Non-native species and urbanization in the context of butterfly communities

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Abstract

Biodiversity is being lost around the world and anthropogenic activities, like non-native species introductions and urbanization, are among the leading causes of decline. Broadening our understanding of human-driven impacts on biodiversity can lead to more effective solutions and contribute towards stemming biodiversity losses. In this thesis, I explored the impacts of non-native species introductions and urbanization on butterfly-plant communities. I evaluated potential factors influencing the range expansion of a newly introduced species (Chapter 1), examined the role of urbanization in structuring biological communities (Chapter 2), and identified important ecological interactions between native and non-native species (Chapter 3). In my first chapter, I found that the newly introduced European Common Blue butterfly (*Polyommatus icarus*) was more abundant in urban and disturbed habitat that was unmown and where their preferred larval host plant (*Lotus corniculatus*), a non-native species, was present. I also found that *P. icarus* was not a strong flier relative to other butterfly species, suggesting that adult dispersal may not be a driving factor in range expansion. Instead, this species could expand its range in the future by colonizing habitats in developed regions across Canada given the association I found between *P. icarus* and disturbed habitat. In my second chapter, I found that urbanization led to the biotic homogenization of butterfly communities around Montréal, QC, favouring a few, highly abundant, non-native species. Homogenization was detected at both the taxonomic and functional levels and was driven by increases in *P. icarus* abundance in the more urban sites. In my third chapter, I found that non-native plants were well integrated into native butterfly nectar diets in an at-risk oak savanna ecosystem on Vancouver Island, BC and that usage of non-native plants increased when they were more available during the season. I also found that native butterflies visited non-native plants more often than flower availability predicted on its own, suggesting that butterflies may even prefer non-native nectar. Findings from my thesis research broaden our understanding of the ways in which butterfly communities can be influenced by human activities like urbanization and the introduction of non-native species, informing conservation efforts and directing future research needs.

Résumé

La biodiversité est en train de disparaître à travers le monde et les activités anthropiques, comme les introductions d'espèces non indigènes et l'urbanisation, sont parmi les principales causes de déclin. En élargissant notre compréhension des impacts humaine sur la biodiversité, nous pouvons créer des solutions plus efficaces afin d'enrayer les pertes de biodiversité. Dans cette thèse, j'ai exploré les impacts des introductions d'espèces non indigènes et de l'urbanisation sur les communautés de papillons et de plantes. J'ai évalué les facteurs potentiels influençant l'expansion de l'aire de répartition d'une espèce nouvellement introduite (chapitre 1), examiné le rôle de l'urbanisation dans la structuration des communautés biologiques (chapitre 2) et identifié d'importantes interactions écologiques entre les espèces indigènes et non indigènes (chapitre 3). Dans mon premier chapitre, j'ai découvert que le papillon Bleu Commun Européen (*Polyommatus icarus*), nouvellement introduit, était plus abondant dans les zones urbaines et perturbées, qui n'étaient pas fauchées et où pousse sa plante hôte préférée par ses chenilles (*Lotus corniculatus)*, une espèce de plante non indigène. J'ai aussi découvert que *P. icarus* n'était pas un vol puissant par rapport aux autres espèces de papillon, ce qui suggère que le vol des adultes n'est peut-être pas un facteur déterminant dans l'expansion de l'aire. Au lieu de cela, cette espèce pourrait étendre son aire à l'avenir en colonisant des habitats dans des régions développées à travers le Canada étant donne d'association que j'ai trouvée entre *P. icarus* et habitat perturbé. Dans mon deuxième chapitre, j'ai découvert que l'urbanisation conduisait à l'homogénéisation biotique des communautés de papillons autour de Montréal, QC, favorisant quelques espèces non indigènes abondantes . L'homogénéisation a été détectée aux niveaux taxonomique et fonctionnel et a été entrainée par des augmentations de l'abondance de *P. icarus* dans les sites plus urbains. Dans mon troisième chapitre, j'ai découvert que les plantes non indigènes étaient bien intégrées dans les régimes alimentaires de nectar de papillons indigènes dans un écosystème de savane à chênes à risque sur l'île de Vancouver, BC, et que l'utilisation par les papillons de ces plantes non indigènes augmentait lorsqu'elles étaient plus disponibles pendant la saison. J'ai aussi découvert que les papillons indigènes visitaient les plantes non indigènes plus souvent que la disponibilité des fleurs ne le prévoyait, ce qui suggère que les papillons peuvent même préférer le nectar non indigène . Les résultats de mes recherches de thèse améliorent notre compréhension de la manière dont les communautés de papillons peuvent être influencées par les activités humaines telles que l’urbanisation et l’introduction d’espèces non indigènes, informant les efforts de conservation et permettant d’orienter les recherches futures.

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Lastly, and on a more personal note, I would like to thank my friends, family, and husband Richard for always supporting and encouraging me.

Table of Contents

List of Publications

This thesis is based on the work contained in the following papers:

I **Rivest SA**, Kharouba HM (2021) Anthropogenic disturbance promotes the abundance of a newly introduced butterfly, the European common blue (*Polyommatus icarus*; Lepidoptera: Lycaenidae), in Canada. *Canadian Journal of Zoology* 99:642–652. doi: 10.1139/cjz-2021-0009.

II **Rivest SA,** Kharouba HM (2022) A few winners replace many losers: Urbanization leads to taxonomic and functional homogenization of butterfly communities in Montréal, Quebec. (*in prep*)

III **Rivest SA,** Wolkovich EM, Kharouba HM (2023) Flowering phenology influences butterfly visitation to non-native plants for nectar in an oak savanna. *Ecology,* manuscript ID ECY22-0801. (*submitted, in review*)

List of Tables

Table 1.1. Criteria for assigning a qualitative index of local-scale habitat disturbance to each site that combined observations about approximate time since disturbance and severity of disturbance. Shown are the four indices of disturbance and their corresponding type/age of vegetation, evidence of human traffic, and examples.

Table 1.2. Results of local- and landscape-scale habitat suitability models for European Common Blue butterflies (*Polyommatus icarus*) using generalized linear models with a negative binomial distribution (n=44 sites). Shown are pseudo-R^2 values for all models and results from likelihood ratio tests (type II anova) including chi-square statistics (χ^2), degrees of freedom (df), and *p*-values. Model coefficients and standard errors are also shown where applicable.

Table 1.3. Results of the mark-release-recapture study conducted on European Common Blue butterfly (*Polyommatus icarus*) adults at 15 semi-disturbed sites in St. Bruno-de-Montarville, Quebec. Values shown include number of marked individuals, numbers of recaptured individuals, recapture ratio (%), maximum dispersal distance (m), and mean dispersal distance (m) for males and females.

Table 2.1. Results of final models analyzing the effects of urban cover on (a-c) richness, abundance, and evenness, (e-g) community-weighted standard deviations of three traits, and (h-j) community-weighted means of three traits using either LMs or GLMs (n=44 sites). Also shown are the results from models analyzing (d) β-diversity as a function of the site grouping (rural vs. urban) and the distance (km) between sites using GLMs (n=498 comparisons). Models are fit on data from entire community, just native species, just non-native species, or the entire community but excluding *P. icarus*. The spatial scale (m) used for each model represents the scale at which the relationship between the response and urban cover was strongest (see **Methods**). Model results include estimates, standard errors (SE), χ^2-values and *p*-values. Estimates and SE for the wingspan model are presented for the log 10 transformed data. Degrees of freedom is 1 in all cases. SA indicates spatial autocorrelation was accounted for by including geographical coordinates.

Table 3.1. Patterns in native butterfly visitation to flowering plants for nectar including the number of native (N) plant species visited, the number of non-native (NN) plant species visited, the total number of visits made, and the percentage of visits that were to NN plants (rounded to nearest unit). Butterfly species are ordered by total number of visits.

Table 3.2. Results of final GLMs analyzing (a) the proportion of non-native (NN) floral area using the beta distribution (n=114 site-visits), and (b-c) the proportion of nectar foraging visits made to NN flowers using the quasibinomial distribution. Model b is based on the full data set (n=58 site-visits) whereas model c is based on data collected before 18 July (n=33 site-visits). Shown are model estimates and standard errors (SE) for standardized model predictors including day of year, site area (m^2),

the proportion of NN plant species richness (SR), and the proportion of NN floral area. Model results from either (a) likelihood ratio tests or (b-c) F-tests including test statistics ([a] chi-square value (χ^2), value; [b-c] *F*-value), degrees of freedom (df: numerator, denominator), and *p*-values (*p*) are also shown. Model visualizations are shown in **Fig. 3.4** and **Fig. 3.5**. NA indicates not applicable.

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List of Figures

GLMs (n=44 sites). Model predictions are from (a-d) LMs, and (e-f) gamma GLMs. Shown are raw data (dots), predicted lines of best fit (black lines), 95% confidence intervals (dotted lines), model estimates (β), standard errors (SE), and results from likelihood ratio tests including χ^2-values and *p*-values. Model predicted lines for larval diet breadth are shown for single-variable models including only urban cover (i.e., not including geographical coordinates). Proportion of urban cover was calculated at spatial scales of (a-b) 200 m, (c-d) 300 m, and (e-f) 100 m. Data for mean butterfly wingspan is log 10 transformed.

Figure 3.1. Map of study sites (n=10; grey circles) around Victoria, BC (black diamond) and an inset showing the location of the study area (red box) within the broader region of Vancouver Island, BC. Size of grey circles is based on the proportion of the total flowering plant species richness across the season that was non-native. Maps were created using R 4.2.0 (R Core Team 2022).

Figure 3.2. Photographs (by S. Rivest) of the top four most visited plant species including the non-native species (a-b) Hairy cat's-ear (*Hypochaeris radicata*), (c-d) Himalayan blackberry (*Rubus armeniacus*), and (e-f) Common vetch (*Vicia sativa*), as well as the native species (g-h) Common camas (*Camassia quamash*). Also show are native butterflies visiting the flowers including (b) Woodland skipper (*Ochlodes sylvanoides*), (d) Gray hairstreak (*Strymon melinus*), (f) Propertius duskywing (*Erynnis propertius*), and (h) Echo azure (*Celastrina echo*).

Figure 3.3. Phenological patterns in (a) floral area (m^2) from non-native and native plants (n=114 site-visits), and (b) the number of foraging visits made by native butterflies to native and non-native plants for nectar (n=58 site-visits). Dashed line in panel b represents 18 July (see **Methods**). To help with visualizations, an outlier in panel a (day of year=125, native floral area=2.6m^2) is not shown and curves were generated from all data points for both panels using geom smooth from the package ggplot2 (Wickham 2016).

Figure 3.4. Effects of significant predictors (x-axes) on (a-b) the proportion of non-native (NN) floral area using beta GLMs (n=114 site-visits), and (c-d) the proportion of nectar foraging visits made to NN flowers using quasibinomial GLMs (n=58 site-visits). Shown are raw data (dots), lines of best fit (solid lines) and 95% confidence intervals (a: ribbons; b-d: dotted lines). Also shown are model estimates (β), standard errors (SE) and *p*-values from either (a-b) likelihood ratio tests (χ^2-value) or (c-d) F-tests (F-value). Panel a shows the interaction between proportion of NN plant species richness (SR) and day of year. To visualize the interaction, the season was divided into equal thirds and model predictions were obtained for three representative time points: early (22 May; purple), mid (24 June; green), and late (27 July; yellow).

Figure 3.5. Test of the null hypothesis that native butterflies forage for nectar in proportion to nectar availability. Presented is the effect of the proportion of non-native floral area

on the proportion of nectar foraging visits made to non-native flowers using quasibinomial GLMs (n=33 site-visits). Shown are raw data (dots), the line of best fit (solid line), the 95% confidence interval (dotted black lines), and the prediction from the null hypothesis based on the quasibinomial model (dotted red line). Also shown are the model coefficient (β), standard error (SE) and *p*-value from an F-test (F-value). Model was fit using only observations before 18 July.

General Introduction

Anthropogenic threats to biodiversity

Biodiversity, defined as the variety of all life on Earth, is intrinsically valuable for its complexity, uniqueness, beauty, and simple existence. Biodiversity is also critical for the preservation of natural ecosystems and, in many cases, having a greater variety of species can positively affect ecosystem functions like biomass production and pollination (van der Plas 2019). All organisms, including humans, rely on naturally functioning ecosystems for their survival and wellbeing. For instance, humans critically rely on ecosystem services like food production, water regulation, and nutrient cycling (Millenium Ecosystem Assessment 2005). Despite widespread knowledge of its value and importance, global biodiversity is in peril. A growing body of evidence shows that over the last century, rates of species extinctions have far exceeded those from pre-human time periods for a variety of taxa (e.g., Raup 1991; Wake and Vredenburg 2008; Ceballos et al. 2015; Payne et al. 2016). Many scientists agree that we are now in the midst of a sixth mass extinction event (Leakey and Lewis 1995; Barnosky et al. 2011; Ceballos et al. 2015).

Modern biodiversity loss is driven by anthropogenic activities that can be divided into several categories: the introduction of non-native species, land use change, over-exploitation, pollution, and climate change (Maxwell et al. 2016). For example, agriculture is a form of land use change that currently threatens 62% of species listed on IUCN’s red list of threatened or near-threatened species (Maxwell et al. 2016). Human influence is now so pervasive that the term ‘Anthropocene’ is used to describe this new epoch of Earth’s history (Crutzen 2002; Lewis and Maslin 2015). The official start date of the Anthropocene is debated, but there is no doubt that human activities have had profound impacts on nature and biodiversity for millennia with the greatest acceleration in global-scale change occurring after the 1950s (Lewis and Maslin 2015). *Studies evaluating the impacts of modern anthropogenic activities on biological communities can help us to understand how and why biodiversity is being lost, hopefully leading to more effective solutions.*

Non-native species

Non-native species pose a large threat to native biodiversity and ecosystem function (Vitousek et al. 1997; Simberloff 2000; Bradley et al. 2019; Pyšek et al. 2020), making their study essential to conservation biologists. Non-native or introduced species can be defined as species that are transported beyond their native range through either accidental or purposeful human transport (Richardson et al. 2000). Since the late 20th century, growing global economies and trade networks combined with advancements in transport efficiency have led to unprecedented increases in the frequency of non-native species introductions worldwide (Meyerson and Mooney 2007; Hulme 2009). As a result, non-native species have become a defining feature of the Anthropocene (Lewis and Maslin 2015) that have the potential to drive global biodiversity change. Since species introductions are predicted to continue increasing until at least 2050 (Seebens et al. 2021), the study of non-native species has never been more critical.

Once introduced, non-native species may establish self-perpetuating populations depending on their ability to survive and reproduce in the new range which is a process referred to as ‘naturalization’ (Richardson et al. 2000). Many non-native species fail to achieve naturalization (Williamson and Fitter 1996; Blackburn et al. 2011), but some will be so successful that they undergo range expansion accompanied by rapid population growth (Sakai et al. 2001). These species are typically referred to as ‘invasive’ and are characterized by their broad distributions, locally abundant/dominant populations, and negative impacts on native species (Richardson et al. 2000; Pereyra 2016). *It is critical that non-native species that have been newly introduced are evaluated to broaden our understanding of the progression from introduction to invasion and the factors that may control its success.*

Non-native species present a range of threats to native biodiversity and human well-being. Non-native species can impact native species richness and abundance through a variety of direct and indirect mechanisms (e.g., predation, competition, habitat alteration, vectors of disease), leading to shifts in native community composition (Mack et al. 2000; Kenis et al. 2009; Bradley et al. 2019). In extreme cases, this can even lead to native species extinctions (Bellard et al. 2016; Blackburn et al. 2019). For example, the Rosy wolfsnail (*Euglandina rosea*) introduced across the South Pacific is thought to be the cause of the extinction of over 100 species of native snails via predation (Blackburn et al. 2019). Non-native species can also alter native communities and populations by impacting their genetic composition (e.g., hybridization), evolutionary trajectory, functional diversity, behaviour, and trophic networks (Suarez and Tsutsui 2008; Kenis et al. 2009; Ricciardi et al. 2013; Pyšek et al. 2020). Scaling up, non-natives can impact ecosystem processes like productivity, nutrient/contaminant cycling, pollination, disturbance regimes (e.g., fire), and hydrology (Mack et al. 2000; Brooks et al. 2004; Pyšek et al. 2020). In addition to these ecological impacts, non-native species can also have significant economic impacts with implications for human well-being (e.g., food production) (Crystal-Ornelas et al. 2021).

While it is clear that we should be wary of the potential threats of non-native species, some non-natives can play a positive role in the persistence of native species and even contribute to achieving conservation goals. Most invasion biology research has focused on the negative impacts of non-native species on ecological communities and ecosystem function (Vitousek et al. 1997; Simberloff 2000; Bradley et al. 2019), but less is known about the positive or neutral effects of non-native species (Rodriguez 2006; Schlaepfer et al. 2011). Some potential benefits of non-native species include providing food and habitat to native species, aiding in restoration progress, acting as ecosystem engineers, and providing ecosystem services (Schlaepfer et al. 2011). For example, reclaimed coal mine grasslands in southwestern Indiana are typically stocked with non-native plants and these areas have been shown to provide habitat for native Henslow's sparrows (*Ammodramus henslowii*), supporting large populations of the bird species that would otherwise be rare (Bajema et al. 2001). *Understanding the potential positive effects of non-native species in native ecosystems is critical and needed for conservation planning and management.*

Research on non-native insects is more recent than that of other animals and plants, but insects are now recognized as one of the most numerous introduced groups (Roques et al. 2009). For instance, in the continental United States, the number of introduced insects has grown from approximately 30 recorded species in 1800 to well over 3500 species by 2015 (Yamanaka et al. 2015). Other countries are similarly inundated with estimates of non-native insects reaching 1306 species in Europe (Roques et al. 2009), 1585 species in New Zealand (MacFarlane et al. 2010) and 2651 species in Hawaii (Yamanaka et al. 2015). Invasive insects, in particular, are among the most damaging of terrestrial invasive species and are notorious for transmitting diseases, causing massive agricultural losses, and increasing the need for pesticide use (Lounibos 2002; Hulme 2014; Bradshaw et al. 2016).

Urbanization

Like non-native species introductions, land use change in the form of urbanization is a defining feature of the Anthropocene that can threaten biodiversity. Urbanization is a process that converts natural and semi-natural land into impervious surfaces, like buildings and roads, for the settlement of dense human populations (Johnson and Munshi-South 2017). Although urban areas account for a small proportion of the Earth's terrestrial surface area (<3%), they contribute to large-scale environmental changes such as global shifts in carbon emissions and water availability (Grimm et al. 2008). This is because urban areas consume large amounts of global resources while simultaneously producing waste (Sanderson et al. 2002; Camaren and Swilling 2012). Some common features of urban areas around the globe are: habitat loss/fragmentation, increased pollution/chemical use, warmer temperatures, and a high abundance and diversity of non-native species, particularly non-native plants (McKinney 2008; Jiang et al. 2010; Pyšek et al. 2010; Pickett et al. 2011; Cadotte et al. 2017; Potgieter et al. 2017). Homogenization of biological communities, at both the taxonomic and functional levels, is another common outcome of increasing urbanization (McKinney 2002b, McKinney 2006). Thus, urban areas typically contain communities with high redundancies in either species identities (taxonomic) or individuals with the same functional forms or traits (functional) (Olden and Rooney 2006).

Although urban areas are typically associated with reduced environmental quality, 'green spaces' within these areas (e.g., parks, gardens) may have the potential to harbour diverse biological communities. A global analysis showed that cities can support diverse communities of birds and plants, particularly where greater proportions of green spaces including intact vegetation are maintained (Aronson et al. 2014). For example, urban green spaces in Dhaka, Bangladesh harbour approximately 50% of the country's butterfly biodiversity (Chowdhury et al.

2021). Cities could even help to support threatened or endemic species, demonstrating their potential value for conservation and restoration (Aronson et al. 2014; Ives et al. 2016). For example, research from Australia has shown that on a per-unit-area basis, urban areas contained more threatened plant and animal species than non-urban areas (Ives et al. 2016). This suggests that conservation efforts in cities could affect a greater number of threatened species than if efforts were concentrated in rural areas where threatened species richness is lower (Ives et al. 2016). To date, most urban biodiversity research has focused on plants and birds (e.g., Marzluff 2001; Wittig 2004), with fewer studies on insects. *More research aimed at understanding and enhancing insect biodiversity in urban areas is needed.*

Importance of spatial scale

Spatial scale is a central consideration in ecological studies. This is because ecological patterns (e.g., species-area relationships) and processes (e.g., competition, dispersal) are known to be scale-dependent, increasing in importance at certain scales over others (Wiens 1989; Levin 1992; Mayor et al. 2009). For example, the abundance of Dryad butterflies (*Minois dryas*) is influenced by the availability of nectar plants at local scales, but plant community composition (e.g., proportion of non-natives) is more important at landscape scales (Kalarus and Nowicki 2017). Spatial scale is particularly important to consider when studying the associations between a species and its habitat since the scale at which environmental variables are measured greatly influences the strength and direction of their effects (Brennan et al. 2002; Mayor et al. 2009). An effective strategy when conducting analyses like this is to use a multi-scale approach where species are surveyed in focal sites and then their abundance and/or occurrence is related to environmental variables measured at multiple spatial scales (Martin and Fahrig 2012; McGarigal et al. 2016). Scale can then be optimized by determining the scale at which the species-habitat relationship is strongest (i.e., 'scale of effect'; Martin and Fahrig 2012; McGarigal et al. 2016; Miguet et al. 2016). Despite evidence of the importance of scale, most species-habitat studies are still commonly conducted at a single scale (Brown et al. 2008; McGarigal et al. 2016). *More species-habitat studies using a multi-scale approach are needed to better understand the responses of biological communities to changes in biotic and abiotic factors.*

Butterflies and plants

A main characteristic of butterflies is that they are phytophagous, relying on plant resources during all life stages (Gilbert and Singer 1975; Boggs and Freeman 2005). As a result, in native butterfly communities, there are several interactions that can occur with native and non-native plants (**Fig. A.1abc**). Interactions with non-native plants may be particularly important to consider in anthropogenic environments since non-native plants tend to be more dominant in these areas (Pyšek et al. 2010). Yet, the overall role of non-native plants in these communities is unclear.

Negative, direct effects (**Fig. A.1a**) of non-native plants on native butterflies can occur when female butterflies oviposit on plants that are toxic to their larvae (i.e., developmental trap; Sands 2008). Negative, indirect effects (**Fig. A.1c**) can occur through competition between native and non-native plants, leading to losses in butterfly host plants or alterations to ecosystem structure and microclimate (Schultz et al. 2011). Alternatively, non-native plants can have positive, direct effects (**Fig. A.1a**) on native butterflies by providing food resources of greater quality, quantity, and/or temporal availability (Graves and Shapiro 2003). Non-native plants also been shown to indirectly (**Fig. A.1c**) benefit butterflies by playing a role in habitat maintenance.

For example, when non-native grasses support the suppression of woody encroachment and contribute to the preservation of ecosystem structure in grasslands (MacDougall and Turkington 2005).

Butterflies and urbanization

In addition to non-native plants, native butterfly communities are impacted by the characteristics of their environment (e.g., urbanization, temperature) through a variety of pathways (**Fig. A.1d**). For example, urbanization is one environmental characteristic that can negatively affect butterflies by reducing the amount of habitable space needed to support sufficient habitat and plant food resources (Blair and Launer 1997; Beninde et al. 2015). Urban areas can include green spaces which may be more suitable for butterflies, however negative impacts can still occur if green spaces are poor quality due to factors like chemical use (e.g., pesticides in gardens), pollution (e.g., soil, air, light, noise), vehicle traffic, and human intervention (e.g., active removals) (Rao and Girish 2007; Wei and Yang 2010; Pickett et al. 2011; Fontaine et al. 2016; Fenoglio et al. 2021).

In contrast, urbanization may positively impact butterflies through increases in temperature (i.e., urban heat island effect; Oke 1973). Since butterflies are ectothermic, increased temperatures in cities could increase their development time and/or reproductive rates (Raupp et al. 2010). However, this will only occur if temperatures do not exceed species-specific critical thermal maxima (CT_{max}) (Fenoglio et al. 2021). Butterflies can also benefit from urbanization if their preferred food plant is grown in urban areas. For example, holly hedges and ivy-covered walls as host plants for the specialist Holly Blue butterfly (*Celastrina argiolus*) in the UK (Hardy and Dennis 1999). Lastly, urbanization can positively affect butterflies by increasing habitat heterogeneity since cities typically have a large variety of different land cover types that occur over relatively small spatial scales (e.g., gardens, transportation, commercial, industrial) (Thompson et al. 2003; Cadenasso et al. 2007). This can benefit some butterflies by providing a greater variety of plant resources. Indeed, plant species richness is often higher in urban areas compared to rural habitats, a pattern which has been explained by a combination of high habitat heterogeneity and the prevalence of non-native plants (McKinney 2002a; Kühn et al. 2004).

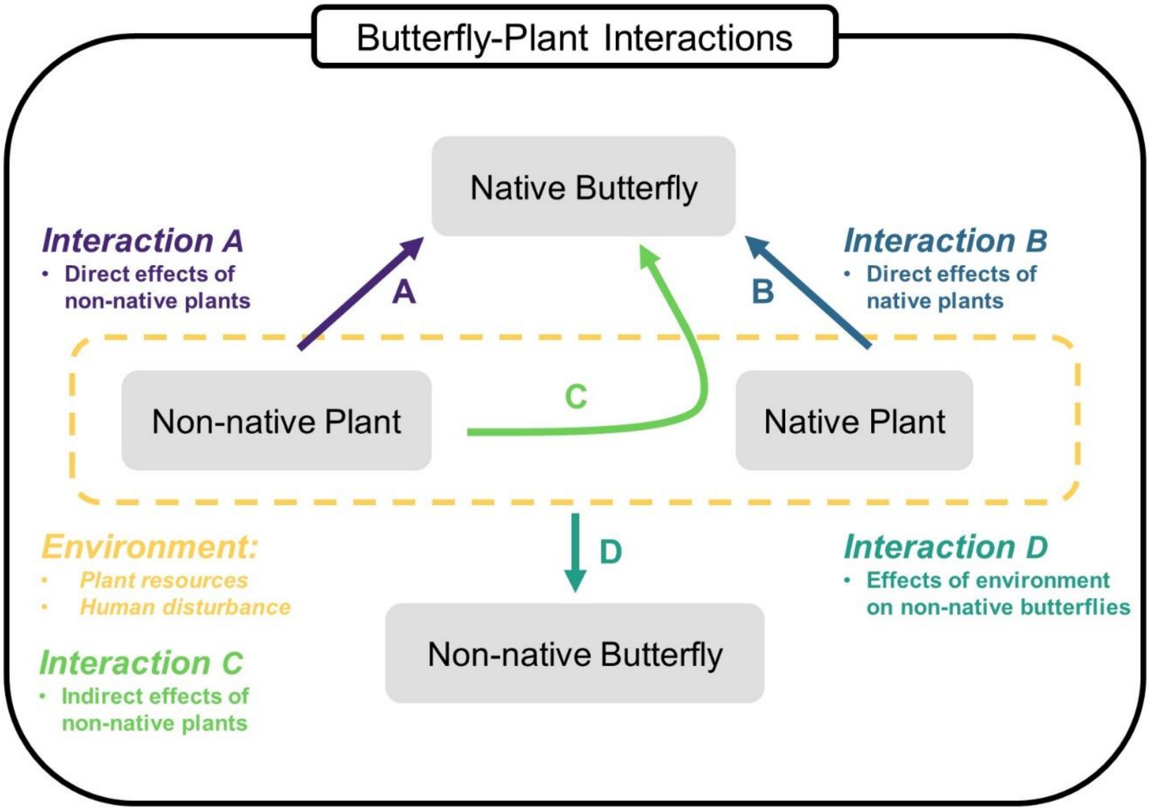
Another key feature of urban areas is the dominance of non-native plants (McKinney 2002a; Kühn et al. 2004; Pyšek et al. 2010; Potgieter et al. 2017) which can have both positive and negative impacts on butterflies, as discussed above.

Thesis objectives

Using two different butterfly-plant communities, my PhD thesis aims to explore two anthropogenic activities that have the potential to threaten biodiversity: non-native species introductions and urbanization. My research is motivated by a need to effectively conserve biodiversity by taking into consideration the range expansion of non-native species, the role of urbanization in native communities, and ecological interactions that can occur between native and non-native species.

In Chapter 1, I examine the interactions between a newly introduced butterfly species in Canada and its environment (**Fig. A.1d**) to identify what habitat characteristics best predict its abundance and gain a better understanding of the factors likely to influence its range expansion. In Chapter 2, I investigate the influence of another environmental characteristic, urbanization, on butterflies (**Fig A.1abd**) in Montréal, Quebec and test the hypothesis that urbanization leads to taxonomic and functional homogenization. To gain insights into how information about species interactions can be integrated into management strategies, I evaluate the role of non-native plants as sources of nectar for native butterflies (**Fig. A.1a**) in Vancouver Island's at-risk Garry oak savanna ecosystem in Chapter 3.

Figure A.1. A schematic diagram representing interactions between butterflies and their environments (yellow-dashed box), including native and non-native food plants, that are the focus of my thesis research.



I. Anthropogenic disturbance promotes the abundance of a newly introduced butterfly, the European common blue (*Polyommatus icarus*; Lepidoptera: Lycaenidae), in Canada

The following thesis chapter is a modified version of a previously published article (citation below). The article was modified to reduce overlap with the general introduction of this thesis. My contributions to this thesis chapter are the conceptions of ideas, design of methodologies, data collection, data analysis, writing, and editing.

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1.1 Abstract

The frequency of introductions of non-native species is increasing worldwide, but only a few introduced species undergo rapid population growth and range expansion, and even fewer become invasive, leading to negative impacts on native communities. Predicting which non-native species are likely to become widespread and abundant can be difficult when there is a lack of species' information in the early stages of colonization. Here, I investigate the ecology of a newly introduced butterfly in Canada, the European Common Blue (*Polyommatus icarus*), by modelling its local and landscape-scale habitat suitability in Montréal, Quebec, Canada, and the surrounding region, and by assessing its dispersal ability using a mark–release–recapture study. At a local scale, I found that *P. icarus* abundance was highest at sites with moderate levels of habitat disturbance (e.g., mowed every 2–3 years), the presence of their preferred larval host plant and low proportional cover of grasses. At a landscape scale, *P. icarus* abundance increased with an increasing proportion of urban area and decreasing proportion of forests. I also found that *P. icarus* is a low to moderate disperser relative to other butterflies. My results suggest that *P. icarus* may become widespread in disturbed and urban areas across Canada, but that further investigation into additional potential range-constraining factors (e.g., microclimate), especially larval preferences, and modelling of the trajectory of *P. icarus* range expansion is needed.

1.2 Introduction

Non-native species characterized by rapid population growth and range expansion (i.e., invasive species) can have negative impacts on native biota (Simberloff 2000; Bradley et al. 2019; Pyšek et al. 2020) and ecosystem function (Vitousek et al. 1997; Guy-Haim et al. 2018).

Consequently, one of the primary aims of invasion biology is to predict which non-native species are likely to become widespread, abundant and potentially invasive, in the future.

Knowledge of the geographical and ecological factors that constrain the distribution of non-native species is essential for predicting their range expansion. Anthropogenic disturbance has long been associated with the successful establishment and spread of non-native species (Elton 1958; Cadotte et al. 2017). For non-native insects, disturbance can accelerate their spread into new sites by increasing propagule pressure along transport pathways (Pyšek et al. 2010; Gippet et al. 2019); increase the diversity and abundance of non-native plants (Jauni et al. 2015) which in turn increases the efficiency of non-native herbivorous insects that forage on non-native hosts (Jactel et al. 2005); and can lead to less diverse communities of enemies and competitors that occur in more natural habitats, resulting in fewer negative biotic interactions (i.e., lower biotic resistance) (Elton 1958). For example, non-native Yellow crazy ants (*Anoplolepis gracilipes*) are more likely to occur in managed agroforests than natural rainforests because of reduced competition with native ants that are largely excluded from the more disturbed sites (Bos et al. 2008).

Anthropogenic disturbance often facilitates the establishment and spread of non-native insects, but not all introduced species respond to disturbance in the same way. While studies generally report higher non-native insect species richness and/or abundance in disturbed habitats (Petit et al. 2008; Roques et al. 2009; Pyšek et al. 2010), the shape of the relationship is not always linear. For instance, Estay et al. (2012) found that the disturbance-richness relationship for non-native forest insects becomes saturated at intermediate levels of disturbance. A study on non-native Argentine ants (*Linepithema humile*) showed that their abundance peaks at intermediate levels of disturbance due to higher resource availability than can be found in more natural habitats and reduced competitive interactions with other non-native ant species that are more dominant in highly disturbed habitats (Vonshak and Gordon 2015). Therefore, specifying how disturbance impacts non-native species is important to guide management efforts (e.g., by prioritizing the right areas for control).

In addition to human disturbance, the spread of non-native species depends on the dispersal ability of the species. Dispersal limitation is considered a significant barrier to range expansions by non-native species (Renault et al. 2018) and, like native species, can prevent them from occupying suitable habitat beyond the edge of their ranges (Tilman 1997; Araújo and Pearson 2005). Given the importance of dispersal to range expansion, quantifying dispersal distance for non-native insects is an important step in understanding their potential for spread. This is particularly important for newly introduced insects whose dispersal ability is likely not known.

Here, I investigate the ecology of a newly introduced butterfly in Canada: the European common blue (*Polyommatus icarus*) (**Fig. 1.1**). Introduced to Montréal, Quebec, Canada from Europe as early as 2005 (Hall 2008), initial observations of this species suggest that it can reach extremely high local densities compared to native butterflies and that it is rapidly expanding its distribution (J. Newman et al. unpublished; M. Larrivée personal communication, 2016). However, the factors that are likely to influence *P. icarus'* range expansion in its range in North America are unknown. The recent introduction of *P. icarus* provides a rare opportunity to study a non-native insect during the early stages of its colonization (e.g., Rosati and VanLaerhoven 2007; Haavik et al. 2015), allowing me to gain further insights into the progression of an invasion.

In this chapter, I ask: (1) what key habitat characteristics best predict *P. icarus* abundance? Additionally, I provide other descriptors of *P. icarus* ecology and its relative abundance in the butterfly community. To do so, I model *P. icarus* habitat suitability by considering the role of plant community characteristics and disturbance at a local scale, and land cover types at a landscape scale, on adult abundance. In addition, I determine (2) the dispersal ability of *P. icarus* adults in its introduced range using a mark-release-recapture study.

1.3 Methods

1.3.1 Study system

The European common blue (*Polyommatus icarus*) is a small, non-migratory butterfly native to temperate Europe and Asia that occurs in discrete closed colonies (i.e., individuals rarely leave natal breeding grounds, especially females) (Thomas 1984; Emmet and Heath 1989; Thomas and Lewington 1991). In its native range, *P. icarus* is tolerant of a range in climatic conditions with a large distribution extending from Northern Africa to Norway and Finland (Thomas and Lewington 1991; Tolman and Lewington 2008). In Europe, *P. icarus* is considered extremely common (i.e., widespread and abundant), occurring in a variety of habitats (e.g., pastures, dunes, heaths, grasslands, roadsides, and waste places; Emmet and Heath 1989).

P. icarus larvae can forage on several leguminous plants (Fabaceae), but have a preference for Bird’s Foot trefoil (*Lotus corniculatus*) (Thomas and Lewington 1991; Tolman and Lewington 2008). *L. corniculatus* was introduced to North America in the mid-1700s and is now extremely widespread and abundant, occurring in every Canadian province (Zandstra and Grant 1968). In Canada, *L. corniculatus* is considered an agricultural escapee. Originally, it was imported as a common hay crop and impurity of seed mixtures, but can now be found growing in pastures, meadows, lawns, roadsides and waste places in every Canadian province (Turkington and Franko 1980). Adult *P. icarus* feed on nectar from a wide variety of plant species from several families (Emmet and Heath 1989), including *L. corniculatus* (Janz et al. 2005).

In Canada, *P. icarus* is in the early phases of its colonization. As of 2017, when this study began, the area inhabited by this butterfly was estimated to be 6000 km^2 and centralized in the largely urban and agricultural region of Montréal, Quebec (**Fig. 1.2a**). It is one of the most densely farmed and populated areas of Canada (Statistics Canada 2014). Aside from urban and agricultural areas, the region is composed of remnant patches of mixed wood forest (most forests in the region are deciduous (57%) or mixed deciduous and coniferous (40.5%)) and an extensive system of waterways including the St. Lawrence river (Wiken 1986). The range of *P. icarus* continues to expand in Montréal with more observations being added each year (e.g., 47 records added in 2019 compared to only 8 records in 2011; eButterfly 2020) and to locations outside the Montréal region (e.g., records in Toronto, Ontario added in 2019 over 400 km away from our study region in Montréal; eButterfly 2020).

1.3.2 Site selection

To assess habitat suitability, I conducted field surveys of adult butterflies and their habitat at 44 open grassland habitats that spanned the introduced range of *P. icarus* as of 2017 (**Fig. 1.2b**). I chose sites along a gradient of anthropogenic disturbance by visually assessing surrounding land cover using satellite imagery, and local site features (e.g., evidence of human presence) upon an initial visit. This was a purely qualitative exercise to approximate differences between sites. To ensure my sampling locations were independent, I chose sites that were at least 7 km apart, a distance that I was confident far exceeded the dispersal abilities of *P. icarus* adults based on European estimates (mean distance 165 to 191m) (Gutiérrez et al. 2001; Kuussaari et al. 2014). It also took into account the patchiness of the landscape and the total extent of the study region (sites > 7 km apart would likely have exceeded the distribution of *P. icarus* based on eButterfly records as of 2017). I visited sites 3-4 times from May to August, with 39 sites surveyed in 2017 and an additional 5 sites in 2018. Beyond the surveys, I checked for the presence of *P. icarus* every 3-4 days in 2017 until 4 November.

1.3.3 Butterfly surveys

I estimated butterfly abundance using the ‘transect walk method’ which is a standardised protocol used in many butterfly monitoring schemes around the world (Thomas 2005; van Swaay et al. 2008). To compare the abundance of *P. icarus* to other butterfly species, I estimated the abundance of all butterfly species. Total site area varied, so I kept my survey area and search time constant. To do so, I walked a spatially fixed 300 m long route, divided into five separate transects of 60 m each arranged side-by-side 15 m apart (i.e., approx. square 60 m by 60 m; **Fig. 1.2c**). Two observers identified and counted all butterflies that flew within 5 m in front of them or on either side of the transect (Pollard and Yates 1993). Transects were walked at a consistent speed of 10 m/min. Although this method has been criticized for its poor ability to detect cryptic species (Pellet et al. 2012), low detection is unlikely to be an issue for *P. icarus* since it is a highly conspicuous butterfly, an active flyer, and has bright blue colouration. Following standard protocols (e.g., Pollard and Yates 1993), surveys were conducted only when butterflies were fully active: 9 am to 4 pm, temperatures of 13-40°C or > 17°C when cloud cover > 75%, wind < 30 km/h, and no rain.

1.3.4 Local habitat surveys

During each site-visit, I characterized habitat at a local-scale (i.e., within the area surveyed for butterflies; **Fig. 1.2c**) by placing five 1 m^2 quadrats along the same five 60 m transects used to survey butterflies. For each visit to a site, I selected the locations of my quadrats before I arrived at the site using an algorithm that randomized the distance from the start (0 to 300 m) and which side of the transect the quadrat would be placed. Once at the site, I ensured the placements of the quadrats adequately covered the site and any larger site features present (e.g., large patch of a single plant species, rock cover).

Within each quadrat, I visually estimated the proportional cover of shrubs, forbs, grasses, bare ground, *L. corniculatus* flowers, and all flowers. I also recorded *L. corniculatus* occurrence (presence/absence) in these quadrats. If I happened to notice *L. corniculatus* on our butterfly surveys, I included this observation as evidence of its occurrence at the site, but this only occurred 4 times over the survey period. As the aim of our study was to describe habitat suitability for *P. icarus* adults, I chose variables most likely to be important for adults. However, some variables (e.g., *L. corniculatus* flower cover) could indicate suitable habitat for both larva and adults based on oviposition preference of females (Janz et al. 2005). I note here that forb cover included the cover of *L. corniculatus* flowers, all other flowers, and plants not flowering at the time of observation. The proportional cover of all quadrats from all seasonal replicates were averaged to produce a site-level estimate. I estimated canopy cover once for each site, during a mid-season visit, using a densiometer at five randomized locations along the 300 m butterfly transect.

At the end of the season, I assigned an index of disturbance to each site. This represented a qualitative measure of local-scale habitat disturbance (four levels) that combined observations about approximate time since disturbance and severity of disturbance. Specifically, I considered the type/age of vegetation (e.g., presence and size of trees, plant height (shorter = younger)), evidence of human traffic, and whether human-made objects were present (e.g., paths, buildings, construction materials) (**Table 1.1**; **Fig. 1.3**).

1.3.5 Landscape habitat surveys

To quantify the landscape surrounding our sites, I used a 30 m resolution 2015 land cover map (Canada Centre for Remote Sensing 2015). For the purposes of this analysis, I aggregated land cover classes to represent seven major types: forest (three classes: needleleaf, broadleaf, and mixed), cropland, wetland, grassland, shrubland, water (i.e., lakes and rivers), and urban land (**Fig. 1.2b**). I aggregated the three classes of forest since we had no a priori reasons to expect that different forest types would impact *P. icarus* abundance differently. I calculated the proportional cover of each land cover type within circular buffers of varying sizes surrounding my sites.

1.3.6 Statistical analysis: habitat suitability modelling

(i) Overall approach

I divided the analysis into two sections: local- and landscape-scale (i.e., within-site and 400 m, respectively; **Fig. 1.2c**). For both scales, I analyzed the total number of *P. icarus* observed across the season. Since *P. icarus* abundance was an overdispersed count (mean:variance = 1:66), I used generalized linear models (GLMs) from the MASS package (Venables and Ripley 2002). I used the negative binomial probability distribution, which has been shown to be the best approach for overdispersed data (Welsh et al. 2000). I combined the two years of surveys since there was no effect of year on the results (**S1.1**; **Table S1.1**). I included the number of visits to sites in all models to account for variation in the number of times a site was surveyed. I assessed non-linear effects by visually checking plots and comparing model fit.

I explored potential relationships amongst my predictor variables in several ways. For continuous variables, I explored collinearity using variance inflation factors (i.e., correlated if VIF > 5; Zuur et al. 2007) from the car package (Fox and Weisberg 2019). To determine overall independence for categorical variables, I used Fisher's exact tests due to my smaller sample sizes in some contingency categories (Bower 2003) and corrected these for multiple comparisons when conducting post-hoc analyses (Shan and Gerstenberger 2017). For the relationships between disturbance index (i.e., categorical) and my continuous variables, I fit beta GLMs (**S1.2**; **Fig. S1.1**) (Ferrari and Cribari-Neto 2004; Cribari-Neto and Zeileis 2010; Douma and Weedon 2019).

Model selection followed a forward step-wise approach based on Akaike Information Criterion (i.e., ΔAIC>2; Burnham and Anderson, 1998) with the final models being those that were the most parsimonious (i.e., lowest AIC). Using the package DHARMa in R, I validated final models by visually assessing scaled residual plots and evaluated spatial autocorrelation with a Moran's I test (p>0.05 for all models) (Hartig 2018). DHARMa uses a simulation-based approach to produce scaled residuals (between 0 and 1) that are readily interpretable for GLMs (Hartig 2018). I used likelihood ratio tests (type II anova) to assess model fit and Nagelkerke pseudo-R^2 values (Nagelkerke 1991), a coefficient of determination for logistic regression, to determine model goodness of fit. Post-hoc comparisons between levels of categorical variables were conducted using a modified Tukey's test from the multcomp package (Hothorn et al. 2008). To account for unequal variances and sample sizes between factor levels (Herberich et al. 2010), this modified test uses a heteroscedastic consistent covariance estimation technique from the sandwich package (Zeileis 2004).

All statistical analyses were performed using R 3.5.3 (R Core Team 2019).

(ii) Local-scale analysis

To identify the local-scale characteristics that best predict the abundance of *P. icarus*, I began with nine predictors: disturbance index (factor with four levels), canopy cover, the occurrence of *L. corniculatus* (two levels: presence, absence), and the mean proportional cover of each of the following: shrubs, forbs, grasses, bare ground, *L. corniculatus* flowers, and total flowers. Proportional cover of shrubs and *L. corniculatus* flowers had insufficient data and were therefore excluded. Preliminary analyses exploring the relationships between my predictor variables showed a high degree of non-independence. Specifically, disturbance index was correlated with all of our other variables (i.e., those describing the plant community structure; **Fig. S1.1**). I therefore chose to model the effects of disturbance (i.e., disturbance model) separately from the effects of plant community structure on *P. icarus* abundance (i.e., plant model). For the plant model, from the remaining six predictor variables, grass and forb were collinear (VIF>5). Therefore, I excluded forb due to its weaker influence on *P. icarus* abundance as determined by model AIC and pseudo-R^2.

(iii) Landscape-scale analysis

To identify the landscape-scale characteristics that best predict the abundance of *P. icarus*, I began with seven predictor variables: the proportional cover of forest, cropland, wetland, grassland, shrubland, water and urban land surrounding the sites. Wetland, grassland,

and shrubland had insufficient data in the study region and were excluded. Cropland and urban land were collinear (VIF>5) at almost all spatial scales assessed (see further discussion below) so I excluded cropland due to its weaker influence on *P. icarus* abundance as determined by model AIC and pseudo-R^2 (400 m scale: β=-1.17 (0.85SE), χ^2=1.43, df=1, *p*=0.232, pseudo-R^2=0.022). Therefore, final models included: the proportional cover of forest, water and urban land surrounding the sites.

Since spatial scale is central to determining species' habitat associations (Levin 1992; Brennan et al. 2002; Mayor et al. 2009), I used a multi-scale approach to determine the scale at which the species-landscape relationship was strongest (Martin and Fahrig 2012; McGarigal et al. 2016; Miguet et al. 2016). As recommended by Jackson and Fahrig (2012), I tested multiple scales that ranged over more than one order of magnitude with the largest scale exceeding nine times the mean dispersal distance (i.e., 75 m; see Results) of the focal organism. This meant that I fit models at scales between 100 m and 2500 m at intervals of 100 m (i.e., 25 scales). Models consisted of all predictors together or each predictor individually. I then evaluated model fit based on AIC. I found that the relationship between *P. icarus* abundance and the three land cover types was strongest at a spatial scale of 400 m (**Fig. S1.2**). This scale was consistent even when I modelled the land cover types separately. Therefore, all landscape-scale analyses were conducted at a 400 m scale.

1.3.7 Mark-release-recapture

To assess the dispersal ability of *P. icarus* adults, I conducted a mark-release-recapture (MRR) study in 2018 at 15 semi-disturbed sites in St. Bruno-de-Montarville, Quebec (**Fig. 1.2d**) which is located approximately 15 km from metropolitan Montréal. I chose sites based on their likelihood to contain *P. icarus* (i.e., close proximity to human developments, floral resources), as my goal was to capture as many individuals as possible. Since measurements of dispersal are directly proportional to total study area (Shreeve 1992; Schneider 2003), I chose sites to maximize the total study area (5.7 km^2), while keeping the study design feasible (larger areas require more sites and sampling effort). This is much larger than other MRR studies looking at adult butterfly movement patterns (e.g., 3 km^2 Dover et al. 1992; 0.11 km^2 Kuussaari et al. 2014). Smaller study areas can underestimate dispersal by restricting the distance of possible movements (Schneider 2003).

I visited sites in rotation (one visit/week) for six weeks in July and August of 2018. During each visit, two observers actively searched for and captured *P. icarus* for 1-2 hours, depending on the number of butterflies present. For all captured individuals, I noted their sex, condition of their wings (e.g., fresh, worn, tattered), time/location of capture, and gave both hind wings a unique mark using a waterproof permanent marker (Sakura Microperm). Butterflies were handled for no more than 2 minutes each and were released at the location of capture. After release, butterflies typically flew a <5 m away before landing on vegetation or bare ground to bask in the sun.

To test for differences in dispersal between male and female *P. icarus*, I conducted a Welch's two sample t-test in R. To determine the sensitivity of our dispersal measurements to an aspect of the study design, I also report results based only on observations of dispersal > 20 m. I chose this threshold because 20 m was the approximate distance that observers would walk in between bouts of capturing and marking individuals. Other MRR studies have made similar methodological choices, but in different ways. For example, by releasing all marked butterflies from a central point at the end of the survey day (e.g., Ricketts 2001) or only recapturing individuals a minimum distance away from a given release area (e.g., 25 m x 25 m area; Kuussaari et al. 2014).

1.4 Results

I counted 1128 P. icarus adults at 35 (80%) of my 44 sites. I observed two generations of *P. icarus* during my survey period in 2017 (1st sighting: 4th June) (**Fig. S1.3**). However, I continued to make anecdotal observations of *P. icarus* adults until 28 October 2017, suggesting that the flight period of *P. icarus* can be up to 5 months long (June-October) and that there are likely more than two generations. I observed *P. icarus* adults foraging for nectar on multiple plant species from at least four plant families (Fabaceae, Asteraceae, Orobanchaceae, Lythraceae).

Relative to other butterfly species I observed, *P. icarus* was the most abundant (mean abundance = 6 individuals (± 1.05 SE)) and reached extremely high densities (maximum abundance in one site-visit = 83 individuals; **Fig. S1.4**). The second most abundant species was the non-native European skipper (*Thymelicus lineola*) (mean abundance = 2 individuals (± 1.05 SE); maximum abundance in one site-visit = 79 individuals; **Fig. S1.4**). In comparison, native butterfly species never exceeded a mean abundance of 2 individuals or a maximum abundance of 29 individuals in one site-visit (**Fig. S1.4**). Interestingly, we observed no individuals of the more recently introduced European peacock (*Aglais io*).

1.4.1 Habitat suitability modelling

At a local-scale, the variables that best predicted *P. icarus* abundance were disturbance index (pseudo-R^2=0.37), the presence of *L. corniculatus,* and the proportional cover of grasses

(**Table 1.2**). *P. icarus* was most abundant at intermediate levels of disturbance (level 3: every 1-5 years (**Table 1.1**); χ^2=27.06, df=3, p<0.0001; **Fig. 1.4a**). *P. icarus* is predicted to be 20 times more abundant in sites with intermediate levels of disturbance (i.e., level 3) compared to low levels (i.e., level 1).

P. icarus was also more abundant where *L. corniculatus* was present (β=1.58 (0.40SE), χ^2=11.3, df=1, p<0.001; **Fig. 1.4b**) and where grass cover was lower (β=-3.50 (1.17SE), χ^2=9.75, df=1, p=0.002; **Fig. 1.4c**). Combined, the two plant variables explained 41% (pseudo-R^2) of the variation in *P. icarus* abundance. *P. icarus* is predicted to be 5 times more abundant where *L. corniculatus* is present compared to where it is absent (**Fig 1.4b**). In addition, *P. icarus* abundance is predicted to increase by a factor of 6 if grass cover is reduced from 50% to 0% (**Fig 1.4c**). Canopy cover and the mean proportional cover of bare ground and total flowers did not predict *P. icarus* counts (**Table S1.2**).

At a landscape-scale, the proportion of urban land and forest surrounding sites (pseudo-R^2= 0.45) best predicted *P. icarus* abundance (**Table 1.2**). Specifically, *P. icarus* was more abundant where the proportion of urban land cover was higher (β=2.81 (0.72SE), χ^2=11.05, df=1, p<0.001; **Fig. 1.5a**) and proportion of forest cover was lower (β=-2.56 (0.90SE), χ^2=6.97, df=1, p=0.008; **Fig. 1.5b**). The proportion of water in the surrounding landscape did not predict *P. icarus* abundance (**Table S1.2**).

1.4.2 Dispersal ability

Over the six weeks of my MRR study, 4629 *P. icarus* adults were captured and 103 were recaptured (2.2% recapture rate; **Table 1.3**). Females were observed less often than males: 23% of initial captures and 16% of recaptures were female (**Table 1.3**). There was no significant difference between males and females in terms of the mean distance dispersed (males: mean=78 m, females: mean=60 m; t=0.82, df=49, p=0.4). Only male *P. icarus* butterflies were detected to have flown longer distances (>350 m, n=4). Based on all observations, the mean, median and maximum distance dispersed was 75 m, 43 m, 862 m, respectively (n=103; **Fig. 1.6a**). When I only included observations that were > 20 m, the mean and median distance dispersed increased to 103 m and 60 m, respectively (n=73; **Fig. 1.6b**).

1.5 Discussion

Here I report the findings of the first investigation of the ecology of *P. icarus,* a newly introduced butterfly in Canada. I found that the level of local-scale habitat disturbance and landscape-scale urban cover were important in shaping the abundance of *P. icarus*. I also found that plant community characteristics, such as local-scale grass cover and landscape-scale forest cover, influenced its abundance. Finally, the presence of the preferred larval host plant of *P. icarus, L. corniculatus,* promoted its abundance.

1.5.1 Habitat suitability

P. icarus was most abundant at sites that were moderately disturbed. These sites had mostly small/young trees, mid-height vegetation (e.g., shrubs, grasses, forbs), and evidence of human traffic such as dirt/gravel paths, litter, construction materials, and hydro towers. This result suggests that sites with greater disturbance—either more recent (e.g. <1 year, any form of land clearing (e.g., buildings, construction)) and/or more frequent (e.g., annual/monthly mowing)—as well as sites with lower disturbance are less suitable for *P. icarus*. This hump-shaped pattern with the disturbance index has been observed for another non-native insect, the

Argentine Ant (*L. humile*; Vonshak and Gordon 2015). My finding that highly disturbed sites are less suitable for *P. icarus* is consistent with studies from its native range that report its occurrence is reduced where habitat management regimes are high in frequency (e.g., mowing, livestock grazing; Gutiérrez et al. 2001). However, I found that sites with low disturbance are less suitable for *P. icarus* which is not supported in the native range where its occurrence was found to be high in unmanaged lands (Gutiérrez et al. 2001). This discrepancy in the type of habitat that is suitable between the native and introduced range is most likely related to the presence of *L. corniculatus,* a non-native plant species in Canada, which tends to occur at disturbed sites in its introduced range (see further discussion below). However, this difference could also be related to the type, frequency, or severity of disturbance. Given that my measure of local-scale disturbance represented a combination of multiple aspects of disturbance, I am unable to tease apart their effects. As such, future work should consider the relative importance of different components of disturbance on *P. icarus* in its introduced range.

In my study, moderate local-scale disturbance likely benefited *P. icarus* by balancing the availability of its main food resource, *L. corniculatus,* and the amount of grass cover. First, *P. icarus* was more abundant where *L. corniculatus* was present. Consistent with other studies (Turkington and Franko 1980), the occurrence of this plant was dependent on disturbance index (p=0.048; **Fig. S1.1a**): *L. corniculatus* occurred most often in moderately disturbed sites. In fact, this plant was completely absent in my least disturbed sites (**Fig. S1.1a**). My results are consistent with the native range where *P. icarus* larvae strongly prefer *L. corniculatus* (Thomas and Lewington 1991; Tolman and Lewington 2008) and adults occur more frequently where this plant occurs or is more abundant (León-Cortés et al. 1999; Gutiérrez et al. 2001). As my study did not include larval surveys, more work is needed on *P. icarus* larvae to confirm whether disturbance promotes abundance via an increase in larval food resources or if a different mechanism is at play.

Second, *P. icarus* was most abundant where the proportional cover of grass was lower. Grass cover was lower in our least to moderately disturbed sites than in the most disturbed sites (χ^2=14.19, *p*=0.003; **Fig. S1.1b**). Since the proportional cover of grass and forb were negatively correlated in my study (Pearson r = -0.81), lower grass cover meant a higher cover of forbs, likely increasing the availability of herbaceous plants that *P. icarus* requires for both larval and adult feeding. However, I did not find an effect of forb cover or the number of total flowers on the abundance of *P. icarus*. It could be that more direct measurements of host plant availability (e.g., plant species identity/diversity, number of individuals, number of open flowers) may have increased my ability to detect an effect of herbaceous plants on *P. icarus* abundance. Alternatively, increased grass cover may reduce the amount of bare ground available, which could create cooler microclimates. Previous work has shown that a cooler microclimate reduces *P. icarus* flight activity in the native range due to its microhabitat use and behaviour (Howe et al. 2007), which could reduce the overall suitability of those sites. Nevertheless, my results suggest that sites with moderate disturbance, the presence of *L. corniculatus* and low grass cover are most suitable for *P. icarus*, and that other vegetation types (e.g., herbaceous host plants, nectar sources) may be required. Future studies should consider the role of microclimate in determining habitat suitability of *P. icarus* in the introduced range.

Anthropogenic disturbance in the surrounding landscape was also important in shaping *P. icarus* abundance. Specifically, *P. icarus* abundance increased with increasing proportional cover of urban land (e.g., cities, buildings, roads). This is inconsistent with studies from its native range which have found negative (Mersey Valley, UK; Hardy and Dennis 1999) and hump-shaped (Prague, CZE; Konvicka and Kadlec 2011) relationships with the amount of urban land cover. As stated previously, discrepancies between the native and introduced ranges could be related to the presence of *L. corniculatus* which tends to occur in disturbed areas in Canada. However, it could also reflect greater tolerance of *P. icarus* in the introduced range to conditions in urban landscapes, differences in how studies define urban land cover (e.g., residential vs. industrial), or the spatial scale of the study, as the relative importance of factors can change with scale. Studies from the native range were conducted at a smaller spatial scale than ours and only at a single scale (Hardy and Dennis 1999; Konvicka and Kadlec 2011).

Urbanization could positively influence *P. icarus* in its introduced range through several mechanisms. Urban areas can have higher diversity of non-native plant species than natural areas (Pyšek et al. 2010; Potgieter et al. 2017), which could benefit *P. icarus* whose primary host plant is non-native in Canada. Urban areas can also alter microclimates by raising ambient temperatures (i.e., urban heat island effect; Oke 1973) which could favour insects like *P. icarus* by increasing their developmental and reproductive rates (Raupp et al. 2010). Overall, urban areas may provide habitat that is conducive to the establishment and proliferation of *P. icarus* in Canada, but more work is needed to elucidate the specific mechanisms.

In contrast to urban land cover, the proportion of forest cover had a negative effect on *P. icarus* abundance, suggesting that forests represent unsuitable habitat (i.e., ‘matrix’; Ricketts 2001). This pattern is consistent with observations in its native range where it is considered a grassland species and is most commonly found in dunes, calcareous grasslands, roadsides, and waste places (Emmet and Heath 1989; van Swaay 2002), not in woodlands. Forests in the surrounding landscape likely act as a barrier and could hamper the ability of *P. icarus* to travel between patches of suitable open habitat. Future studies could determine the effective isolation of habitat surrounded by forest cover by measuring dispersal distances of *P. icarus* adults in heavily forested landscapes.

1.5.2 Dispersal ability

Based on my MRR study (mean and median distances dispersed were 75 m and 43m, respectively), *P. icarus* is a low to moderate disperser relative to other butterfly species. In a review of 46 MRR studies of non-migratory butterflies of various sizes, the majority of species (57%) had a mean dispersal distance of less than 200 m, but estimates varied from just 23 m in the Tailed copper (*Lycaena arota*) to 600 m in the Common alpine (*Erebia epipsodea*) (Sekar 2012). Using less precise methods than MRR (i.e., tracking eggs), Jones et al. (1980) measured the dispersal range of non-native Cabbage white butterflies (*Pieris rapae*) to be 250-600 m. Overall, my results suggest that *P. icarus* has a low ability for dispersal relative to other butterfly species.

My estimates of the dispersal ability of *P. icarus* in its introduced range show both similarities and differences to estimates from its native range. Qualitative studies in the native range have described *P. icarus* as forming closed populations where individuals, especially females, tend to remain in natal breeding grounds (Thomas 1984; Emmet and Heath 1989; Thomas and Lewington 1991). These behavioural descriptions are similar to my findings that *P. icarus* tends to disperse short distances (82% of observations <100 m). However, I did not find differences between sexes. As my estimate of female dispersal was less precise than of males, a larger sample size is needed to determine if females disperse shorter distances than males in the introduced range. My estimates for mean (75 m) and maximum (862 m) dispersal are lower and higher, respectively, than estimates obtained in the native range (**Table S1.3**; Gutiérrez et al.

2001; Kuussaari et al. 2014). It is unclear whether there are actual differences in the dispersal ability between the native and introduced range, or whether it is because there are methodological differences across studies (**Table S1.3**). Dispersal measurements can be sensitive to study design (Shreeve 1992; Schneider 2003) as evidenced by my sensitivity analysis. Nevertheless, *P. icarus* seems to be a low-moderate disperser across both its native and introduced ranges.

My recapture rate (2.2%) was low given that the butterflies did not disperse far between captures and in comparison to other MRR studies measuring butterfly dispersal (e.g., depending on the species: 4-41% Ricketts 2001, 2-43% Kuussaari et al. 2014). It could be that the time between revisits was too long (~weekly) relative to their lifespan (i.e., individuals died before I could recapture them), however, their lifespan is uncertain. The longest time I recorded between captures was 11 days, but this was only based on 103 recaptured individuals. It could also be that the extremely high densities of *P. icarus* adults in my MRR study region had a dilution effect making it difficult to recapture marked individuals. For instance, I captured and marked 4629 *P. icarus* adults in just 6 weeks, while Ricketts (2001) captured 1039 individuals of the same species in its in native range in 10 weeks. Regardless, my recapture rate is still comparable to some previous butterfly MRR studies.

1.5.3 Implications & conclusions

My results have implications for habitat management/restoration and predicting range expansion. First, my finding that *P. icarus* abundance was lower in grassier sites suggests that disturbed habitats could be restored with grass mixes to prevent the establishment of this non-native butterfly or reduce its abundance. Preserving forest fragments could also be an effective management strategy given the negative correlation I observed between forest cover and *P. icarus* abundance. However, I note that negative impacts of *P. icarus* on native biota have not been assessed so the degree of management and restoration needed is uncertain. Second, my study can inform future modelling efforts aimed at predicting range expansion. For example, the associations between *P. icarus* abundance and landscape composition reported here could be used to determine where range expansion is most likely to occur (i.e., in more urbanized landscapes with lower forest cover). These predictions could then be used to prioritize areas for control or assess potential negative impacts on native biota.

While my results suggest that *P. icarus* is limited by the local-scale availability of its larval host, *L. corniculatus*, this plant species is widespread across Canada (Zandstra and Grant 1968; Turkington and Franko 1980) and thus may not limit future range expansion of *P. icarus*. Instead, range expansion may be constrained by the low to moderate dispersal ability of *P. icarus* adults. Still, range expansion could be facilitated by rare long-distance dispersal events and spill-over effects due to the extremely high densities of *P. icarus* individuals. Indeed, *P. icarus* has recently colonized sites in Toronto, Ontario (eButterfly 2020), over 400 km away from my study region. This could be the result of rare natural long-range dispersal, human-mediated dispersal via transport pathways, or independent introductions from Europe. Human-mediated long-range dispersal via highways has been implicated in the range expansion of another non-native insect in the U.S.: the Emerald ash borer (*Agrilus planipennis*; Muirhead et al. 2006). Future studies could use genetic analyses (e.g., Ficetola et al. 2008) to determine the geographic origin, number of introductions, and genetic diversity of Canadian populations *P. icarus*.

Overall, I found that anthropogenic disturbance at two spatial scales is an important determinant of *P. icarus* habitat suitability in Montréal, Canada. Building on this initial assessment of the ecology of *P. icarus,* modelling the trajectory of range expansion across Canada is needed. Further investigation into additional potential range-constraining factors (e.g., microclimate), especially larval preferences, would also be helpful.

Tables

Table 1.1. Criteria for assigning a qualitative index of local-scale habitat disturbance to each site that combined observations about approximate time since disturbance and severity of disturbance. Shown are the four indices of disturbance and their corresponding type/age of vegetation, evidence of human traffic, and examples.

	Level 1 Low	Level 2 Low-Mid	Level 3 Mid-High	Level 4 High
Approximate time since last disturbance	>15 years	5-15 years	1-5 years	<1 year
Type/age of vegetation	Numerous large/tall trees, high vegetation height	Numerous trees with a mix of large/tall and small/short, high vegetation height	Some trees that are mostly small/short, mid-length vegetation height	Few to no trees that are mostly small/short, short vegetation height
Evidence of human traffic	No evidence	Trampled vegetation, dirt paths, remnants of buildings or stone fencing	Dirt or gravel paths, litter, construction materials, hydro towers	Paved paths, litter, parking lots, buildings, hydro towers, benches, playgrounds
Examples	Natural meadow, forest clearing	Semi-natural meadow, abandoned farmstead, low traffic nature trail	Abandoned commercial lot, unmowed hydro field, high traffic nature trail	City park, roadside, residential lawn, mowed areas

Table 1.2. Results of local- and landscape-scale habitat suitability models for European Common Blue butterflies (*Polyommatus icarus*) using generalized linear models with a negative binomial distribution (*n*=44 sites). Shown are pseudo-R^2 values for all models and results from likelihood ratio tests (type II anova) including chi-square statistics (χ^2), degrees of freedom (df), and *p*-values. Model coefficients and standard errors are also shown where applicable.

Scale	Model	Model R^2	Term	Coefficient	Standard Error	χ^2	df	*p*-value
Local	Disturbance	0.37	Disturbance Index	N/A	N/A	27.06	3	<0.0001
	Plant	0.41	Bird's Foot Trefoil, *Lotus corniculatus*	1.58	0.40	11.30	1	<0.001
			Grass	-3.50	1.17	9.75	1	0.002
Landscape	N/A	0.45	Urban	2.81	0.72	11.05	1	<0.001
			Forest	-2.56	0.90	6.97	1	0.008

Table 1.3. Results of the mark-release-recapture study conducted on European Common Blue butterfly (*Polyommatus icarus*) adults at 15 semi-disturbed sites in St. Bruno-de-Montarville, Quebec. Values shown include number of marked individuals, numbers of recaptured individuals, recapture ratio (%), maximum dispersal distance (m), and mean dispersal distance (m) for males and females.

	Marked Individuals	Recaptured Individuals	Recapture Ratio (%)	Maximum Distance (m)	Mean Distance (m)
Female	1060	16	1.5	227	60
Male	3569	87	2.4	862	78
Total	*4629*	*103*	*2.2*	*862*	*75*

Figures

Figure 1.1. Photograph (by S. Rivest) of two European Common Blue butterflies (*Polyommatus icarus*) including a male (left) and female (right) perched on a dried flower in Montréal, Quebec.

Figure 1.2. Maps of the study region. (a) Occurrence records (n=204 sightings) of European Common Blue butterflies (*Polyommatus icarus*), shown by red dots, in eastern Ontario and western Quebec, Canada from eButterfly (eButterfly 2020) as of 2017 when this study began. The cities of Ottawa, Ontario and Montréal, Quebec are represented by yellow diamonds. (b) Location of sites (n=44 sites), shown by red dots, used for the local- and landscape-scale habitat suitability modelling centered in Montréal, Quebec overlaid on a 30 m resolution 2015 land cover map (Canada Centre for Remote Sensing 2015). (c) Close-up view of one focal site showing the two sampling areas used in our local- (inner red square, radius 30 m) and landscape-scale (outer red ring, radius 400 m) analyses. (d) Location of sites (n=15 sites), shown by red dots, used for the mark-release-recapture study conducted in St. Bruno-de-Montarville, Quebec and an indication of their area (size of red dot). Maps were created using R 3.5.3 (R Core Team 2019) and google maps.

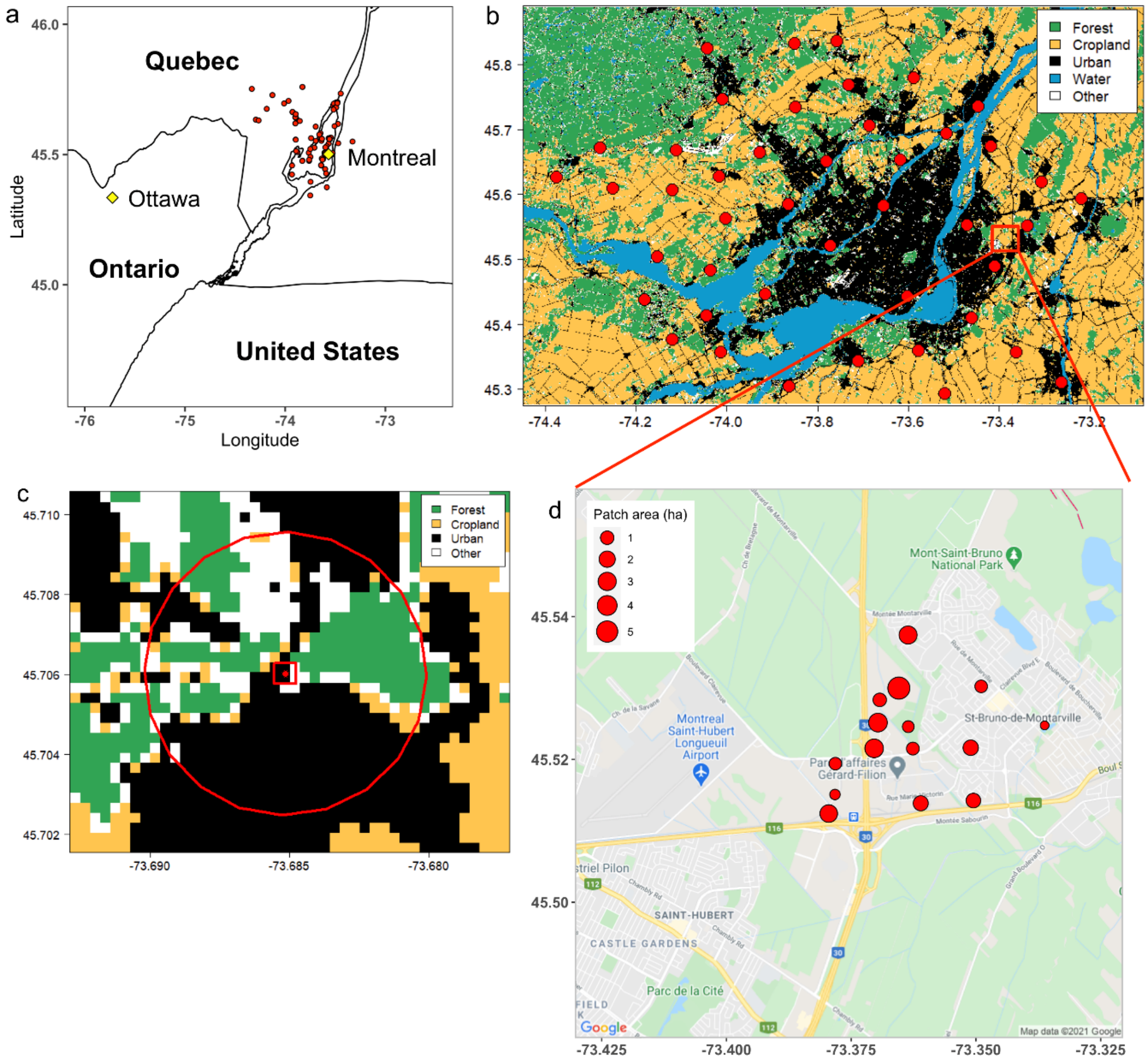


Figure 1.3. Photographs (by S. Rivest) of field sites spanning a gradient of disturbance (level 1-4) based on a qualitative assessment of the site (see **Table 1.1**). Shown are: (a) site 28 on August 11th, 2017; (b) site 10 on June 4th, 2017; (c) site 40 on June 22nd, 2017; (d) site 30 on August 25th, 2017; (e) site 14 on June 15th, 2017; (f) site 45 on July 20th, 2018; (g) site 25 on August 1st, 2017; (h) site 39 on August 29th, 2017.

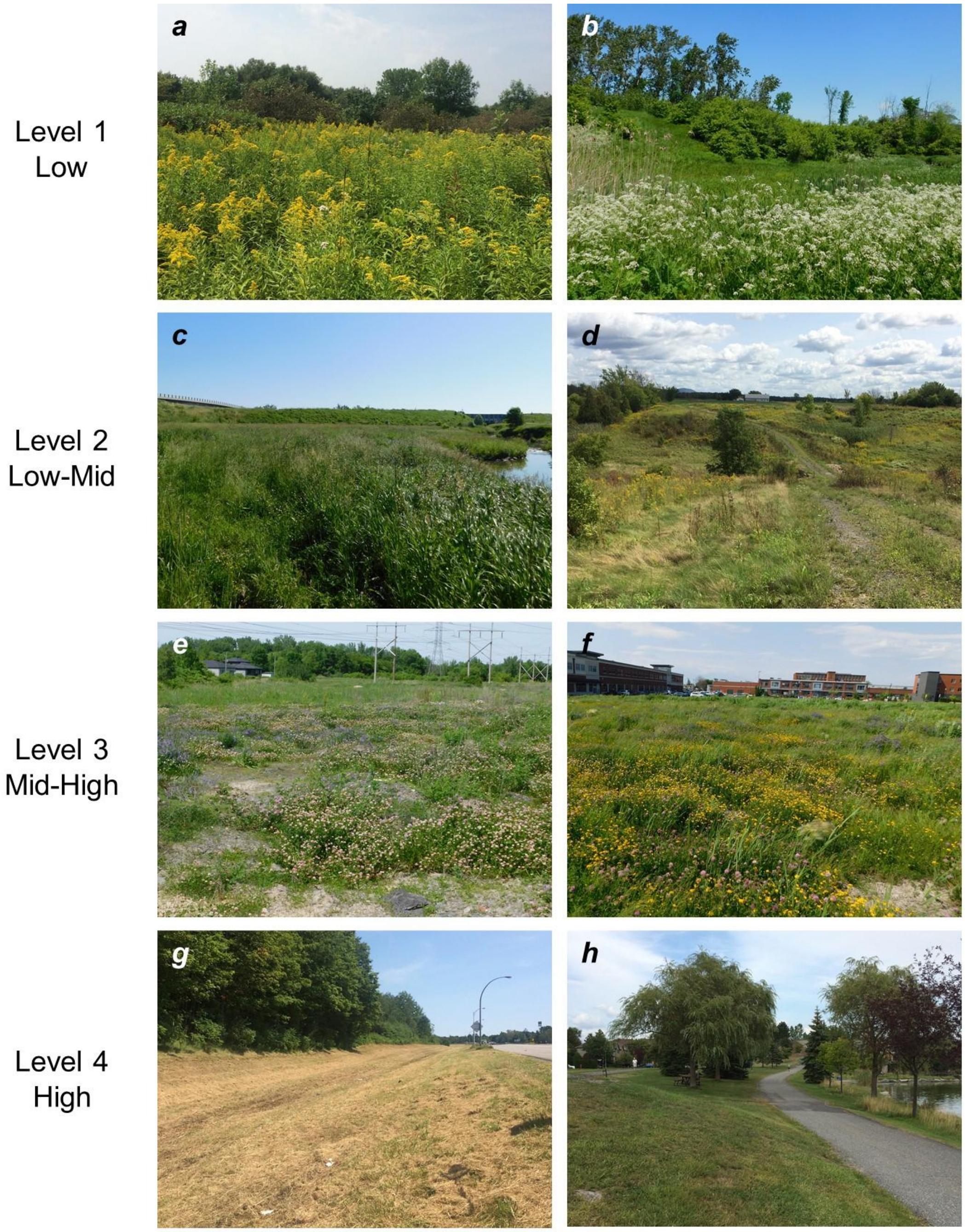


Figure 1.4. Effects of local-scale habitat factors on the abundance of European common blue (*Polyommatus icarus*) butterflies using generalized linear models with a negative binomial distribution (n=44 sites). The relationship between *P. icarus* abundance and local-scale (a) disturbance index, (b) bird's foot trefoil (*Lotus corniculatus*) occurrence, and (c) proportional cover of grasses. Shown are the mean predicted values (grey bars; a, b) or predicted line of best fit (black solid line; c) and 95% confidence intervals (error bars (a, b) and broken lines (c)). Raw data (solid circles) have been jittered in panels a and b to increase visibility. Lowercase letters in panels a and b represent significant (p<0.05) pairwise comparisons. For details on the meaning of disturbance indices refer to **Table 1.1**.

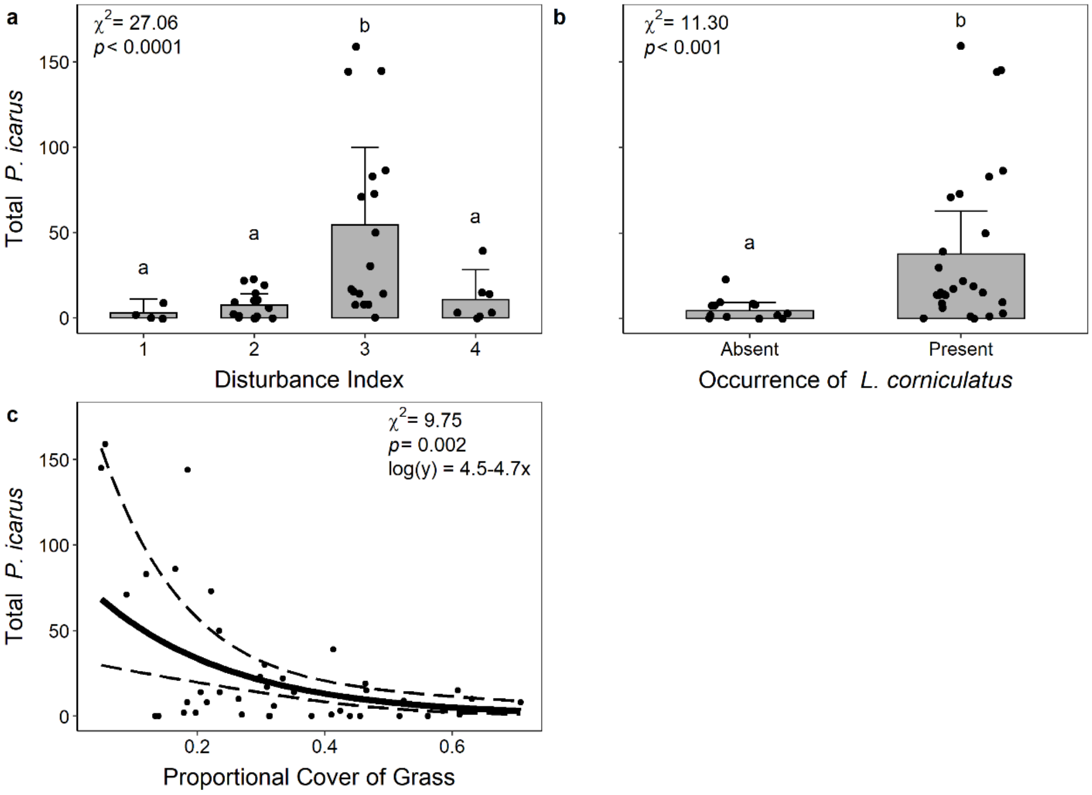


Figure 1.5. Effects of landscape-scale habitat factors on the abundance of European common blue (*Polyommatus icarus*) butterflies using generalized linear models with a negative binomial distribution (n=44 sites). The relationship between *P. icarus* abundance and (a) proportional cover of urban land and (b) proportional cover of forest. Shown are the predicted lines of best fit (solid line), 95% confidence intervals (broken lines), and raw data (solid circles).

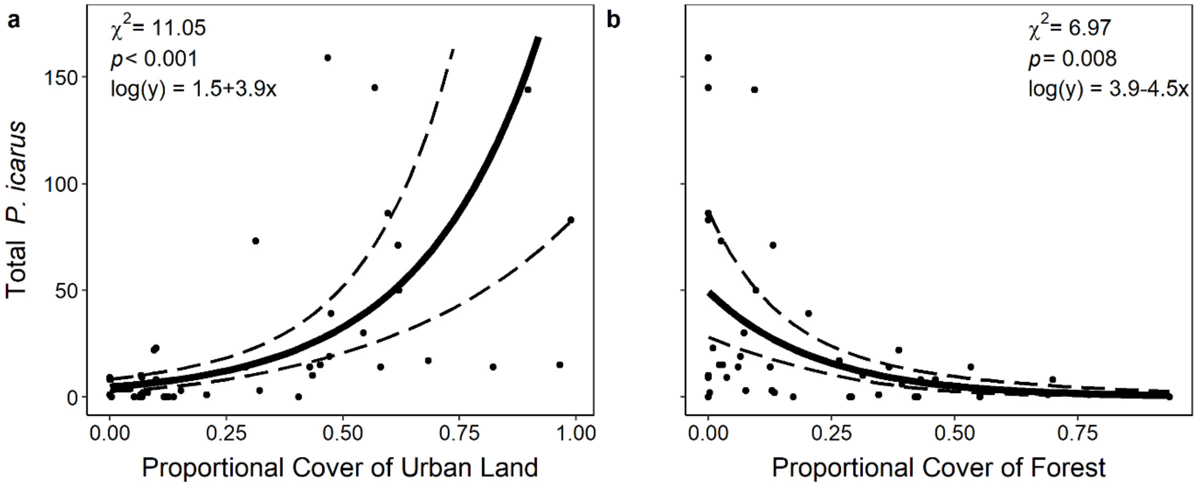
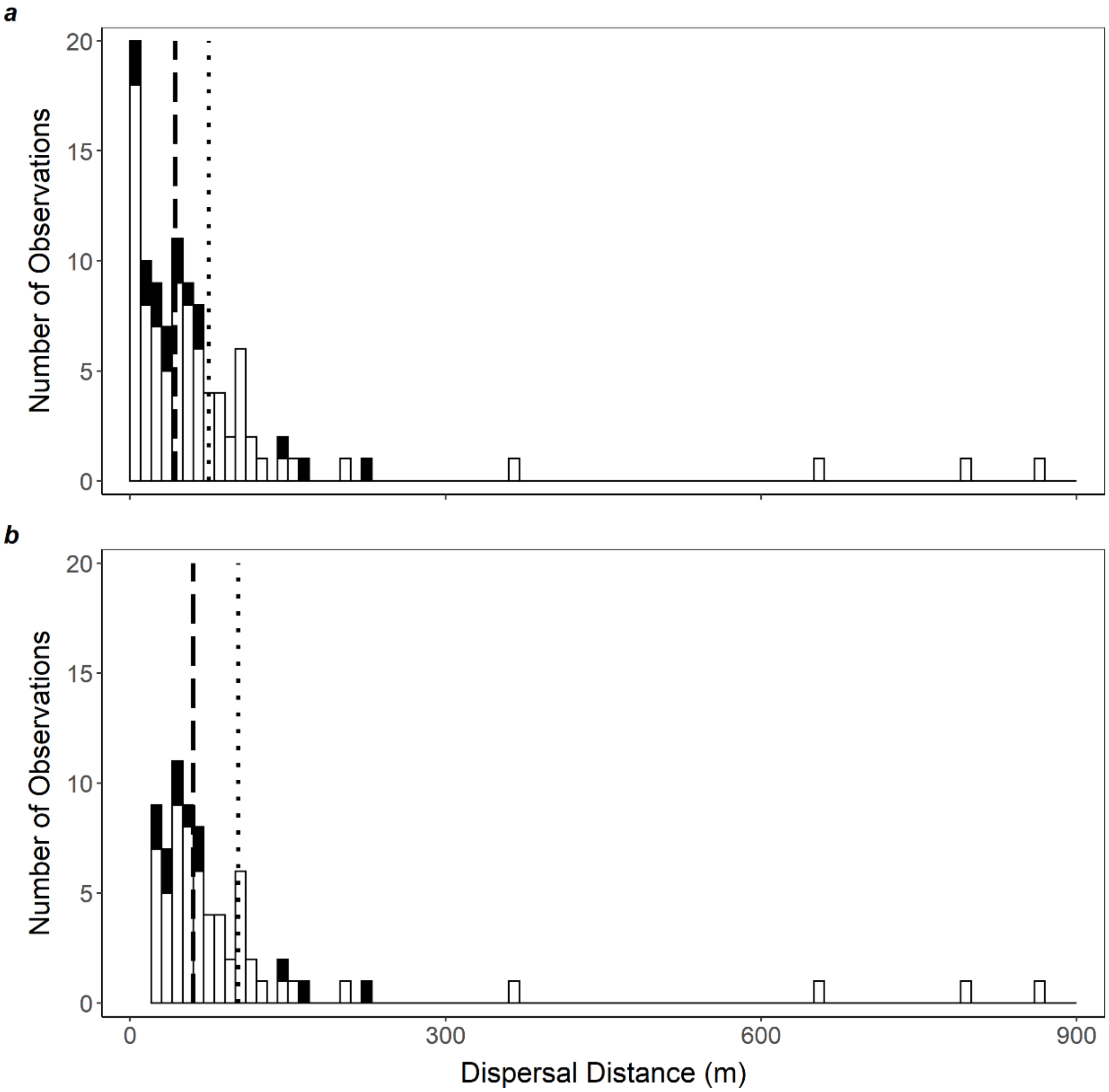


Figure 1.6. The distribution of dispersal distances (m) for European common blue (*Polyommatus icarus*) butterflies (total: n=103; female: n=16; male: n=87) based on a mark–release–recapture study conducted in 2018 at 15 sites in St. Bruno-de-Montarville, Quebec, for (a) all observations or (b) only observations >20 m. The median (broken vertical line) and mean (dotted vertical line) dispersals are also shown.



II. A few winners replace many losers: urbanization leads to taxonomic and functional homogenization of butterfly communities in Montréal, Quebec

My contributions to this thesis chapter are the conceptions of ideas, design of methodologies, data collection, data analysis, writing, and editing.

2.1 Abstract

Urbanization is on the rise globally, driving many conservation biologists to examine its effects on ecological communities. While changes in butterfly community structure in response to urbanization have been well studied, less is known about whether urbanization favours species with specific traits (i.e., functional dominance) or if this can lead to biotic homogenization. Urbanization-driven biotic homogenization has been reported for taxa such as birds and plants, but similar work for butterflies is lacking. Here, I examine patterns of change in the composition of butterfly communities in response to urbanization by conducting field surveys in 44 sites spanning an urbanization gradient in Montréal, Quebec, Canada and test the hypothesis that urbanization leads to taxonomic and functional homogenization. I found that there were clear shifts in the structure of urban butterfly communities in favour of a few, highly abundant, non-native species. These shifts were driven by losses of native species richness and abundance combined with increases in non-native species abundance, resulting in taxonomic homogenization. I also found evidence for reduced variation in butterfly wingspan, resulting in functional homogenization for this trait. Lastly, I show that there were no trends in functional dominance for three key traits (wingspan, voltinism, and larval diet breadth) in response to urbanization for most of the butterfly community. Together, my results indicate that urban areas support less diverse butterfly communities than surrounding areas and that native species should be the focus of future conservation efforts. Since urban areas are growing worldwide, documenting biotic homogenization in cities will be important to better understand what type of insect communities exist in cities and how best to support them.

2.2 Introduction

Urbanization, the process of conversion of natural and semi-natural land into impervious surfaces (e.g., roads, buildings; Johnson and Munshi-South 2017), is on the rise globally, driving many conservation biologists to examine its effects on ecological communities. Currently, over half of the global human population, and 87% of Canadians, live in urban areas and this is projected to increase over the next several decades (Statistics Canada 2017; United Nations 2019). Urbanization results in habitat loss and fragmentation (McKinney 2002b; Liu et al. 2016), driving biodiversity declines worldwide (Czech et al. 2000; McKinney 2008; Faeth et al. 2011; Elmqvist et al. 2016). However, green spaces within cities (e.g., parks, gardens) have the potential to harbour diverse biological communities and, in some cases, can be an opportunity to support threatened or endemic species (Aronson et al. 2014; Ives et al. 2016). It is therefore essential to understand how biodiversity is influenced by urbanization to better inform policy, management, and urban planning.

The documented effect of urbanization on butterfly community structure is generally negative. Butterfly richness and abundance are most frequently reported as decreasing with urbanization (Stefanescu et al. 2004; Lizée et al. 2011; Olivier et al. 2016; Dylewski et al. 2019; Merckx and Van Dyck 2019; Kuussaari et al. 2021), a result which is supported by a recent global meta-analysis (Ramírez-Restrepo and MacGregor-Fors 2017). However, some studies have reported peaks in butterfly richness and/or abundance in areas of moderate urbanization (e.g., suburbs) (Blair and Launer 1997; Hogsden and Hutchinson 2004) or found that certain species can reach extremely high densities in cities (Shapiro 2002; Williams 2009; Ramírez-Restrepo and Halffter 2013). These findings suggest that not all butterfly species are impacted by urbanization in the same way, hampering our ability to effectively inform conservation actions in cities.

One process that has not been well studied in urban butterfly communities is biotic homogenization (Ramírez-Restrepo and MacGregor-Fors 2017). This occurs when communities increase in similarity over time or space, typically due to species invasions and/or native species extirpations (*sensu* McKinney and Lockwood 1999). It can occur at the taxonomic level as a decrease in β-diversity and at the functional level if the losses and gains of species are related to the roles and/or traits of those species (Olden and Rooney 2006). Both processes can lead to redundancies in either species identities or individuals with the same functional forms or traits (Olden and Rooney 2006).

Urbanization-driven biotic homogenization occurs when biological communities in cities become more similar to each other than communities in rural or natural areas (McKinney 2002b, 2006). Studies documenting urbanization-driven biotic homogenization for plants and birds are fairly common (e.g., McKinney 2006; Marcacci et al. 2021), yet there has been relatively little research done on insects such as butterflies (Lokatis and Jeschke 2022). To my knowledge, only one previous study has appropriately evaluated biotic homogenization in urban butterfly communities (Merckx and Van Dyck 2019). This study identified functional homogenization by evaluating whether there were declines in interspecific trait variation within communities. Thus, it remains unclear whether urbanization leads to the taxonomic and functional homogenization of butterfly communities.

If urbanization drives functional homogenization of butterfly communities (i.e., reduced variation in a trait), then this may result in certain types of species being favoured in urban areas based on their traits (i.e., functional dominance). For example, some studies have shown that butterflies with increased body size and/or wingspans, factors known to be correlated with butterfly dispersal ability (Sekar 2012), are more common in urban areas (Merckx et al. 2018; Merckx and Van Dyck 2019; Kuussaari et al. 2021). This is because dispersal ability is thought to mitigate against habitat or resource fragmentation (Cote et al. 2017), a common feature of urban areas (Liu et al. 2016). Species with higher reproductive capacities may also be favoured in urban areas because they are expected to be more resilient to perturbations like habitat degradation (McKinney and Lockwood 1999). Studies evaluating the number of generations per year (i.e., voltinism), a proxy for butterfly reproductive capacity (Altermatt 2010), have generally found support for this prediction (Blair and Launer 1997; Hogsden and Hutchinson 2004; Niell et al. 2007; Lizée et al. 2011). Lastly, butterflies whose larvae are diet generalists may be more common in urban areas than specialists since they are most likely to be able to exploit urban plant resources (Blair and Launer 1997; Hogsden and Hutchinson 2004; Niell et al. 2007; Lizée et al. 2011), but see Merckx and Van Dyck (2019). Most past work evaluating the influence of urbanization on the dominance of traits within butterfly communities has been conducted in Europe, with fewer studies from North America, and only one study also evaluated functional homogenization (Merckx and Van Dyck 2019).

In this chapter, I investigate patterns of change in butterfly community composition in response to urbanization by conducting field surveys across Montréal, Quebec, Canada. Specifically, I evaluate whether urbanization leads to (1) negative effects on the components of α-diversity (richness, abundance, evenness); (2) taxonomic-; and (3) functional homogenization; and (4) functional dominance for three key traits. To identify taxonomic and functional homogenization, I tested for declines in β-diversity and community-weighted standard deviations for three traits (wingspan, voltinism, larval diet breadth) across the urban gradient, respectively.

To evaluate functional dominance in each trait, I tested for predicted patterns in community-weighted means in these same three traits across the urban gradient. I predict that urban habitats will favour butterflies with larger wingspans, increased voltinism, and that are larval diet generalists. I consider ‘functional' in the sense that these traits impact fitness by influencing a species’ response to environmental change, rather than a species’ role in ecosystem function per se (Wong et al. 2019).

2.3 Methods

2.3.1 Study area

This study was conducted in the Greater Montréal region (82 municipalities within 4604 km^2; Statistics Canada 2017) of Quebec, Canada in 2017 and 2018. This region is characterized by mainly urban and agricultural land, but also includes remnant patches of mixed wood forests and an extensive system of waterways (Wiken 1986). Montréal is the second largest city in Canada with over 4 million inhabitants (Statistics Canada 2017). Most of the population lives on Montréal Island, with relatively lower density settlements in the surrounding municipalities. These surrounding areas have seen the largest gains in population size since 1966, signifying a general migration from the downtown core to the suburbs (Dupras et al. 2016). Indeed, urban sprawl (i.e., measure of built-up area, dispersion, and built-up area/inhabitant) in Montréal has been continuously accelerating since 1951 (Nazarnia et al. 2016).

2.3.2 Site selection

Field surveys were conducted in the same sites used for **Chapter 1** of this thesis. Thus, I examined butterfly communities in 44 sites of open grassland habitat that spanned an urban gradient in Montréal, Quebec (**Fig. 1.2**; **Fig. 2.1**). To select sites that varied in the amount of urbanization, I visually assessed surrounding land cover using satellite imagery and local site features (e.g., evidence of human presence). Rural sites were often situated within landscapes that had a mix of agricultural land, forest fragments, and smaller human settlements. Whereas urban sites were typically located closer to denser human settlements (e.g., suburbs, apartments), commercial buildings, and industrial areas. Thus, none of my sites were completely unaffected by human activities (e.g., nature preserves). Sites were located at least 7 km apart and were visited 3-4 times from May to August in 2017 (n=39 sites) or 2018 (n=5 sites). Additional sites were selected in 2018 to increase the number of urban sites that were surveyed. For example, at the 300 m scale, most sites surveyed in 2017 (69%; 27/39) had less than 50% urban cover in the surrounding landscape.

2.3.3 Butterfly surveys

To estimate species richness and abundance, I used the transect walk method which is a standardized protocol used in many butterfly monitoring schemes around the world (Pollard and Yates 1993; Thomas 2005; van Swaay et al. 2008). During each site-visit, two observers walked a spatially fixed 300 m long route, divided into five separate transects of 60 m each arranged side by side 15 m apart (i.e., approximate square 60 m 60 m). In addition to *P. icarus* butterflies counted for **Chapter 1** of this thesis, observers also identified and counted all other butterfly species that flew within 5 m in front of them or on either side. Transects were walked at a consistent speed of 10 m/min. Following standard protocols (e.g., Pollard and Yates 1993), surveys were conducted only when butterflies were fully active: 9 am to 4 pm, temperatures of 13-40°C or > 17°C when cloud cover exceeded 75%, wind below 30 km/h, and no rain.

2.3.4 Trait data

To evaluate the role of traits in mediating the effects of urbanization, I collected information on butterfly traits from a variety of previously published sources (**Table S2.1**). Mean butterfly wingspan was based on measurements of specimens from across the species' Canadian range from the Canadian National Insect Collection maintained by Agriculture and Agri-Food Canada and was obtained from (Layberry et al. 1998). Voltinism was measured as the mean number of generations per year across the species' Canadian range (Layberry et al. 1998; Kharouba et al. 2014). Larval diet breadth was scored from 1 to 5 based on whether larvae were known to feed on (1) one plant species, (2) one plant genus, (3) one plant family, (4) one plant order, or (5) multiple plant orders within its Canadian range (Layberry et al. 1998; Douglas and Douglas 2005; Wagner 2005; Brock et al. 2006). Trait data for the European Common Blue (*Polyommatus icarus*), a newly introduced species in Canada, was compiled from studies conducted in both the native (Thomas and Lewington 1991; Nygren et al. 2008) and introduced ranges (Rivest and Kharouba 2021).

2.3.5 Landscape data

To quantify the amount of urbanization in the landscape surrounding the sites, I used a 30 m resolution 2017 land cover map (Agriculture and Agri-Food Canada 2017) (**Fig. 2.1**). I aggregated land cover classes to represent eight major types: urban, forest (three classes: needleleaf, broadleaf, and mixed), crops (30 classes), wetland, grassland, shrubland, and water (i.e., lakes and rivers). Urban areas were defined as built-up or developed land used for human infrastructure like roads, buildings, and industrial sites. I calculated the proportional cover of each land cover type in circular buffers of varying radii (i.e., spatial scales) surrounding my sites (see **Statistical analysis**). Depending on the spatial scale, the proportion of urban cover surrounding sites varied. For example, at the 300 m scale mean urban cover was 0.39 (range=0–1) whereas at the 2600 m scale mean urban cover was 0.36 (range=0–0.85).

2.3.6 Statistical analysis

(i) Overall approach

I structured the analysis into four sections and fit a series of models within each section. First, I analyzed changes in the components of α-diversity (species richness, abundance, and evenness) across the urban gradient. Second, I tested whether these changes led to taxonomic homogenization in urban areas by analyzing β-diversity in urban sites compared to rural sites. Third, I tested whether urbanization led to functional homogenization by analyzing community-weighted standard deviations for three traits (wingspan, voltinism, larval diet breadth) across the urban gradient. Lastly, to evaluate overall functional dominance, I analyzed changes in community-weighted means for the same three traits across the urban gradient.

Model fitting followed the same approach in all sections. Where data met the assumptions of normality and homoscedasticity, I used linear models (LM); otherwise, I used generalized linear models (GLM). I tested for an effect of year in all models by comparing Akaike Information Criterion (AIC) and included it as a covariate when it improved model fit (i.e., $\Delta AIC<2$; Burnham & Anderson 1998). I explored potential non-linear effects of covariates by visually checking plots and comparing AIC with models where covariates had linear fits. Final models were validated by visually assessing residual plots. For GLMs, residual plots were produced using the package DHARMa which uses a simulation based approach to produce scaled residuals (between 0 and 1) that are readily interpretable for generalized models (Hartig 2018). Spatial autocorrelation was evaluated using Moran’s I tests (Hartig 2018). To evaluate the contribution of covariates to model fit, I used likelihood ratio tests (type II ANOVA). All statistical analyses were performed using R 4.2.0 (R Core Team 2022).

Since spatial scale is central to determining associations between species and their environment (Levin 1992; Brennan et al. 2002; Mayor et al. 2009), I used a multi-scale approach to determine the scale at which species–landscape relationships were strongest (Martin and Fahrig 2012; McGarigal et al. 2016; Miguet et al. 2016). This meant that I fit all models at scales between 100 m and 5000 m at intervals of 100 m (i.e., 49 scales). I compared models at these different scales using AIC where best-fitting models were those that were most parsimonious (i.e., lowest AIC). I found that the relationships with urban cover were best explained at the following scales: species richness=2600 m, total abundance and voltinism=300 m, mobility and wingspan=200 m, and larval diet breadth=100 m (**Fig. S2.1**). All analyses were conducted at these scales.

(ii) Components of α-diversity

To evaluate changes in butterfly community structure across the urban gradient, I first combined butterfly observations across visits for each site (n=44 sites). I calculated species richness and total abundance for three groups: the entire community, only native species, and only non-native species (vegan package; Oksanen et al. 2019). I also calculated evenness for the entire community using the commonly used measure (e.g., Tu et al. 2020): Pielou’s J, or Shannon’s evenness, which is taken as the ratio between Shannon’s diversity index (H’) and the maximum possible diversity if all species were equally abundant (H’ max) (Pielou 1966). This index ranges from 0 to 1, with 1 indicating complete evenness (i.e., abundance evenly distributed amongst species) (Pielou 1966).

To analyze changes in richness and abundance across the urban gradient, I fit GLMs with the proportional cover of urban land surrounding sites as a predictor. I analyzed species richness (discrete count; >0) using GLMs fit with the poisson probability distribution from the MASS package (Venables and Ripley 2002). Total abundance (discrete count; >0) was overdispersed (mean:variance = 1:48), so I used GLMs fit with the negative binomial probability distribution which has been shown to be the best approach for overdispersed count data (Welsh et al. 2000). For both models, I included the number of visits to sites as a covariate to account for variation in the number of times that a site was surveyed.

To analyze changes in evenness (continuous; [0,1]) across the urban gradient, I fit GLMs with the beta probability distribution from the packages gam and mgcv (Wood 2011; Hastie 2019) with the proportional cover of urban land surrounding sites as a predictor. Since evenness sometimes took on the value of one but the beta distribution assumes values in the open interval (0,1), I rescaled the values by applying the transformation: $y'=(y*(n-1)+0.5)/n$, where n is the sample size (Smithson and Verkuilen 2006).

(iii) Taxonomic homogenization

To determine whether butterfly communities are taxonomically homogenized in urban areas relative to rural areas, I first divided sites into two groups according to the proportion of urban cover surrounding sites in a 300 m radius: urban (≥ 50% urban, n=16 sites) and rural (< 50% urban, n=28 sites). I chose 300 m since this was the spatial scale where butterfly abundance was best modelled (**Fig S2.1**). Within each group, I calculated Bray-Curtis dissimilarity indices (i.e., β-diversity) for all pairwise site comparisons based on abundance (Bray and Curtis 1957) using the package vegan (Oksanen et al. 2019). The Bray-Curtis index ranges from 0 to 1 and represents the proportion of the total abundance that is different between two communities (i.e., low β-diversity, high homogenization). Many metrics for β-diversity exist, but Bray-Curtis is desirable because it is more robust to potential sampling errors than other indices (e.g., Sorenson, Simpson) when abundance data is available (Schroeder and Jenkins 2018).

To test for changes in β-diversity (continuous; [0,1]) between urban site comparisons and rural site comparisons, I used GLMs fit with the beta probability distribution from the packages gam and mgcv (Wood 2011; Hastie 2019) with the site grouping (rural vs. urban) as a predictor. I included the distance between sites as a covariate to account for decreasing similarity between biological communities with distance and tested for a two-way interaction between the covariates.

(iv) Functional homogenization

To determine whether butterfly communities are functionally homogenized in urban areas relative to rural areas, I first calculated community-weighted standard deviations for wingspan, voltinism, and larval diet breadth based on species’ abundances at each site (n=44 sites). To test for declines in the community-weighted standard deviations across the urban gradient, I fit LMs with the proportional cover of urban land surrounding sites as a predictor. For these trait-level calculations, I excluded butterflies for which reliable data was not available (n=3 genera). For example, *Colias* spp. was only identified to genus in the field and was thus excluded.

(v) Functional dominance of traits

To evaluate trends in the dominance of functional traits across the urban gradient, I calculated community-weighted means for wingspan, voltinism, and larval diet breadth based on species' abundances at each site (n=44 sites). This metric indicates the overall dominance of a trait within a community (e.g., Roscher et al. 2012; Merckx and Van Dyck 2019). As above, I excluded butterflies without reliable trait data.

To analyze changes in trait means across the urban gradient, I fit a combination of LMs and GLMs with the proportional cover of urban land surrounding sites as a predictor. Mean butterfly wingspan and voltinism (continuous) were analyzed using LMs, but wingspan was log 10 transformed to help achieve normality. Mean larval diet breadth (continuous) was highly skewed and transformations did not help achieve normality, so I fit GLMs with the gamma probability distribution and the log link from the packages gam and mgcv (Wood 2011; Hastie 2019). Spatial autocorrelation was detected for the mean larval diet breadth model, so I included geographical coordinates using splines as a trend-surface (Dormann et al. 2007; Wood 2011).

2.4 Results

I observed a total of 2794 butterflies from 42 species across the two years of surveys (for results by year, see **Table S2.2**). Per site, mean species richness was 9.5 (range=4–17), median species richness was 9 (range=4–17), mean abundance was 63.5 (range=5–202), and median abundance was 44 (range=5–202). Only three non-native species occurred in the area, but they had a combined abundance of 1642 individuals (59%) (**Fig. S2.2**). The most common and abundant species was non-native *P. icarus* which I observed 1128 times in 80% of sites (35/44).

2.4.1 Components of α-diversity

Urban habitats supported a few, highly abundant butterfly species that were typically non-native (**Table 2.1; Fig. 2.2**). First, I found that species richness decreased with urban cover (β=-0.70(0.21SE), χ^2=11.85, df=1, *p*<0.001; **Fig. 2.2a**), declining by 50% across the urban gradient. This decline was driven by a decrease in native species richness in urban areas (β=-1.0(0.25SE), χ^2=17.39, df=1, *p*<0.001; **Fig. 2.2b**). In contrast, non-native species richness did not change across the gradient (β=0.08(0.38SE), χ^2=0.043, df=1, *p*=0.8; **Fig. 2.2c**).

Second, total abundance was the same across the urban gradient (β=0.46(0.31SE), χ^2=2.53, df=1, *p*=0.1; **Fig. 2.2d**). However, dividing the community based on species origin revealed that the abundance of non-natives increased (β=1.47(0.36SE), χ^2=19.74, df=1, *p*<0.001; **Fig. 2.2f**) while natives decreased (β=-0.87(0.38SE), χ^2=5.59, df=1, *p*=0.02; **Fig. 2.2e**) with urban cover. Across the gradient, non-native species abundance increased by 336% while native abundance decreased by 58%. The survey year also had an effect (*p*<0.001 all models; **Table 2.1**) with more individuals counted per site in 2018 compared to 2017 (**Table S2.2**).

In accordance with patterns of richness and abundance, evenness decreased with urban cover (β=-1.20(0.31SE), χ^2=12.46, df=1, *p*<0.001; **Fig. 2.2g**), indicating that urban butterfly communities typically included a few, highly abundant species.

2.4.2 Taxonomic homogenization

Urbanization led to the taxonomic homogenization of these butterfly communities (**Table 2.1**; **Fig. 2.3**). β-diversity was lower across urban sites than rural sites (mean difference=0.15, χ^2=81.36, df=1, *p*<0.001; **Fig. 2.3**). On average, β-diversity was 22% lower across urban sites than rural sites (mean=0.54 and 0.69, respectively). Distance between sites had no effect on β-diversity (β=0.0026(0.002SE), χ^2=2.41, df=1, *p*=0.12).

2.4.3 Functional homogenization

Urbanization led to the functional homogenization of these butterfly communities (**Table 2.1**; **Fig. 2.4**). I found that the standard deviation of wingspan decreased across the urban gradient (β=-9.45(SE2.42), χ^2=13.63, df=1, *p*<0.001; **Fig. 2.4a**), providing evidence for convergence in this trait. There was no difference in the standard deviation of voltinism (β=-0.14(SE0.09), χ^2=2.44, df=1, *p*=0.1; **Fig. 2.4b**) or larval diet breadth (β=-0.24(SE0.13), χ^2=3.39, df=1, *p*=0.07; **Fig. 2.4c**) across the gradient. The survey year had an effect on the standard deviation of larval diet breadth with lower values (i.e., smaller range) reported in 2018 compared to 2017 (mean difference=0.3, χ^2=4.35, df=1, *p*=0.04).

2.4.4 Functional dominance of traits

When considering all species, urban habitats supported more butterflies with smaller wingspans, that had more generations per year, and that had more specialized larval diets (**Table 2.1**; **Fig. 2.5**). As urban cover increased, butterfly communities showed a shift towards species with smaller wingspans (β=-0.12(0.03SE), χ^2=12.62, df=1, *p*<0.001; **Fig. 2.5a**), increased voltinism (β=0.75(0.15SE), χ^2=19.69, df=1, *p*<0.001; **Fig. 2.5c**), and decreased larval diet breadth (β=-0.1(0.03SE), χ^2=21.83, df=1, *p*=0.001; **Fig. 2.5e**).

However, *P. icarus* was by far the most abundant butterfly species in these communities (**Fig. S2.3**), so I also examined trends in functional dominance when *P. icarus* was excluded (**Table 2.1**). This analysis revealed that mean wingspan, voltinism, and larval diet breadth for the rest of the community did not differ across the urban gradient (**Fig 2.5bdf**). Relative to other species in the community, *P. icarus* is a small butterfly that has more generations per year and that can feed on several plant species from the same family (wingspan=29.5 mm; voltinism=3 generations per year; larval diet breadth=level 3; **Table S2.1**). Thus, when *P. icarus* was included in the analysis, its high abundance in urban sites influenced trait means such that they approximated towards *P. icarus'* characteristics.

2.5 Discussion

Urbanization-driven biotic homogenization has been well documented for many taxa, but less so for invertebrates like butterflies. Here, I demonstrate that urbanization in Montréal, Quebec has led to the taxonomic and functional homogenization of butterfly communities in open grassland habitats. I show that there were clear shifts in the structure of the urban butterfly communities in favour of a few, highly abundant, non-native species. These shifts were driven by losses of native species richness and abundance combined with increases in non-native species abundance, resulting in taxonomic homogenization. I also found evidence for reduced variation in butterfly wingspan, resulting in functional homogenization for this trait. Lastly, I show that there were no trends in functional dominance for three key traits in response to urbanization for most of the butterfly community.

2.5.1 Components of α-diversity

Increasing urban cover had a negative effect on native butterfly species richness, abundance, and evenness, consistent with the majority of past work on butterflies in developed regions (Stefanescu et al. 2004; Lizée et al. 2011; Olivier et al. 2016; Ramírez-Restrepo and

MacGregor-Fors 2017; Dylewski et al. 2019; Merckx and Van Dyck 2019; Kuussaari et al. 2021). This result is not particularly surprising given that urban areas are associated with multiple factors that could all be negatively impacting native butterflies like habitat loss/fragmentation, vehicle traffic, human interventions, and increased pollution/chemical use (McKinney 2002b; Rao and Girish 2007; Jiang et al. 2010; Wei and Yang 2010; Pickett et al. 2011; Liu et al. 2016; Fontaine et al. 2016; Fenoglio et al. 2021). Future research should evaluate the relative importance of these factors to better understand the mechanisms underlying native butterfly declines in cities. This will help habitat managers prioritize and mitigate which threats to focus on.

Increasing urban cover had a positive effect on non-native abundance which was driven by increases in just one species, *P. icarus*. Indeed, when *P. icarus* is excluded from the analysis, non-native abundance did not change across the urban gradient (**Fig. S2.4**). This is consistent with past work showing that non-natives can reach high densities in cities (i.e., urban exploiters; McKinney 2006), including butterflies (Petit et al. 2008), potentially as a result of increased propagule pressure (Meyerson and Mooney 2007; Hulme 2009). In addition, previous work from this region has shown that *P. icarus* abundance is related to human disturbance at local and landscape scales as well as the presence of its preferred larval host plant, Bird's Foot Trefoil (*Lotus corniculatus*) (Chapter 1: Rivest and Kharouba 2021) which is a non-native plant in Canada common in disturbed environments (Turkington and Franko 1980).

2.5.2 Biotic homogenization

Urbanization led to the taxonomic and functional homogenization of butterfly communities in Montréal, Quebec. To my knowledge, only one previous study has evaluated urbanization-driven homogenization for butterflies (Merckx and Van Dyck 2019), making comparisons with the literature difficult. This study concluded that functional homogenization was occurring, but not taxonomic. My finding that urbanization-driven biotic homogenization is occurring is more consistent with studies on the taxonomic homogenization of true bug and leafhopper communities (Knop 2016), the taxonomic and functional homogenization of moth communities (Merckx and Van Dyck 2019), as well as reports of taxonomic homogenization of butterfly and moth communities across other types of anthropogenic gradients (e.g., management intensity in agricultural systems; Ekroos et al. 2010). My findings add to a growing body of literature showing support for the urbanization-driven biotic homogenization hypothesis across multiple taxa and regions (Lokatis and Jeschke 2022).

The cause of biotic homogenization in the communities I studied likely relates to two factors: habitat and non-native species introductions. First, cities are built for the needs of humans so urban habitats tend to be similar in terms of their physical characteristics, promoting colonization by the same species with similar habitat needs (McKinney 2006). This resulted in urban butterfly communities that had fewer butterfly species overall. Second, cities are hubs of transport and trade which is known to increase the propagule pressure of non-native species (Meyerson and Mooney 2007; Hulme 2009). This likely also contributed to the homogenization I observed here since a greater share of urban butterfly communities were made up of non-native species.

2.5.3 Functional homogenization

I found reduced variation in butterfly wingspan where urban cover was higher, resulting in functional homogenization. Since I found no trends in functional dominance for wingspan (i.e., no change in community-weighted mean wingspan) when *P. icarus* was excluded (see further discussion below), this indicates that both smaller and larger butterflies were absent from urban sites. This is surprising given that previous work has shown that larger-winged or larger-bodied butterflies are more common in urban areas (Merckx et al. 2018; Merckx and Van Dyck 2019; Kuussaari et al. 2021). My result was likely driven by decreases in native richness and abundance combined with increases in non-native abundance. These structural changes likely reduced the amount of variation in butterfly wingspan present in urban sites. Additionally, the substantial gains in *P. icarus* abundance in urban sites also likely contributed to the functional homogenization in wingspan that I detected since a greater share of the total butterfly abundance was made up of just a single species.

2.5.4 Functional dominance of traits

When *P. icarus* was excluded, there was no functional dominance for three key butterfly traits across the urban gradient. This is inconsistent with past work which suggests that butterflies with larger wingspans/greater mobility, higher voltinism, and broader diet breadths are more common in urban areas (Blair and Launer 1997; Hogsden and Hutchinson 2004; Niell et al. 2007; Bergerot et al. 2011; Lizée et al. 2011; Merckx et al. 2018; Merckx and Van Dyck 2019; Kuussaari et al. 2021). However, my results do align with one urban gradient study that also found no trends in larval diet breadth (Merckx and Van Dyck 2019).

The lack of trends I found here could be related to the low interspecific variation in two of the traits that I considered. Across the entire urbanization gradient, I found low variation in the types of larval feeding habits present. Most butterfly species I observed (74%; 31/42) fed on plants from either one genus (level 2) or one family (level 3) (**Table S2.1**). In contrast, species that were extreme specialists (level 1) or extreme generalists (level 5) were both rare in my study (1 and 8 species, respectively; **Table S2.1**). It is possible that butterflies that are extreme specialists are already absent from this landscape, even in my most rural sites, given that this region has a long history of human activities in addition to urbanization (e.g., agriculture; Statistics Canada 2014). Similarly, for voltinism, most butterfly species I observed (59%; 25/42) had on average less than 2 generations per year whereas very few species had 3 generations (3 species; **Table S2.1**). This lack of interspecific variation across the entire urbanization gradient may have led to my inability to detect trends.

The way traits were measured may have also influenced my ability to detect functional dominance in these traits. Trait values were obtained by taking the average value across a butterfly species' entire Canadian range which may be less meaningful for predicting patterns at local scales. Indeed, intraspecific variation in insect community trait analyses is often assumed to be negligible and all individuals from the same species are typically assigned a single trait value (Gentile et al. 2021). The traits I examined could therefore be important for predicting the response of butterfly communities to urbanization, but the level at which they were measured (i.e., at species-level) may have been less informative. Furthermore, insect trait analyses for species assemblages that are highly diverse have been shown to be more robust to the presence of intraspecific variation (Gentile et al. 2021). Therefore, the ability to detect functional dominance in urban sites may increase by including surveys of a greater variety of non-urban sites (e.g., woodlands, wetlands), and thus a more diverse pool of butterfly species.

2.5.5 Implications & conclusions

My findings indicate that the preservation and restoration of native butterfly communities in urban areas is greatly needed. However, it remains difficult to make specific conservation recommendations about managing urban butterfly communities without a better understanding of the underlying mechanisms. Future studies should identify what specific urban characteristics (e.g., host plant availability, temperature, pollution, landscape configuration) have the biggest impacts on butterflies, so that they can be mitigated and important habitats can be prioritized for protection. For example, if fragmentation is a driving factor, then park connectivity should be prioritized whereas if host plant availability is a driving factor, planting native plants should be prioritized, thus requiring different resources. Future studies could also expand on the work that I have done here by evaluating other butterfly traits such as thermophily/heat tolerance, overwintering stage (e.g., pupa, adult), habitat affinity (e.g., moist, arid, canopy, forest edge), or oviposition style (e.g., eggs laid singly, clustered). These traits could be important for mediating the effects of urbanization on butterfly communities. For example, due to the urban heat island effect, species tolerant of higher temperatures may be better suited for urban environments (e.g., beetles and butterflies; Piano et al. 2017; Merckx and Van Dyck 2019).

One implication from my findings is that biotic homogenization may lead to a reduction in ecosystem functions and services in urban areas since there are fewer different species with distinct roles (Olden et al. 2004). For example, a reduction in the variation of butterfly wingspan in urban areas may have cascading impacts on their predators (e.g., birds) since different predators feed on differently sized butterflies. This could lead to shifts in nutrient cycling in urban areas since the butterfly community might support a reduced diversity of birds or some birds might experience shifts in their resource use.

Since butterflies are often used as indicator species for other insects (Thomas 2005), the urban butterfly community structure that I documented here could be a signal of widespread homogenization in other insect communities in cities. Indeed, striking declines in insect populations and biomass have been documented globally across a range of taxa and environments (Conrad et al. 2006; van Swaay et al. 2013; Hallmann et al. 2017), but research on urbanization-driven homogenization is lacking. Since urban areas are growing worldwide, documenting homogenization in cities is important so that we can understand what type of communities exist following insect declines. Since non-native species were the winners and native species were the losers in this study, my results highlight the need for more research aimed at making cities more habitable places for native species to live.

Tables

Table 2.1. Results of final models analyzing the effects of urban cover on (a-c) richness, abundance, and evenness, (e-g) community-weighted standard deviations of three traits, and (h-j) community-weighted means of three traits using either LMs or GLMs (n=44 sites). Also shown are the results from models analyzing (d) β-diversity as a function of the site grouping (rural vs. urban) and the distance (km) between sites using GLMs (n=498 comparisons). Models are fit on data from entire community, just native species, just non-native species, or the entire community but excluding *P. icarus*. The spatial scale (m) used for each model represents the scale at which the relationship between the response and urban cover was strongest (see **Methods**). Model results include estimates, standard errors (SE), χ^2-values and *p*-values. Estimates and SE for the wingspan model are presented for the log 10 transformed data. Degrees of freedom is 1 in all cases. SA indicates spatial autocorrelation was accounted for by including geographical coordinates.

Section	Model	Response	Spatial Scale (m)	Predictor	Estimate	SE	χ^2	*p*
Components of α-Diversity	a	Species Richness	2600					
		Entire Community		Urban Cover	-0.70	0.21	11.85	<0.001
		Native Species		Urban Cover	-1.0	0.25	17.39	<0.001
		Non-native Species		Urban Cover	0.08	0.38	0.043	0.8
	b	Total Abundance	300					
		Entire Community		Urban Cover	0.46	0.31	2.53	0.1
				Year	1.2	0.33	16.51	<0.001
		Native Species		Urban Cover	-0.87	0.38	5.59	0.02
				Year	1.31	0.40	13.64	<0.001
		Non-native Species		Urban Cover	1.47	0.36	19.74	<0.001
				Year	1.15	0.38	11.69	<0.001
	c	Evenness	300	Urban Cover	-1.20	0.31	12.46	<0.001
Taxonomic Homogenization	d	β-Diversity	300	Site Grouping	-0.64	0.07	81.36	<0.001
				Distance	0.0026	0.002	2.41	0.1
Functional Homogenization	e	SD Wingspan	200	Urban Cover	-9.45	2.42	13.63	<0.001
	f	SD Voltinism	300	Urban Cover	-0.14	0.09	2.44	0.1
	g	SD Larval Diet Breadth	100	Urban Cover	-0.24	0.13	3.39	0.07
				Year	-0.30	0.15	4.35	0.04
Functional Dominance of Traits	h	Mean Wingspan	200					
		Entire Community		Urban Cover	-0.12	0.03	12.62	<0.001
		Excluding *P. icarus*		Urban Cover	-0.02	0.03	0.53	0.46
	i	Mean Voltinism	300					
		Entire Community		Urban Cover	0.75	0.15	19.69	<0.001
		Excluding *P. icarus*		Urban Cover	0.22	0.14	2.54	0.11
	j	Mean Larval Diet Breadth $_{\text{SA}}$	100					
		Entire Community		Urban Cover	-0.1	0.03	21.83	0.001
		Excluding *P. icarus*		Urban Cover	-0.02	0.04	2.21	0.33

Figures

Figure 2.1. Map of study sites (n=44 sites; red dots) in Montréal, Quebec overlaid on a 30 m resolution 2017 land cover map (Agriculture and Agri-Food Canada 2017) used to calculate the percentage of urban land surrounding sites. Map was created using R 4.2.0 (R Core Team 2022).

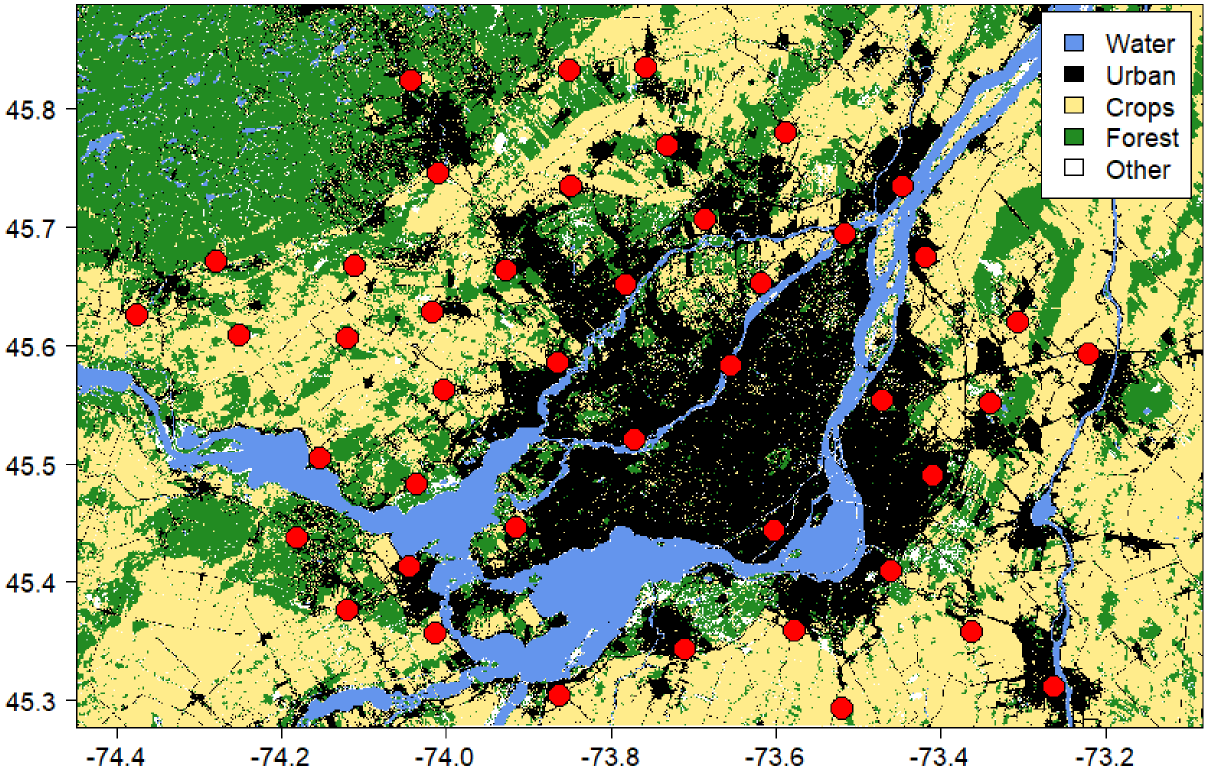


Figure 2.2. Effects of urban cover on butterfly community structure based on (a-c) species richness, (d-f) total abundance, and (3) evenness using GLMs (n=44 sites). Model predictions are from (a-c) poisson GLMs, (d-f) negative binomial GLMs, (g) and beta GLMs. Shown are raw data (dots), predicted lines of best fit (black lines), 95% confidence intervals (dotted lines), model estimates (β), standard errors (SE), and results from likelihood ratio tests including χ^2-values and *p*-values. The year of survey had a significant effect on abundance (d-f), so model predictions are shown for the year 2017 and raw data are colour-coded by year (2017=black, 2018=white). Proportion of urban cover was calculated at spatial scales of (a-c) 2600 m and (d-g) 300 m.

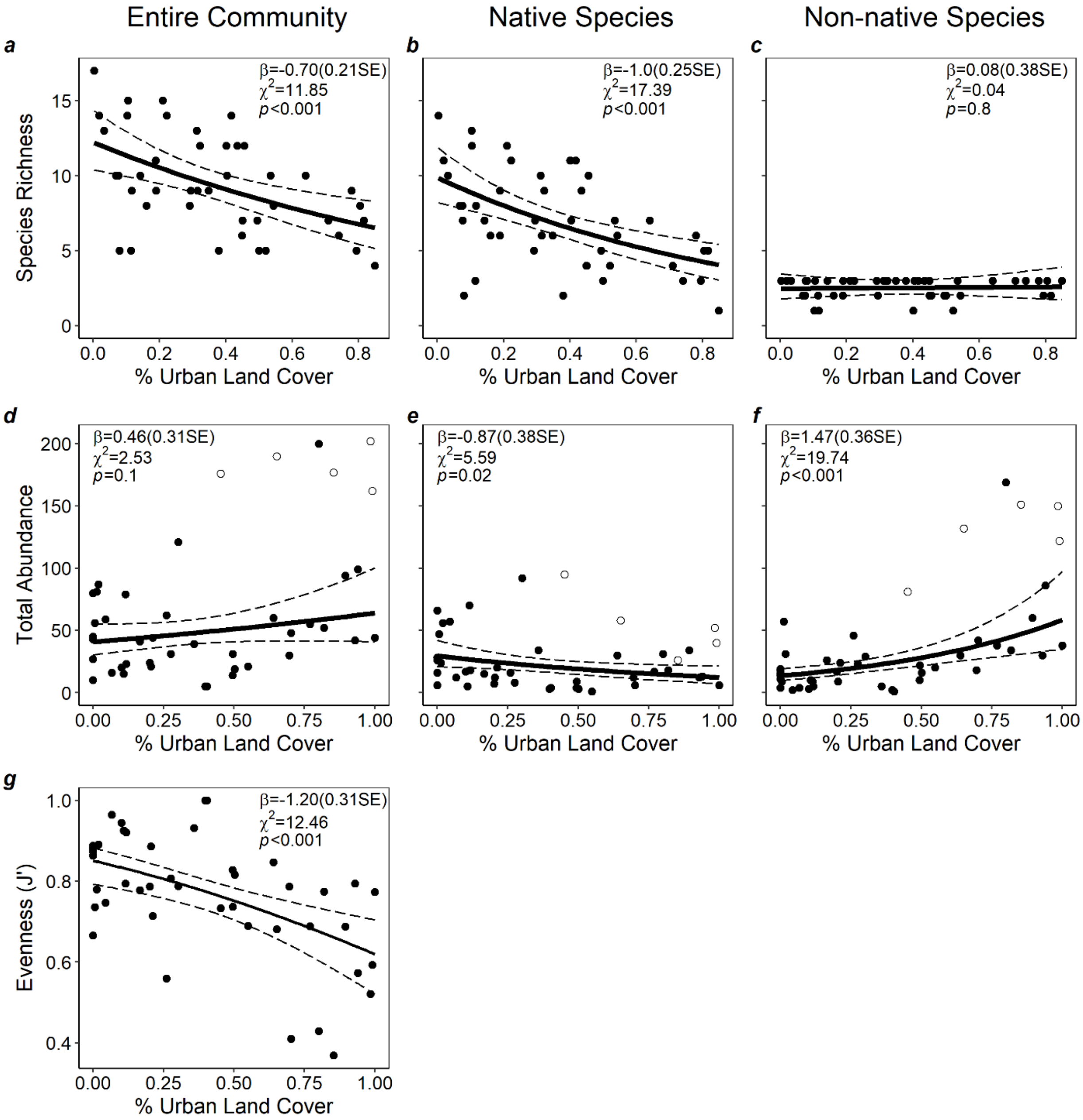


Figure 2.3. Effect of site grouping on β-diversity (Bray-Curtis dissimilarity index) using beta GLMs (n=498 comparisons) (mean difference=0.15, χ^2=81.36, df=1, *p*<0.001). Shown are predicted means (white bars) and upper 95% confidence intervals (error bar). Model predictions were obtained when holding distance between sites constant at its mean. Sites were grouped based on the amount of urban cover within circular buffers of radius 300 m (urban: >50%, n=16 sites vs. rural: <50%, n=28 sites).

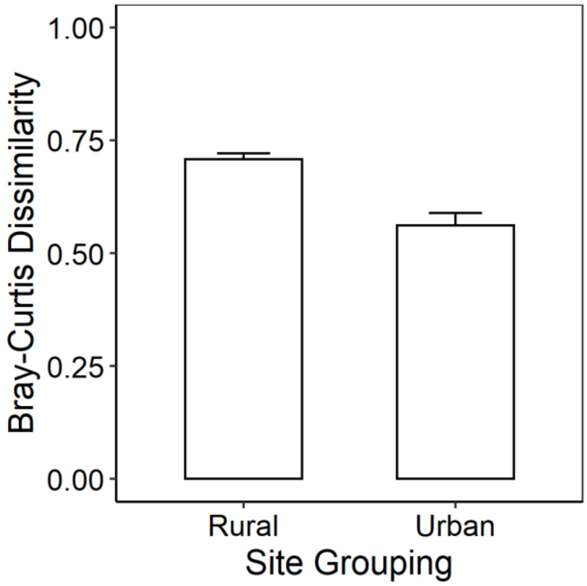


Figure 2.4. Effects of urban cover on community-weighted standard deviations (SD) for butterfly traits including (a) wingspan (mm), (b) voltinism, and (c) larval diet breadth using linear models (n=44 sites). Shown are raw data (dots), predicted lines of best fit (black lines), 95% confidence intervals (dotted lines), model estimates (β), standard errors (SE), and results from likelihood ratio tests including χ^2-values and *p*-values. The year of survey had a significant effect on SD larval diet breadth (c), so model predictions are shown for the year 2017 and raw data are colour-coded by year (2017=black, 2018=white). Proportion of urban cover was calculated at spatial scales of (a) 200 m, (b) 300 m, and (c) 100 m.

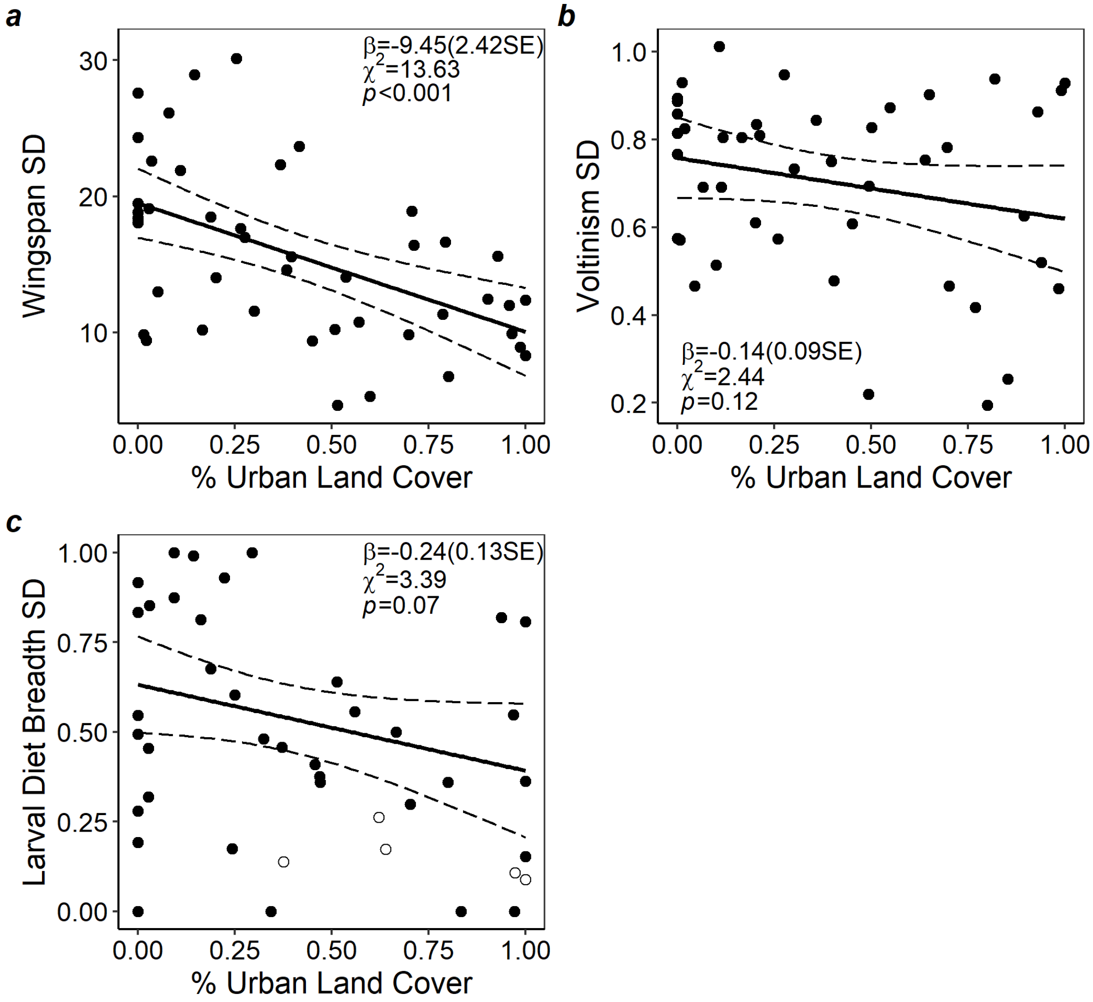
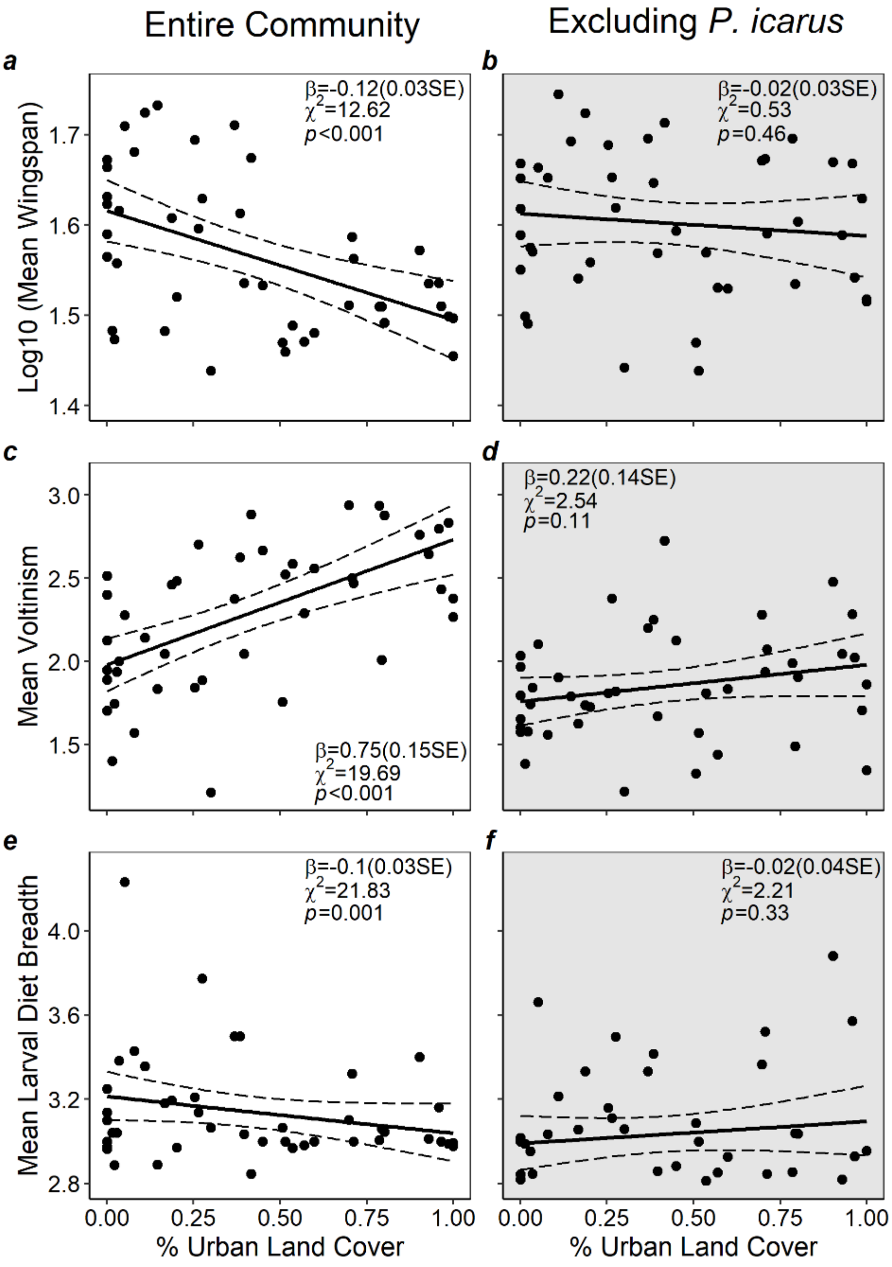


Figure 2.5. Effects of urban cover on community-weighted means for butterfly traits including (a-b) wingspan (mm), (c-d) voltinism, and (e-f) larval diet breadth using LMs and GLMs (n=44 sites). Model predictions are from (a-d) LMs, and (e-f) gamma GLMs. Shown are raw data (dots), predicted lines of best fit (black lines), 95% confidence intervals (dotted lines), model estimates (β), standard errors (SE), and results from likelihood ratio tests including χ^2-values and *p*-values. Model predicted lines for larval diet breadth are shown for single-variable models including only urban cover (i.e., not including geographical coordinates). Proportion of urban cover was calculated at spatial scales of (a-b) 200 m, (c-d) 300 m, and (e-f) 100 m. Data for mean butterfly wingspan is log 10 transformed.



III. Flowering phenology influences butterfly visitation to non-native plants for nectar in an oak savanna

The following thesis chapter is a modified version of an article under review (citation below). Since the article was submitted as a shorter Report intended for fast publication, it was modified by including more figures, tables, and background information. My contributions to this thesis chapter are the conceptions of ideas, design of methodologies, data collection, data analysis, writing, and editing.

Article Citation: Rivest SA, Wolkovich EM, Kharouba HM (2023) Flowering phenology influences butterfly visitation to non-native plants for nectar in an oak savanna. *Ecology,* manuscript ID ECY22-0801. (*submitted, in review*)

3.1 Abstract

Non-native species have the potential to interact with native species, altering ecosystems and leading to changes in community dynamics. Previous work has mainly focused on the negative impacts of non-native species on ecological communities, but some non-native species can play a positive role in the persistence of native species and even contribute to achieving conservation goals. One way that non-native plants can positively interact with native butterflies is by provisioning nectar. Relatively little is known about the role of phenology in determining native butterfly visitation to non-native plants for nectar, yet flowering time directly controls nectar availability. Here, I investigate the phenological patterns of flowering by native and non-native plants and nectar foraging by native butterflies in an at-risk oak savanna, and test whether native butterflies select nectar sources in proportion to their availability. I conducted weekly field surveys in 10 sites of Garry oak savanna on Vancouver Island, British Columbia, Canada. I found that shifts in flower availability between native and non-native plants had a large impact on butterfly foraging: visitation to non-native plants increased later in the season when native plants were no longer flowering. Across the entire season, non-native nectar was well integrated into native butterfly diets (83% of all foraging visits). When I tested butterfly resource selection during times in the season when native and non-native flowers were both available, butterflies selected non-native flowers more often than expected based on their availability, suggesting that these plants represent a potentially valuable resource that butterflies may prefer. My study shows that non-native species have the potential to drive key species interactions in seasonal ecosystems. Therefore, management regimes focused on eradicating non-native plants may need to consider their aims and evaluate resources that non-native species provide, especially when resources from native species are less abundant.

3.2 Introduction

The negative impacts of non-native species on ecological communities and ecosystem function have been well documented (Bradley et al. 2019; Vitousek et al. 1997). However, some non-native species can play a positive role in the persistence of native species and even contribute to achieving conservation goals. For example, they have been shown to provide food and habitat to native species, act as ecosystem engineers and provide ecosystem services (Schlaepfer et al. 2011). Some non-native species are so well integrated into the ecosystem that their removal has threatened the recovery of endangered species (Casazza et al. 2016). In anthropogenic environments, non-native species tend to be more dominant (e.g., plants and insects; Pyšek et al. 2010; Jauni et al. 2015), so their role in supporting native species in these habitats may be particularly important. For example, non-native honeysuckles (*Lonicera* spp.) in central Pennsylvania grow best near urban environments (Luken and Thieret 1996) and are a significant food resource for native birds such as robins (*Turdus migratorius*) and catbirds (*Dumetella carolinensis*) (Gleditsch and Carlo 2011). As more non-native species are introduced into biological communities, interactions with native species are predicted to increase (Pearse and Altermatt 2013). Therefore, evaluating the roles that non-native species play in ecosystems is critical.

Native butterflies are likely to interact with non-native plants because they rely on plant resources during all life stages, yet the overall role of non-native plants in butterfly communities remains unclear. One understudied, yet potentially important, interaction between native butterflies and non-native plants is nectar provisioning. For many adult butterflies, nectar is an essential resource that provides water, sugar, and amino acids important for flight and reproduction (Gilbert and Singer 1975; Mevi-Schütz and Erhardt 2005). In some species, late-season egg-laying can entirely depend on the adult female's nectar diet (O'Brien et al. 2004). Male nectar foraging can also impact a female's reproductive output via the donation of nuptial gifts (Boggs and Gilbert 1979; Boggs 1990, 1995). Previous work has shown that native butterflies can forage for nectar on non-native plants, but it is not clear to what extent and under what conditions. Some studies report high usage (e.g., 71% of foraging visits to non-natives in urban sites; Jain et al. 2016), some report moderate usage (e.g., ~50% of foraging visits to non-natives across all sites (Hardy and Dennis 2008; Bergerot et al. 2010)), while others report very low usage or a even a preference for native plants (e.g., 20% of foraging visits to non-natives for female *Plebejus icarioides fenderi*; Thomas and Schultz 2016). Knowing how often native butterflies interact with non-native plants while nectar foraging is essential for maximizing the effectiveness of potential conservation actions.

Flowering phenology may be an important factor influencing native butterfly visitation to non-native plants since flowering time directly controls nectar availability, but few studies have addressed this. Theoretical predictions (Wolkovich and Cleland 2011) and empirical evidence (Gerlach and Rice 2003; Willis et al. 2010) suggest that non-native plants can flower longer and/or at different times compared to natives. For native butterflies, this could mean there are times during their flight period when non-native flowers are more available than native flowers and/or that their flight periods could lengthen if nectar is available for longer. Yet only a handful of studies have explored phenological patterns in the availability of butterfly nectar resources (e.g., Szigeti et al. 2018), and to our knowledge, only one study has specifically considered the flowering of non-native plants (Thomas and Schultz 2016).

It is also unclear how butterflies would respond to differences in native and non-native flowering phenology if they were to occur. Since adult butterflies are typically generalist nectar feeders (Hardy and Dennis 2008), they may forage based on nectar availability, regardless of plant characteristics or origin (i.e., null hypothesis from resource selection studies; Manly et al. 2002). Indeed, flower abundance can explain butterfly visitation for certain butterfly-plant species pairs (Grundel et al. 2000; Munguira et al. 1997; Szigeti et al. 2018). Alternatively, butterflies may choose plants based on other factors (e.g., sugar quantity; Thomas and Schultz 2016). Since past work has focused on resource selection by single butterfly species, we have a limited understanding of foraging patterns at the community-level. Further, few studies exploring butterfly resource selection have compared the composition of non-native flowering plants in the diet of butterflies compared to native plants (but see Thomas and Schultz (2016)).

In this chapter, I investigate native butterfly nectar foraging in relation to the flowering phenology of plants in an oak savanna ecosystem and ask: (1) How much are native butterflies using non-native plants as a source of nectar? (2) How does phenology influence nectar availability? (3) How does phenology influence nectar foraging by native butterflies and do native butterflies select nectar sources in proportion to their availability? For my third question, I predict that butterfly visitation to non-native plants will increase proportionally with non-native flower availability.

3.3 Methods

3.3.1 Study area

I conducted field surveys of native butterflies and flowering plants in 10 sites of remnant Garry oak savanna in Victoria, British Columbia, Canada (**Fig. 3.1**). Remnant patches of Garry oak savannas in this region are characterized by rocky outcroppings, a diverse forb understory, and an open canopy of trees including Garry oak (*Quercus garryana*), Douglas fir (*Pseudotsuga* *menziesii*), and Arbutus (*Arbutus menziesii*) (Fuchs 2001). The climate is Mediterranean-like, with wet winters and dry summers ending in late-season drought (Klassen et al. 2015).

Garry oak savannas in this region have been strongly impacted by human activities (e.g., urbanization, agriculture, forestry), the loss of natural disturbance regimes, and abundant non-native plant introductions (Lea 2006; GOERT 2013). Since Europeans settled in 1840, the extent of Garry oak savanna has declined by 90%, making it one of the most at-risk ecosystems in Canada (Lea 2006). This ecosystem is highly biodiverse and contains more than 100 species at-risk (BC red list) including seven butterfly species (GOERT 2013; BC Conservation Data Centre 2021). It also contains a high diversity of non-native flowering plants (Lilley and Vellend 2009), making it an ideal study system to consider my research questions. Management of Garry oak savannas is ongoing, so understanding how non-native plants interact with native butterflies is essential.

3.3.2 Site selection

I selected my 10 sites by first consulting a vascular plant dataset based on surveys of 43 sites of Garry oak savanna in Victoria, BC in 2006 (Lilley and Vellend 2009). Since I was primarily interested in phenological variation, I minimized site-level differences such as site area and the proportion of the total flowering plant species richness across the season that was non-native. After minimizing these differences, my 10 sites still varied somewhat in these two factors (site area varied 0.6-8.8 ha; species richness varied 40-71% non-native (**Fig. 3.1**)). Where possible, I also tried to minimize variation in local habitat conditions such as canopy openness and human disturbance (e.g., dirt/paved paths, buildings). The minimum distance between sites was 2 km.

3.3.3 Nectar foraging surveys

From 6 May to 12 August 2019, I surveyed sites in rotation approximately once per week. Recent work from this area has shown that butterflies are typically present from April to September, but that May to August represents the main period of butterfly activity (Zand et al. 2017; Kharouba unpubl.). Summer weather conditions in Victoria, BC in 2019 were similar to recent climate normals (1981-2010): daily average temperatures were 1.5°C and 0.7°C warmer in May and August, respectively, and there was 9.7mm (~9%) less precipitation from May to August in 2019 (Environment Canada, 2022a; Environment Canada, 2022b). At the start of each visit to a site, two observers recorded butterfly nectar foraging events for approximately 60-90 minutes by walking a 300 m long route, divided into five transects of 60 m each arranged side by side 15 m apart. For any native butterfly observed foraging (i.e., proboscis entered flower) within 5 m of the transect, I noted the species of butterfly and plant. Since butterfly activity tended to be low, I walked the entire transect, but prioritized areas where butterflies were active. Butterflies were identified on the wing and could be confidently resolved to species. Individuals were not distinguished as marking butterflies in the field is time-consuming and disturbs short-term behaviour. However, when a single individual was observed, the number of foraging observations recorded was restricted to five (< 30% of total observations). Following standard protocols (Pollard and Yates 1993), surveys were conducted only when butterflies were fully active: 9 am to 4 pm, temperatures of 13–40°C or > 17°C when cloud cover > 75%, wind < 30 km/h, and no rain.

3.3.4 Flower availability surveys

Next, I estimated nectar availability from all flowering forbs and shrubs either on the same or following day as the butterfly surveys by placing a 1 m^2 habitat quadrat at five locations along the same 300 m route described above. For each site-visit, quadrat locations were selected using an algorithm that randomized the distance from the start (0-300 m) and the side of the transect (left or right). However, I ensured the placement of quadrats adequately covered the floral resources present in a site. For example, if a quadrat was located on a rocky outcropping, I moved the quadrat forward on the transect until the next patch of flowers. Within each quadrat, I counted the number of open flowering units for each plant species. Plant species were identified by taking photographs and/or a sample of the plant and consulting online resources like the BC Conservation Data Centre (2021). In particular, an active group of local community members on iNaturalist (2019) were instrumental for correctly identifying plant species. Through the field work conducted as a part of this thesis chapter, I contributed 172 records of 109 species of plants and animals observed in Victoria which were identified by 79 different community members (iNaturalist 2019).

Depending on the species of plant, a flowering unit could be a single flower, cluster of flowers (inflorescence), or branching stem. Flowers were considered open if floral parts were expanded enough to allow potential pollinators to obtain food rewards and if they had not dried or wilted. I assumed only open flowers produced nectar and that flowers that were shriveled or dying did not produce nectar. It is possible that some open flowering units may have been older and no longer producing nectar which I was unable to detect with my approach. Sampling nectar directly would have taken substantial time and effort, limiting my ability to visit sites at a high enough frequency to detect changes in flowering phenology, which was the focus of my research. Then, I estimated nectar availability by multiplying the number of flowering units counted with their mean surface area in mm^2, thus accounting for differences in flower size. I estimated the mean surface area of flowering units by measuring the dimensions of 10–20 randomly chosen individuals for each plant species (**Table S3.1**). Area was calculated for circular flowers using πr^2, for oblong and rectangular flowers using length*width, and for circular flowers with a depth dimension using the equation of a bottomless cylinder: $2\pi rh + \pi r^2$ (Hegland and Totland 2005) (r=radius; h=height). This approach has been used in the past (e.g., Hegland and Totland 2005) and is an effective way to increase the accuracy of flower count variables (e.g., number shoots, flowers/stem) while minimizing the time and effort spent on nectar surveys (Szigeti et al. 2016). The assumption that flower size is positively correlated with nectar quantity (i.e., nectar production, volume, and/or sugar concentration) is supported by empirical work from multiple systems and multiple levels of organization (within species (Cresswell and Galen 1991; Fenster et al. 2006), genera (Inoue et al. 1995; Galetto and Bernardello 2004) and communities (Tavares et al. 2016; Parachnowitsch et al. 2019)).

I reviewed scientific and grey literature to determine whether the plant species I observed produce nectar rewards. Species known to produce no nectar rewards (e.g., *Cytisus scoparius* (Scotch Broom); Parker 1997) were excluded (n=11). I also determined plant species origin using online databases (Jepson Flora Project 2020; BC Conservation Data Centre 2021; Flora of North America Editorial Committee 2021) (**Table S3.1**).

3.3.5 Statistical analysis

(i) Overall approach

I structured the analysis into two sections and fit a series of generalized linear models (GLM) in each. The same modelling approach was followed in both sections. All statistical analyses were performed in R 4.2.0 (R Core Team 2022).

All predictor variables were standardized by subtracting the mean and dividing by the standard deviation. To avoid problems with collinearity between my predictor variables, I visually assessed pairwise plots. I explored potential two-way interactions between all predictors and determined whether they significantly improved model fit by comparing models using Akaike Information Criterion (ΔAIC>2; Burnham and Anderson 1998).

Model selection followed a backward step-wise approach to find the best fitting model with the lowest AIC. Predictors that did not significantly improve model fit (i.e., ΔAIC<2) were removed. Final models were validated by visually assessing either (1) pearson residual plots (Ferrari and Cribari-Neto 2004) or (2) residual versus fitted plots. To assess the fit of covariates, I used either (1) likelihood ratio tests from the package lmtest (Zeileis and Hothorn 2002) or (2) F-tests, which is more appropriate for models with quasi-likelihoods (Venables and Ripley 2002; Zuur et al. 2009).

(ii) Influence of phenology on nectar availability

To estimate trends in the phenology of nectar availability, I first summed my floral area data across the five habitat quadrats within each site-visit (n=114). I analyzed the proportion of floral area from non-native plants compared to native plants. Given this was a continuous proportion (i.e., derived from a continuous measurement), I fit GLMs with the beta probability distribution using the packages gam and mgcv (Hastie 2019; Wood 2011). Since the response sometimes took on the value of 1 but the beta distribution assumes values in the open interval

(0,1), I rescaled the values by applying the transformation: y'=(y*(n−1)+0.5)/n, where n is the sample size (Smithson and Verkuilen 2006). To understand phenological trends, I included day of year as a predictor. I also included two site-level covariates: site area and the proportion of the total flowering plant species richness across the season that was non-native. Although I minimized site-level variation in these factors through site selection, I included the two covariates to account for any remaining variation.

(iii) Influence of phenology and availability on nectar foraging

To explore trends in the phenology of nectar foraging and test the hypothesis that native butterflies select nectar sources in proportion to their availability, I fit two models. I first combined observations of nectar foraging across butterfly species within each site-visit. Nectar foraging was only observed during 58 out of a possible 114 site-visits (n=58). I analyzed the proportion of nectar foraging visits made to non-native flowers compared to native flowers. Since this was a discrete proportion (i.e., derived from counts) with minor overdispersion (dispersion parameter~4), I fit GLMs with the quasibinomial probability distribution (Zuur et al. 2009). I included the predictors day of year, the proportion of floral area from non-native plants compared to native plants, and two site-level covariates: site area and the proportion of the total flowering plant species richness across the season that was non-native.

To test my hypothesis, I used the same nectar foraging model as above but excluded periods of time when butterflies did not have a choice between native and non-native flowers (i.e., when only non-native flowers were available; after July 18). As such, I fit my second nectar foraging model on a reduced dataset that only included observations before 18 July (**Fig. 3.2b**).

After this point in the season, 100% of foraging visits were to non-native plants and relative availabilities of non-native floral area were ≥ 99% for 80% of my visits to sites (see Results).

3.4 Results

3.4.1 Summary of descriptive patterns

Across the season, I observed nectar foraging on 1143 occasions by 14 native butterfly species from 5 families: Lycaenidae (n=3), Hesperiidae (n=2), Nymphalidae (n=3), Pieridae (n=3), and Papilionidae (n=3). Summed across the season, 83% (946/1143) of all foraging visits were to non-native plants. I found that 64% (9/14) of butterfly species visited non-native flowers more often than native flowers (i.e., >50%), whereas 29% (4/14) species visited native flowers more often and one species visited native and non-native flowers equally (**Table 3.1**). However, some butterflies were rare in my sites (e.g., Anise swallowtail (*Papilio zelicaon*) is more common in woodlands than in savannas), leading to lower confidence in my estimates for these species. Notably, out of a potential seven at-risk butterfly species in this region, I only observed two: Propertius duskywing (*Erynnis propertius*) and Vancouver ringlet (*Coenonympha tullia insulana*) which are both critically imperiled (S1 ranking; BC Conservation Data Centre 2021). These two butterflies made 60% (121/201) and 67% (6/9) of their nectar foraging visits to non-native flowers, respectively (**Table 3.1**).

I observed 81 species of flowering plants with nectar rewards from 23 plant families (**Table S3.1**). Of these species, 55% (45/81) were non-native. The amount of floral area recorded for each plant species varied across species, sites, and the season (**Figs. S3.1**; **Fig. S3.2**). Some plants were highly available: eight species (3 native, 5 non-native) made up 87% of all floral area recorded (**Fig. S3.3**). Other plant species were rare: nine species (3 native, 6 non-native) were only recorded in a single site-visit (**Fig. S3.1**; **Fig. S3.2**). I tested the sensitivity of my analyses to these rarer plants by excluding them from the calculation of total plant species richness and re-fitting models. The only difference was that site area no longer contributed to explaining variation in the proportion of floral area that was non-native (i.e., model “a”; **Table S3.2**). Since my main findings were the same, I included the rare plant species in my calculation of species richness. Thus, amongst my sites, the total flowering plant species richness varied from 40 to 71% non-native (**Fig. 3.1**).

The number of foraging visits was unevenly distributed amongst flowering plants with only 36% (29/81) of available plant species being visited by butterflies, 59% (17/29) of which were non-native (**Fig. S3.4**). Indeed, 71% (812/1143) of all foraging visits were to just four flowering plant species including the non-native species *Hypochaeris radicata* (Hairy Cat’s-ear), *Rubus armeniacus* (Himalayan Blackberry), and *Vicia sativa* (Common Vetch) as well as the native species *Camassia quamash* (Common Camas) (**Fig. S3.4**).

3.4.2 Influence of phenology on nectar availability

The availability of native and non-native flowering plants fluctuated across the season. While non-native floral area stayed at relatively low, but constant, levels across the season, native floral area started the season at high levels and then declined over time until eventually reaching zero in several of my sites (**Fig. 3.3a**). In fact, in the last 3-4 weeks of the survey period (18 July-12 August), I recorded relative availabilities of non-native floral area that were ≥ 99% in 80% of my visits to sites (31/39 site-visits).

The proportion of non-native floral area was higher in sites with a higher proportion of non-native plant species, but the magnitude of this effect was dependent on day of year (χ^2=4.6, df=1, *p*=0.032, n=114 site-visits; **Fig. 3.4a**; **Table 3.2**: Model a). Later in the season when native floral area declined, all sites had high relative availabilities of non-native floral area, regardless of the proportion of non-native plant species richness (**Fig. 3.4a**). The proportion of non-native floral area was also higher in larger sites (β=0.21 (0.10SE), χ^2=4.1, df=1, *p*=0.043, n=114 site-visits; **Fig. 3.4b**; **Table 3.2**: Model a).

3.4.3 Influence of phenology and availability on nectar foraging

As expected based on the trends in flowering phenology, the proportion of nectar foraging visits made by native butterflies to non-native flowers compared to native flowers increased later in the season (β=1.4 (0.5SE), $F_{1,55}$=10.5, *p*=0.002, n=58 site-visits; **Fig. 3.4c**; **Table 3.2**: Model b). During the beginning of the season, butterflies visited both native and non-native flowers (**Fig. 3.3b**). Whereas in the last 3-4 weeks of field surveys, 100% of foraging visits were to non-native flowers (**Fig. 3.3b**). The proportion of nectar foraging visits made to non-native flowers was also higher in sites with a higher proportion of non-native plant species richness (β=1.6 (0.4SE), $F_{1,55}$=23.1, *p*<0.001, n=58 site-visits; **Fig. 3.4d**; **Table 3.2**: Model b).

When I tested butterfly selection of nectar sources when native and non-native flowers were both available (i.e., before 18 July), I found that native butterflies increased their visitation to non-native flowers when the relative availability of non-native flowers increased (β=1.1 (0.4SE), $F_{1,31}$=11.0, *p*=0.002, n=33 site-visits; **Fig. 3.5**; **Table 3.2**: Model c). However, this increase was not in proportion to availability as predicted by the null hypothesis. Instead, butterflies selected non-native flowers more often than expected based on their availability (i.e., predicted curve is above null expectation curve; **Fig. 3.5**). For example, 50% of nectar foraging visits were to non-native flowers when only 27% of available flowers were non-native (**Fig. 3.5**).

3.5 Discussion

Relatively little is known about how differences in native and non-native flowering phenology can influence butterfly nectar foraging, yet this knowledge is essential to maximize the effectiveness of conservation actions. Our study contributes three key findings. First, we show that across the entire season, non-native nectar was well integrated in native butterfly diets (83% of all foraging observations). Second, we found that seasonal shifts in flower availability had a large impact on butterfly nectar foraging patterns: visitation to non-native plants increased later in the season when native plants were no longer flowering. Lastly, we show that when both native and non-native flowers were available, butterflies visited non-native plants more often than expected, suggesting that these plants represent a potentially valuable resource.

Across the entire season, we found that non-native flowers were a heavily used source of nectar for native butterflies. Our estimate of usage may even be an under-estimate since our sites were adjacent to suburbs, public gardens, and other urban land uses which could have provided additional non-native nectar sources that were not measured here. Even still, our low-end estimate is higher than previous reports which have documented low to moderate usage of non-native plants (i.e., 20-50% of foraging visits to non-natives (Bergerot et al., 2010; Hardy & Dennis, 2008; Thomas & Schultz, 2016), but see 71% of visits in Jain et al. (2016)). Our findings are more consistent with reports of high usage of non-native plants as larval hosts for native butterflies (Shapiro, 2002). We may have found higher estimates of non-native usage than other studies due to site-level characteristics such as the high species richness of non-native flowering plants that we found here. Differences across studies could also be due to a combination of site-level factors and resource selection since we know butterflies can select certain resources over others despite patterns in resource quantity (e.g., Thomas & Schultz, 2016). Future studies should examine how site-level factors, in particular land-use history (e.g., urbanization), influence the usage of non-native nectar by butterflies.

Non-native flowers were the main source of nectar in the last 3-4 weeks of the butterfly flight period due to a seasonal decline in native flowers and butterflies responded by increasing their visitation to non-native plants during this time. This result is consistent with past work showing that insect pollinators can increase their visitation to non-native flowers when they are relatively more available (e.g., later in season; Salisbury et al., 2015). Our results also support previous work done in this system (Simon et al., 2021) and in others (Gerlach & Rice, 2003; Pearson et al., 2012) showing that non-native plants flower later in the season than native plants. However, given that our work is based on a single year, future studies could evaluate if the patterns we observed here are sensitive to interannual variability (e.g., weather, population dynamics).

Since late season plant community dynamics in Garry oak savannas, and other Mediterranean-like ecosystems, are driven by drought (Klassen et al., 2015), flowering later than natives could be a result of increased drought tolerance in certain non-native plant species. For instance, in this system, non-native floral area was found to be negatively correlated with soil moisture (Simon et al., 2021). However, since historical data on flowering times in Garry oak savannas are unavailable, it is unknown whether non-native plants are occupying vacant temporal niches and/or if they have become more abundant than native plants that were historically present late in the season when conditions are drier. Current plant species lists compiled for this ecosystem indicate that 10 native plant species are expected to flower, at least in part, in August (GOERT, no year). We only observed one of these 10 plant species (i.e., *Symphoricarpus albus* (Common Snowberry)) while a previous study done in the same sites observed three (Lilley & Vellend, 2009). As we surveyed a non-random subset of remaining patches of Garry oak savanna, we may have underestimated the number of late-season native plant species. More work is needed to determine what changes are occurring in the native plant community. Regardless, the later flowering of non-native plants relative to native plants could mean that the nectar foraging period, and thus the flight season, for butterflies has lengthened with the introduction of non-native plants. This could allow some late-season butterfly species (e.g., Woodland Skipper (*Ochlodes sylvanoides*)) to accumulate more resources and produce additional generations which could accelerate population growth (Altermatt, 2010). Whether this occurs will also depend on late-season environmental conditions (e.g., temperature) remaining suitable for butterflies and their larval host plants.

We found that butterflies selected non-native flowers more often than expected based on non-native flower availability. This suggests that non-native nectar is a valued resource and that butterflies may prefer non-native flowers over native flowers in some contexts, though a choice-experiment could be used to determine this with greater confidence. Our results are similar to one single-species study that found ovipositing females preferred non-native plants (*Euphydryas editha*; Haan et al., 2021), but are unlike another single-species study that found that nectar foraging adults preferred native flowers (*Plebejus icarioides fenderi*; Thomas & Schultz, 2016). This reinforces the notion that studies of multiple species offer insights into general tendencies of the community. Of the top five most visited plant species, three were also amongst the top five species that provided the greatest amounts of total floral area (**Fig. S3.3**; **Fig. S3.4**). Yet, other plant species that provided very high amounts of floral area (e.g., native *Plectritis congesta*) were not highly visited by butterflies, suggesting that factors other than flower availability are influencing foraging decision-making. Overall, our study suggests that non-native plants can be a valued resource for native butterfly communities.

Several possible factors could have influenced why butterflies chose non-native nectar sources so often such as flower colour and shape (Tiple et al., 2006), or nectar characteristics like sugar concentration (Pivnick & McNeil, 1985), alkaloid content (Ramos et al., 2019), and amino acids (Mevi-Schütz & Erhardt, 2005). For example, we observed that native butterflies visited yellow flowers most often (52% of visits; 598/1143) (**Fig. S3.5**) which is consistent with past work (Grundel et al., 2000; Yurtsever et al., 2010). Since most yellow flowering plant species in our study were non-native (75% of species; 9/12) (**Fig. S3.5**), this may help to explain why we observed such high visitation to non-natives plants. Future work could evaluate differences between native and non-native flowers to determine why butterflies are selecting non-natives so frequently.

We found that non-native flowers were well integrated into native butterfly nectar diets, but there was also variation across butterfly species in the degree of usage of non-native flowers. This is consistent with community-level work where interspecific variation in nectar foraging is thought to be influenced by differences in proboscis lengths among butterfly species (Bergerot et al., 2010). Interspecific variation could also be related to the timing of butterfly flight periods (**Fig. S3.6**). For instance, the high number of visits to non-native flowers by *Ochlodes sylvanoides* (Woodland Skipper) could be influenced by its high abundance in July and August when native flowers were least available. In contrast, the high number of visits to native flowers by *Celastrina echo* (Echo Azure) could be explained by its high abundance in May and June when native flowers were most available. To best inform regional conservation practices, future studies could assess nectar foraging in relation to flower availability for individual butterfly-plant species pairs, especially for at-risk butterflies.

Although we show that non-native nectar was well integrated into native butterfly diets, it could be lower quality than native nectar and lead to negative effects on butterfly fitness. Nectar quality differences between native and non-native plants have not been well studied and research on pollen quality is inconclusive: some researchers report no nutritional differences (Harmon-Threatt & Kremen, 2015) whereas others report increased quality of non-native pollen (Russo et al., 2019). In theory, butterflies should select nectar sources that provide sufficient rewards of adequate quality. But previous work has shown that butterflies can sometimes have maladaptive strategies (i.e., developmental traps), like when females oviposit on non-native plants that are toxic to their larvae (Sands, 2008). This may occur because toxic non-native host plants are closely related to native hosts or because they possess similar chemical cues (e.g., glucosinolate profiles as cues for ovipositing *Pieris napi macdunnoughii*; Rodman & Chew, 1980). Alternatively, if non-native nectar is of similar or better quality than native nectar, then non-native plants may help buffer native butterflies against losses in native flowers. An important next step will be to evaluate the consequences of non-native nectar diets on native butterflies.

3.5.1 Implications & conclusions

Our findings have important implications for the conservation of butterflies in seasonal invaded ecosystems. Our work shows that non-native flowers can be an important resource for butterflies throughout the season, and particularly at key times. This is at odds with current management regimes, including those for Garry oak savannas (e.g., Trowbridge et al., 2017), that typically recommend the eradication of non-native plants which could leave butterflies and other pollinators without sufficient nectar resources, especially during periods of drought later in the season. To mitigate the removal of potentially important nectar resources, managers could combine their eradication efforts with supplemental plantings of native flowers that provide nectar at the necessary times. We also caution that the presence of non-native plants may help to achieve conservation goals where native plants are less common or less likely to persist (e.g., disturbed habitats). Overall, our work highlights the need for evaluating the phenological patterns of non-native plants to better understand their role in the diets of native insects.

Tables

Table 3.1. Patterns in native butterfly visitation to flowering plants for nectar including the number of native (N) plant species visited, the number of non-native (NN) plant species visited, the total number of visits made, and the percentage of visits that were to NN plants (rounded to nearest unit). Butterfly species are ordered by total number of visits.

	Butterfly Species	# N Species Visited	# NN Species Visited	Total Visits	# Visits to NN	% Visits to NN
More Visits to NN	*Ochlodes sylvanoides*	0	4	571	571	100
	Erynnis propertius[A]	8	7	201	121	60
	Vanessa cardui	2	4	105	96	91
	Strymon melinus	3	8	97	87	90
	Papilio rutulus	0	1	23	23	100
	Coenonympha tullia insulana[A]	1	2	9	6	67
	Papilio eurymedon	0	1	7	7	100
	Neophasia menapia	0	1	4	4	100
	Anthocharis julia flora	0	1	2	2	100
More Visits to N	*Limenitis lorquini*	2	2	67	23	34
	Celastrina echo	3	3	52	5	10
	Callophrys augustinus iroides	2	0	2	0	0
	Papilio zelicaon	1	0	1	0	0
Equal Visits	*Pieris marginalis*	1	1	2	1	50

[A] at-risk species (BC red list)

Table 3.2. Results of final GLMs analyzing (a) the proportion of non-native (NN) floral area using the beta distribution (n=114 site-visits), and (b-c) the proportion of nectar foraging visits made to NN flowers using the quasibinomial distribution. Model b is based on the full data set (n=58 site-visits) whereas model c is based on data collected before 18 July (n=33 site-visits). Shown are model estimates and standard errors (SE) for standardized model predictors including day of year, site area (m^2), the proportion of NN plant species richness (SR), and the proportion of NN floral area. Model results from either (a) likelihood ratio tests or (b-c) F-tests including test statistics ([a] chi-square value (χ^2), value; [b-c] *F*-value), degrees of freedom (df: numerator, denominator), and *p*-values (*p*) are also shown. Model visualizations are shown in **Fig. 3.4** and **Fig. 3.5**. NA indicates not applicable.

Model	Response	Predictors	Estimate	SE	Test Statistic	df	*p*
a	Proportion NN Floral Area	Day of Year	1.07	0.10	NA	NA	NA
		Proportion NN Plant SR	0.24	0.10	NA	NA	NA
		Site Area	0.21	0.10	4.1	1	0.04
		Proportion NN Plant SR:Day of Year	NA	NA	4.6	1	0.03
b	Proportion Visits to NN	Proportion NN Floral Area	1.2	0.4	9.1	1,55	0.004
		Day of Year	1.4	0.5	10.5	1,55	0.002
		Proportion NN Plant SR	1.6	0.4	23.1	1,55	<0.001
c	Proportion Visits to NN	Proportion NN Floral Area	1.1	0.4	11.0	1,31	0.002
		Proportion NN Plant SR	2.0	0.9	14.9	1,31	<0.001

Figures

Figure 3.1. Map of study sites (n=10; grey circles) around Victoria, BC (black diamond) and an inset showing the location of the study area (red box) within the broader region of Vancouver Island, BC. Size of grey circles is based on the proportion of the total flowering plant species richness across the season that was non-native. Maps were created using R 4.2.0 (R Core Team 2022).

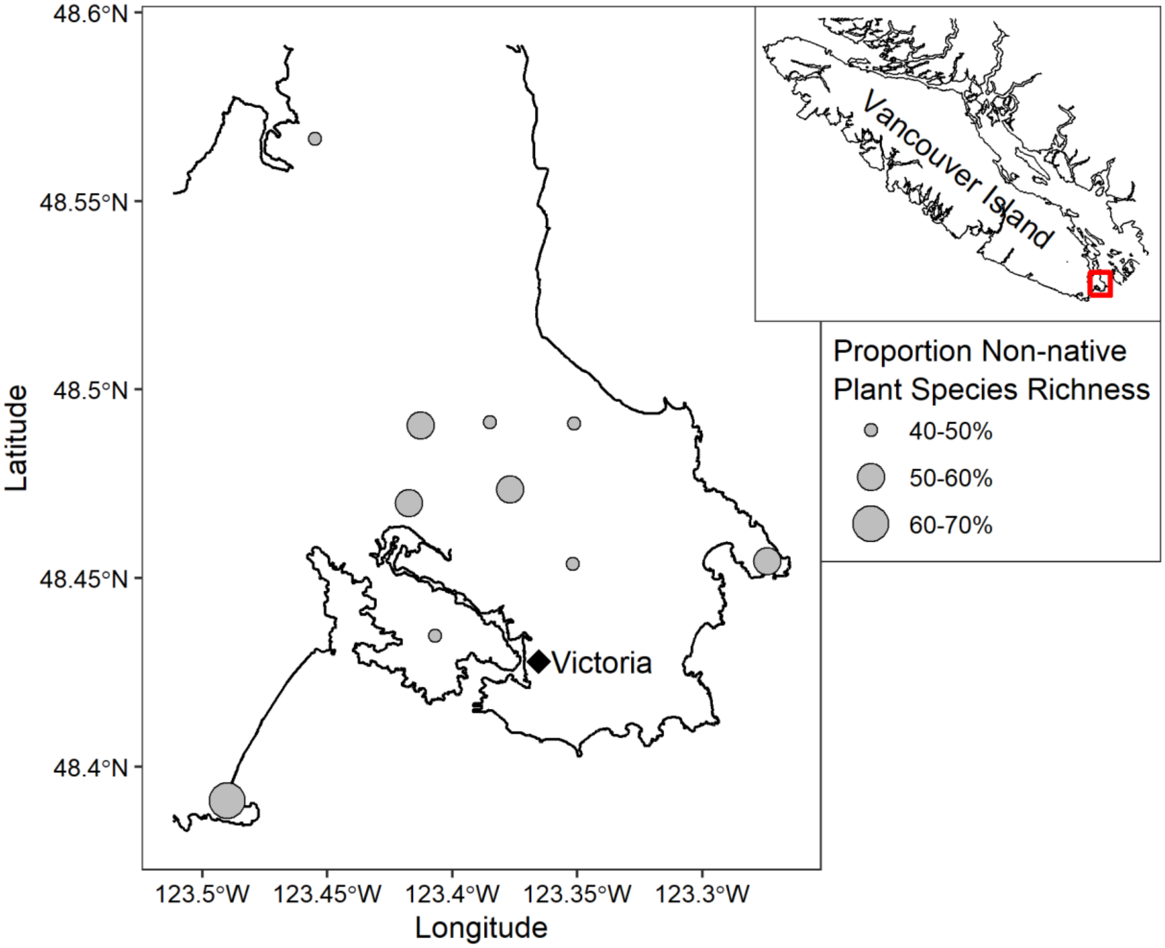


Figure 3.2. Photographs (by S. Rivest) of the top four most visited plant species including the non-native species (a-b) Hairy cat's-ear (*Hypochaeris radicata*), (c-d) Himalayan blackberry (*Rubus armeniacus*), and (e-f) Common vetch (*Vicia sativa*), as well as the native species (g-h) Common camas (*Camassia quamash*). Also show are native butterflies visiting the flowers including (b) Woodland skipper (*Ochlodes sylvanoides*), (d) Gray hairstreak (*Strymon melinus*), (f) Propertius duskywing (*Erynnis propertius*), and (h) Echo azure (*Celastrina echo*).

Figure 3.3. Phenological patterns in (a) floral area (m^2) from non-native and native plants (n=114 site-visits), and (b) the number of foraging visits made by native butterflies to native and non-native plants for nectar (n=58 site-visits). Dashed line in panel b represents 18 July (see **Methods**). To help with visualizations, an outlier in panel a (day of year=125, native floral area=2.6m^2) is not shown and curves were generated from all data points for both panels using geom smooth from the package ggplot2 (Wickham 2016).

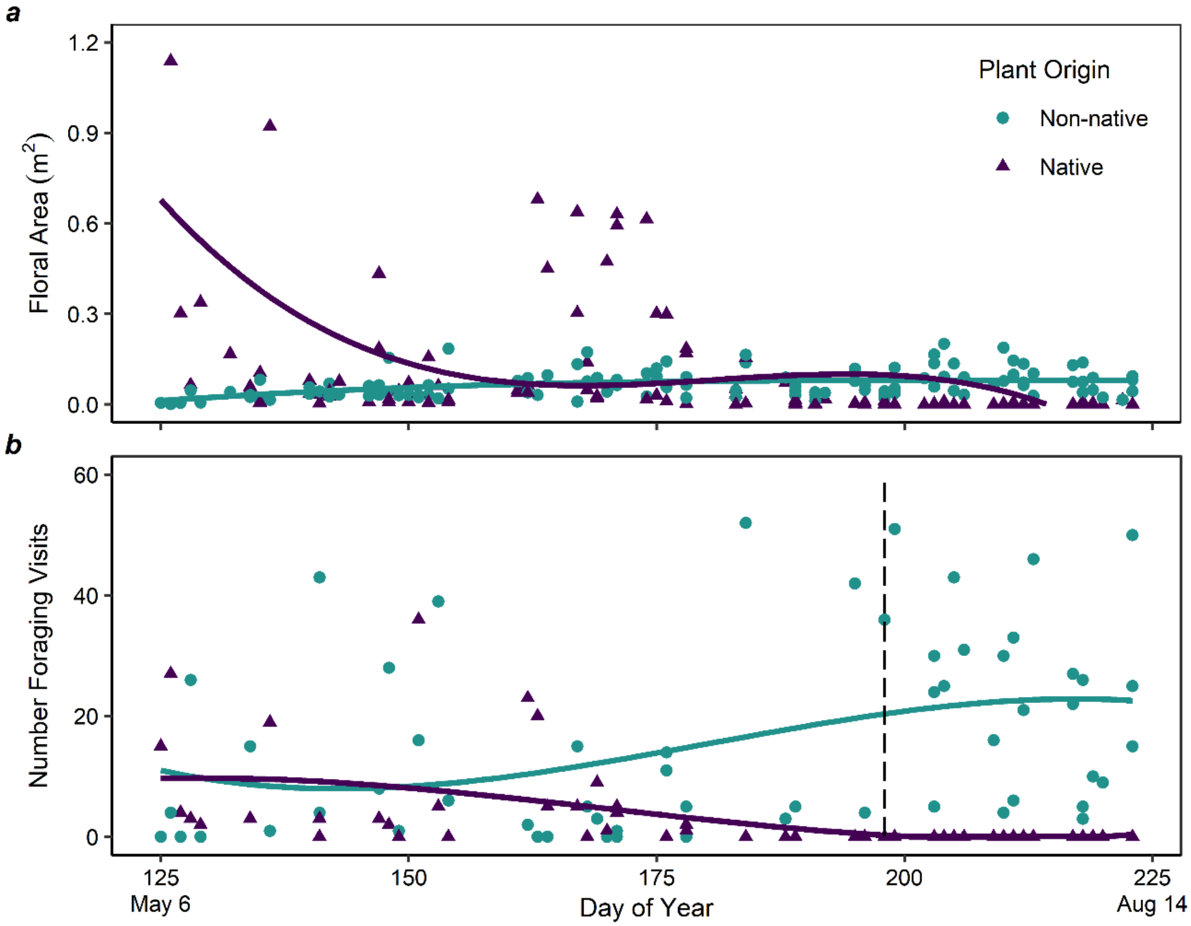


Figure 3.4. Effects of significant predictors (x-axes) on (a-b) the proportion of non-native (NN) floral area using beta GLMs (n=114 site-visits), and (c-d) the proportion of nectar foraging visits made to NN flowers using quasibinomial GLMs (n=58 site-visits). Shown are raw data (points), lines of best fit (solid lines) and 95% confidence intervals (a: ribbons; b-d: dotted lines). Also shown are model estimates (β), standard errors (SE) and *p*-values from either (a-b) likelihood ratio tests (χ^2-value) or (c-d) F-tests (F-value). Panel a shows the interaction between proportion of NN plant species richness (SR) and day of year. To visualize the interaction, the season was divided into equal thirds (early=purple squares; mid=green triangles; late=yellow circles) and model predictions were obtained for the midpoint of each third (22 May=purple lines; 24 June=green lines; 27 July=yellow lines).

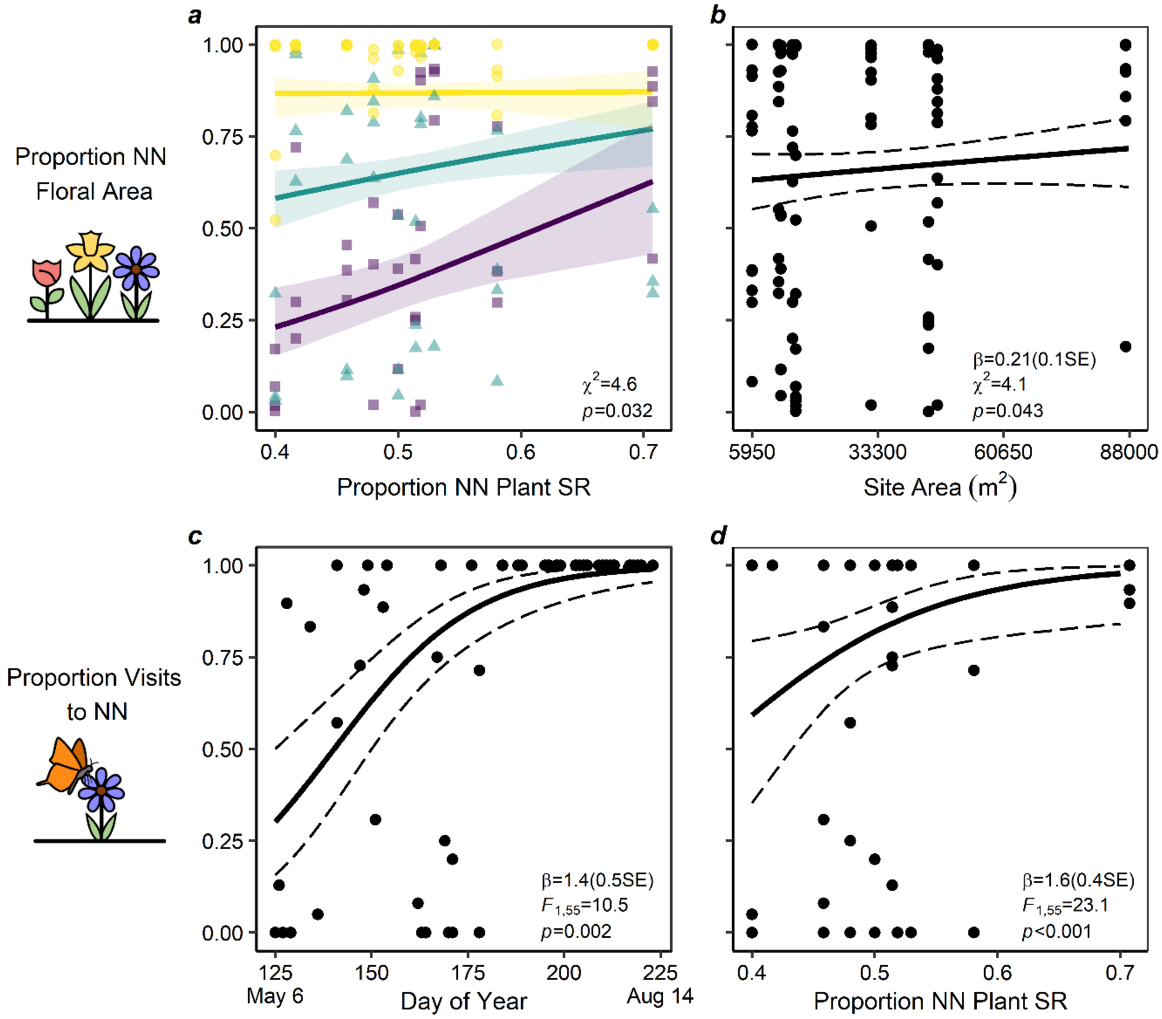
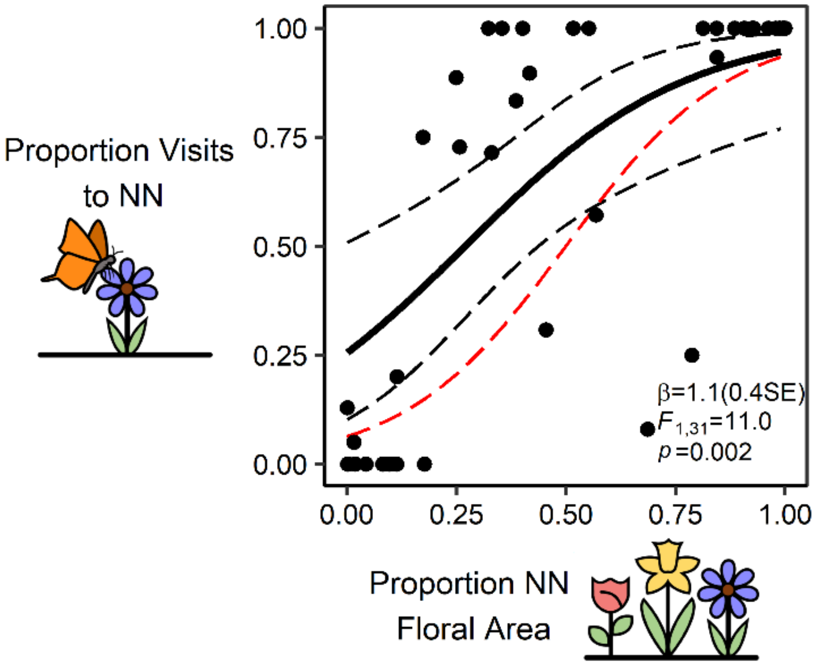


Figure 3.5. Test of the null hypothesis that native butterflies forage for nectar in proportion to nectar availability. Presented is the effect of the proportion of non-native floral area on the proportion of nectar foraging visits made to non-native flowers using quasibinomial GLMs (n=33 site-visits). Shown are raw data (dots), the line of best fit (solid line), the 95% confidence interval (dotted black lines), and the prediction from the null hypothesis (dotted red line) which was derived by fitting a quasibinomial model to data where foraging was in perfect proportion to availability. Also shown are the model coefficient (β), standard error (SE) and *p*-value from an F-test (F-value). Model was fit using only observations before 18 July.



General Conclusions

Stemming modern biodiversity loss is an important challenge for conservation biologists that is critical for the preservation of nature, ecosystems, and the services and functions that they provide. Studying the effects of different anthropogenic activities, like the introduction of non-native species and urbanization, on butterfly-plant communities can broaden our understanding of the ways in which we can conserve biodiversity. In this thesis, I contributed several key findings to this challenge. In chapter 1, I identified key factors likely to contribute to the range expansion of a newly introduced butterfly species. This will help to inform future predictions about range expansion for this species and will aid in understanding the progression of invasion success more generally. In chapter 2, I documented biotic homogenization of butterfly communities across an urban gradient, resulting in urban habitats that favoured a few, highly abundant, non-native species. This will help us to better understand the influence of urban land on the formation of biological communities and to inform management strategies aimed at supporting urban insect diversity. In chapter 3, I evaluated the relationship between native butterflies and non-native plants with respect to a key interaction—nectar provisioning—to better understand the potential positive impacts of non-native species in native ecosystems. Overall, my research provides new insights into invasion progression, urbanization, and the roles of non-native species in ecological communities, advancing our knowledge of how species are influenced by characteristics of their environment and species interactions so this information can be best utilized to mitigate anthropogenic threats and biodiversity loss.

Summary of research: Chapter 1

Predicting the range expansion of newly introduced species is critical because non-native species that are widespread and abundant have a higher likelihood of negatively impacting native biota and ecosystems (Richardson et al. 2000; Pereyra 2016). To make accurate predictions about non-native species' range expansion, detailed and relevant information on a species' ecology (e.g., resource requirements, dispersal, reproduction, species interactions) are needed, but for newly introduced species this type of information from the introduced range is typically rare. In chapter 1 of my PhD thesis, I took advantage of the presence of a newly introduced species of butterfly in Montréal, Quebec, the European Common Blue (*Polyommatus icarus*), to study the habitat suitability and dispersal abilities of a non-native insect during the early stages of its colonization, gaining insights into the progression of species invasions. At both local and landscape scales, I found that anthropogenic disturbance was important in shaping *P. icarus* abundance. At local-scales, *P. icarus* was more abundant in moderately disturbed habitat and at landscape-scales, *P. icarus* was more abundant where urban cover was higher.

My findings suggest that *P. icarus* has increased its tolerance for disturbed habitat compared to its native range in Europe which could indicate that *P. icarus* has undergone a niche shift since its introduction. Species' niches may contract, expand, or shift over time and space (Pearman et al. 2008). Since modelling efforts (i.e., species distribution models; SDMs) aimed at predicting species' distributions assume that niches are conserved, it is critical to evaluate potential niche shifts in non-native species (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). Niche shifts in the introduced range could lead to inaccurate predictions of habitat suitability if data from the native range is used to inform model predictions. However, for newly introduced species, data from the native range is often the only information available. For *P.*

icarus, more direct and standardized comparisons of habitat suitability, as well as the climatic niche, between the native and introduced ranges are needed to make definitive conclusions about whether a niche shift has occurred. These types of niche comparisons should be conducted for other newly introduced species, particularly those with negative impacts on native biodiversity, as this information is critical for accurately predicting range expansion.

One limitation of my work, and a key challenge for predicting species distributions in general, is the degree to which a species is at equilibrium with its environment (i.e., when a species occupies all suitable habitats available to it; Guisan and Thuiller 2005). For non-native species in the early stages of invasion, this assumption is typically violated (Gallien et al. 2012). This means that models based on a non-native species' distribution in the introduced range before equilibrium has been reached are likely to misrepresent suitable habitat (Barbet-Massin et al. 2018). Additionally, when equilibrium has not yet been reached, researchers may not be able to disentangle potential niche shifts from lags in niche filling (Petitpierre et al. 2012). Therefore, although my results will likely better inform predictions of *P. icarus'* distribution in Canada compared to solely using data from the native range, predictions may still be inaccurate if *P. icarus* is currently in the process of filling its niche (i.e., not at equilibrium). Unfortunately, effective control of non-native species often hinges on how quickly actions are taken before the species becomes widespread, despite potentially not being at equilibrium yet. This remains a key challenge for the study and control of all non-native species.

Results from my research also showed that *P. icarus* abundance was negatively impacted by forest cover, consistent with studies from Europe where *P. icarus* is a known grassland species (Emmet and Heath 1989; van Swaay 2002). This information can help to increase the accuracy of models predicting *P. icarus* range expansion since forests can be identified as obstacles to spread. Additionally, my results can inform management plans to control *P. icarus* spread, if desired. For instance, the preservation and/or restoration of forest fragments could help to prevent or slow *P. icarus* range expansion.

Results from this chapter provide several interesting directions for future research. I identified several biotic (e.g., presence of *L. corniculatus*) and abiotic (e.g., urban cover) factors that influenced *P. icarus* abundance, but future studies could evaluate other biotic interactions that may be important for range expansion like myrmecophily (i.e., association with ants) or interactions with other host plant species. In Europe, *P. icarus* larvae are known to have facultative mutualistic relationships with ants where nutritious secretions from caterpillars are exchanged for protection from parasitoids and/or predators (Fiedler 1990). Indeed, recent work from Montréal has documented this type of interaction between *P. icarus* and a native ant species *Lasius neoniger* (Dexheimer et al. 2021) that is known to be dominant in urban habitats (Lessard and Buddle 2005). Whether *P. icarus* interacts with any other ant species and the degree to which these myrmecophilous relationships influence its range expansion remain important areas of future research. Furthermore, I identified an association between adult *P. icarus* abundance and the presence of *L. corniculatus*, but more recent work has reported *P. icarus* oviposition on other non-native plants species (*Trifolium pratense, Medicago lupulina*; Dexheimer 2021), so future work should determine the relative importance of all possible host plants.

Building on my initial assessment, future studies are greatly needed to model the potential spatial and temporal patterns of *P. icarus* range expansion in Canada. Additionally, future studies could use genetic analyses (e.g., Ficetola et al. 2008) to determine the geographic origin, number of introductions (if >1), and genetic diversity of Canadian populations of *P. icarus*. This information could help inform range expansion predictions and subsequent management decisions. For example, non-native species that have undergone genetic bottlenecks, could be more limited in their ability to adapt to novel conditions and expand their ranges, however, this question is still under debate (Dlugosch and Parker 2008; Prentis et al. 2008). Lastly, future research is needed to evaluate the potential impacts of *P. icarus* in Canada so that the degree of management needed is better understood. The preferred larval host plant for *P. icarus* is *L. corniculatus*, but larvae can forage on other legumes from the Fabaceae family (Thomas and Lewington 1991; Tolman and Lewington 2008). As Canada grows a lot of legume crops including chickpeas, soybeans, and lentils (Statistics Canada 2022), *P. icarus* could have an impact on these agroecosystems. Similar impacts have been reported for other non-native butterflies like the Cabbage White butterfly (*Pieris rapae*) which is a known pest on cultivated mustards such as cabbage, broccoli, and cauliflower (Layberry et al. 1998). *P. icarus* may also impact native butterflies by competing for resources like habitat, larval host plants, and mutualistic ant partners since several species of Canadian butterflies are myrmecophilous and/or overlap in host plant usage with *P. icarus*. For example, native Eastern-tailed Blue (*Cupido comyntas*) larvae are myrmecophilous and can readily feed on non-native Red Clover (*Trifolium pratense*) which are also fed on by *P. icarus* larvae in Canada (Layberry et al. 1998; Dexheimer 2021).

Summary of research: Chapter 2

Evaluating the effects of urbanization on native biodiversity is critical given that more than half of the global human population, and 87% of Canadians, live in cities with further increases predicted over the next several decades (Statistics Canada 2017; United Nations 2019). While changes in butterfly community structure in response to urbanization have been well studied (Ramírez-Restrepo and MacGregor-Fors 2017), less is known about whether urbanization favours species with particular functional attributes (i.e., traits). Yet, this information is necessary to accurately predict which species are most prone to decline. Furthermore, relatively little is known about whether urbanization leads to the biotic homogenization of butterfly communities. In chapter 2 of my PhD research, I evaluated the effects of urban land cover on butterfly communities in Montréal, Quebec and tested the hypothesis that urbanization leads to biotic homogenization. I found that there were clear shifts in the structure of urban butterfly communities in favour of a few, abundant, non-native species, resulting in biotic homogenization. I also found that these shifts were not influenced by three key butterfly traits (wingspan, voltinism, larval diet breadth).

My results indicate that urban areas support less diverse butterfly communities than surrounding areas and that native butterflies should be the focus of future conservation efforts. Continued urban growth may lead to further reductions in the amount and quality of habitable space for butterflies, potentially contributing to future species declines and extinctions. Furthermore, urban growth could promote the establishment of new non-native butterflies or the proliferation of existing ones (see Chapter 1) which could have numerous impacts on native species and ecosystems. Since non-native plants tend to be more dominant in urban areas (Pyšek et al. 2010; Potgieter et al. 2017), urban growth could also have indirect implications for butterfly communities via changes in plant community composition.

Beyond the structural outcome of biotic homogenization (i.e., non-natives replace natives), my results could have higher order implications for ecosystem functions and services. Research suggests that homogenized communities can have reduced ecosystem functionality given that there are fewer different species with distinct roles (Olden et al. 2004; van der Plas et al. 2016). This can lead to reductions in ecosystem stability and resilience, increasing the vulnerability of ecosystems to environmental changes (Olden et al. 2004). Indeed, the composition and variety of functional traits (‘response’ and/or ‘effect’ traits) in a community can influence ecosystem function and stability (Cadotte et al. 2011; Díaz et al. 2013). For example, van der Plas et al. (2016) showed that landscapes with lower turnover in tree species composition, in other words, taxonomic homogenization, typically had fewer functions (e.g., timber production, litter decomposition) compared to landscapes with higher turnover. For butterflies, common ecosystem functions include pollination and nutrient cycling (Merckx et al. 2013). Disruptions in either of these functions as a result of reduced functional diversity could have impacts on species that interact with butterflies (e.g., predators) or species that occupy similar habitats (e.g., flowering plants). Future studies should quantify ecosystem functions provided by butterflies in urban compared to rural environments to better understand the consequences of biotic homogenization.

A limitation of this work, and a key knowledge gap in urban-insect research, is our lack of understanding about the mechanisms underlying native biodiversity declines in cities. This poses a problem since knowledge of the most important factors driving changes in butterfly communities could be used to make specific conservation recommendations. My research has focused on the patterns between butterfly communities and urban land cover as an important first step, but future studies should identify what specific urban characteristics (e.g., host plant availability, temperature, pollution/chemical use, landscape configuration, habitat size, vehicle traffic, human interventions) have the biggest impact on butterflies. For example, if temperature is a driving factor of butterfly declines in cities, tree planting could be used as a strategy to reduce microclimate temperatures whereas prioritizing the connectivity of parks would be a better strategy if fragmentation is a driving factor.

Summary of research: Chapter 3

The frequency of species introductions is on the rise globally (Meyerson and Mooney 2007; Hulme 2009), leading to increases in the interactions between native and non-native species (Pearse and Altermatt 2013). The negative impacts of non-native species have been well-documented (e.g., Bradley et al. 2019), but less is known about the positive or neutral effects. In chapter 3 of my PhD research, I studied the role of non-native plants in the nectar diets of native butterflies in an at-risk Garry oak savanna on Vancouver Island, British Columbia. I found that non-native flowers were well integrated into butterfly nectar diets, that butterflies increased their usage of non-native nectar later in the season when native plants were no longer flowering, and that butterflies selected non-native flowers more often than expected based solely on flower availability.

I found that non-native flowers were the only source of nectar available to native butterflies later in the season which could indicate that the nectar foraging period, and thus the flight season, for butterflies has lengthened over recent decades. However, whether this is the case depends on the historical context of the flowering plant community which we have limited knowledge of. Most non-native plant species in southeastern Vancouver Island have been present since the 1960s, but have expanded their ranges to occupy more sites in recent years (McCune and Vellend 2013). In Garry oak savannas, all sites surveyed in 2009 had at least some non-native plant species, whereas in the 1960s many sites had only native plant species (Roemer 1972; McCune and Vellend 2013). Unfortunately, historical data on the flowering times for these plant species is lacking, making it difficult to conclude how the butterfly nectar foraging period may have changed in recent decades. If native plants were historically restricted in how late they could bloom (e.g., due to drought intolerance), then the non-native plants I observed may have colonized vacant temporal niches. In this case, native butterflies foraging on non-native flowers later in the season may have extended their flight period to utilize these newly available nectar sources. However, it is also possible that some native plants historically flowered later in the season, but have been outcompeted by non-native plants in recent decades. In this case, native butterflies present later in the season may have recently switched to foraging on non-native plants, but the length of the nectar foraging period would have remained the same. My research indicates that the temporal context within a growing season is important for evaluating butterfly visitation to flowering plants, but the larger historical context is needed to determine whether butterfly nectar foraging periods have lengthened.

My findings also have implications for best practices in habitat management and restoration. Non-native plant eradication and control are common management strategies used in many ecosystems, including Garry oak savannas (GOERT 2011). This practice is likely appropriate when non-native plants have clear negative impacts on native biodiversity, but the benefits of removing non-native plants may decrease if some native species rely on these plants as sources of food or habitat. Therefore, knowing when and where non-native plant removals will have negative impacts on native species is critical for maximizing conservation benefits. For example, managers in the Garry oak ecosystem could focus their eradication efforts on non-native plants that flower earlier in the season, since butterflies are likely to still have sufficient food resources in the spring even after non-native plants have been removed. Alternatively, if managers are motivated to eradicate all non-native plants species because of known negative impacts, then my results could be used by managers to prioritize the timing of supplemental native species plantings to ensure butterflies have adequate food resources across the entire season.

In practice, the decision to eradicate non-native plants remains complex since there are many native species that interact with non-native plants, beyond just butterflies, with implications for the entire ecosystem. For example, non-native Himalayan blackberry (*Rubus armeniacus*) was a highly visited nectar source amongst native butterflies in my study, but this plant is also known to provide habitat to non-native herbivores (e.g., rabbits, deer) that in turn negatively impact native plants (e.g., spring forbs) through grazing (GOERT 2011). Lessons learned from my research indicate that management teams should carefully evaluate the temporal context, both within a season and across past decades, of the interactions that occur between native and non-native species, before taking any action.

To help bridge the gap between my findings and conservation decision-making, there are several important directions for future research. First, future studies could examine native butterfly preferences for different flowers by conducting controlled choice experiments. Second, to better understand native butterfly decision-making, future work could explore factors other than flower availability that might be driving butterflies’ selection of nectar sources like flower morphology, colour, scent, as well as nectar characteristics like viscosity, amino acid content, and sugar concentration. Third, future research is needed to evaluate whether the patterns I found here (i.e., high usage of non-native plants) occur in other ecosystems. For instance, in systems where less invasion has occurred or where invasion has occurred over a shorter time period.

Lessons and limitations

My thesis research has relied on methodologies that have some limitations. First, my studies were based on observational field surveys conducted over 1–2 years. Field surveys are useful for understanding patterns and processes at ecologically relevant scales, providing insights that lab studies cannot. However, interannual variability in different factors (e.g., weather) may limit the applicability of conclusions from field studies when they are conducted over relatively short time periods (i.e., year effects; Vaughn and Young 2010). For example, in chapter 1 of my thesis research, weather conditions in 2017 and 2018 could have been particularly optimal for *P. icarus*, leading to higher estimates of abundance than would have been recorded in other years. Furthermore, my research has been observational which, although useful, is limited by its inability to elucidate underlying mechanisms. For example, in chapter 2 of my thesis research, I examined spatial correlations between butterfly communities and urban land cover. This approach can tell us the way in which urbanization influences butterfly community structure (i.e., reduced diversity/richness), but it does not help us figure out how or why these patterns occur.

Overall conclusions

My thesis research was motivated by a need to effectively conserve biological communities in an age of major biodiversity loss. I have explored two anthropogenic threats, non-native species introductions and urbanization, in the context of butterfly-plant communities to better understand how species are influenced by characteristics of their environments and by key species interactions. I have focused on specific study systems, Montréal, QC and Victoria, BC, to achieve my research goals which has enabled me to better inform management strategies in these locations. I have also focused my research on butterflies which are often used as indicator species that can represent responses from other insect groups (Thomas 2005). Despite insects being one of the most abundant and diverse groups of species, research, monitoring, policy, and conservation have all lagged behind compared to other taxonomic groups, but are greatly needed to help stem global insect declines (van der Sluijs 2020). My thesis research has contributed to solving some of these issues by revealing new insights into the responses of butterflies to urbanization and the introduction of non-native species, helping to inform and prioritize management efforts. During the Anthropocene, finding smarter and more efficient ways to maximize conservation gains is critical given that time, effort, and money spent on conservation is limited, yet the impacts from human activities are only increasing.

Supplementary Materials S1: Chapter 1

A) Additional Information for Analyses

S1.1. Effect of year
S1.2. Effect of disturbance on local-scale continuous predictors

B) Tables

Table S1.1. Results of local-scale models using only data from 2017
Table S1.2. Results of full local- and landscape-scale models
Table S1.3. Differences across mark-release-recapture studies of *P. icarus* in the native range

C) Figures

Figure S1.1. Relationships between disturbance level and plant community structure
Figure S1.2. AIC values for landscape-scale habitat suitability models for *P. icarus* at multiple spatial scales
Figure S1.3. Abundance of *P. icarus* butterflies across the season
Figure S1.4. Mean and maximum abundance of all butterfly species

A) Additional Analyses and Results

S1.1. Effect of year

Data collection for our habitat suitability analyses occurred over two years with 39 sites surveyed in 2017 and an additional 5 sites in 2018. To explore potential differences in counts of European Common Blue butterflies (*Polyommatus icarus*) due to year, we modelled abundance using the 2017 data only. Results from this model were similar to results from models fit using the full data set (**Table S1.2**). Therefore, we combined the two years of survey data for both the local- and landscape-scale analyses.

S1.2. Effect of disturbance on local-scale continuous predictors

To model the influence of disturbance level on our continuous plant community structure variables (i.e., grass, forb, bare ground, total flowers, canopy cover), we fit individual beta regression models from the betareg package since all response variables in these analyses were continuous proportions (Ferrari and Cribari-Neto 2004; Cribari-Neto and Zeileis 2010; Douma and Weedon 2019). Total flowers and canopy cover had insufficient data to be analysed. We used likelihood ratio tests to assess model fit and pseudo-R^2 values to determine model goodness of fit.

Disturbance level was a significant predictor of all continuous plant community structure variables analysed ($p \leq 0.003$ in all cases; **Fig. S1.2bcd**). For each predictor, we also conducted post-hoc comparisons of marginal means between the levels of disturbance using Tukey's tests from the multcomp package (**Fig. S1.2**) (Hothorn et al. 2008).

B) Tables

Table S1.1. Results of local-scale habitat suitability models for European Common Blue butterflies (Polyommatus icarus) using generalized linear models with a negative binomial distribution and only the data from 2017 (n=39 sites). Shown are pseudo-R^2 values for all models and results from likelihood ratio tests (type II anova) including chi-square statistics (χ^2), degrees of freedom (df), and *p*-values. Model coefficients and standard errors (SE) are also shown where applicable.

Model	R^2	Term	Coefficient	SE	χ^2	df	*p*-value
Disturbance	0.25	Disturbance Index	N/A	N/A	13.19	3	0.004
Plant	0.30	Bird’s Foot Trefoil, *Lotus corniculatus*	N/A	N/A	8.02	1	0.004
		Grass	-2.67	1.34	5.27	1	0.02

Table S1.2. Results of full models for European Common Blue butterflies (*Polyommatus icarus*) using generalized linear models with a negative binomial distribution and data from 2017 and 2018 (n=44 sites). Shown are pseudo-R^2 values for all models and the results from likelihood ratio tests (type II anova) including chi-square statistics (χ^2), and p-values. Model coefficients and standard errors (SE) are also shown where applicable. Degrees of freedom was 1 in all cases.

Scale	Model	R^2	Term	Coefficient	SE	χ^2	p-value
Local	Plant	0.45	Birds’ Foot Trefoil, *Lotus corniculatus*	N/A	N/A	8.50	0.004
			Grass	-1.71	1.72	1.13	0.29
			Canopy Cover	-0.61	1.75	0.11	0.74
			Bare Ground	3.80	2.04	3.29	0.07
			Total Flowers	5.83	9.09	0.51	0.47
Landscape	N/A	0.48	Urban	2.82	0.70	11.24	<0.001
			Forest	-2.59	0.88	7.35	0.007
			Water	-3.51	2.20	2.26	0.13

Table S1.3. Differences across mark-release-recapture studies of European Common Blue butterflies (*Polyommatus icarus*) in the native range including the general methodological approach, study area (km^2), recapture rate (%), and estimate of dispersal including mean (m) and maximum (m).

Methodology description	Area	Recapture Rate	Mean	Maximum	Reference
Could recapture marked individuals anywhere. Recaptures on the same day as marking were excluded.	0.49	12%	165	671	Gutiérrez et al. 2001
Could recapture marked individuals only outside of a 25 m x 25 m “release area”.	0.11	20%	191	510	Kuussaari et al. 2014

C) Figures

Figure S1.1. The effect of disturbance level on plant community structure variables including (a) Bird's Foot Trefoil (*Lotus corniculatus*) occurrence and the proportional cover of (b) grass, (c) forb, and (d) bare ground (n=44 sites). Raw data (closed circles) have been jittered in panels b, c and d to increase visibility. Results of overall Fisher's exact tests (panel a) and beta regression models (panels b, c, d; see **S1.2.**) indicate an overall significant effect of disturbance level (p<0.05 in all cases). However, post-hoc analyses conducted in panel a were unable to detect significant pair-wise differences between disturbance levels after the Bonferroni correction, likely due to our smaller sample size. Note that the y-axis range varies across panels.

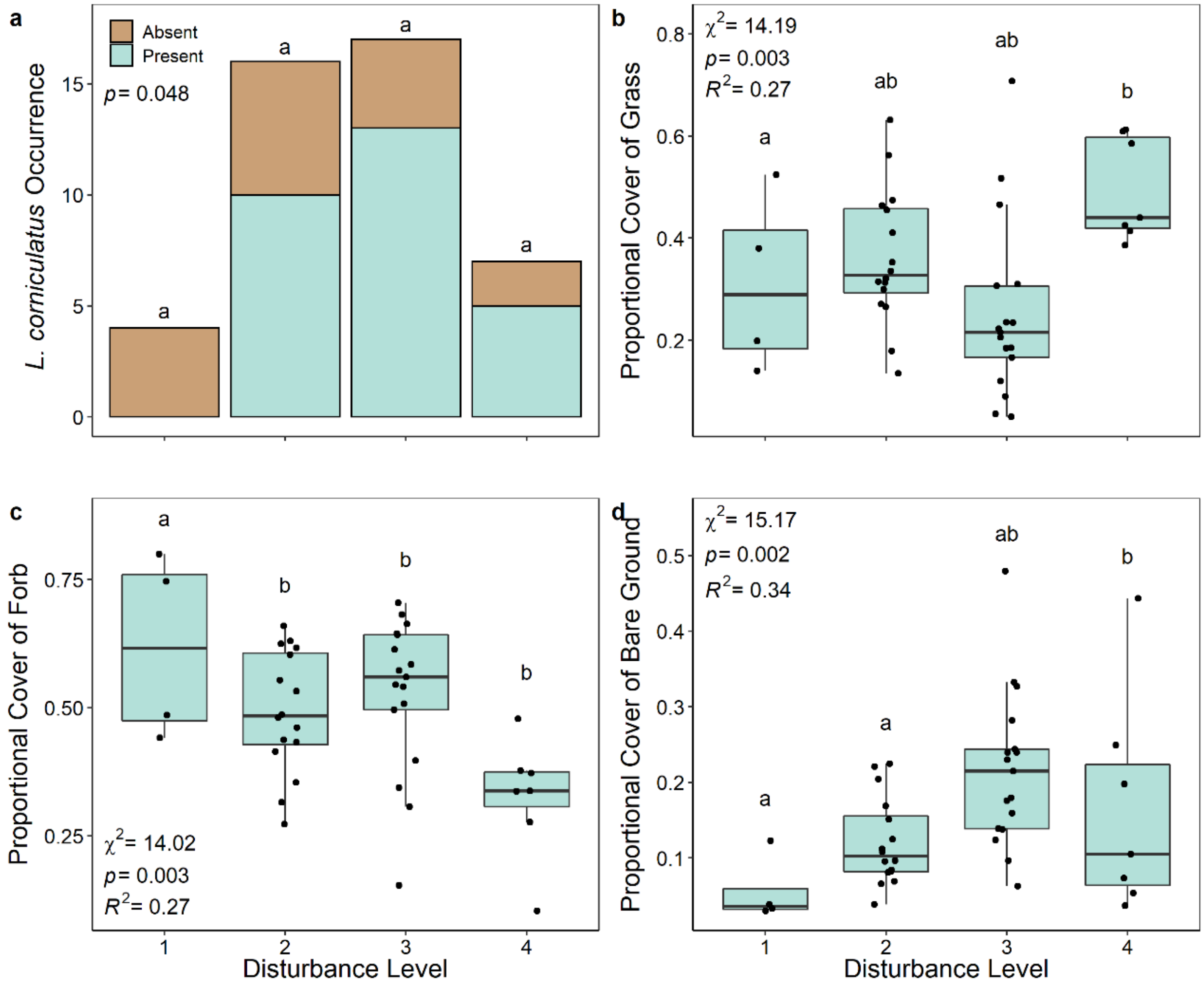


Figure S1.2. AIC values for landscape-scale habitat suitability models for European Common Blue butterflies (*Polyommatus icarus*) using generalized linear models with a negative binomial distribution at multiple spatial scales (*n*=44 sites). The landscape scale (m) represents the radius of a circular area surrounding each site within which the land cover types were measured. All models include the proportional cover of urban land, forest, and water in the surrounding landscape.

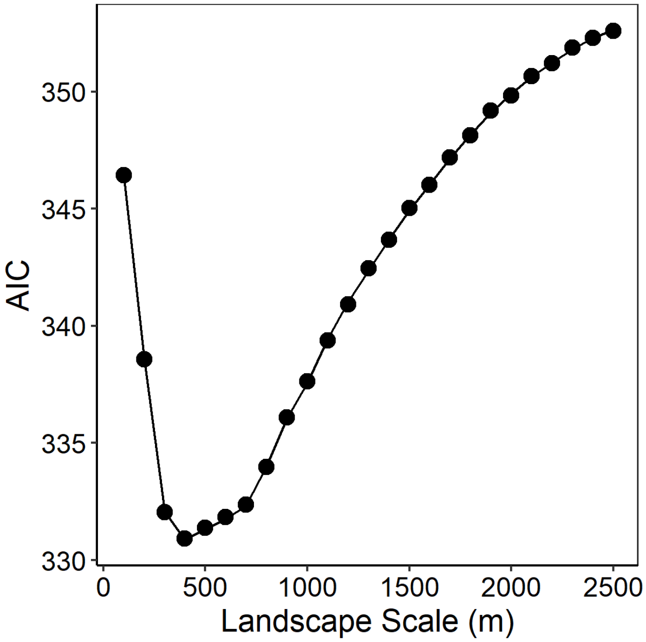


Figure S1.3. Abundance of European Common Blue butterflies (*Polyommatus icarus*) counted during each site-visit at all 44 sites across Montréal, Quebec from May to August 2017 and 2018.

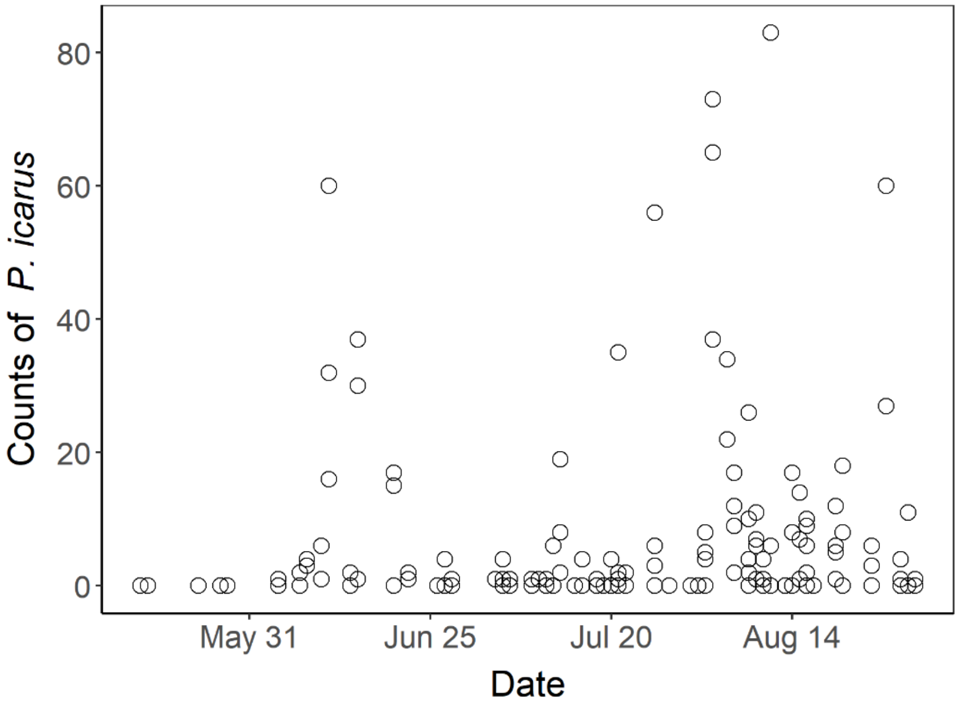
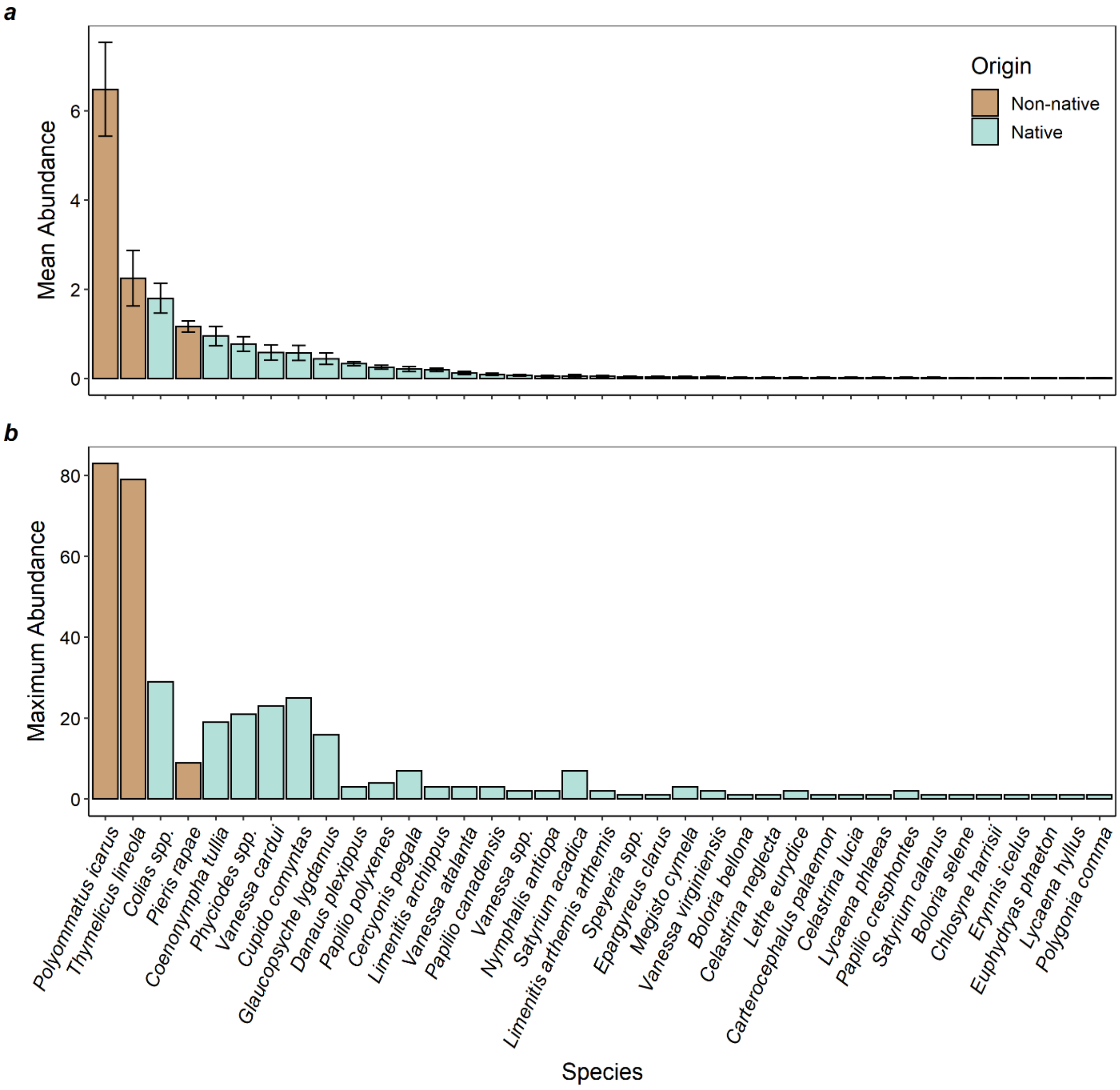


Figure S1.4. Comparison of all butterfly species observed including (a) mean abundance per site-visit (± standard error) and (b) maximum abundance recorded during a single site-visit.



Supplementary Materials S2: Chapter 2

A) Tables

B) Figures

A) Tables

Table S2.1. Traits of 42 butterfly species observed including family, mean wingspan (mm), mean voltinism (number generations per season), and larval diet breadth (1=one plant species, 2=one plant genus, 3=one plant family, 4=one plant order, 5=multiple plant orders). Non-native species are in bold.

Family	Species	Wingspan	Voltinism	Larval Diet
Hesperiidae	*Carterocephalus palaemon*	25.5	1	3
Hesperiidae	*Epargyreus clarus*	41	1.5	3
Hesperiidae	*Erynnis icelus*	26.5	1	5
Hesperiidae	***Thymelicus lineola***	**22.5**	**1**	**3**
Lycaenidae	*Celastrina lucia*	23	1	5
Lycaenidae	*Celastrina neglecta*	26	2.5	5
Lycaenidae	*Cupido comyntas*	21	2.5	3
Lycaenidae	*Glaucopsyche lygdamus*	23	1	3
Lycaenidae	*Lycaena hyllus*	30.5	1.5	3
Lycaenidae	*Lycaena phlaeas*	25.5	1.5	2
Lycaenidae	***Polyommatus icarus***	**29.5**	**3**	**3**
Lycaenidae	*Satyrium acadica*	28	1	2
Lycaenidae	*Satyrium calanus*	29.5	1	4
Nymphalidae	*Boloria bellona*	39.5	2	2
Nymphalidae	*Boloria selene*	43	1.5	2
Nymphalidae	*Cercyonis pegala*	48	1	3
Nymphalidae	*Chlosyne harrisii*	35.5	1	1
Nymphalidae	*Coenonympha tullia*	33	1.5	3
Nymphalidae	*Danaus plexippus*	99	2.5	2
Nymphalidae	*Euphydryas phaeton*	57	1	5
Nymphalidae	*Lethe eurydice*	43	1	2
Nymphalidae	*Limenitis archippus*	67	2	3
Nymphalidae	*Limenitis arthemis arthemis*	62.5	2	5
Nymphalidae	*Megisto cymela*	35.5	1	3
Nymphalidae	*Nymphalis antiopa*	62	3	5
Nymphalidae	*Phyciodes batesii*	31.5	1	2
Nymphalidae	*Phyciodes cocyta*	30	1.5	2
Nymphalidae	*Phyciodes tharos*	27.5	2.5	2
Nymphalidae	*Polygonia comma*	46.5	2	4
Nymphalidae	*Speyeria cybele*	75	1	2
Nymphalidae	*Speyeria aphrodite*	62	1	2
Nymphalidae	*Speyeria atlantis*	57	1	2
Nymphalidae	*Vanessa atalanta*	51	2.5	3
Nymphalidae	*Vanessa cardui*	54	2.5	5
Nymphalidae	*Vanessa virginiensis*	46.5	2.5	3
Papilionidae	*Papilio canadensis*	71.5	1	5
Papilionidae	*Papilio cresphontes*	98	2	3
Papilionidae	*Papilio polyxenes*	73	2	3
Pieridae	*Colias philodice*	43	1	3
Pieridae	*Colias eurytheme*	44.5	2.5	3
Pieridae	*Colias interior*	41	1	2
Pieridae	***Pieris rapae***	**39.5**	**3**	**3**

Table S2.2. Summary statistics for butterfly communities surveyed in 2017 or 2018 including number of sites surveyed, species richness, and total abundance. Also included are site-level statistics including the mean and median richness and abundance per site.

	Number of sites	Species richness	Total abundance	Mean richness per site	Median richness per site	Mean abundance per site	Median abundance per site
2017-only	39	36	1887	9.7	10	48.4	43
2018-only	5	11	907	8	8	181.4	177
Both years	44	42	2794	9.5	9	63.5	44

B) Figures

Figure S2.1. AIC values for models analyzing the effects of urban cover across a range of spatial scales on (a) species richness, (b) total abundance, (c) evenness, (d) wingspan (mm), (e) voltinism, and (f) larval diet breadth (n=44 sites). Model fits are from (a) poisson GLMs, (b) negative binomial GLMs, (c) beta GLMs, (d, e) LMs, and (f) gamma GLMs. The spatial scale (m) represents the radius of a circular area surrounding each site within which the proportion of urban land cover was measured. Number insets represent the scale at which AIC was lowest.

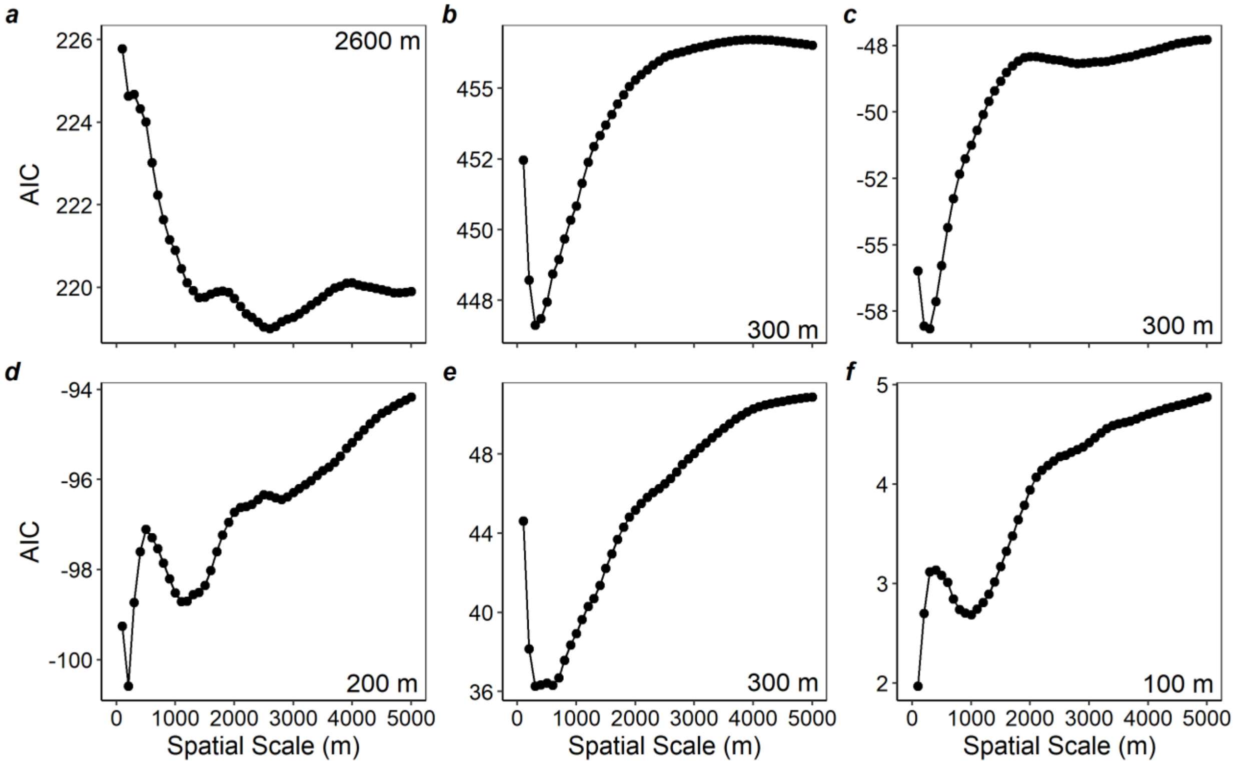


Figure S2.2. Total abundance per site (n=44 sites) for the three non-native butterfly species that occur in the study region across the urban gradient (n=1642 individuals). Urban cover was measured within circular buffers of radius 300 m.

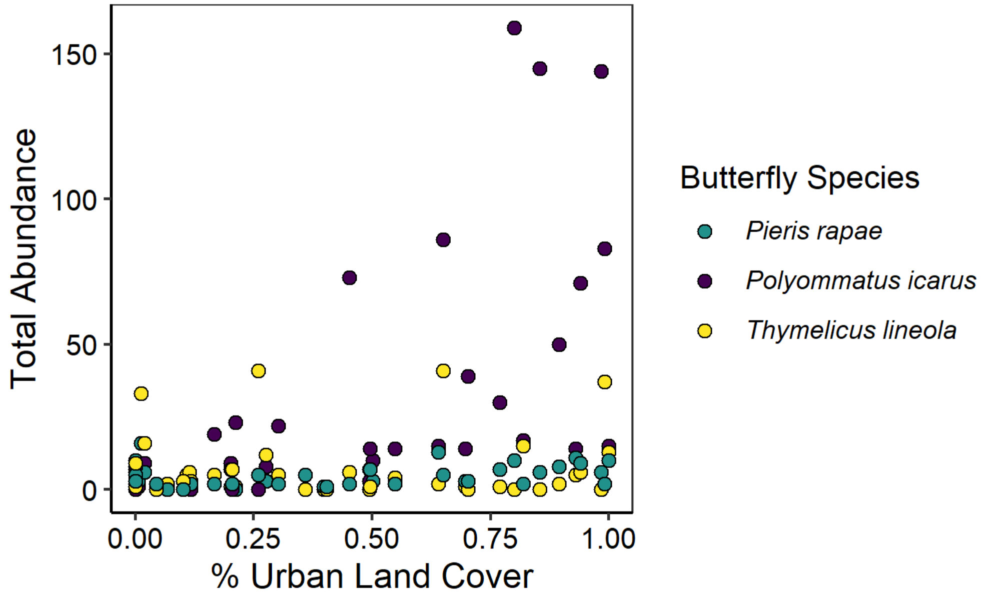


Figure S2.3. Comparison of all butterfly species observed including (a) total abundance summed across all sites and visits, and (b) mean abundance per site-visit (± standard error).

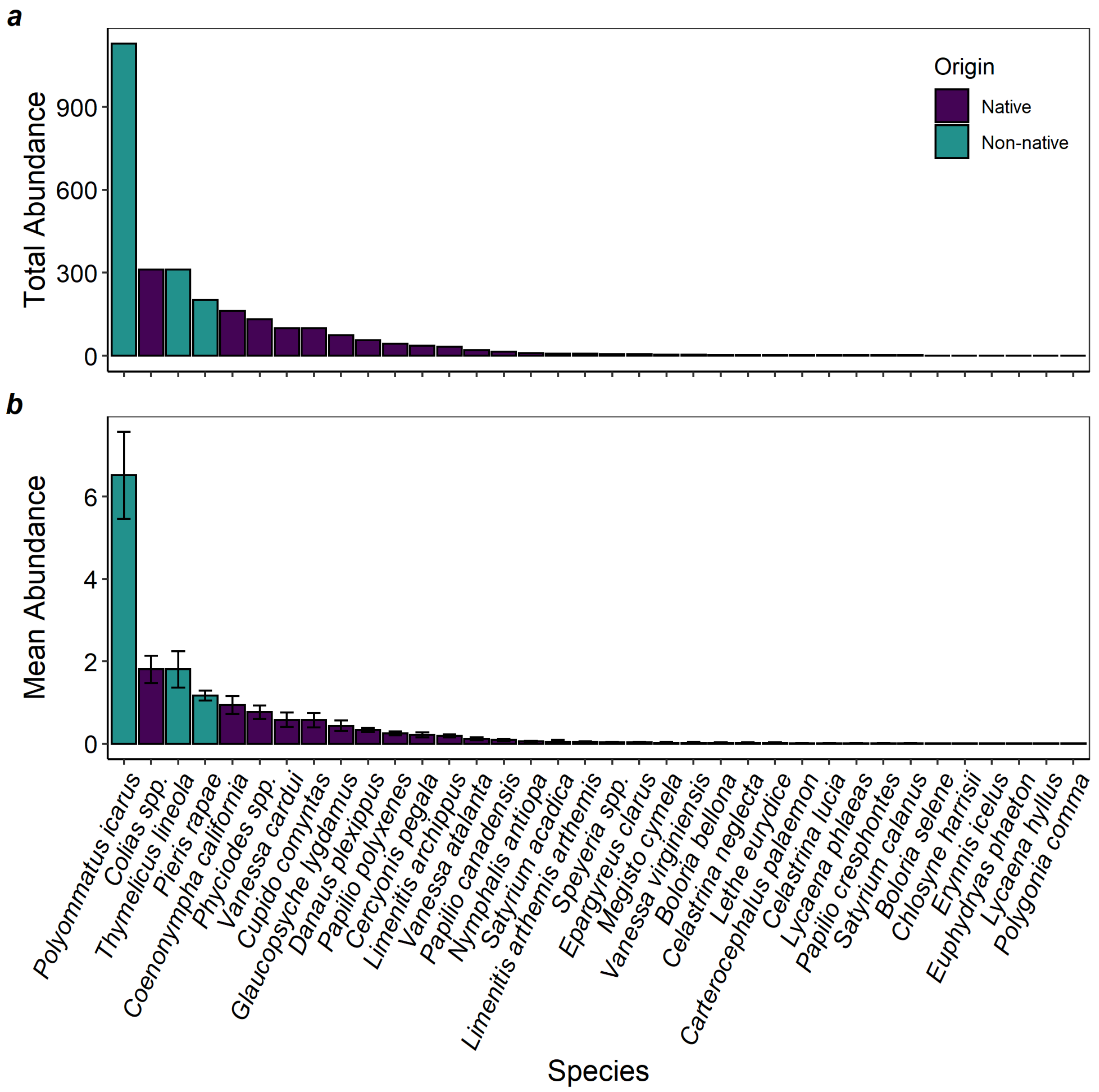
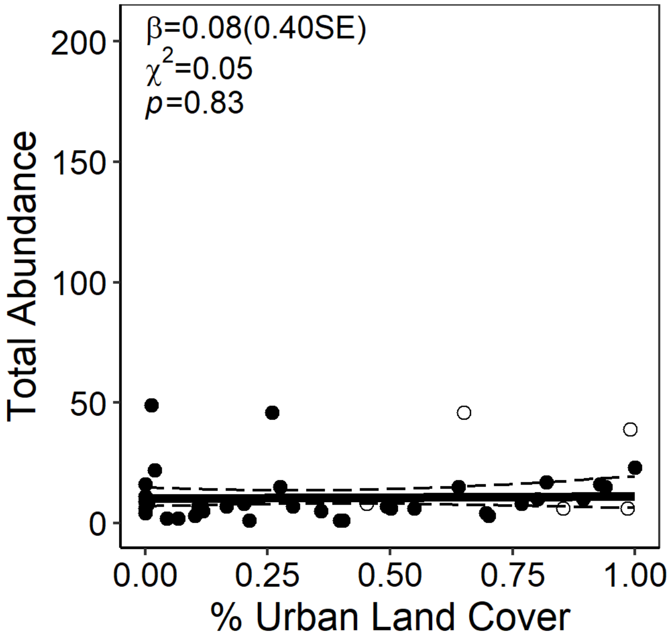


Figure S2.4. Effect of urban cover on non-native total abundance when excluding *P. icarus* using negative binomial GLMs (n=44 sites). Shown are raw data (dots), predicted line of best fit (black line), 95% confidence intervals (dotted lines), model estimate (β), standard error (SE), and results from a likelihood ratio test including χ^2-value and p-value. The year of survey had a significant effect, so model predictions are shown for the year 2017 and raw data are colour-coded by year (2017=black, 2018=white). Proportion of urban cover was calculated at spatial scales of 300 m.



Supplementary Materials S3: Chapter 3

A) Tables

B) Figures

A) Tables

Table S3.1. Flowering plant species with nectar rewards (n=81) including scientific names, origin (N=native; NN=non-native) and flower characteristics such as symmetry, shape, and colour. Also shown are the equations used to estimate flower surface area (l=length; w=width; r=radius; h=height) and the corresponding mean surface area (mm^2) for each plant species calculated from 10-20 randomly chosen individuals. The presence and/or quantity of nectar rewards is noted based on past work that either measured nectar directly or made observations of animals (e.g., butterflies, birds, bees) visiting flowers to obtain nectar rewards.

Scientific Name	Origin	Symmetry	Shape	Colour	Surface Area Equation	Mean Surface Area	Nectar Presence or Quantity	Nectar Presence References
Achillea millefolium	NN	Radial	Open	White	lw	4674	>10 μg/day	Hicks et al. (2016)
Acmispon micranthus	N	Bilateral	Tubular	Yellow	lw	31	Unknown	
Allium acuminatum	N	Radial	Tubular	Red-pink	πr^2	108	Present	Prior et al. (2009)
Allium cernuum	N	Radial	Tubular	Red-pink	πr^2	58	Present	Hilty (2020a)
Anthriscus caucalis	NN	Radial	Open	White	lw	214	Present	Winkler et al. (2009)
Anthemis cotula	NN	Radial	Tubular	Yellow	πr^2	278	Present	Yurtsever et al. (2010)
Bellis perennis	NN	Radial	Tubular	Yellow	πr^2	295	>10 μg/day	Hicks et al. (2016)
Brassica rapa	NN	Radial	Open	Yellow	lw	152	Present	Davis et al. (1996)
Brodiaea coronaria	N	Radial	Tubular	Blue-violet	πr^2	604	Present	Prior et al. (2009)
Camassia quamash	N	Radial	Open	Blue-violet	πr^2	1320	Present	Prior et al. (2009)
Capsella bursa-pastoris	NN	Radial	Open	White	lw	37	9.052 μg/day	Hicks et al. (2016)
Centaurea cyanus	NN	Radial	Tubular	Multi	πr^2	1007	>10 μg/day	Hicks et al. (2016)
Cerastium arvense	NN	Radial	Open	White	πr^2	191	Present	LeBeau et al. (2017)
Cirisium vulgare	NN	Radial	Tubular	Red-pink	$2\pi rh+\pi r^2$	1493	>10 μg/day	Hicks et al. (2016)
Clarkia amoena lindleyi	N	Radial	Open	Red-pink	πr^2	346	Present	Young-Mathews (2012)
Claytonia perfoliata	N	Radial	Open	White	πr^2	44	Present	Russell (2013)
Collinsia parviflora	N	Bilateral	Tubular	Blue-violet	lw	30	Unknown	
Coriandrum sativum	NN	Radial	Open	White	lw	1173	Present	Vattala et al. (2006)
Cotoneaster franchetii	NN	Radial	Open	Red-pink	πr^2	20	Present	Brun (2021)
Daucus carota	NN	Radial	Open	White	πr^2	5972	>10 μg/day	Hicks et al. (2016)
Delphinium menziesii	N	Bilateral	Tubular	Blue-violet	πr^2	515	Present	Caldwell (2014)
Eriophyllum lanatum	N	Radial	Tubular	Yellow	πr^2	1225	Present	Pavek (2012)
Eschscholzia californica	NN	Radial	Open	Yellow	πr^2	1018	10.317 μg/day	Hicks et al. (2016)
Fumaria officinalis	NN	Bilateral	Tubular	Red-pink	lw	28	>10 μg/day	Hicks et al. (2016)
Galium aparine	N	Radial	Open	White	πr^2	8	Present	Russell (2013)
Geranium molle	NN	Radial	Open	Red-pink	πr^2	72	>10 μg/day	Hicks et al. (2016)
Geranium robertianum	NN	Radial	Open	Red-pink	πr^2	176	>10 μg/day	Hicks et al. (2016)
Hieracium albiforum	N	Radial	Tubular	White	πr^2	68	Present	Caldwell (2014)
Holodiscus discolor	N	Radial	Open	White	πr^2	4257	Present	Russell (2013)
Hyacinthoides spp.	NN	Radial	Tubular	Blue-violet	πr^2	219	Present	Corbet (1999)

Hypochaeris glabra	NN	Radial	Tubular	Yellow	πr^2	42	Unknown	
Hypochaeris radicata	NN	Radial	Tubular	Yellow	πr^2	684	>10 µg/day	Hicks et al. (2016)
Lapsana communis	NN	Radial	Tubular	Yellow	πr^2	113	>10 µg/day	Hicks et al. (2016)
Leptosiphon minimus	N	Radial	Open	White	πr^2	12	Present	Schmitt (1983)
Ligustrum vulgare	NN	Radial	Open	White	πr^2	800	Present	Percival (1955)
Linaria dalmatica	NN	Bilateral	Tubular	Yellow	lw	110	Present	Minnesota Wildflowers (2021)
Lomatium nudicaule	N	Radial	Open	Yellow	$2\pi rh+\pi r^2$	352	Present	Caldwell (2014)
Lomatium utriculatum	N	Radial	Open	Yellow	lw	1380	Present	Caldwell (2014)
Lonicera hispidula	N	Bilateral	Tubular	Red-pink	lw	64	Present	Caldwell (2014)
Lotus corniculatus	NN	Bilateral	Tubular	Yellow	lw	116	Present	Hicks et al. (2016)
Lunaria annua	NN	Radial	Open	Red-pink	πr^2	430	Present	Gardener and Gillman (2002)
Lupinus polycarpus	N	Bilateral	Tubular	Blue-violet	lw	20	Present	Caldwell (2014)
Medicago lupulina	NN	Bilateral	Tubular	Yellow	$2\pi rh+\pi r^2$	57	Present	Caldwell (2014)
Montia parvifolia	N	Radial	Open	Red-pink	πr^2	211	Unknown	
Myosotis discolor	NN	Radial	Open	Multi	lw	23	31 µg/day	Schultz and Dlugosch (1999)
Navarretia squarrosa	N	Radial	Open	Blue-violet	πr^2	17	Unknown	
Nemophila parviflora	N	Radial	Open	White	πr^2	12	Present	Caldwell (2014)
Perideridia gairdneri	N	Radial	Open	White	lw	1813	Present	Caldwell (2014)
Platanthera elegans	N	Bilateral	Tubular	White	πr^2	1612	Present	Caldwell (2014)
Platanthera unalascensis	N	Bilateral	Tubular	Green	lw	725	Present	Caldwell (2014)
Plectritis congesta	N	Bilateral	Tubular	Red-pink	πr^2	1215	Present	Prior et al. (2009)
Plectritis macrocera	N	Radial	Tubular	Red-pink	πr^2	65	Unknown	
Polygonum aviculare	NN	Radial	Open	White	πr^2	7	Present	Caldwell (2014)
Ranunculus occidentalis	N	Radial	Open	Yellow	πr^2	333	>10 µg/day	Hicks et al. (2016)
Rosa gymnocarpa	N	Radial	Open	Red-pink	πr^2	735	Present	Caldwell (2014)
Rosa nutkana	N	Radial	Open	Red-pink	πr^2	1979	Present	Pavek and Skinner (2013)
Rosa rubiginosa	NN	Radial	Open	Red-pink	πr^2	2124	Unknown	
Rubus armeniacus	NN	Radial	Open	Red-pink	πr^2	1122	Present	Boersma et al. (2006)
Sanicula crassicaulis	N	Radial	Open	Yellow	lw	193	Unknown	
Sedum spathulifolium	N	Radial	Open	Yellow	πr^2	167	Present	Langellotto (2017)
Sherardia arvensis	NN	Radial	Open	White	πr^2	8	Present	Caldwell (2014)
Silene gallica	NN	Radial	Tubular	White	πr^2	30	Present	Witt et al. (2013)
Sisymbrium officinale	NN	Radial	Open	Yellow	lw	72	3.675 µg/day	Hicks et al. (2016)
Sonchus asper	NN	Radial	Tubular	Yellow	πr^2	129	>10 µg/day	Hicks et al. (2016)
Sonchus oleraceus	NN	Radial	Tubular	Yellow	πr^2	302	>10 µg/day	Hicks et al. (2016)
Spergularia rubra	NN	Radial	Open	Red-pink	πr^2	27	Present	Caldwell (2014)
Stellaria media	NN	Radial	Open	White	πr^2	15	11.918 µg/day	Hicks et al. (2016)
Symphoricarpos albus	N	Radial	Open	Red-pink	πr^2	13	Present	Russell (2013)
Taraxacum officinale	NN	Radial	Tubular	Yellow	πr^2	730	>10 µg/day	Hicks et al. (2016)
Toxicoscordion veneosus	N	Radial	Open	Yellow	πr^2	62	Present	Caldwell (2014)
Trifolium campestre	NN	Bilateral	Tubular	Yellow	$2\pi rh+\pi r^2$	220	Present	Hilty (2020b)
Trifolium dubium	NN	Bilateral	Tubular	Yellow	πr^2	26	Present	LeBeau et al. (2017)

Triteleia hyacinthina	N	Radial	Open	White	πr^2	115	Present	Heritage Seedlings (2021)
Trifolium repens	NN	Bilateral	Tubular	White	$2\pi rh+\pi r^2$	713	12.135 μg/day	Hicks et al. (2016)
Trifolium subterraneum	NN	Bilateral	Tubular	White	lw	7	Unknown	
Trifolium variegatum	N	Bilateral	Tubular	Multi	πr^2	44	Present	SPLASH Education (2021)
Veronica arvensis	NN	Radial	Open	Blue-violet	πr^2	9	Present	Hilty (2020c)
Vicia americana	N	Bilateral	Tubular	Red-pink	lw	114	Present	LeBeau et al. (2017)
Vicia cracca	NN	Bilateral	Tubular	Blue-violet	lw	25	>10 μg/day	Hicks et al. (2016)
Vicia hirsuta	NN	Bilateral	Tubular	White	lw	49	>10 μg/day	Hicks et al. (2016)
Vicia sativa	NN	Bilateral	Tubular	Red-pink	lw	134	Present	LeBeau et al. (2017)

Table S3.2. Sensitivity analysis for results of final generalized linear models when excluding plant species represented by very small amounts of floral area (i.e., recorded in a single site-visits; n=9 species) from calculations of the proportion of the total flowering plant species richness (SR) that was non-native (NN). Results are shown for analysis of (a) the proportion of NN floral area using the beta distribution (n=114 site-visits), and (b-c) the proportion of nectar foraging visits made to NN flowers using the quasibinomial distribution. Model b is based on the full data set (n=58 site-visits) whereas model c is based on data collected before 18 July (n=33 site-visits). Shown are model estimates and standard errors (SE) for standardized model predictors including day of year, site area (m^2), the proportion of NN plant SR, and the proportion of NN floral area. Model results from either (a) likelihood ratio tests or (b-c) F-tests including test statistics ([a] chi-square value; [b-c] *F*-value), degrees of freedom (df: numerator, denominator), and *P*-values (*P*) are also shown. NA indicates not applicable.

Model	Response	Predictors	Estimate	SE	Test Statistic	df	*P*
a	Proportion NN Floral Area	Day of Year	1.07	0.10	NA	NA	NA
		Proportion NN Plant SR	0.24	0.10	NA	NA	NA
		Site Area	0.18	0.10	4.1	1	0.07
		Proportion NN Plant SR:Day of Year	NA	NA	4.6	1	0.03
b	Proportion Visits to NN	Proportion NN Floral Area	1.1	0.4	7.8	1,55	0.007
		Day of Year	1.6	0.5	13.9	1,55	0.005
		Proportion NN Plant SR	1.7	0.4	26.9	1,55	<0.001
c	Proportion Visits to NN	Proportion NN Floral Area	1.0	0.4	9.4	1,31	0.005
		Proportion NN Plant SR	2.3	0.9	19.1	1,31	<0.001

B) Figures

Figure S3.1. Phenological patterns in floral area (m^2) of all native plant species (n=36 species) known to produce nectar surveyed from 10 sites. To help with visualizations, an outlier for *Plectritis congesta* (day of year=125, native floral area=$2.6m^2$) is not shown.

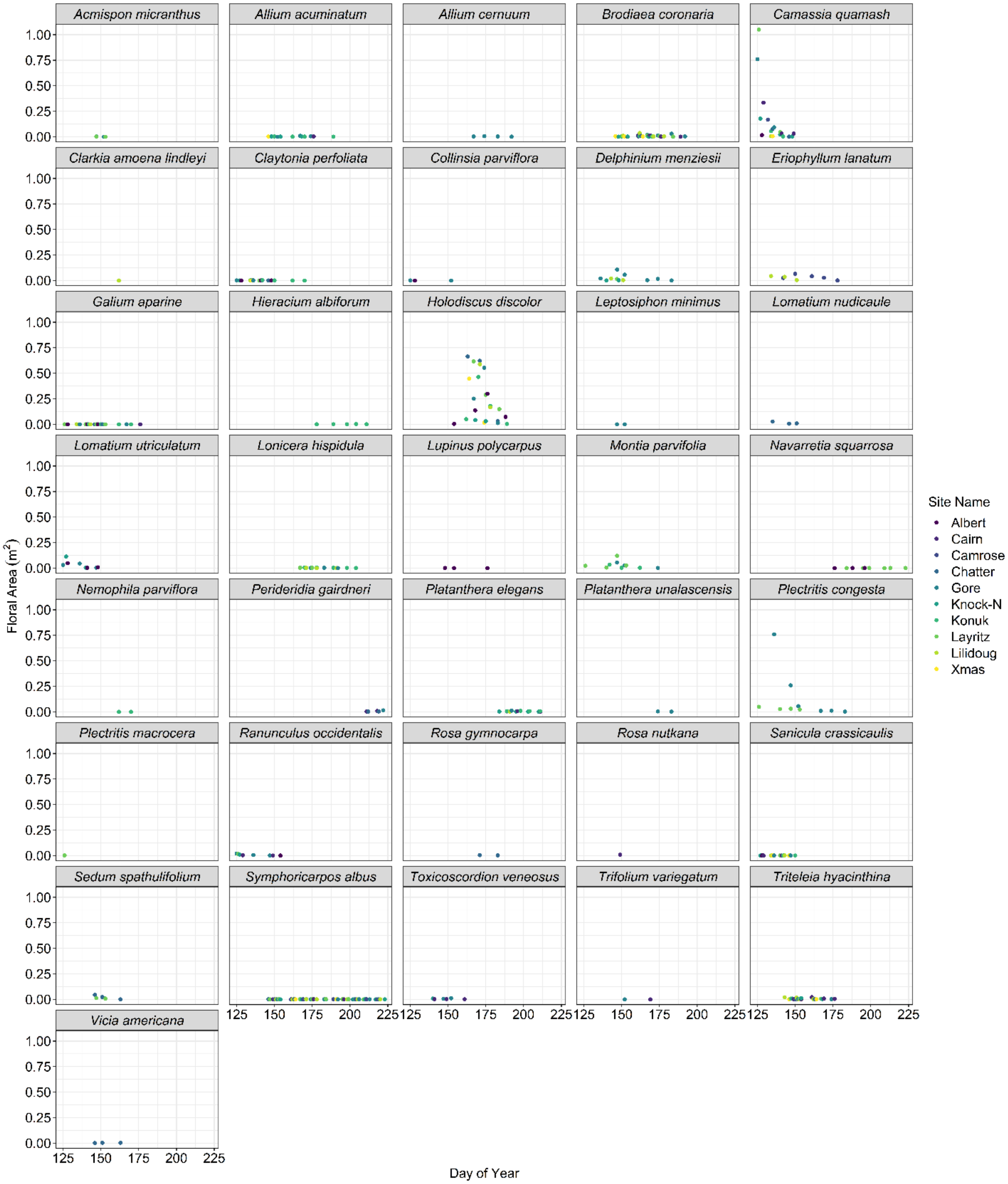


Figure S3.2. Phenological patterns in floral area (m^2) of all non-native plant species (n=45 species) known to produce nectar surveyed from 10 sites.

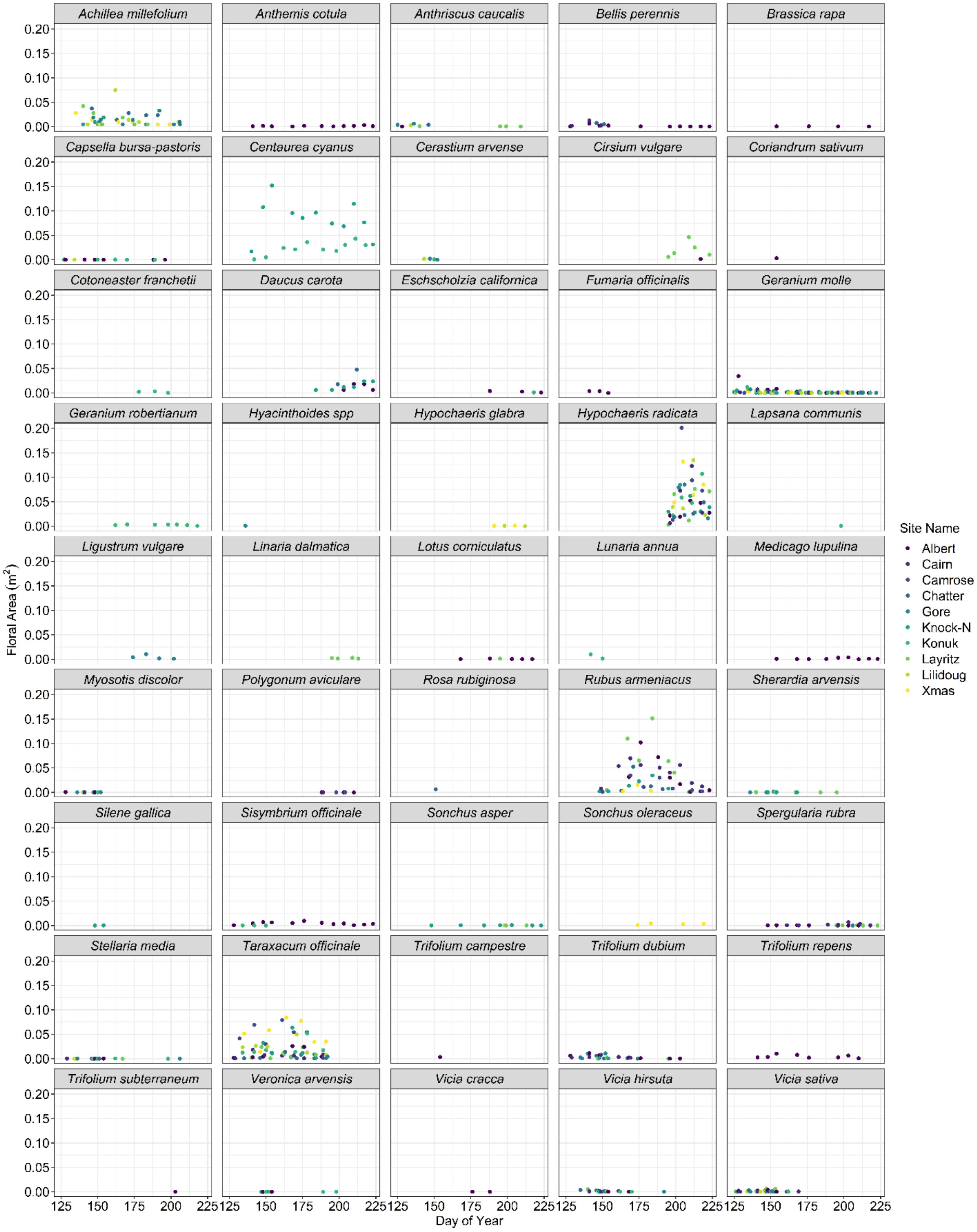


Figure S3.3. Total floral area (m^2) from all (a) native and (b) non-native plant species known to produce nectar summed across all visits and sites.

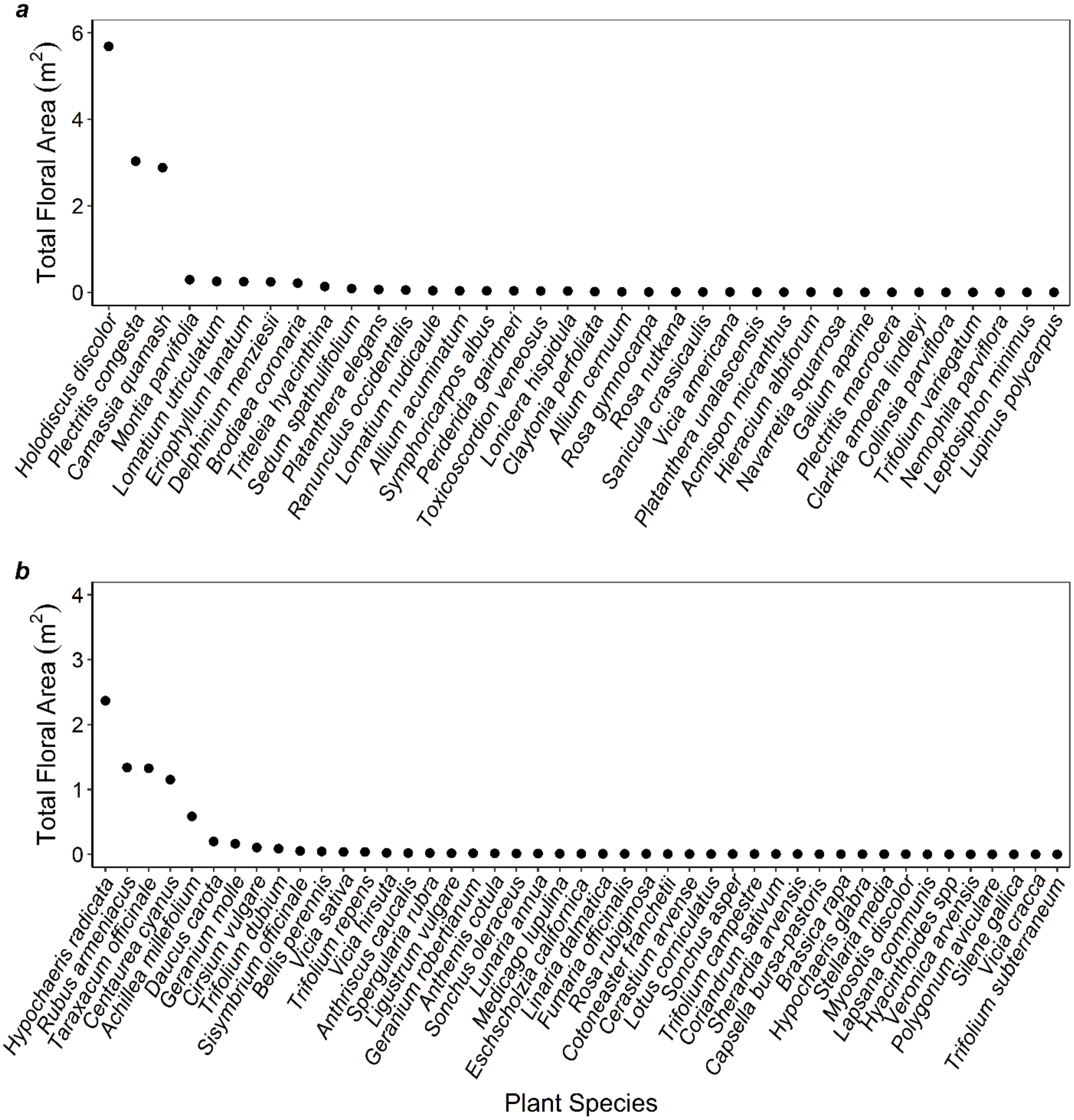


Figure. S3.4. Number of nectar foraging visits (>0) made by native butterflies to species of flowering plants (n=29 plant species) summed across the season.

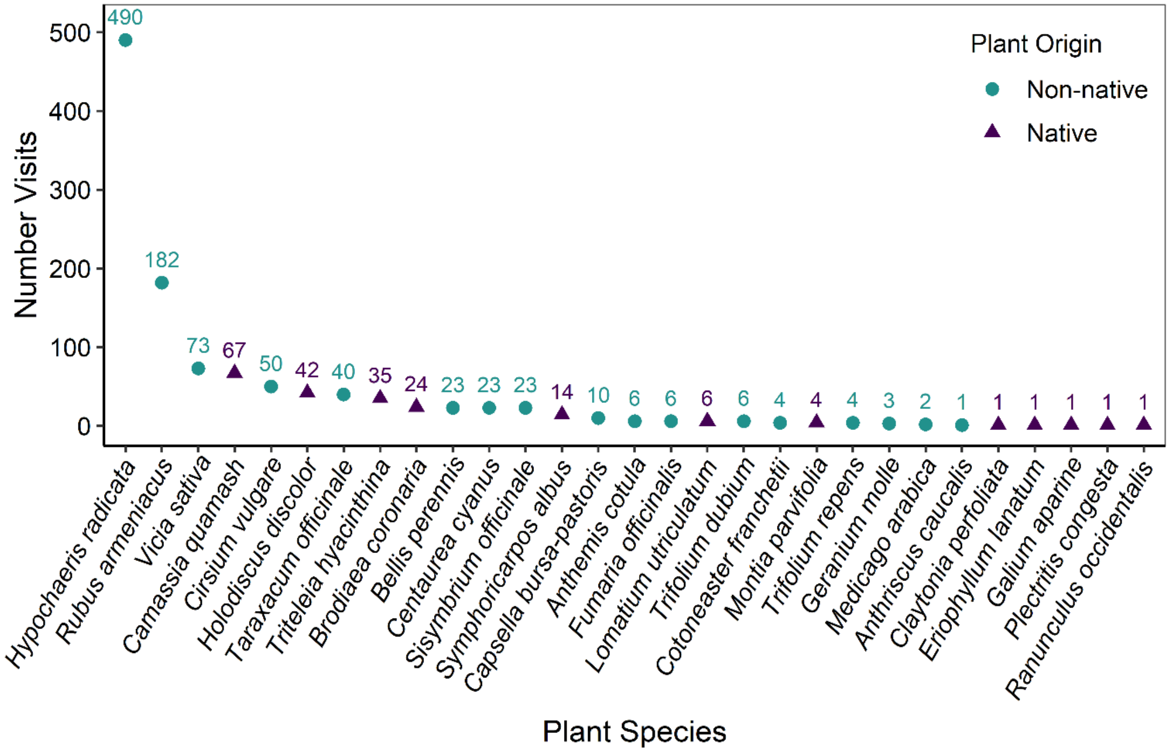


Figure S3.5. Trends in flower colour, symmetry, and shape showing (a-c) the number of nectar foraging visits made by 14 species of native butterflies across the season (n=1143 foraging visits) and (d-f) the number of plant species that were non-native compared to native (n=29 plant species). Only plant species that were visited by butterflies are included.

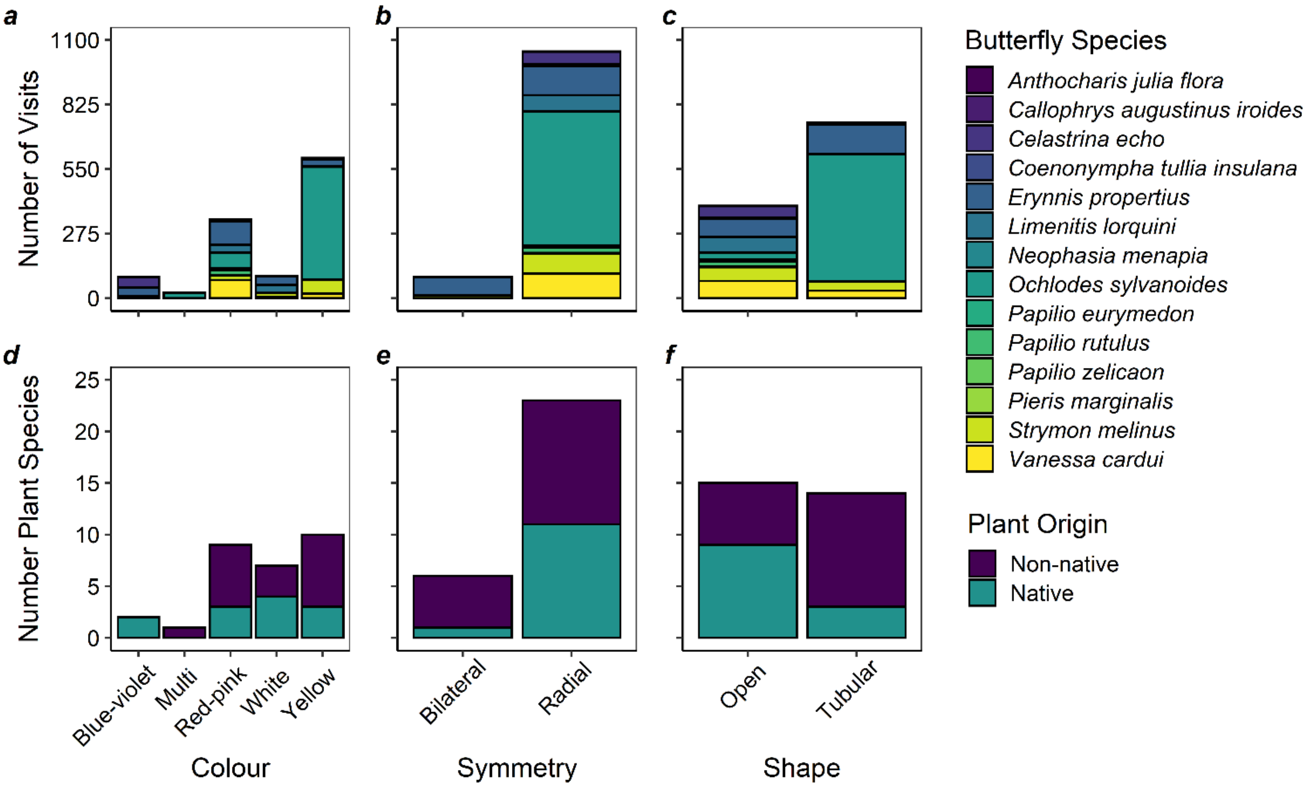
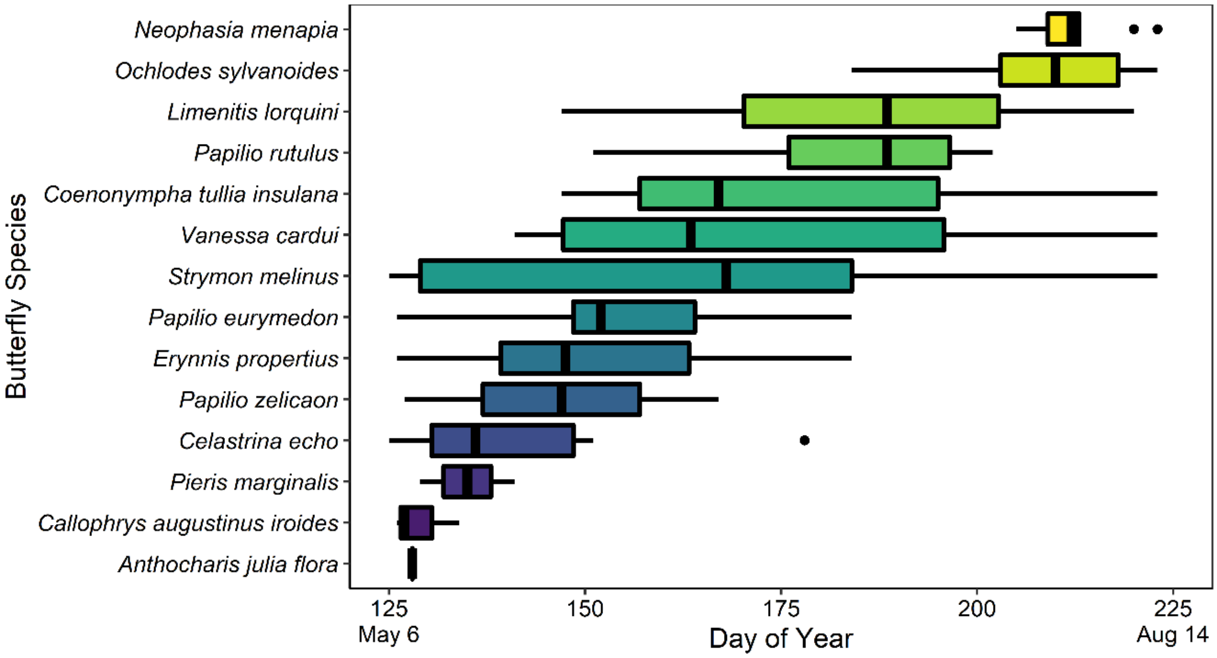


Figure S3.6. Flight period of 14 native butterfly species observed in Garry oak savannas based on whether the species was recorded as present or absent during all site-visits across the season. For each butterfly, the median (centre lines), interquartile range (length of box), minimum/maximum (whiskers), and outliers (dots) are shown.



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