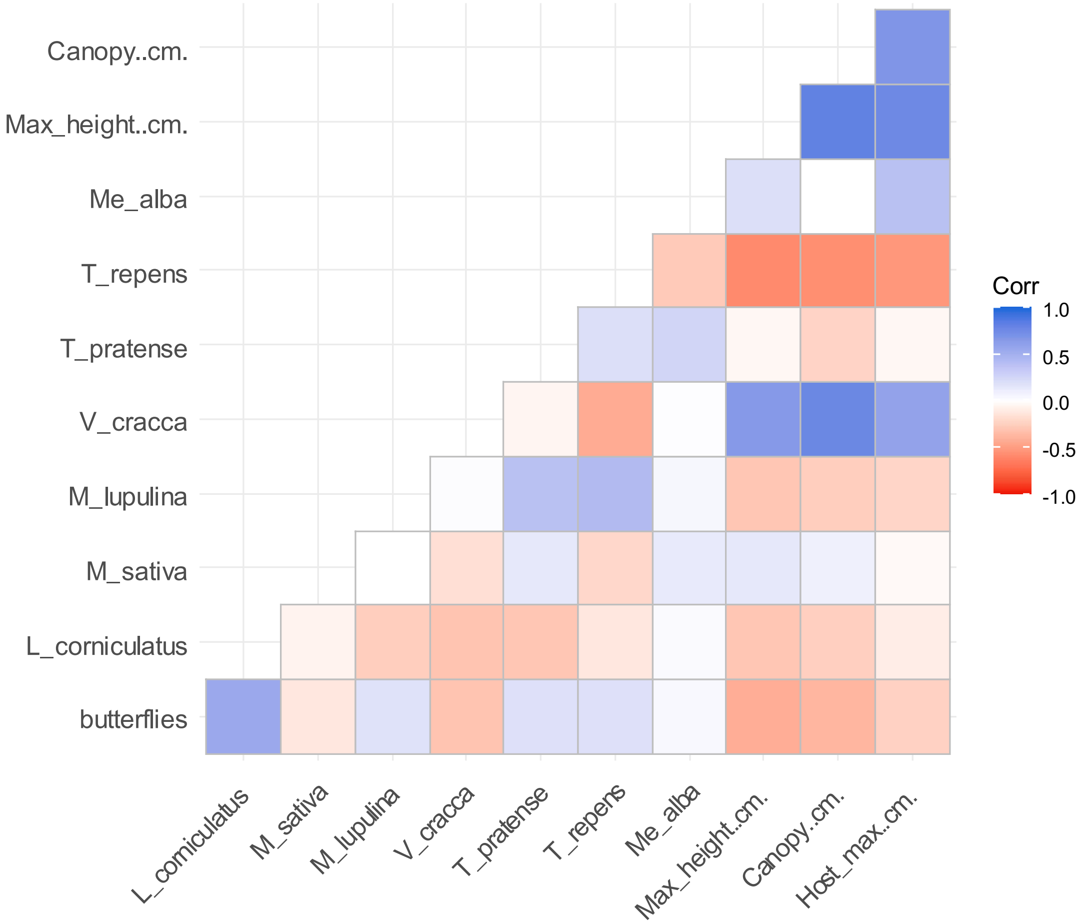

Figure 9. Correlation matrix between butterfly abundance and the independent variables (measured during the summer 2020).

The correlation matrix suggests that adult abundance is favored by *L. corniculatus* availability, and by *M. lupulina*, *T. pratense* and *T. repens* to a lesser extent (Figure 9). Another noticeable correlation is found between *V. cracca* abundance and the three plant height measurements, and the negative correlation of *T. repens* with these same height measurements. To assess the statistical significance of these correlations, GLMMs were used since the dependent variables were in counts, presenting left-skewed distributions.

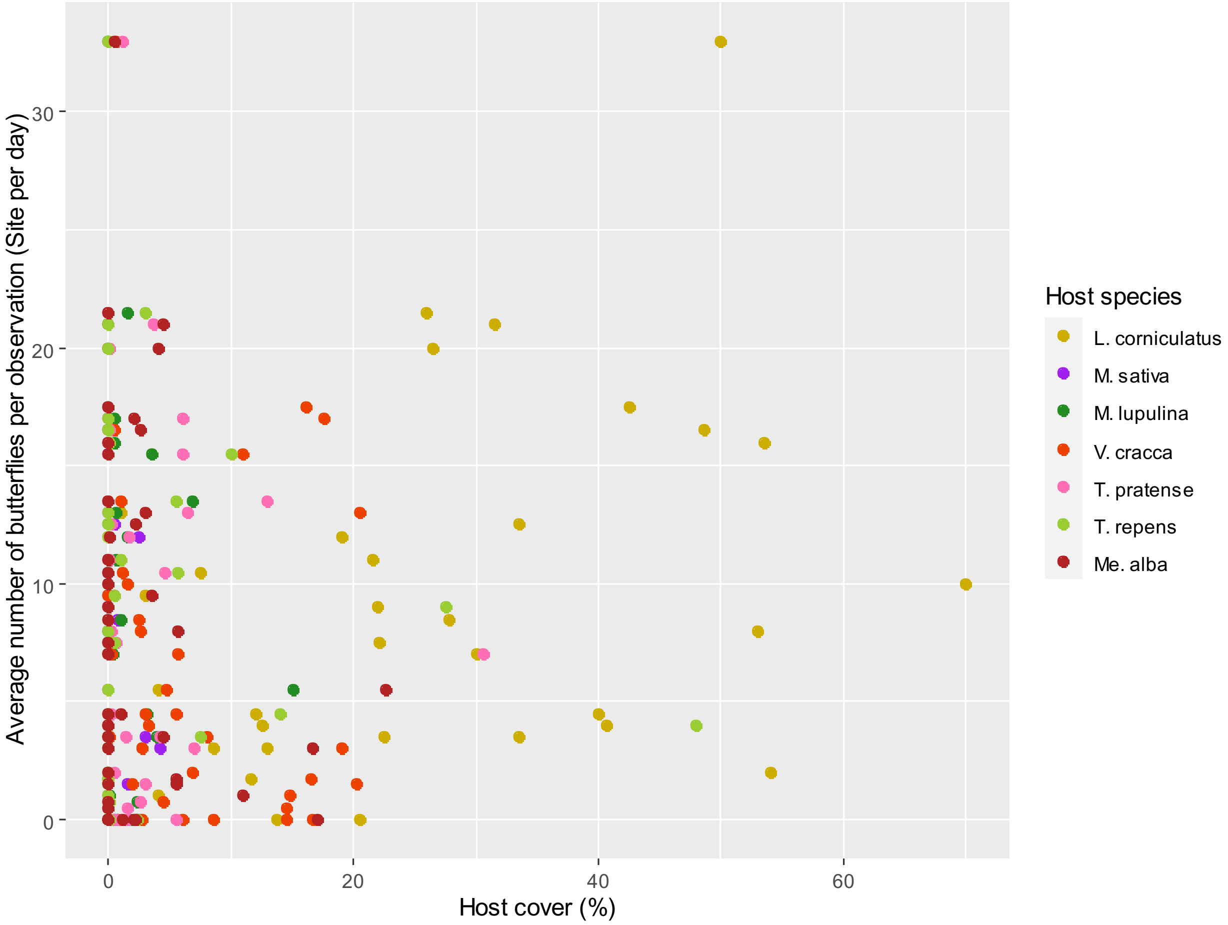

Figure 10. Average number of butterflies across the transect measurements of each site visit against host plant surface cover.

| *Parameter* | *Estimate* | *Standard Error* | *z value* | *p-value* |
|---|---|---|---|---|
| (Intercept) | 1.23 | 0.46 | 2.70 | <0.05** |
| L. corniculatus | 0.03 | 0.01 | 4.03 | <0.05 *** |
| T. repens | 0.00 | 0.02 | 0.17 | 0.87 |
| T. pratense | 0.06 | 0.02 | 2.73 | <0.05** |
| M. lupulina | 0.19 | 0.07 | 2.77 | <0.05** |
| M. sativa | -0.18 | 0.11 | -1.67 | 0.10. |
| Me. alba | -0.07 | 0.03 | -2.06 | 0.04* |
| V. cracca | 0.04 | 0.03 | 1.18 | 0.24 |
| Canopy | -0.03 | 0.01 | -2.45 | 0.01* |

Table 3. GLMM output table for adult abundance.
Formula: butterflies ~ L_corniculatus + T_pratense + T_repens + V_cracca + M_lupulina + Canopy..cm. + (1 | Site/volt), family = "poisson"
AIC=317.7 BIC=334.9 logLik=-149.8 Deviance=299. 7 Df=41
*Voltinism X Site variance = 0.43 Site variance = 0.26*

The GLMM showed that butterfly abundance increased with *L. corniculatus* cover, and to a lesser extent with that of *T. pratense* and *M. lupulina*, but decreased with average vegetation height (Figure 10, Table 3).

### *3.3.3. Oviposition*

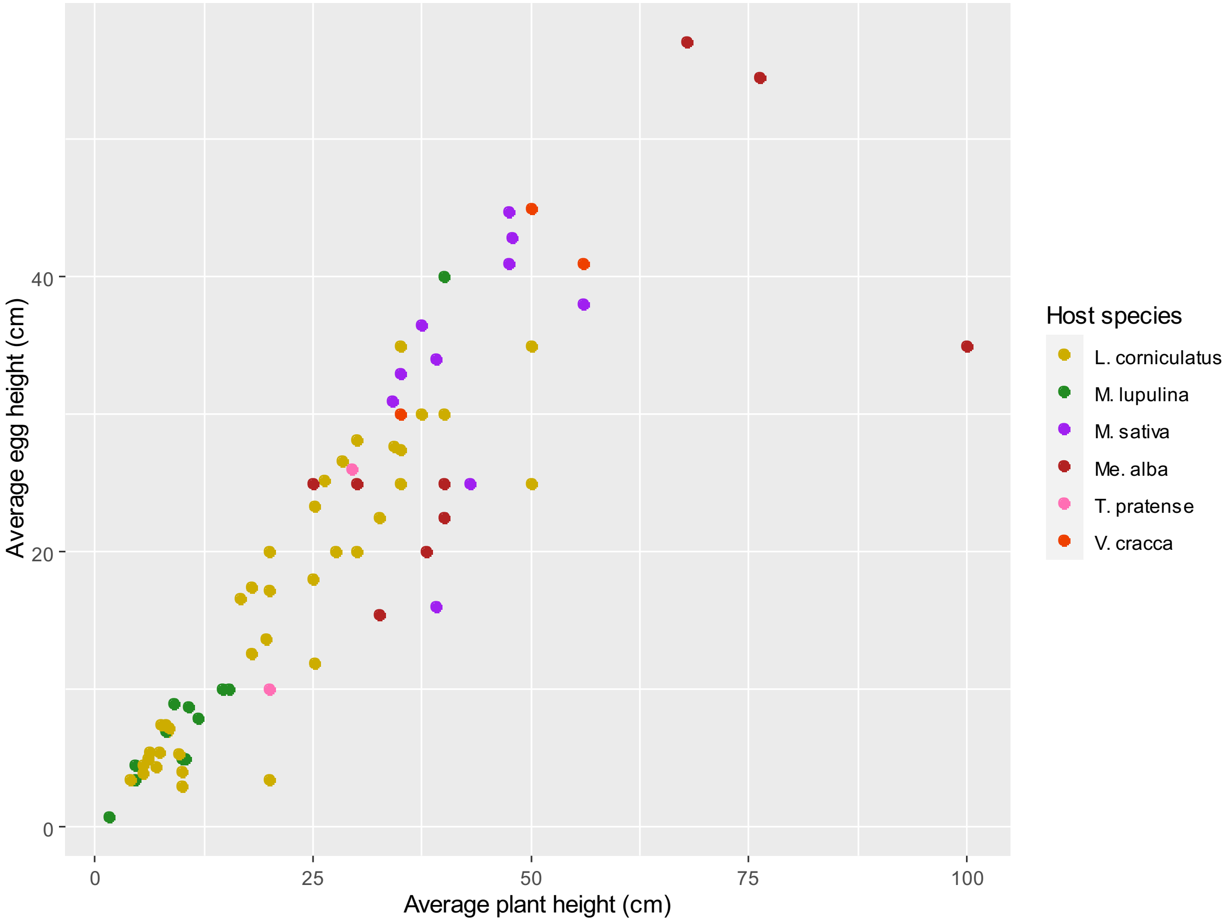

Figure 11. Egg elevation plotted against height of the receiving host plant across host species.

| *Parameter* | *Estimate* | *Standard. Error* | *z value* | *p-value* |
|---|---|---|---|---|
| (Intercept) | 2.14 | 0.17 | 12.47 | <0.05 *** |
| Mean plant height | 0.02 | 0.01 | 8.46 | <0.05 *** |

Table 4. GLMM output table for the effect of vegetation height on egg height position on the plant. Formula: mean.egg.height ~ mean.plant.height + (1|summ.eggs$Host_sp) + (1|summ.eggs$Site), family = "poisson"

AIC=290.5 BIC=297.2 logLik=-141.3 Deviance=282.5 Df=35

Site variance = 0.10 Host variance = 0.06

The elevation of the egg above ground was positively correlated with the height of the receiving plant (Figure 11). Adults laid eggs at approximately 80% of the average heigh of available host plants, regardless of species (Figure 11, Table 4).

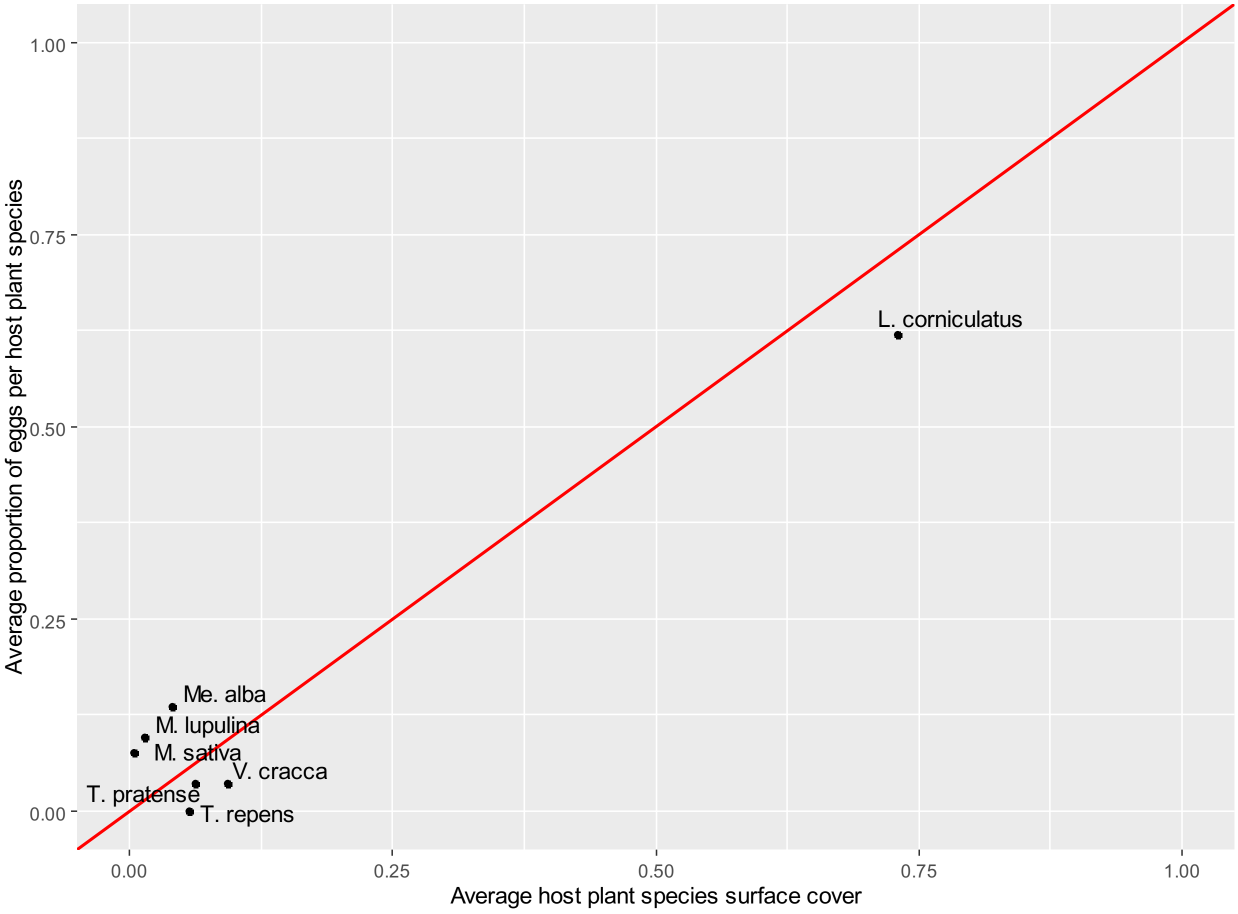

Figure 12. Average proportion of eggs on each host plant against the average proportion cover of each host species out of all hosts present. The red line represents the f(y)=x function.

| *Parameter* | *Estimate* | *Std. Error* | *z value* | *Pr(>\|z\|)* |
|---|---|---|---|---|
| (Intercept) | 0.38 | 0.41 | 0.92 | 0.36 |
| Host cover | 0.02 | 0.01 | 2.84 | <0.05 ** |
| Me. alba | -1.84 | 0.45 | -4.09 | <0.05 *** |
| T_pratense | -3.55 | 0.83 | -4.30 | <0.05 *** |
| V_cracca | -3.70 | 0.88 | -4.21 | <0.05 *** |
| Host_cover: Me. alba | 0.19 | 0.05 | 3.91 | <0.05 *** |
| Host_cover: T_pratense | 0.16 | 0.07 | 2.26 | 0.02* |
| Host_cover: V_cracca | 0.17 | 0.065 | 2.56 | 0.01* |

Table 5. GLMM output table for egg abundance against host cover per host species.
Formula: egg.count~Host_sp*Host_cover+(1|Site)+(1|Date), family=”poisson”.
AIC=260.4 BIC=285.6 logLik deviance=240.4 df.resid=82
Date variance = 0.6774 Site = 0.1438

The model presented in Table 5 presents the correlation of host abundance on egg abundance in interaction with availability (Host cover). Figure 12 presents the data used as average proportions of eggs per host species against host availability. Less eggs were laid on *Me. alba*, *T. pratense*, and *V. cracca* compared to *L. corniculatus*. Host availability was positively correlated with egg abundance, meaning butterflies laid eggs selectively on the most abundant host species. An interaction was found between the availability of these same plants and the number of eggs laid on them, reflected by the deviation from the 1:1 slope in Figure 12. This indicates that these host species received more eggs than would be expected if host selection were random.

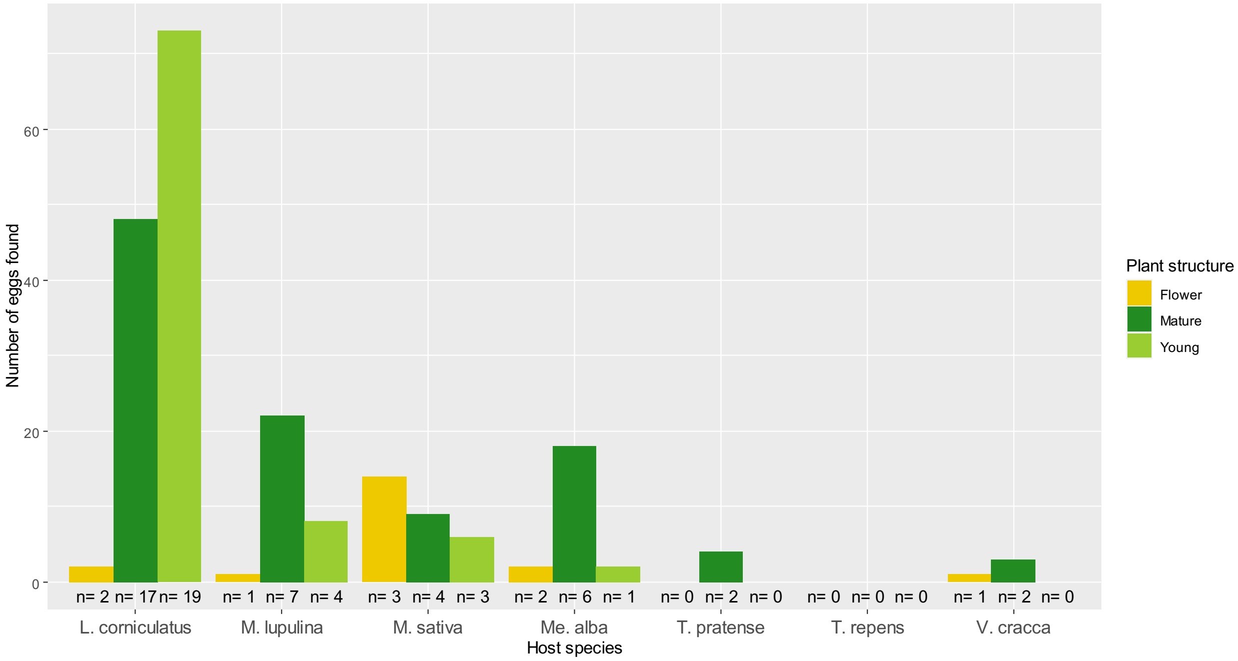

Figure 13. Number of eggs across plant structures (mature leaves, young leaves, and flowers) and host species. Sample sizes are shown by n.

According to the egg survey, preference for different plant structures varied across host species but this trend did not turn out significant. No statistical analysis was executed on this data, due to small sample sizes stretched by replication.

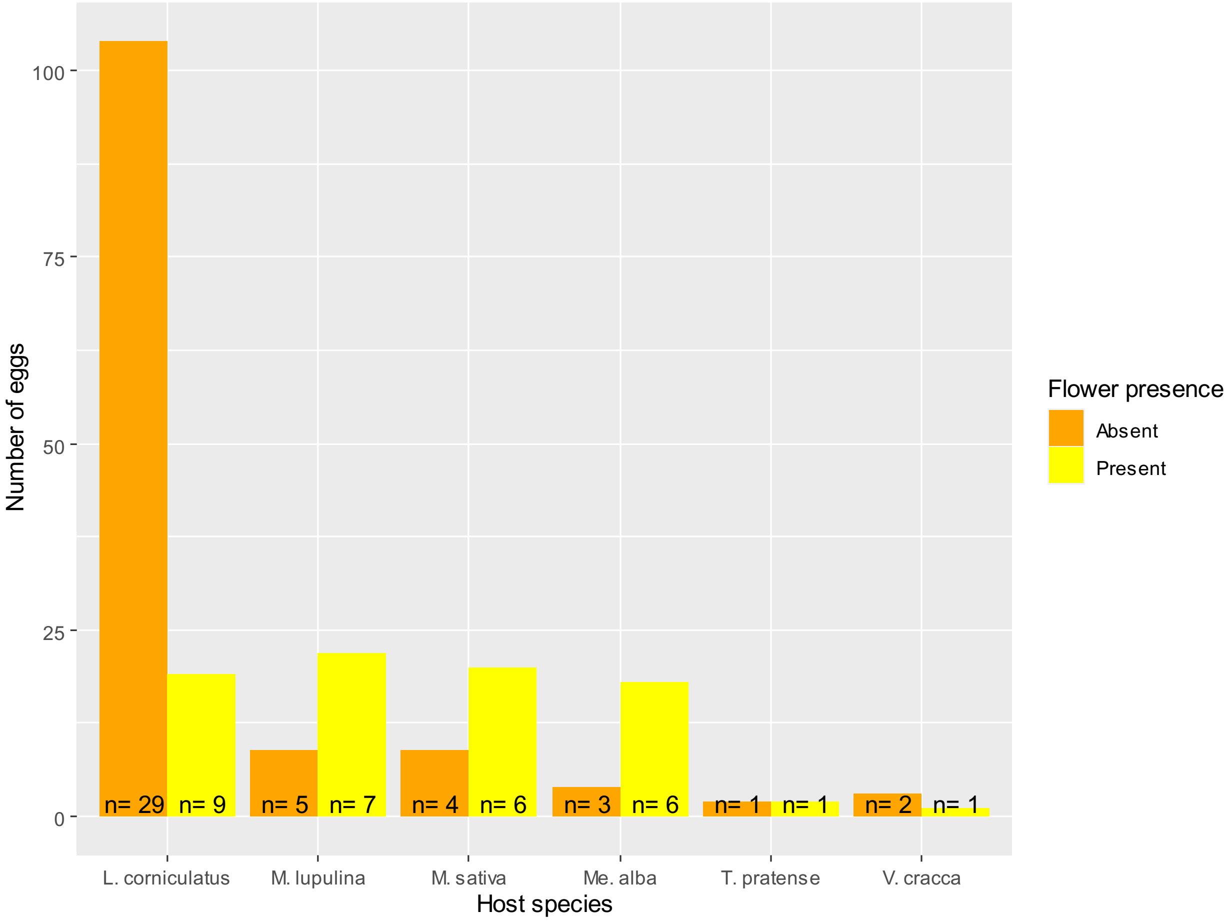

Figure 14. Egg abundance across host species laid under meristems with and without flowers counted over the summer 2020.

| *Parameter* | *Estimate* | *Standard Error* | *z-value* | *P-value* |
|---|---|---|---|---|
| (Intercept) | 1.27 | 0.19 | 6.61 | <0.05*** |
| Flower present | -0.44 | 0.27 | -1.66 | 0.10. |
| *M. lupulina* | -0.95 | 0.40 | -2.39 | 0.02* |
| *M. sativa* | -0.89 | 0.40 | -2.21 | 0.03* |
| *Me. alba* | -0.77 | 0.55 | -1.39 | 0.16 |
| *T. pratense* | -0.25 | 0.84 | -0.30 | 0.77 |
| *V. cracca* | -0.50 | 0.63 | -0.79 | 0.43 |
| Flower:*M. lupulina* | 1.27 | 0.50 | 2.52 | 0.01* |
| Flower:*M. sativa* | 1.05 | 0.48 | 2.17 | 0.03* |
| Flower:*Me. alba* | 0.97 | 0.65 | 1.49 | 0.14 |
| Flower:*T. pratense* | -0.30 | 1.16 | -0.26 | 0.80 |
| Flower:*V. cracca* | 0.06 | 1.19 | 0.05 | 0.96 |

Table 6. GLMM output table on effect of flower presence on egg abundance.
Formula: egg.count ~ Flower * Host_sp + (1 | Site) + (1 | Date).
AIC= 337.4 BIC=369.7 logLik=-154.7 deviance=309.4 df.resid=60
Date variance = 0.24038 Site variance = 0.06581

There was no significant difference between the number of eggs laid under meristems with and without flowers. Eggs were laid significantly more often under meristems with flowers of *M. lupulina*, *M. sativa* and *Me. Alba*. Eggs laid on *L. corniculatus* were laid significantly more often under meristems without flowers (Table 6).

### 3.4. Discussion

In its native range, *P. icarus* is associated with a range of grassland types: in Wales, it is most often associated with rough coastal and limestone grasslands and is most abundant where vegetation is short (León-Cortés et al., 1999). Adult presence was best predicted by the abundance of certain host plants found in the field sites, namely *L. corniculatus*, *M. sativa* and *T. pratense*. Butterfly abundance was smaller with higher cover of *Me. alba* and higher average vegetation height, the latter correlation confirming the finding of León-Cortés et al. (1999). This is further supported by *V. cracca* being the least used host for oviposition. As a climbing plant, *V. cracca* possesses tendrils that allow it to grow among tall vegetation, making it well adapted to compete for light amidst tall grass species. Its prevalence in areas with tall vegetation may partly explain why it is not used as a host by *P. icarus*, which was less abundant in such habitats. However, *V. cracca* flowers were frequently used by adults as a source of nectar, and would therefore constitute adult habitat (Appendix 4).

While it is clear that vegetation structure is an important habitat factor, a mechanistic explanation as to why open habitats are privileged remains to be provided for this species. One plausible explanation is the use of habitat structure as a refuge, roosting or for overwintering as larvae (Dover et al., 1997). Regarding oviposition behavior; the observed preference for young leaves to lay eggs on is likely explained by their tenderness compared to mature leaves, and provide better nutrition as plants concentrate nutrients in developing meristems (Lyndon, 1998).

Preference among host species was determined given that host abundance had been accounted for, however it is possible that the availability of the different host plants in Quebec varies over time and differs between species. Furthermore, plant structures such as flowers may present an even narrower window of opportunity for *P. icarus* to feed on and use as a larval food source, since this species is known to utilize host nectar as a cue for oviposition (Janz et al., 2005).

This means that the flowering periods of each host species may be important in determining host selection and habitat use. Thus, *P. icarus* might switch between hosts as they become available throughout the year. Female butterflies were observed ovipositing on *T. repens* flowers in early June (Figure 15), but laid no eggs on this host species throughout the rest of the summer. This might indicate that this species is a secondary host plant, which may be selected only when alternative hosts are absent. Thus, host selection may be dependent on host phenology and flowering period. Populations of generalist butterfly species such as *Papilio machaon* (Papilionidae) may locally specialize on one host species, based on its abundance and the diversity of host plants present (Singer, 1971; Wiklund, 1981; Wiklund et al., 2018). Our results suggest that *P. icarus* eggs were laid preferentially on the most abundant host species at each site, giving rise to an apparent local specialization.

To properly explore this hypothesis in future studies, a summer-long survey of host availability (measured as surface cover) could be done along with direct measurements of oviposition events. Herbivorous insects and their host plants typically have coevolved phenology, with herbivores emerging shortly after their hosts become available. In addition, polyphagous species were also found to switch between hosts across the year following the flowering periods of the different host species present (Fogelstroem et al., 2017; Toftegaard et al., 2019; Wiklund, 1984).

Plant structure availability may play an important role in host switching as host species often differ in their respective flowering periods. Generalist butterflies do not match their emergence period with the host plant flowering (Phillimore et al., 2012), but in the case of *P. icarus*, host flowers may be preferred as larval food as they contain flavonoids, a pigment sequestered by larvae and displayed in adult wings, which increases female attractiveness to males, and therefore fitness (Burghardt et al., 1997, 2000, 2001). This was the case of *M. sativa*, which received eggs on flowers more than on leaves. In addition, flowers are used by adults as a source of nectar, and as a cue for oviposition, meaning that host flowers mark prime habitat for both adults and larvae (Janz et al., 2005).

Figure 15. Female *P. icarus* butterfly ovipositing in a *T. repens* inflorescence in June 2020 on a mixed lawn patch adjacent to Saint Jacques street, Montreal. Photo: Eric Dexheimer.

Other important factors in the host choice of herbivorous insects are host plant physiology and chemical defense (Bauerfeind & Fischer, 2013; E. A. Bernays & Chapman, 2007; Ehrlich & Murphy, 1988; Kuczyk et al., 2021). Suitability can vary among individuals of a host species depending on soil nutrient composition, temperature, light and water availability (Bauerfeind & Fischer, 2013; Buse et al., 1998; Curtis & Wang, 1998; Kuczyk et al., 2021; Zvereva & Kozlov, 2006). Thus, combining host and soil quality with their distributions in spatial analyses would contribute to predicting habitat suitability for *P. icarus* in North America. Finally, previous studies on herbivorous insects found that predation also shifted host plant selection towards enemy-free spaces (E. A. Bernays & Chapman, 2007; Rausher, 1981).

*P. icarus* is a multivoltine species, meaning that it has a variable number of generations per year. This number of generations is dependent on climate regime, specifically ambient temperature, which positively correlates with development speed and voltinism in insects (Altermatt, 2010; Chen et al., 2011; Tobin et al., 2008; Zeuss et al., 2017). Thus, *P. icarus* populations in Scotland and Scandinavia have two generations, while populations in the southmost reaches of its range have three or four. According to e-Butterfly, there appears to be two generations in Quebec, with the start of a third in September (Figure 16). Since *P. icarus* overwinters as late-instar larvae, it is likely that the last generation of adults perishes along with any eggs laid during the following winter. However, with warming climes, this last generation is likely to have an increased window for reproduction and thus may become viable.

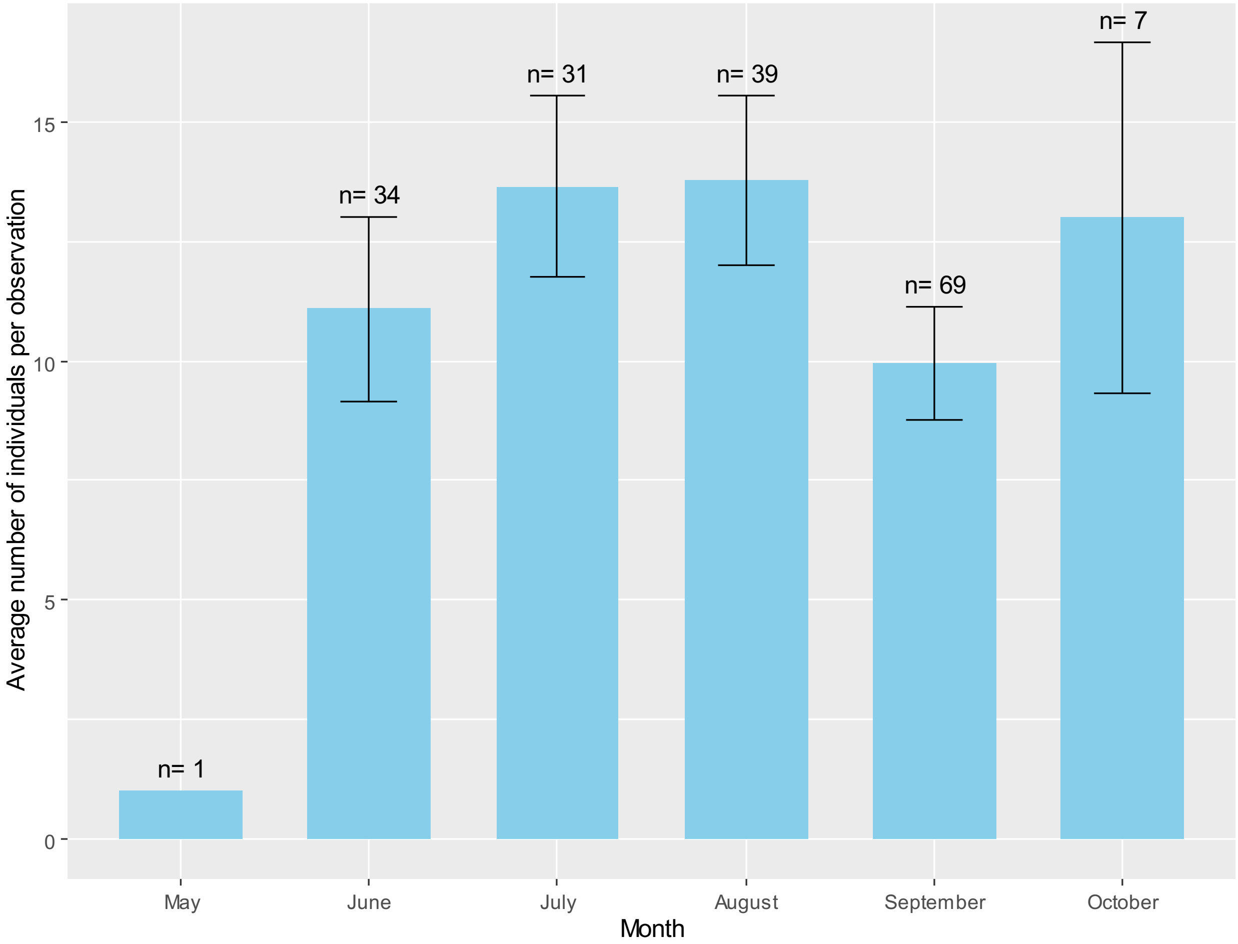

Figure 16. Average number of *P. icarus* butterflies per observations submitted to e-Butterfly between 2017 and 2019. N indicates the cumulated number of submitted observations between 2017 and 2019 for each month.

As an introduced butterfly feeding on non-native hosts that thrive in disturbed areas, *P. icarus* seems to have a limited presence if at all in native ecosystems since observations are more scarce beyond urban areas (*EButterfly*, 2020; *GBIF Secretariat: GBIF Backbone Taxonomy*, 2021). That being said, introduced species that become prolific have a significant chance to be encountered by local fauna. Thus, in large densities, *P. icarus* may induce changes in food web dynamics by attracting the attention of native predators through a bottom-up effect, as has been the case for other prolific species (Altieri et al., 2010; Jordan et al., 2008; Mondor & Addicott, 2007; Rodriguez, 2006). Overall, *P. icarus* thus seems to be established as an important component of disturbed and urbanized grasslands in the Montreal area, but its reliance on introduced plants for larval development and its preference for short vegetation will likely limit its spread to native habitats.

## 4. General conclusion

Myrmecophilous interactions in invasion biology are uncommon (Dekoninck et al., 2007; Ikenaga et al., 2020; Kistner et al., 2007), and are an understudied facet of invasion biology. As an introduced species in North America, *P. icarus* presents an opportunity to learn about biological invasions and the role played by mutualisms in species establishment. In addition, the present thesis attempted to identify the habitat occupied by this species in its new range in North America, through the study of its mutualism with ants and by identifying resource usage.

The results show that *P. icarus* remains a generalist species in its new range, as both adult presence and oviposition were driven by the most abundant host species, *L. corniculatus*. Vegetation structure also predicted adult abundance, although the mechanism explaining this preference in habitat remains to be determined.

This thesis is new as it looks this species from an invasion biology perspective. Future studies could attempt to investigate the remaining important factors that shape the niche of this species in its new range, in particular intra-host selection and host plant physiology. Additionally, genetic analyses would be useful in identifying the population of origin from the species' native range, and estimate the number of individuals from which the population in North-America was able to establish. This species is also currently expanding its range, with occurrences reported for the first time in Quebec City and Toronto in 2020 (*EButterfly*, 2020; *GBIF Secretariat: GBIF Backbone Taxonomy*, 2021).

The host choice and habitat use data presented here could be incorporated in spatial analyses to predict habitat suitability for *P. icarus* in North America. Lastly, since the species has become prolific in its new range in Quebec, it is likely that the species' abundance will alter the trophic and pollination web dynamics of urbanized ecosystems as a food item to native predators and parasitoids.

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## 6. Appendix

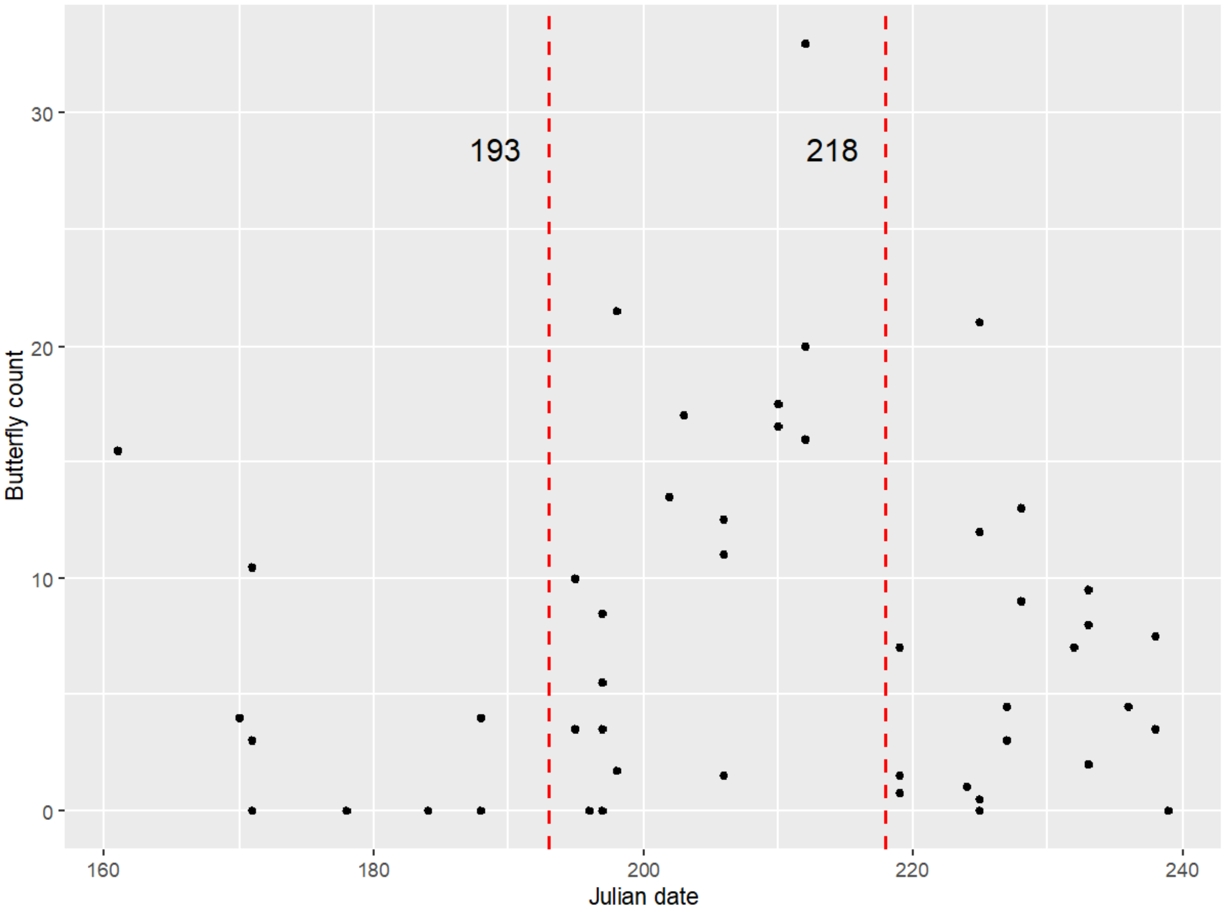
| **Subfamily** | **Vernacular name** | **Scientific name** | **Tending ant species** | **Host plants** |
|---|---|---|---|---|
| Polyommatinae | Spring Azure | *Celastrina ladon* | *Formica subsericea*, *Camponotus nearcticus*, *Crematogaster lineolatus* | *Prunus* spp., *Vacciunium* spp., *Viburnum* spp. |
| | Summer Azure | *Celastrina neglecta* | Unspecified | |
| | Cherry gall Azure | *Celastrina* sp. | | *Prunus* spp., *Viburnum* spp. |
| | Square-spotted Blue | *Euphilotes battoides* | Unspecified | *Eriogonum* spp. |
| | Rocky mountain dotted Blue | *Euphilotes ancilla* | Unspecified | *Eriogonum* spp. |
| | Western tailed Blue | *Everes amyntula* | Unspecified | Fabaceae (*Lathyrus* spp.) |
| | Silvery Blue | *Glaucopsyche lygdamus* | *Formica microgyna* (?), *Formica subsericea*, *Formica oreas comptula*, *Tapimona sessile* | Fabaceae |
| | Reakirt's Blue | *Hemiargus isola* | Unspecified | *Prosopis* spp. |

| | | | | |
|---|---|---|---|---|
| | Melissa Blue | *Lycaeides melissa* | Unspecified | *Lupinus* spp. |
| Lycaeninae | American Copper | *Lycaena phlaeas* | Unspecified | Polygonaceae |
| | Lustrous Copper | *Lycaena cuprea* | Unspecified | Polygonaceae |
| | Grey Copper | *Lycaena dione* | Unspecified | Polygonaceae |
| | Bronze Copper | *Lycaena hyllus* | Unspecified | Polygonaceae |
| | Ruddy Copper | *Lycaena rubida* | Unspecified | Polygonaceae |
| | Blue Copper | *Lycaena heteronea* | Unspecified | Polygonaceae |
| | Bog Copper | *Lycaena epixanthe* | Unspecified | *Vaccinium* spp. |
| | Dorcas Copper | *Lycaena dorcas* | Unspecified | *Potentilla* spp. |
| | Maritime Copper | *Lycaena dospassosi* | Unspecified | *Potentilla* spp. |
| | Purplish Copper | *Lycaena helloides* | Unspecified | Polygonaceae |
| | Lilac-bordered Copper | *Lycaena nivalis* | Unspecified | Polygonaceae |
| | Mariposa Copper | *Lycaena mariposa* | Unspecified | Ericaceae,<br>Polygonaceae |

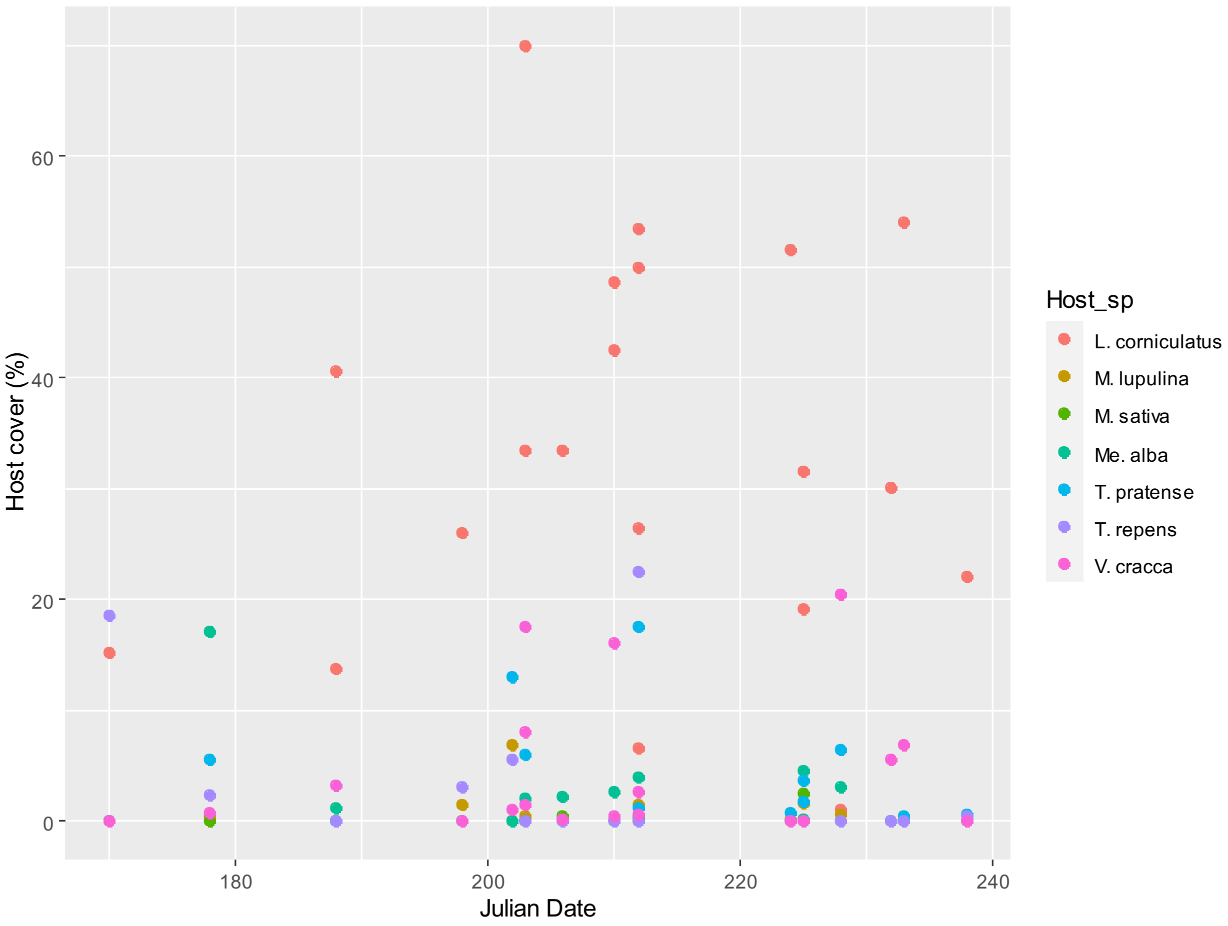
Appendix 1. Table 7. Supplementary table 1 for the 2nd chapter. Table 1. Lycaenidae in Quebec known to form myrmecophilous associations. (From: Canadian Biodiversity Information Facility website, 2019). Louis Handfield, 1999.

| **Subfamily** | **Species** |
|---|---|
| Myrmicinae | *Crematogaster lineolatus* |
| Formicinae | *Camponotus nearcticus* |
| | *Formica comptula* |
| | *Formica exssectoides* |
| | *Formica integra* |
| | *Formica microgyna* |
| | *Formica rufa* Group |
| | *Formica subsericea* |
| | *Tapimona sessile*<br>*Lasius americanus* |
| | *Lasius neoniger* |

Appendix 2. Table 8. Supplementary table 2 for the 2nd thesis chapter. Table 2. Ant species in Quebec known to tend Lycaenidae larvae (From: Le guide des papillons du Québec, 1999).



Appendix 3. Butterfly abundance data collected in the Summer 2020. The red dashed lines indicate the three arbitrary time periods that defining the “volt” random factor (designated as “Voltinism” in the main text).



Appendix 4. Host plant cover per species over the Summer 2020.