THE TAXONOMIC AND FUNCTIONAL DIVERSITY OF URBAN GROUND ARTHROPODS WITH A SPECIAL FOCUS ON PHORIDS

by

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B.Sc., McGill, 2020

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES-BIOLOGY

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

July 2024

ABSTRACT

Urban environments can host diverse arthropod communities that provide critical ecosystem services. Yet cities are complex, heterogenous habitats with many different land management practices at small spatial scales, often with variable effects on arthropods. Arthropods should be considered during urban development, which often involves habitat modification that alters arthropod biodiversity and the services they provide, such as pollination and pest-control. In this study, I investigated how urban land use types impact the taxonomic and functional diversity of ground arthropods. I compared arthropod communities from industrial, greenbelt, and residential land use types across twelve sites (n=4 per land use type) in Prince George, a mid-sized British Columbia city, sampled in 2015. I also focused on phorids (Diptera: Phoridae) in chapter two, which represent one of the most taxonomically rich and abundant insect groups in urban spaces. I sampled phorids from 30 sites during the summer of 2022. For ground arthropods, neither functional nor taxonomic diversity differed significantly between land use types. Composition of communities, however, was distinct and urbanized land use types favoured herbivorous taxa. For the 2022 data, 99 operational taxonomic units were detected with DNA barcoding, with greenbelt, edge, and residential areas harbouring the most diverse and abundant fly communities. Overall, Prince George hosts species-rich, functionally diverse arthropod communities, even in its most urbanized land use types.

This suggests that highly modified habitats can be managed to support high arthropod diversity and ecosystem function, especially in large grassy areas and

should be included in urban conservation projects. However, not all taxa tolerate industrial sites well, including phorids, which are some of the most taxonomically and ecologically diverse arthropods. Therefor, other land use types must be preserved to ensure that high gamma diversity in maintained. This work provides a foundation for management and preservation of biodiversity and ecosystem services in similar urban habitats.

ACKNOWLEDGEMENTS

I would like to extend an enormous thank you to Dezene Huber for encouraging and guiding me throughout this project, Lisa Poirier, for providing a lab space, expertise, and invaluable support, Che Elkin, and Felix Sperling for being a part of my committee and helping advise and improve my work, and Alicja Muir for collecting and sorting the 2015 data.

I would also like to thank the BC Ministry of Advanced Education and Skills Training, the Fonds de Recherche du Quebec: Nature et technologies, and the Natural Sciences and Engineering Research Council of Canada for funding this research.

Lastly, I would like to thank the Prince George residents, and business owners who let me sample their properties, and without whom this research would not have been possible.

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Chapter one

1.1. Background

Cities are expanding. Conservative estimates project that global urban land area will double within this century (Gao et al. 2020), with roughly 68% of the world's population expected to inhabit cites by 2050 (United Nations 2018). But urban planners must balance the need to develop against the need to protect rapidly changing ecosystems.

Arthropods are by far the most abundant (Bar-On et al. 2018), and diverse group of animals on the planet (Hébert 2023). Many reports identify urbanization as one of the main culprits driving declines in global arthropod abundance and diversity (Fenoglio et al. 2020; van Klink et al. 2020). As cities develop, they break up natural habitat, create novel environments, expose native species to invasive competitors, and warm the surrounding area through the urban heat island effect (Fenoglio et al. 2020; Fenoglio et al. 2021). This can affect arthropod communities and the ecosystem services they provide.

1.2. Urban entomology

Despite their importance, urban arthropods have long been overlooked by the scientific community. Urban entomology is a term that was coined in 1884 but wasn't popularized until the 1970s. Most urban entomologists researched pest-control (Rust et al. 2024), until the early 2000s when more literature on the biodiversity of insects in cities began to emerge (Brown 2018).

Most urban animal biodiversity work focuses birds and mammals, leaving arthropods largely understudied (Collins et al. 2021).Unlike many larger animals, insects breed quickly, disperse easily, and need little space to persist (New 2015), allowing them to adapt to and even flourish in cities (Diamond et al. 2023). This makes them useful for gauging the effects of different kinds of disturbance (Kotze et al. 2011; Lewthwaite et al. 2024).Their ubiquity and incredible biological diversity also make them excellent subjects for urbanization studies, as well as bioindicators of ecosystem health (Schowalter et al. 2018).

The need to understand the ecological effects of urbanization has fuelled a rise in the number of urban wildlife publications in the last decade, including those dealing with arthropods (Collins et al. 2021). The growing body of research has diverged to include lesser-known taxa and gathered sufficient data for researchers to conduct meta-analyses for various groups. This helps us understand how arthropods respond to urbanization at a global scale (Collins et al. 2024).

1.3. Effects of urbanization on taxonomic diversity

The effects of urbanization on arthropod communities can be complex and diverse. While urbanization has been linked to widespread arthropod decline (van Klink et al. 2020), in other cases urbanization has yielded positive or no effects on arthropod diversity (Bang and Faeth 2011; Piano et al. 2020).This may partially be explained by how different taxa, from the species to the order level, respond differently to urbanization based on their respective niches. Bees, butterflies, and beetles are the most commonly studied groups, and often respond negatively to

urbanization (Merckx and Van Dyck 2019; Fenoglio et al. 2020; Fenoglio et al. 2021), while fruit flies do not (Avondet et al. 2003).

Experimental design also explains variation between studies. Traditionally, urbanization has been explored along urban-rural gradients, but defining and comparing urban areas between studies can prove challenging (Moll et al. 2019). An urban area typically involves a developed area within a population center, but can include everything from landfills and industrial parks, to recreation grounds and gardens (New 2015). Studies may only compare areas within a city center, or include suburban areas, managed parks, and natural areas (Beninde et al. 2015; Turrini and Knop 2015). Additionally, rural areas can host lower diversity than urban ones when managed intensively (Turrini and Knop 2015). Studies that survey only a small area or short time period may not prove sufficient to capture large-scale or long-term trends (Fenoglio et al. 2020). Likewise, at a local scale, urbanization may increase biodiversity, but homogenize it at a regional scale if species being introduced in different cities are the same (McKinney 2006).

1.4. Urbanophile insects

While many insects avoid highly built-up, disturbed urban environments, some species have adapted to tolerate, or even specialize to human associated habitats (Florencio et al. 2015). Pioneer and edge species often thrive in cities because open city spaces can resemble early successional stages (McKinney 2006). Herbivores can also reach high population densities in these areas due to predator release (Kruess and Tscharntke 1994). Additionally, cities often host introduced or invasive species because human transport concentrates around heavily populated areas

(Gippet et al. 2019). With climate change, many species ranges will shift, leading to new introductions, especially in urban areas. In temperate climates, biodiversity losses may be offset by new insects moving polewards, but not in tropical climates where many species have reached their maximum temperature thresholds (Diamond et al. 2023).

1.5. Functional diversity and ecosystem services

Functional diversity is a field of research that examines a species' ecological role or traits, rather than their taxonomy (Petchey and Gaston 2006; Gu et al. 2016). This approach is becoming increasingly popular in the literature as functional traits can often shed more light on how organisms interact with their environment than their taxonomic names alone (Petchey et al. 2009). This is especially relevant for arthropods as they provide many ecosystem services such as pollination, decomposition, and nutrient cycling (Schowalter et al. 2018).

Often urbanization is detrimental to these services (Civeira et al. 2020). For example, as development intensifies, it can undermine ecosystem services ants provide like soil production and aeration (Sanford et al. 2009). When habitat fragmentation negatively affects predators and parasitoids, it can limit bio-control services (Kruess and Tscharntke 1994). Arthropod populations also forge a critical link in the food web. Fewer arthropods in cities can result in poorer diets for birds like great tits (Sinkovics et al. 2021), and increasing urban arthropod abundance could greatly improve bird diversity (Planillo et al. 2021).

1.6. Taxonomic diversity in different land use types

Different sections of a city are zoned and managed to fulfill different needs. These can include industrial, commercial, residential, park, and recreational areas among others. Consequently, cities develop as mosaics of different kinds of land use types or habitat patches. Two patches might border each other, but undergo vastly different management regimes (Pickett et al. 2017). Industrial and residential sites tend to be planted with non-native species, regularly mown, and are subject to pesticide and fertilizer treatments (Proske et al. 2022). Green spaces or other natural or semi-natural areas are often far less maintained. This can alter the resources available to arthropod communities, their structure, and the ecological benefits they provide (McIntyre et al. 2001).

Sites within the same land use type may also vary in their physical characteristics. Differences within land use types can reveal much about what conditions underlie biodiversity trends (McIntyre et al. 2001). For instance, urban ecologists measure gradients in vegetation cover, structure (Beninde et al. 2015; Herrmann et al. 2023), and the area of impervious surfaces to explore differences in arthropod communities (Su et al. 2011; Geslin et al. 2016).

1.7. Functional diversity in different land use types

High levels of biodiversity are often assumed to improve ecosystem services, but this relationship depends on how species vary in their functional traits (Leps et al. 2006) — high species richness does not necessarily equate with high functional diversity (Sobral et al. 2014; Freitas et al. 2021). When beneficial guilds of

arthropods like predators and pollinators are negatively impacted by urbanization, it can compromise ecosystem functions (Civeira et al. 2020), such as biological control services (Kruess and Tscharntke 1994), and pollination (Liang et al. 2023). To protect biodiversity and ecosystem function, researchers must consider functional traits along with species diversity (Auber et al. 2022).

Urbanization filters out some species from communities based on the suitability of their traits related to their habitat (Gathof et al. 2022). The urban filter often favours generalist species at low trophic levels (Fenoglio et al. 2020). Likewise, the prevalence of different functional traits can reveal much about the selection pressures a community faces (Gerlach et al. 2013). Urbanization tends to shorten food chains (Kruess and Tscharntke 1994; Fenoglio et al. 2020) because natural enemies rely on prey populations and often need larger habitat areas to persist (Cardoso et al. 2011). This can lead to a loss of biological control services (Korányi et al. 2022). Urbanization also tends to select for dietary generalists because if a food source is compromised, generalist species can exploit other resources (Vázquez and Simberloff 2002; Concepción et al. 2015).

1.8. Insect conservation

Few people appreciate the conservation potential of cities (New 2015). For the last century, most urban entomology research has focused on how to best eliminate unwanted insects. Pest species such as cockroaches, bedbugs, and termites thrive in urban conditions, and spread with human trade. This fuels a growing and costly demand for pest-control services and research (Rust et al. 2024). Unfortunately, urbanization can also deepen the public's aversion to insects,

including harmless species (Fukano and Soga 2021). When people rarely encounter insects, they learn little of native species (McKinney 2006), and tend to think of insects as only pests in their home, further undermining conservation efforts (Fukano and Soga 2021).

However, insects are fundamental to many ecosystem processes (Lewthwaite et al. 2024). Since urban areas are one of the fastest growing habitat types (Menke et al. 2011), and many insects species are suffering steep population declines (Habel et al. 2019), working to improve urban insect diversity is one of the few ways to reconcile development and conservation interests. Likewise, some areas in cities can be biodiversity hotspots (Connor et al. 2002), unique novel ecosystems, and havens for vulnerable species (Hall et al. 2017).

In the last 25 years, there has been a growing recognition of the need to protect insects and explore their diversity in cities (Brown 2018; Collins et al. 2024). This is reflected in the literature by the growing number of urban biodiversity studies (Collins et al. 2021), surveys of understudied urban taxa (Hartop et al. 2015), and proposals for ways to improve insect conservation (Samways et al. 2020; Brandl et al. 2022). The awareness of issues insects face has helped both scientists and the public reimagine cities from ecological deserts to potential refuges for insects amidst widespread biodiversity loss due to climate change and human habitat destruction (Diamond et al. 2023).

However, much work remains to be done. Media reports of an “insect apocalypse” have sensationalized real invertebrate declines, to point of becoming counter productive. In truth, many arthropods remain undescribed, and often little is

known of the life history of discovered species (Saunders et al. 2020). Many of the most widely cited papers discuss the general effects of urbanization on insect communities (habitat suitability). Few focus on faunistics, insect biology, or ecological theory (Brown 2018). Likewise, many solutions have been proposed to help support insect diversity: everything from bee hotels to planting gardens of native host plants. However, conservation efforts often target narrow groups of insects, and if left untested, these strategies risk being ineffective, or even becoming ecological traps (Brown 2018; Diamond et al. 2023).

Future research needs to consider more nuanced approaches that investigate mechanisms behinds how arthropods respond to different urban disturbances, as well as vet restoration approaches to ensure they're effective (Samways et al. 2020; Diamond et al. 2023). It is also clear that conservation cannot done by scientists alone. Generally, insects are underappreciated by most people, and disliked by many (Fukano and Soga 2021). Their importance must be communicated to stakeholders, policy makers, and the public for conservation efforts to succeed. Promoting citizen science and public education can help people realize the value of insects, increase support for conservation, and improve well-being for both insects and humans (Samways et al. 2020).

1.9. Project goals

This project seeks to determine how land use type impacts the taxonomic and functional diversity of arthropod communities, as well as inventory which species are present, as northern British Columbia is comparatively understudied. As phorids are one of the largest and most ecologically diverse families of insect, I focus further

analysis on this group. I aim to quantify their abundance and diversity in different land use types and assess how they respond to environmental variables like season and temperature.

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Chapter two: The taxonomic and functional diversity of ground arthropods in different land use types

2.1. Background

As cities develop, managers must consider how to best meet human demands, but also preserve or improve ecosystem health and the benefits arthropods provide. In my research I investigated how urbanization affects the taxonomic and functional diversity of ground arthropods in Prince George, a mid-sized British Columbia (BC) city. Urban biodiversity studies typically take place in larger, southerly cities, leaving the insect fauna of northern BC largely understudied. The city of Prince George provides an opportunity to study insect biodiversity in the context of an urbanized area mostly surrounded by forests.

2.2. OBJECTIVES

The main objectives for the first part of my thesis research were to establish a baseline of which ground-dwelling arthropod species were present in Prince George, explore their taxonomic diversity, and compare those trends with patterns of functional diversity across different land use types using pitfall trap-derived data from industrial, residential, and greenbelt areas. I aimed to answer four questions:

i) How does land use type impact taxonomic diversity?

ii) How do different local physical land features impact species richness?

iii) How does land use type impact functional diversity?

iv) Do different land use types exert stronger selection pressure for certain traits in arthropod communities such as host specialization and habitat preference?

2.3. PREDICTIONS

i) Greenbelt and residential sites should have the highest species richness as they have the more vegetated area within a 50 m radius compared to industrial sites. I expected residential sites to have higher species richness than industrial sites but similar or fewer species than greenbelt sites as they had less vegetation, but also very varied vegetation and additional food sources such as composts, trash, and gardens.

ii) a) Species richness would be positively related to total vegetation and vegetation evenness (measured as the Pielou evenness index for trees, shrubs, grass and gardens at each site). Vegetated area is considered favourable habitat to arthropods, so increasing vegetation increases potential habitat for arthropod taxa (Beninde et al. 2015; Turrini and Knop 2015). Increasing habitat heterogeneity can also increase species richness (Cramer and Willig 2005), so increasing vegetation evenness (more balanced vegetation structure), should increase diversity.

b) Industrial and greenbelt communities were most different in terms of their geospatial variables (high lawn and hard surface cover compared to high tree cover, respectively), so I also expected them to be very different in terms of community composition.

iii) Functional diversity would be lowest in industrial sites. Industrial sites lacked resources like woody debris, and gardens which supplied flowers, which could be important to decomposers (Tóth et al. 2021), and natural enemies respectively (Corcos et al. 2019).

iv) a) There would be higher proportions of natural enemies at greenbelt sites compared to industrial sites as greenbelt sites had more vegetation cover and could potentially support more predator and parasitoid taxa by providing habitat for both herbivore prey and the natural enemies (Kruess and Tscharntke 1994).

b) There would be more polyphagous taxa and habitat generalists/open habitat taxa at industrial sites. Urbanization typically selects for dietary and habitat generalists (Concepción et al. 2015; Magura et al. 2020), so I expected more heavily managed and developed land use types to support more generalist taxa.

2.4. METHODS

2.4.1. Study sites

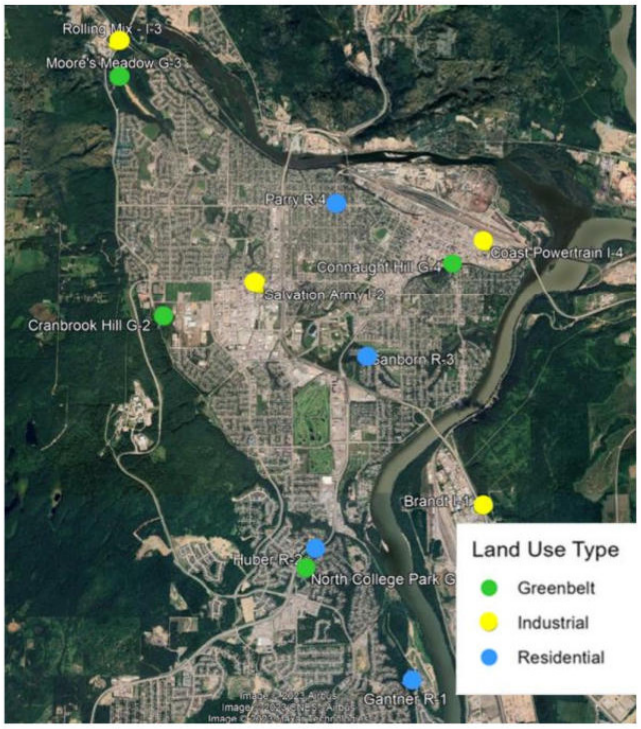
Prince George falls within the Sub-Boreal Spruce biogeoclimatic zone, which supports mostly mixed forests of gymnosperm (e.g., *Picea* spp., *Pinus contorta*, *Pseudotsuga menziesii*) and angiosperm (e.g. *Populus* spp., *Betula papyrifera*, *Alnus* spp.) trees and associated understory plants. It experiences warm, wet, short summers and long cold winters (Meidinger and Pojar 1991). The mean annual

temperature of the region has warmed by 1.3°C in the last century, and will likely rise another 2.2°C to 3.7°C in the next 60 years (Coady and Picketts 2012).

Prince George supports a population of 77000 people (Statistics Canada 2023) spread over an area of 329 km^2 (City of Prince George 2023). It encompasses several industrial zones including pulp mills, an oil refinery and chemical plant (Prince George Area Industrial Land Profile 2008), along with residential areas of mostly low-density housing (City of Prince George 2023). The city contains at least 6000 hectares of productive forest on municipal and crown land (Timberline Forest Inventory Consultants 2006), and 65% of the land is considered greenbelt when including parks together with natural forests (Coady and Picketts 2012).

The study area for this project encompassed 50 km^2 in the main urbanized portion of the city – much of the outlying area remains unurbanized – in three different land use types: industrial, residential, and greenbelt spaces. Industrial areas consisted of local businesses dominated by lawns and pavement. Commercial areas were included with industrial areas in this project as both contained lots of hard surfaces and lawns. Residential areas included private residences with lawns and gardens, while greenbelt areas were forested spaces within and around Prince George generally lacking substantial management or roadways. The residential sites in this study were confirmed to be pesticide free with homeowners, while industrial and greenbelt sites (within treeline) likely were as well. Industrial and greenbelt sites were selected by driving in Prince George and randomly choosing sites in four of the city's industrial areas. Residential sites were selected by recruiting local

homeowners to the project and selecting residences that were situated in different parts of the city.



Site	Latitude	Longitude
R1	53.856950°	-122.755560°
R2	53.873243°	-122.775723°
R3	53.898214°	-122.764266°
R4	53.919023°	-122.770138°
G1	53.870774°	-122.777743°
G2	53.903715°	-122.809661°
G3	53.936776°	-122.820802°
G4	53.910720°	-122.744167°
I1	53.878739°	-122.738973°
I2	53.907891°	-122.787999°
I3	53.941743°	-122.821441°
I4	53.913714°	-122.736775°

Figure 2.1. Map of 2015 study sites on a satellite map of Prince George from Google Earth. Colored points indicate land use types. Sites (R = Residential, G = Greenbelt, I = Industrial) are shown in the table beside.

2.4.2. Geospatial land feature data

Using 2014 orthophoto data of the sites provided by the City of Prince George, circles were drawn around each site with 50 m, 25 m, and 10 m radii. Physical features such as tree canopy, sidewalk, roads, gravel, buildings, lawn etc. were measured in pixels (~1m) within each circle. I combined these features into seven variables: the area of total vegetation, trees, shrubs, lawns, gardens, hard surfaces, and buildings for each site. Hard surfaces included gravel and pavement. Different types of vegetation included both planted and naturally occurring vegetation.

2.4.3. Sampling

To survey Prince George, five pitfall traps were set in four-meter transects at twelve sites in industrial, residential, and greenbelt land use types (n = 4 sites for each land use type) with traps spaced one meter from each other. The traps contained 50% propylene glycol and were collected every week from July to late August 2015. Specimens were stored in 95% ethanol and initially processed by students in Dezene Huber and Lisa Poirier's labs using guides such as Ubick et al.'s 2017 Spiders of North America: An Identification Manual (2nd ed.), Roth's 1993 Spider Genera of North America (3rd ed.), Marshall's 2017 Insects, their Natural History and Diversity (2nd ed.).

Later, Huber and Poirier refined identifications and selected 420 specimens which they believed to represent distinct morphospecies to the Centre for Biodiversity Genomics at the University of Guelph for DNA barcoding (CO1-5P-

gene). These specimens were vouchered, photographed, and added to the Barcode of Life database (BOLD). BOLD can generate identifications by comparing query sequences from specimens with those in its reference library (Ratnasingham and Hébert 2007). Huber and Poirier used these to develop pictorial catalogs to help identify local species. Using the above-mentioned guides, pictorial catalogues, and online resources such as Ant Web, Bug Guide, and Facebook groups for fly and wasp identification, Honour's student Alicja Muir further sorted specimens from four sampling periods (the weeks beginning on 17 July, 24 July, 6 August, and 28 August) to the lowest taxon she could (from species to order level). Two taxa, *Megaselia* and Platygastridae, were known for high diversity but difficult to sort, so an additional 285 specimens were submitted to BOLD.

2.4.4. Statistical analyses

All statistical analyses were conducted in R version 4.2.2. I analyzed presence-absence data due to the biased nature of species abundances when using pitfall traps (Hohbein and Conway 2018). Most specimens were identified to genus or species. All genera and broader taxa were treated as unique identifications that I refer to as operational taxonomic units (OTUs). All OTU occurrences are recorded in (Table 5.1.2.) I assessed normality of data using histograms of residuals, plots of residuals vs fitted values, and normal Q-Q plots. For comparisons of categorical variables, I conducted ANOVA tests, except if the data's residuals were non-normal, in which case, I used Kruskal-Wallis tests.

2.4.4.2. Baseline of species richness in Prince George

Using the *specaccum* function in the R vegan package, I built species richness curves for OTU counts using the method “random”. I estimated the OTU richness for the regional species pool using the *specpool* function which calculates estimates using the Chao 2 index, first and second order jackknifing, and bootstrapping.

2.4.4.3. Comparison of land use types

To ensure that sites within the same land use type were similar enough to be considered replicates, I used the geospatial data to build Bray-Curtis NMDS plots for each spatial scale.

For each land use type, I compared the richness of species (OTUs), genera, and families of arthropods present. Species vary in their activity and capture rates in pitfall traps. Because I was comparing a broad range of taxa, with varying mobility, I avoided using abundance based diversity indices, as relative abundances from my trap yields would be unreliable (Topping and Sunderland 1992). For each taxonomic level, I estimated an upper value of richness where all OTUs were included, and a lower value of richness in which all broad taxa were excluded from the analysis (eg. if comparing genera, any categorization broader than genus would be excluded). I then conducted Kruskal-Wallis tests to compare richness values between land use types.

2.4.4.4. Community similarity

I calculated the Bray-Curtis dissimilarities between sites, which when using presence absence data is equivalent to the Sørensen index. Unlike other indices, Bray-Curtis and Sorensen do not consider sites that don't share a species (double zero problem) as similar to each other as sites that do share a species (Ramette 2007; Ricotta and Podani 2017). I drew ellipses around groups of sites belonging to the same land use type using the *ordellipse* function which calculates the standard error of the weighted centroids of for each group of sites. I conducted ANOSIM and PERMANOVA tests to see if the dissimilarity between land use types was significant at the OTU level. I also conducted ANOSIMs at the genus and family level where broader taxa were excluded.

PERMANOVA is usually more sensitive to changes in community structure, and less affected by heterogenous dispersions between groups (Anderson and Walsh 2013). However, because they test different hypotheses, they can also be considered complimentary (Somerfield et al. 2021). These tests make no assumptions about the normality of the data and are compatible with Bray-Curtis dissimilarities (Anderson 2017). I conducted pairwise ANOSIM and PERMANOVA tests post-hoc to see which land use types were significantly different from each other. I adjusted p-values using the method *fdr* which calculates the false discovery rate for p-values (Jafari and Ansari-Pour 2019).

2.4.4.5. Habitat preference

Urban areas typically favour open habitat species and habitat generalists. I categorized OTUs as preferring open, semi-open, closed habitats by reading about their habitat preferences in the literature (Table 5.1.3.). I classified OTUs that preferred a specific habitat, but likely occurred in others as “more open” or “more closed”. I classified OTUs as “semi-open” if they were edge species or preferred heterogenous habitats like prairie parkland. I would classify OTUs as “both” when they occurred in more than one habitat type without a clear preference. Because most OTUs had unknown habitat preferences, I could not perform a statistical analysis. I also tested whether any species were associated with different land use types using the r_{pb} index from the indicspecies package. The function *multipatt* runs permutations of random communities to test the significance of species correlations with groups of sites (De Cáceres et al. 2010).

2.4.4.6. Geospatial modelling

I modelled how upper estimates of species richness responds to seven geospatial land variables at all three spatial scales (50 m, 25 m, 10 m). I also included an additional variable called vegetation evenness, which measured how even or dominant different vegetation types (vegetable and flower garden, lawns, trees, and shrubs) were at each site using Pielou’s evenness index. Because the dataset was small, and there were many explanatory variables, including correlated ones, I used iterative forward selection where explanatory variables were only added to the final model if they were significant. I checked the normality of these models using Shapiro-Wilkes tests and histograms of residuals. While most Shapiro-Wilkes

tests had p-values larger than 0.05, suggesting normal distributions, visual inspection of the histograms showed some models had bimodal, right, or left-skewed distributions. Log and square-root transformations did not correct most of these distributions, so the variables were left untransformed. I also ran these models a second time using land use type as an interaction term (species richness = geospatial variable*land use type), as I expected arthropods from different land use types might respond differently to vegetative resources (e.g., grass could provide good habitat for industrial site-dwelling species but not necessarily for forest-dwelling species).

I also fitted environmental variables to NMDS Bray-Curtis ordination plots to investigate community similarity using the function *envfit* from vegan at all three spatial scales. This function assesses the association between environmental variables and communities by modelling environmental variables as a function of ordination axis scores. It tests the significance of the relationship by randomly reordering the dependent variable through 10000 permutations and testing whether the original R^2 is different from R^2 distribution calculated through random permutations (Simpson 2018).

2.4.4.7. Functional diversity

At its core, functional diversity involves grouping together ecologically similar species to better describe animal communities and how they respond to their environment (Wilson 1999). Functional groups refer to groups of species that perform the same roles in the ecosystem while guilds refer to groups of species that use similar resources, but both terms are often used interchangeably (Blondel 2003;

Cardoso et al. 2011). The simplest way to determine functional diversity is to measure the unique number of trait combinations present in a community. But researchers have developed a suite of more complex indices, many of which focus on trait richness (Mammola et al. 2021). Each index has strengths and weaknesses, so often it is important to include more than one index to ensure robust results (Petchey et al. 2009) or to measure complimentary facets of diversity (Legras et al. 2018).

Functional traits can encompass various aspects of a species niche from their diet or habitat to their body size (Gu et al. 2016). I decided to focus on feeding guilds because these relate to some of the main ways arthropods contribute to the nutrient cycle and what resources they depend on to survive. I selected five guilds: herbivores, natural enemies (predators and parasites), decomposers, fungivores, and honeydew feeders. I chose very broad feeding guilds for three reasons. Over-splitting guilds could lead to some groups being overrepresented in the dataset or becoming redundant (e.g., many different feeding styles of herbivores or decomposers, if all were explicitly mentioned there would be far more herbivore and decomposer guilds than fungivore, and natural enemy guilds; or predators and parasitoids have very different lifestyles but essentially perform the same function of regulating other arthropod species). Including more traits would also likely make my functional diversity measures correlate too strongly with species richness and thus make it redundant (Petchey and Gaston 2006). And lastly, because many OTUs lacked taxonomic resolution, they were easier to sort into broader functional guilds

than into more specific ones. Narrower guilds would have led to a larger number of OTUs being excluded.

Herbivores included arthropods that fed on any part of a plant and other non-animal organism including pollen, nectar, lichen, mosses, and algae. Natural enemies included parasitoids and predators. Decomposers included arthropods that fed on any dead or rotting material including dead plants, carrion, or dung. Some decomposers may feed on decomposing microorganisms more so than the material under decomposition, but these were still considered decomposers due to their reliance on dead organic material. Many fungivores were also decomposers, so arthropods were only labelled as fungivores if fungi or fungal spores were explicitly mentioned to be a component of their diet. Honeydew feeders rely on plant juices obtained through a secondary species such as aphids, scale insects, or some fungi (Hardy 1988; Shaaban et al. 2021). Ants, in particular, are known for honeydew feeding, often even protecting the insects that supply these resources (Nielsen et al. 2010).

Each OTU was ranked as having a strong (3), moderate (2), weak (1), or no (0) affinity for each guild, based on data from the literature (Table 5.1.1.). An OTU could belong to several different guilds, as many arthropods are omnivorous or feed on different food sources throughout their life cycle. Arthropods were ranked as three for a guild if it was their main feeding style, or main feeding style in their juvenile stage. Arthropods were ranked 2 if a food source was known to be important to their diet, or more important than other food sources, but not their main food source. They were ranked 1 for a food source if they fed on it facultatively, opportunistically, or

much less than other food resources. OTUs were ranked as 0 when the feeding style was extremely rare, not recorded in North America, or not present in that group. I excluded 18 OTUs of the 134 recorded due to uncertainty regarding their niches .

Many adult insects, including flies and parasitoid wasps, feed on pollen, nectar, or honeydew. Often these were ranked as 1 for herbivory or honeydew feeders as feeding could be opportunistic, or the juvenile feeding stage was more strongly emphasized in the literature. Some OTUs had uncertain functional attributes. For broader taxa, I checked BOLD identifications from barcoded specimens, and referred to Canadian and provincial checklists (Campbell and Davies 1991; Campbell and Davies 1991; Hamilton 1998; Maw 2000; Beaulieu and Wheeler 2001; Lienhard 2018; Bennett et al. 2021; Langor and Langor 2022) to determine which species were most likely to occur in Prince George. OTUs that could represent two or more species with conflicting life histories were excluded from the functional analysis. When the feeding style was uncertain, OTUs were sorted into the guild of a closely related species, the most prevalent guild in a broader taxon, or the most likely guild based on ecological data.

I used three different indices to measure functional diversity: the number of unique functional trait combinations (F_{Ric}), Petchey and Gaston's 2002 FD_{PG} , and the functional mean pairwise distances (FMPD) (Chapman et al. 2018). FD_{PG} is a dendrogram based method where OTUs are sorted into a tree based on similarities in their functional traits. FD_{PG} for a community is measured as total branch length required to include every member of the community (Petchey and Gaston 2002). FMPD measures the average distances between pairs of species from the same

community on a dendrogram (Tsirogiannis and Sandel 2014; Chapman et al. 2018). I used the FD package to calculate F_{Ric}, and methodology followed by Chapman et al. 2018 to calculate both FD_{PG} and FMPD with the fundiv and picante R packages.

To build my functional dendrogram, I used Gower's distance which is appropriate for ordinal data (Podani and Schmera 2007; Mouchet et al. 2008). Several clustering algorithms can be used to build a tree, but the choice of algorithm can influence results. I selected algorithms recommended by Mouchet et al. 2008, used by Chapman et al. 2018 and Clark et al. 2012 in similar studies, and available in the fundiv package. I calculated the cophenetic correlations of all algorithms with my original distance matrices (Mouchet et al. 2008), and selected the unweighted pair group method with arithmetic mean (UPGMA) clustering algorithm as it scored the highest cophenetic correlation. I calculated the FD_{PG} values for all sites and divided them by the FD_{PG} value of a hypothetical community containing all OTUs to standardize them. I compared the functional diversity between land use types using a Kruskal Wallis test. I also tested their relationship with species richness using simple linear models.

2.4.4.8. Guild prevalence

To analyze whether certain guilds were better represented in some land use types, I compared the proportion of each guild between land use types using Kruskal-Wallis tests. I used proportions to control for the effect of species richness between sites. For herbivores, decomposers, natural enemies, and fungivores, I only included OTUs that ranked moderate or higher in their feeding affinities to eliminate opportunistic and occasional feeders. I did not do this for honeydew feeders as most

OTUs in this guild were omnivorous and only ranked as weak. I also tested the association of different guilds with different land use types using richness data and the r_{pb} index from the R package indicspecies. I expected guilds to have higher richness in land use types they were more strongly associated with (Panda et al. 2021).

2.4.4.9. Host specialization

I ranked herbivores with a guild affinity of moderate or higher into three feeding categories: polyphagous OTUs that fed on many plant families (3), oligophagous OTUs that fed within a single family (2), and monophagous OTUs that feed on a single genus (1) (Table 5.1.4.). I included 33 taxa whose host specialization was known out of 39 taxa that were known to be herbivorous (Table 3.4.). I performed Kruskal Wallis tests to compare the proportions of each host specialization category between land use types and corrected the p-values using the false detection rate function *fdr*. I also calculated the mean host specialization of each site and compared it between land use types.

2.5. RESULTS

2.5.1. Land use type classification

These figures plot sites in NMDS space based off their geospatial dissimilarities (differences in area of grass, hard surfaces, trees, shrubs, buildings, and gardens) at the 10 m, 25 m, and 50 m scales. These results show that sites within the same land use type are similar in their geospatial composition but distinct from other land use types at every spatial scale.

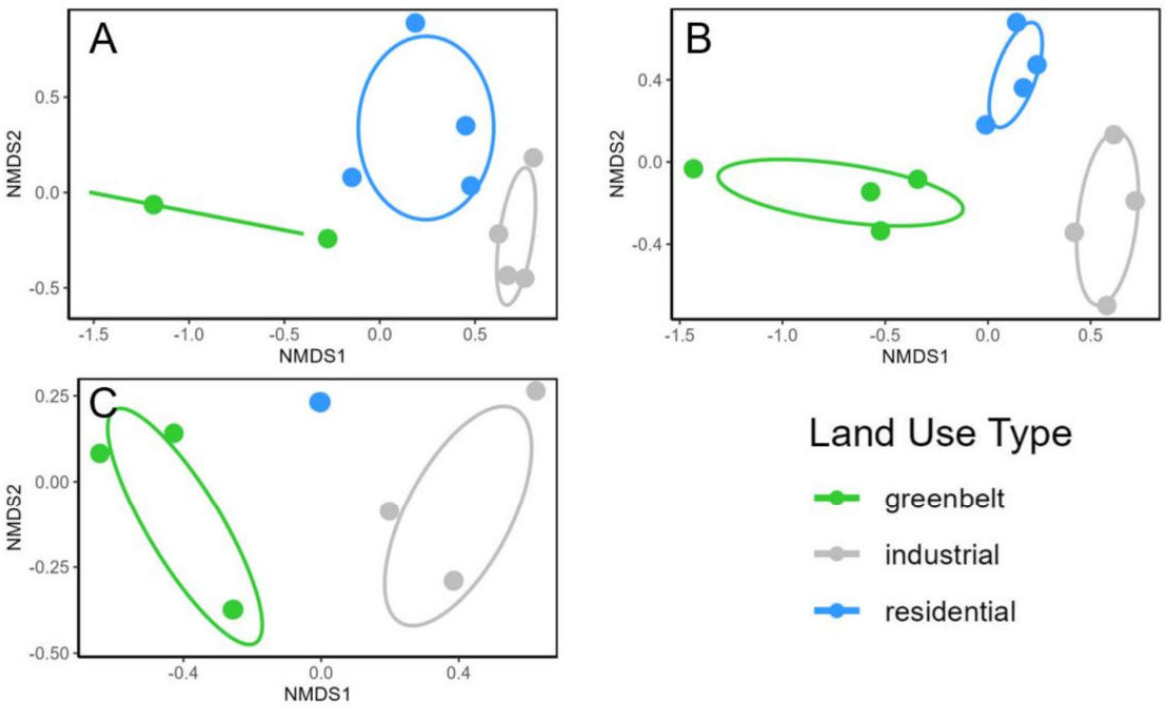


Figure 2.2. NMDS Bray-Curtis dissimilarity plots where points represent sites and ellipses represent the standard error of weighted centroids. Plots were constructed using vegan in R and the function *metaMDS*, from geospatial data at the 10 m, 25 m, and 50 m scales. The data were standardized with square-root transformations, then the Wisconsin double standardization. Plot A represents sites at the 10 m scale (dissimilarity = "bray", k = 3, permutations = 20, stress = 0.0031). Plot B represents sites at the 25 m scale (distance = Bray, k = 3, permutations = 20, stress = 0.014). Plot C represents sites at the 50 m scale (distance = bray, k = 3, permutations = 20, stress = 0.0027). Note: Some points overlap in figures.

2.5.2. Species baseline

2.5.2.1. Data quality

In 2015, 8645 specimens were sorted into 134 operational taxonomic units (OTUs), where OTUs represented the lowest taxonomic level to which a species could be identified. Thirty-six percent of OTUs were identified to species (5% of specimens), 35% to genus (86% of specimens), and 25% to family (6% of specimens). The proportion of OTUs identified to genus or lower was weakly correlated with OTU richness (Pearson's, t = 2.3, df = 10, cor = 0.59, p=0.044), but

these proportions did not differ significantly between land use types (ANOVA, df = 2,9, F = 3.45, p = 0.077). While taxonomic resolution may have affected species richness values, the resolution was similar across greenbelt, industrial, and residential sites.

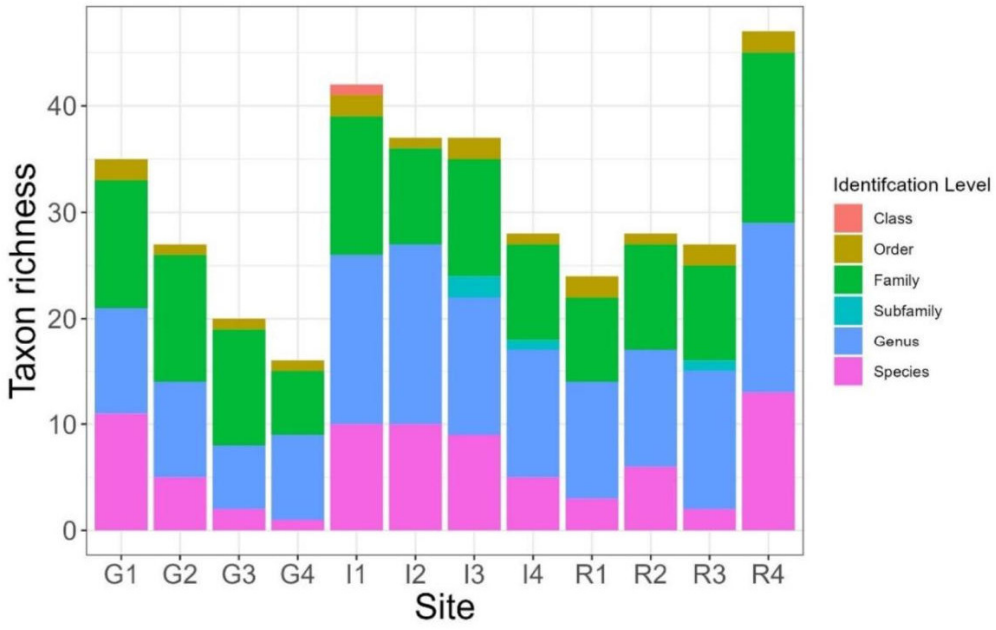


Figure 2.3. The OTU richness at each site. Different colors indicate the proportion of OTUs at each site that represent species-, genus-, family-, and order-level identifications.

2.5.2.2. Richness estimates

Overall, 134 morphological OTUs were detected across 89 genera and 63 families from initial barcoding and sorting with guides and pictorial catalogs. Barcoded specimens represented 118 molecular OTUs, with 33 OTUs belonging to *Megaselia*. BOLD records included an additional 130 OTUs that were sampled outside the initial collection periods Alicja Muir studied (17 July, 24 July, 6 August, 28 August) for a total of 248 molecular OTUs recorded in Prince George. Given the position of the curve in Figure 2.4., this likely represents most of the OTUs that can

be found through morphological sorting alone. Morphological OTU estimates for the regional species pool ranged from 161 +/- 10 (bootstrap index) to 246 +/- 38 (chao 2 index) indicating that between 54% to 83% OTUs in the regional species pool were sampled.

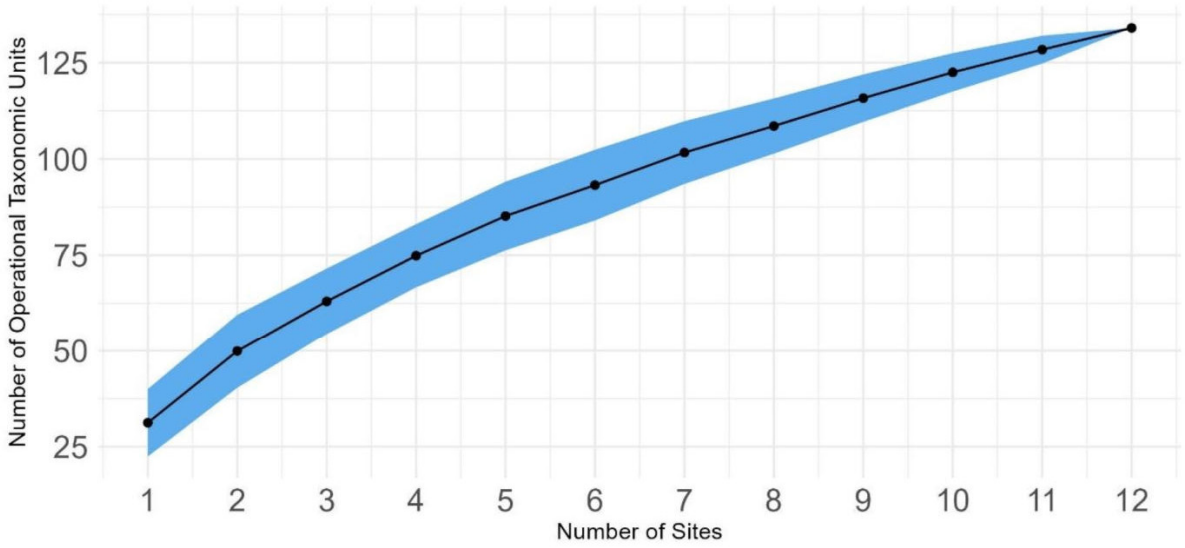


Figure 2.4. The OTU accumulation curve of OTUs detected from the 8645 specimens across 12 sites and four sampling periods. Using the *specaccum* (method=*random*) package from vegan in R, sites were added randomly in 100 permutations of the data to find the mean species accumulation curve. Dots represent the mean number of OTUs found per number of sites sampled (+/- the standard deviation in blue). A total 134 OTUs were sampled across the sites and collecting periods.

Table 2.1. Estimates of OTU richness for the regional species pool and each land use type, along with their standard error for the chao 2 index, jackknife 1, jackknife2, and bootstrap estimators.

Land use type	OTU richness	Chao 2	Jack 1	Jack 2	Bootstrap
All	134	246 +/- 38	198 +/- 23	241	161 +/- 11
greenbelt	57	91 +/- 16	82 +/- 16	94	68 +/- 8
industrial	83	141 +/- 24	119 +/- 22	138	99 +/- 10
residential	68	100 +/- 15	95 +/- 20	108	80 +/- 10

2.5.3. Richness between land use types

When including all OTUs at the finest taxonomic level, industrial sites had the highest overall mean richness, a residential site had the highest absolute richness value, and richness did not differ significantly between land use types (Kruskal-Wallis, χ^2 = 4.29, df = 2, p = 0.12). Upper and lower estimates for genus and family richness did not significantly differ either.

Table 2.2. Comparisons of richness values between land use types where upper estimates of richness include all taxa and lower estimates exclude broader taxa. (df = degrees of freedom, res. df. = residual degrees of freedom, p = p-value).

Response variable	Type of test	F-statistic	χ^2	res. df.	df.	p
Species richness upper estimate	Kruskal Wallis		4.29		2	0.12
Species richness lower estimate	Kruskal Wallis		1.53		2	0.47
Genus richness upper estimate	Kruskal Wallis		4.29		2	0.12
Genus richness lower estimate	ANOVA	3.47		9	2	0.08
Family richness upper estimate	Kruskal Wallis		4.02		2	0.13
Family richness lower estimate	ANOVA	1.93		9	2	0.20

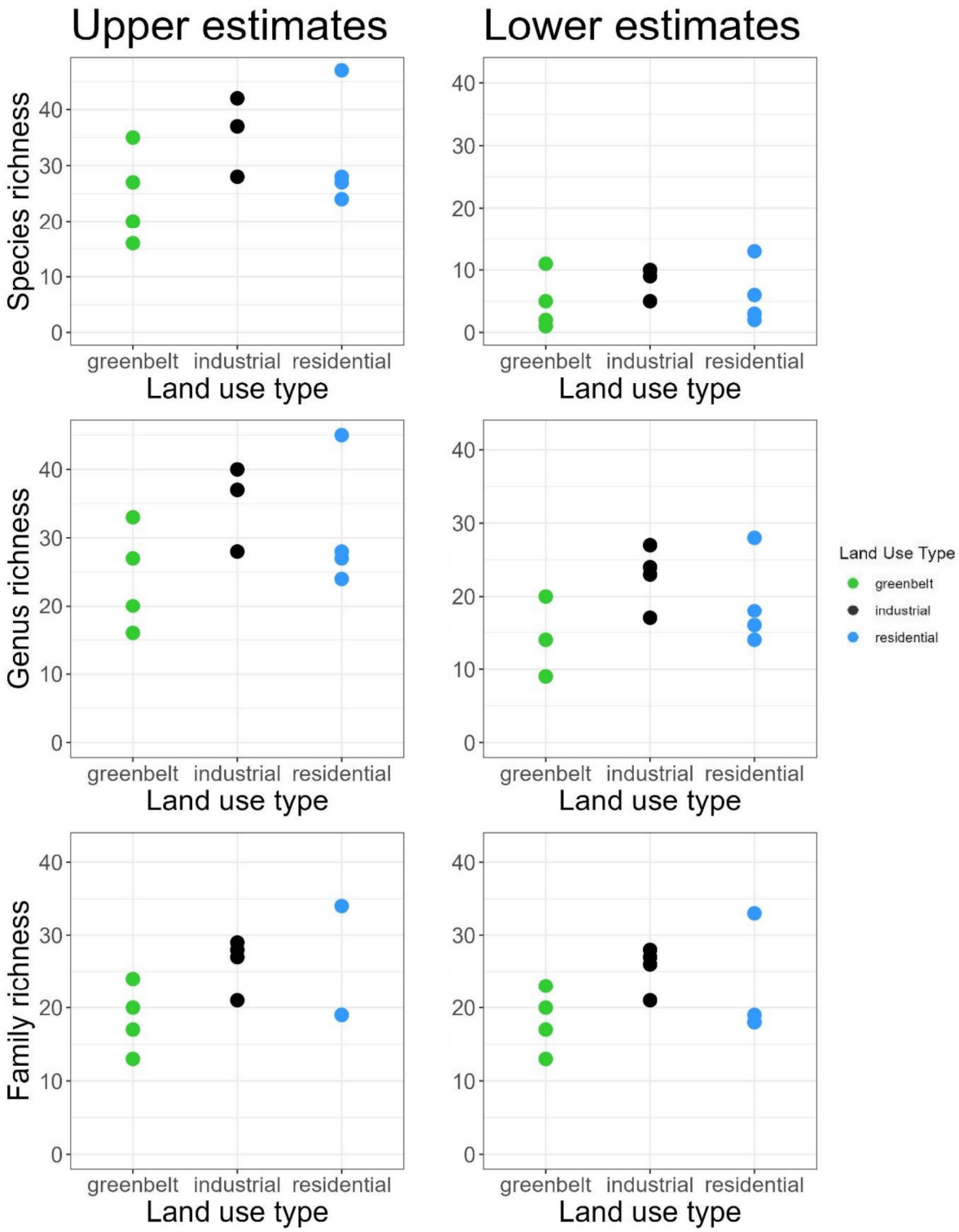


Figure 2.5. Dot plots representing upper (left column), and lower (right column) estimates for species, genus, and family richness between land use types. Upper estimates include all taxa. Lower estimates excluded broad taxa.

2.5.4. Geospatial land feature modelling

Contrary to what was expected, neither the total area of vegetation, nor vegetation evenness predicted species richness. Of the 54 models tested, only three proved significant, the area covered by trees at the 25 m scale, and the area of trees and grass at the 10 m scale. The first model was non-normal. The last two were strongly correlated (Pearson's correlation = -0.81, t = -4.3, df = 10, p = 0.0015), and so were not combined into a single, final model.

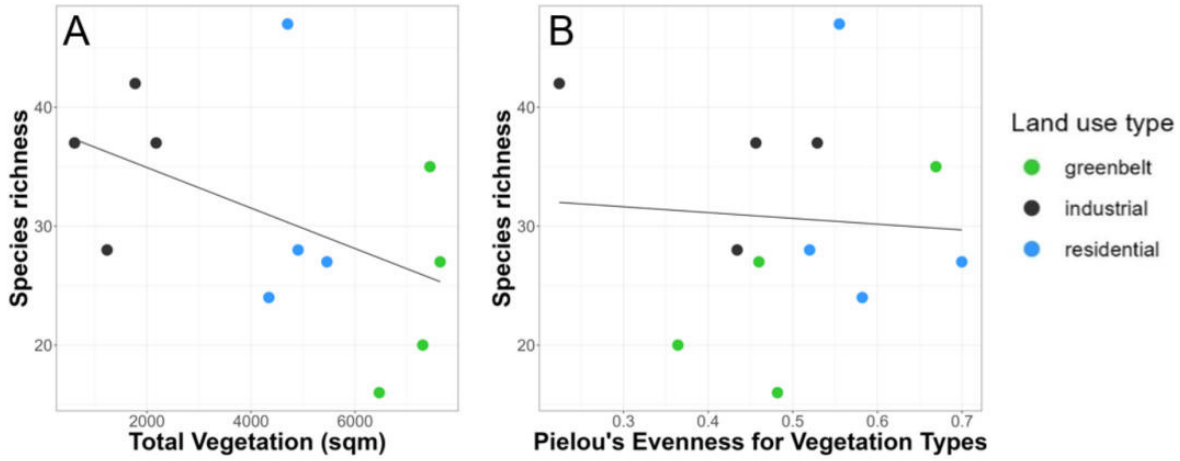


Figure 2.6. Scatterplots of species richness as a function of total vegetated area (A) and as a function of Pielou's evenness (B) for different vegetation types within a 10 m radius.

Table 2.3. The results of simple linear regressions where the total vegetated area (tot. veg.) and Pielou's evenness vegetation type (veg. evenness) are used to predict species richness (SR). (Adj. R^2 = Adjusted R^2)

Equation	Scale (m)	Slope	F-statistic	Res. df	df	Adj. R^2	p
SR~ total veg.	50	-0.0017	2.88	10	1	0.15	0.12
SR ~ total veg.	25	-0.0074	3.47	10	1	0.18	0.092
SR ~ total veg.	10	-0.03	0.74	10	1	-0.024	0.41
SR ~ veg. evenness	50	-4.87	0.05	10	1	-0.095	0.83
SR ~ veg. evenness	25	-6.57	0.52	10	1	-0.046	0.49
SR ~ veg. evenness	10	3.01	0.14	10	1	-0.085	0.72

Table 2.4. The results of two simple linear regressions; species richness (SR) as a function of grass area, and species richness as a function of forest area, both at a ten-meter scale. Both models are significant, but grass area negatively correlates with tree area, so these results are not independent.

Equation	Scale	Slope	F-statistic	Res. df.	df	Adj. R^2	p
SR ~ lawn area	10 m	0.079	10.31	10	1	0.46	0.0093
SR ~ tree area	10 m	-0.04	5.41	10	1	0.29	0.042

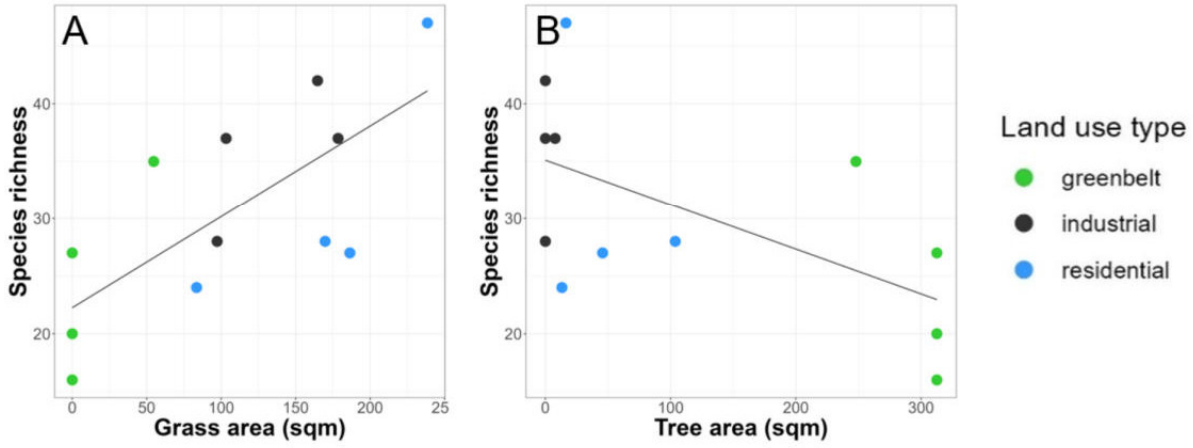


Figure 2.7. Linear regression plots of upper OTU richness estimates as a function of grass area (A) and forest area (B) within ten meters of a site.

2.5.5. Community similarity

Greenbelt and industrial arthropod communities were expected to be distinct from each other because they represented two extremes of vegetation types (tall vegetation, shaded, lots of woody debris vs. short, dense, open vegetation). Overall, industrial, residential, and greenbelt communities were significantly dissimilar from each other at the OTU, genus, and family level (Table 2.5.). The area of trees, grass, hard-surfaces, and buildings were all significantly associated with community composition (Figure 2.9.). When OTUs were pooled for each land use type, industrial and residential communities shared more OTUs with each other than with greenbelt sites. However, industrial communities had the greatest number of OTUs, and the most unique OTUs overall (Figure 2.8.). Geographic distance between sites did not correlate with community dissimilarity (Pearson's $r = 0.084$, $t = 0.68$, $df = 64$, $p = 0.5$).

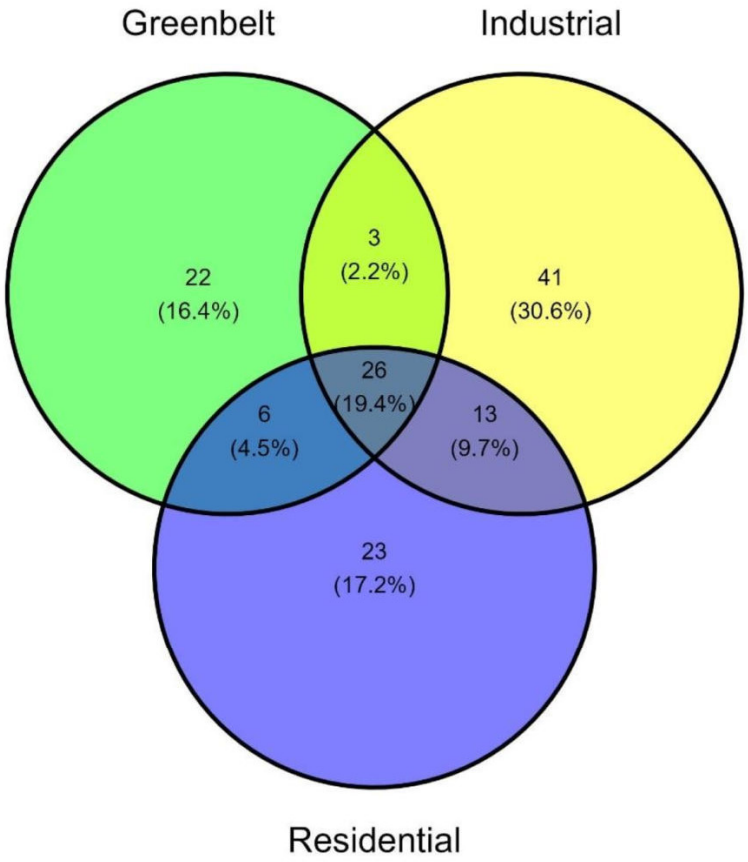


Figure 2.8. A Venn Diagram of the number of OTUs that are unique or shared between land use types (constructed from pooled data for each land use type). The percentages indicate what proportion of the total OTU pool each category makes up.

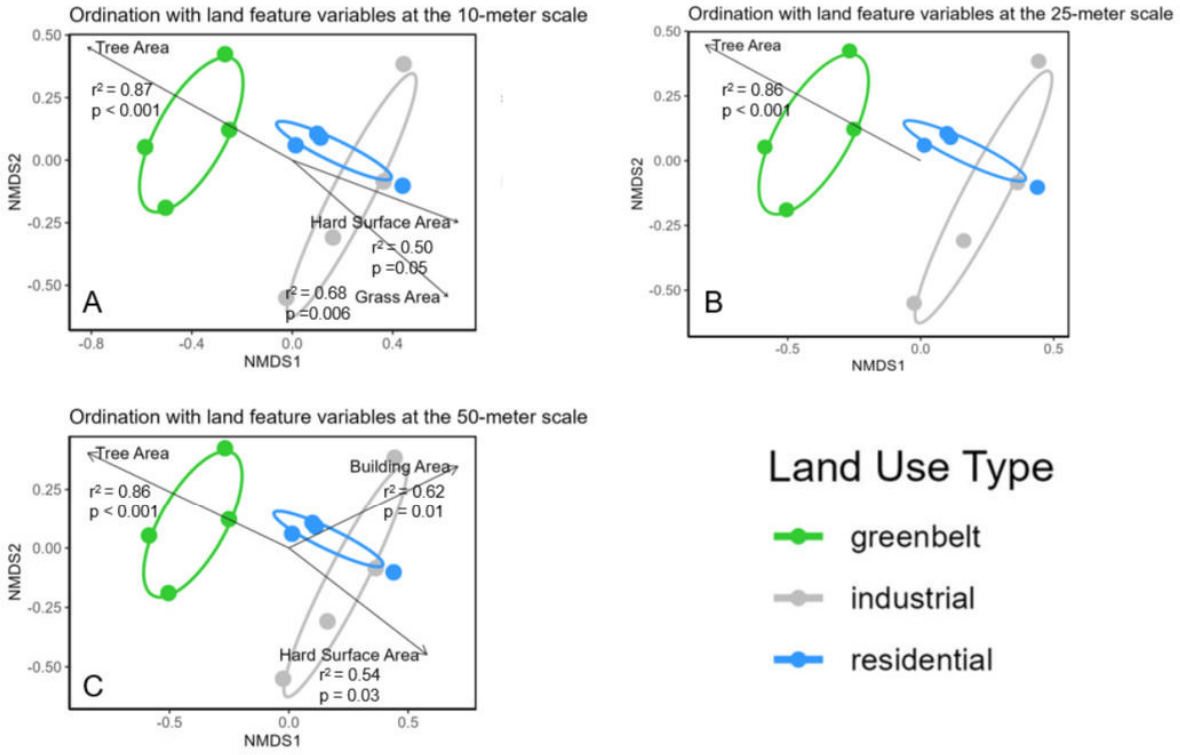


Figure 2.9. Bray Curtis ordination (dissimilarity = "bray", dimensions = 4, permutations = 10000, stress = 0.052) plots arthropod communities in NMDS space where points represent sites, and color indicates land use type (meta.mds function from vegan in R). Ellipses were drawn around sites of the same land use type using the standard error of weighted centroids. Residential sites overlap more strongly with industrial sites, indicating they have more similar species communities than greenbelt sites which are more distinct from the other two. Vectors indicate the relationship of environmental variables to communities using the *envfit* function from the vegan package. Longer arrows indicate a stronger relationship. These were tested at the 10 m (A), 25 m (B), and 50 m (C) scale with 10000 permutations. Tree area and grass area correlate with each other at the 10 m scale, so these results are not independent.

Table 2.5. Results of ANOSIM (ANO) and PERMANOVA (PERM) tests which compared the similarity of greenbelt, residential, and industrial communities. All analyses were conducted using Bray-Curtis dissimilarity with 10000 permutations. (Gb. = Greenbelt, Ind. = Industrial, Res. = Residential)

Communities	Taxon Level	Test	ANOR	Res. df.	df	R^2	Res. R^2	F-Statistic	p	fdr adj. p
All	OTU	ANO	0.62						0.0002	
Gb & Ind.	OTU	ANO	0.74						0.03	0.03
Res. & Gb.	OTU	ANO	0.65						0.03	0.03
Res. & Ind.	OTU	ANO	0.57						0.03	0.03
All	OTU	PERM		9	2	0.32	0.68	2.16	0.0002	
Gb & Ind.	OTU	PERM								0.03
Res. & Gb.	OTU	PERM								0.03
Res. & Ind.	OTU	PERM								0.03
All	Genus	ANO	0.68						0.0002	
All	Family	ANO	0.51						0.0003	

2.5.6. Habitat preference

Based on abundance data, Only *Megaselia* and *Lasius* were significantly associated with greenbelt and residential habitats respectively (r_{pb} = 0.58, p = 0.03; r_{pb} = 0.97, p = 0.01). However, species within these genera can have differing habitat preferences. A few other OTUs were strongly associated with different land use types, but a larger sample size would be needed to confirm these preferences (Table 3.3.). No analyses could be performed for habitat preference as the majority of OTUs' niches remain unknown. However most known OTUs seem to prefer semi-open habitat or are habitat generalists found in more than one type of environment. Closed habitat taxa are mostly found at greenbelt sites and open habitat taxa are mostly found at residential and industrial sites.

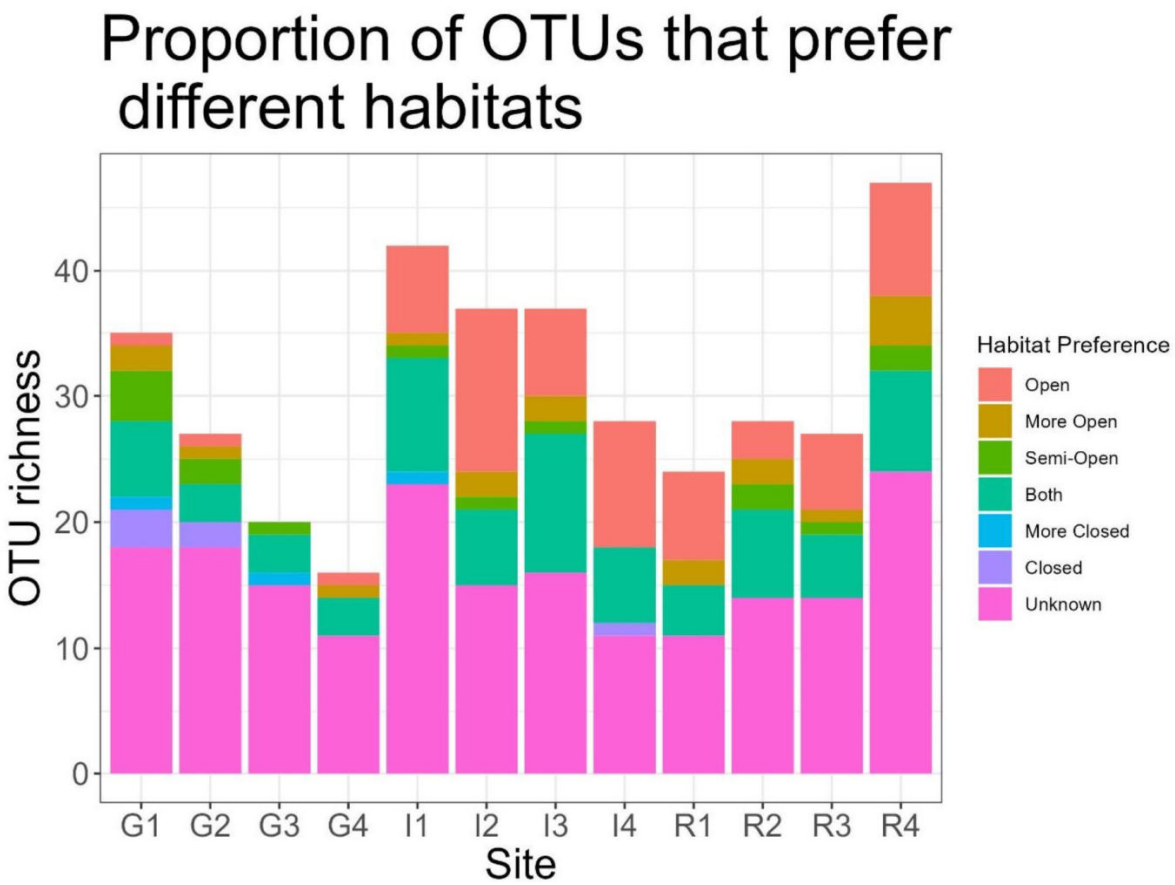


Figure 2.10. Bar plot of the habitat preference for different OTUs, where bars represent OTU richness and different colors represent habitat preference as described in the literature.

2.5.7. Functional diversity

Although urbanization was expected to negatively impact functional diversity, diversity was similar across land use types, regardless of the index used. Species richness significantly predicted FD_{pg} and F_{Ric} but not FMPD, suggesting results are robust.

Table 2.6. The results of three Kruskal Wallis tests that compared functional richness values of three different indices against land use type.

Statistical Test	Index	χ^2	df.	p
Kruskal-Wallis	FD(pg)	3.23	2	0.20
Kruskal-Wallis	F(Ric)	1.61	2	0.45
Kruskal-Wallis	FMPD	1.42	2	0.49

Table 2.7. The results of three simple linear regressions that model functional richness as a function of species richness. FD_{pg} and F_{Ric} are both strongly affected by species richness while FMPD is not.

Index	Slope	F-statistic	Res. df.	df.	Adj. R^2	p
FD_{PG}	0.0089	8.36	10	1	0.40	0.016
F_{Ric}	0.242	37.38	10	1	0.77	0.00011
FMPD	0.0021	0.65	10	1	-0.03	0.44

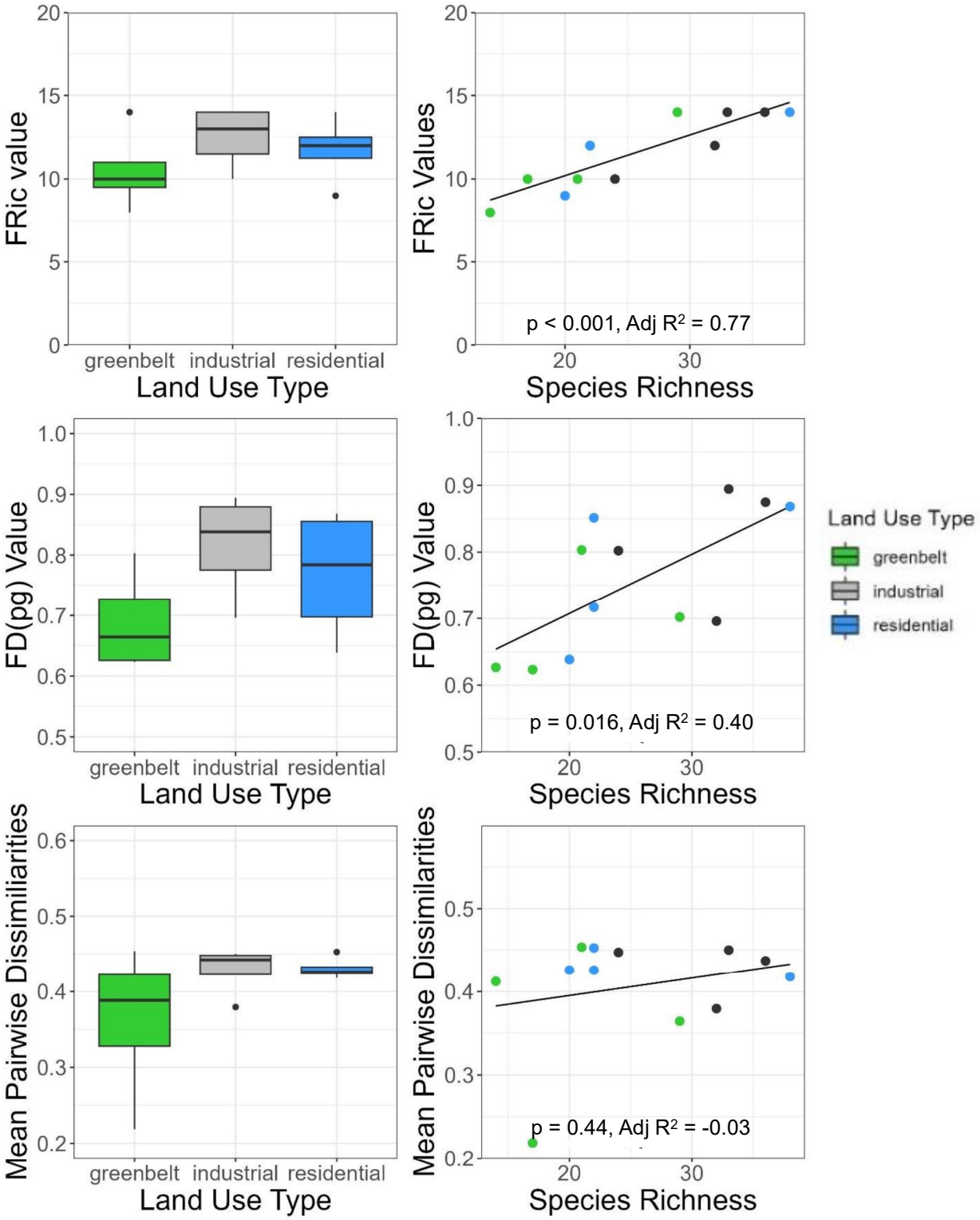


Figure 2.11. The three box and whiskers plots above compare the median functional richness values (F_{Ric}, FD_{pg}, FMPD) of different land use types, while the regression plots below show functional richness as a function of OTU richness.

2.5.8. Guild prevalence

Urbanization was expected to select for lower trophic positions. Residential and industrial areas did have higher proportions of herbivores and lower proportions of natural enemies, and these differences were significant for herbivores in residential areas compared to greenbelt areas (χ^2 = 6.99, df = 2, p = 0.03). The proportions of decomposers, fungivores, and honeydew feeders were statistically similar across land use types. Herbivore richness was most strongly associated with industrial and residential sites (r_{pb} = 0.87, adjusted p = 0.026), while no other guilds correlated significantly with land use types (Table 2.9.).

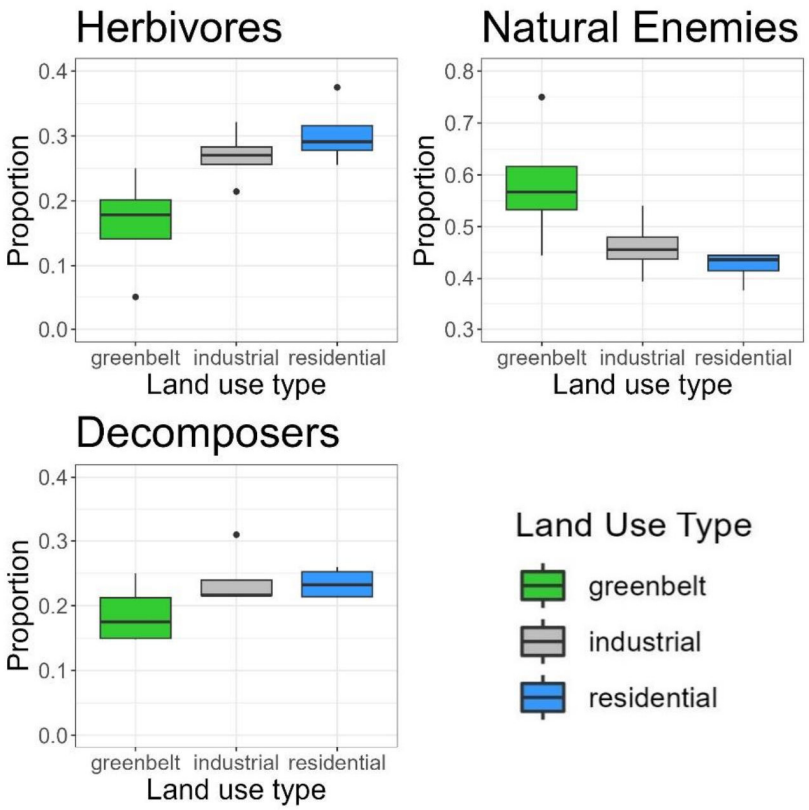


Figure 2.12. The box and whiskers plots compare the proportion taxa bellowing to herbivores (top left), natural enemies (top right), and decomposers (bottom left) out of all potential taxa at each site between land use types.

Table 2.8. The results of Kruskal-Wallis and Dunn tests comparing the proportions of different guilds against land use types. (Herb. = Herbivore, Nat. En. = Natural Enemy, Decom = Decomposer, fdr adj. p =fdr adjusted p-value)

Statistical Test	Guild	Comparison	χ^2	df	p	fdr adj. p
Kruskal-Wallis	Herb.		6.97	2	0.03	
Dunn-Test	Herb.	Gb. – Ind.	6.97		0.03	0.05
Dunn-Test	Herb.	Gb. – Res.	6.97		0.005	0.02*
Dunn-Test	Herb.	Ind. – Res.	6.97		0.3	0.2
Kruskal-Wallis	Nat. En.		5.10	2	0.08	
Kruskal-Wallis	Decom.		3.27	2	0.2	

Table 2.9. The associations of guilds with land use types. Correlations were calculated using the r_{pb} index from the *indicspecies* package in R (permutations = 10000). Zeroes and ones indicate positive or no association between guilds and land use types. r_{pb} is the correlation between guilds and groups of sites for their strongest association (single or multiple land use types). P-values were adjusted using the *fdr* method.

Guild	Gb.	Ind.	Res.	r_{pb}	p	fdr. adj. p
Herbivores	0	1	1	0.87	0.005	0.026*
Natural Enemies	0	1	0	0.33	0.58	0.68
Decomposers	0	1	1	0.62	0.10	0.24
Fungivores	0	1	0	0.34	0.68	0.68
Honeydew Feeders	0	1	0	0.35	0.65	0.68

2.5.9. Host specialization

Industrial areas were expected to have higher proportions of polyphagous OTUs. Overall, there were higher proportions of specialists at greenbelt sites, and more generalists at residential and industrial sites, but there were no significant differences. Generalists were the most common host specialization level, followed by oligophagous taxa, suggesting that a broad diet may be beneficial overall in urban environments. Mean host specialization also showed no significant differences between land use types. A larger sample size may be needed to draw more conclusive results.

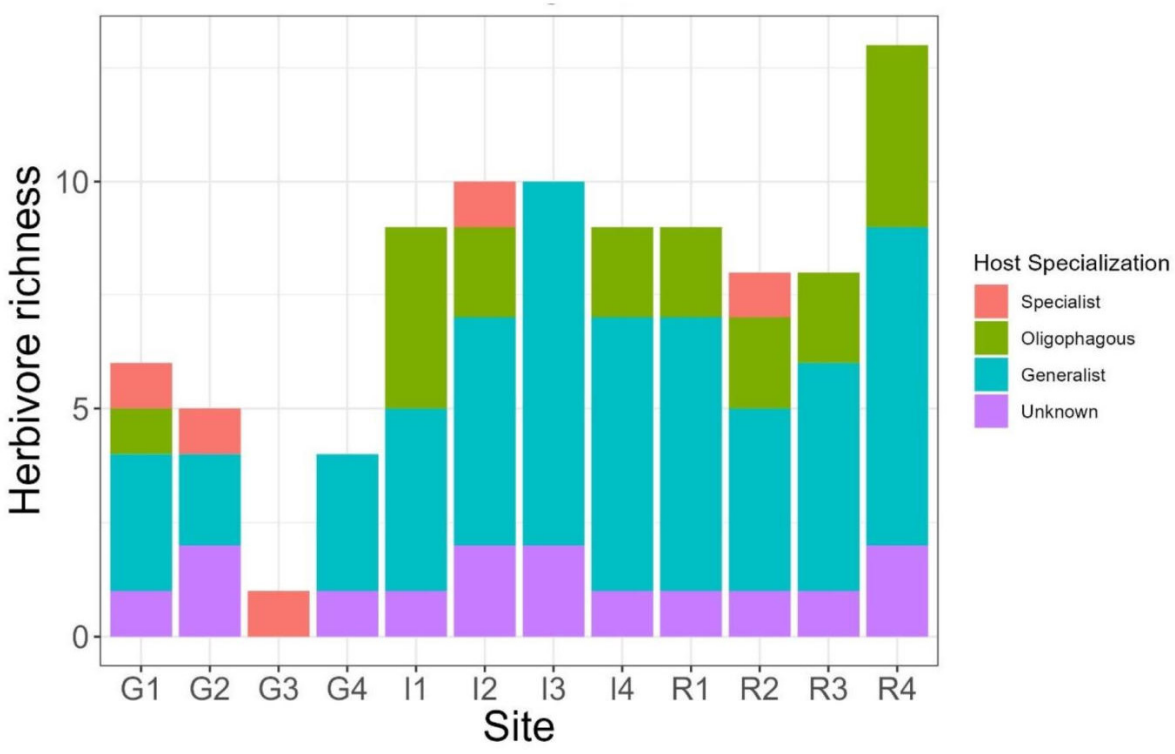


Figure 2.13. The proportions of different host specialization categories in different colors over the total number of herbivores collected for each site.

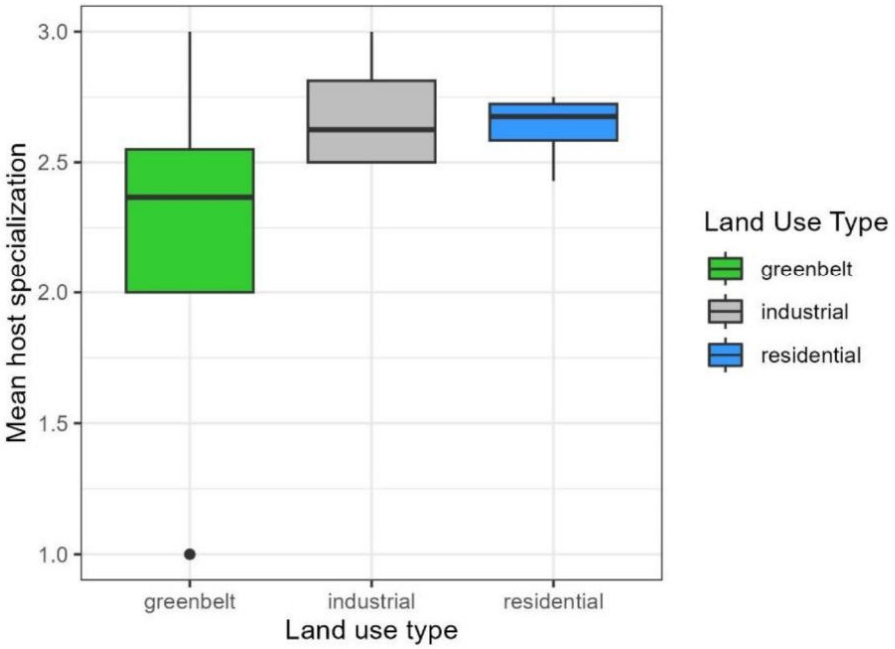


Figure 2.14. Box and whiskers plot of mean host specialization by land use type, calculated using the CWM.type method, in *dbFD* function from the FD package in R. Specialists were ranked as 1, oligophages as 2, and generalists ranked as 3.

Table 2.10. The results of Kruskal-Wallis tests for the proportions of generalist, oligophagous, and specialist OTUs compared between land use types, as well as the means between land use types.

Statistical Test	Dependent Variable	χ^2	df	p	fdr adj. p
Kruskal-Wallis	Proportion of Generalists	1.44	2	0.49	0.49
Kruskal-Wallis	Proportion of Oligophages	6.39	2	0.04	0.12
Kruskal-Wallis	Proportion of Specialists	4.35	2	0.11	0.17
Kruskal-Wallis	Mean host specialization	2.23	2	0.33	

2.6. DISCUSSION

While many studies highlight the negative impacts of urbanization on arthropod communities (Vergnes et al. 2014; Chatelain et al. 2023), these findings suggest that land use type had no strong effects on diversity. However, communities from different land use types were distinct, highlighting how many different styles of land management can foster high gamma diversity across a city (Sattler et al. 2011). McIntyre et al. 2001 found similar results where land use type did not affect taxon richness but did alter community composition. Sattler et al. 2010 also found little difference in arthropod richness along urban gradients, which they attributed to the fine-scale habitat heterogeneity that cities create.

Urban habitats filter species from the regional species pool based on their ecological traits (Aronson et al. 2016) and are typically considered harsh environments in which only few species can survive (Sol et al. 2014). But urban conditions can also promote higher than average diversity, especially when food availability is high. Often, well-adapted, non-native species are introduced (Gippet et al. 2019), or early seral species colonize urban habitats (McKinney 2006). While urbanization may be cause for concern on a large scale, the conservation value of industrial and residential areas should not be ignored as they can support taxonomically diverse arthropod communities.

Although increased total vegetation and vegetation evenness would be expected to positively affect biodiversity, neither of these variables had any effect. Lawn at the ten-meter scale was found to positively affect arthropod richness, while tree area decreased it. This could be due in part to greenbelt sites tending to have

lower species richness than grassier industrial and residential sites. However, of the taxa with known habitat preferences, only a handful preferred closed habitats. Many greenbelt species appeared to be habitat generalists or preferred semi-open habitats. In other land use types, taxa tended to be habitat generalists or open habitat species. Overall, most OTUs were positively associated with industrial (53%) and residential (34%) areas.

Urban areas often favour habitat generalists and open-habitat species (Magura et al. 2010; Olivier et al. 2015; Magura et al. 2020). Since lawn is one of the most common vegetative characteristics in cities (Proske et al. 2022), and most taxa in Prince George prefer or tolerate lawns, it follows that increasing lawn area, and consequently, decreasing tree area, could promote higher OTU richness, potentially even in forested areas. Urban forests are often invaded by open-habitat species from the surrounding landscape, especially as urban forests tend to be drier and warmer than natural forests (Magura et al. 2020). Lawn at the ten-meter scale might also act as a better proxy for habitat patch size in residential and industrial sites than at larger spatial scales as it is less likely to be measuring vegetation separated by fences, buildings, roads, or other physical obstacles. Thus, increases in lawn area may relate to increases in overall habitat size. Note that lawns in this study tended to be lightly managed with infrequent mowing and little to no use of herbicides and pesticides.

Functional diversity was also similar between land use types, regardless of the index used. Because abundance was not considered, only functional richness could truly be evaluated, but this suggests that taxa fill the same basic niches in

various land use types, and members of those communities are, on average, equally dissimilar from each other. Both F_{Ric} and FD_{PG} were significantly related to species richness, as communities with larger species pools are more likely to have functionally different species (Petchey et al. 2009). However, a strong relationship with species richness can make it hard to disentangle the effect of richness from the effect of functional differences within a community (Dalerum et al. 2012). FMPD was not significantly affected by species richness but was still similar across land use types, suggesting these results are robust.

While arthropod communities in different land use types may offer the same range of ecosystem services, different guilds may be better represented in different land use types. Proportions of honeydew feeders, fungivores, and decomposers were similar between land use types. But greenbelt communities supported higher proportions of natural enemies while residential areas harboured significantly higher proportions of herbivores. Herbivores were also significantly associated with industrial and residential sites. Natural enemies are especially vulnerable to environmental disturbance (Cardoso et al. 2011). They often require a wide array of resources to complete their life cycles, from nectar to prey sources (Corcos et al. 2019). Natural enemies need larger, more well-connected habitats than their prey (Kruess and Tscharntke 1994), and urban features like roads and walls can represent dispersal barriers (Peralta et al. 2011). Greenbelt sites represented the largest, most continuous habitat patches as they had the highest total vegetation, and smallest areas of buildings and hard surfaces.

Greenbelt sites were also mainly unmanaged, which could better support longer food chains. Rigal et al. 2018 found intensive pasture selected for pierce-cutting herbivores compared to more diverse assemblages in natural forests. Likewise Hironaka and Koike 2013 found semi-natural grasslands better supported large carnivorous arthropods compared to managed grasslands. Additionally, decreasing native plant richness and habitat complexity at urbanized sites can reduce predator pressure (Raupp et al. 2010), which may explain higher proportions of herbivores at industrial and residential sites. Yet even if some groups are underrepresented at various land use types, the mosaic nature of cities helps compensate for this as different functional groups can be promoted in different land use types (Pinto et al. 2021).

Urbanization tends to select for generalist species (Clavel et al. 2011), but host specialization was similar for herbivores across land use types. This suggests herbivores face similar selection pressures for this trait regardless of land management style, however, a larger sample size would be needed to confirm these results.

On a global scale, urbanization threatens biodiversity by removing an increasing number of vulnerable species from regional pools (Clavel et al. 2011), and homogenizing remaining communities (McKinney 2006). As cities sprawl, novel habitats become increasingly important for protecting biodiversity as natural areas alone prove insufficient (Lundholm and Richardson 2010). On a local level, urban planners and landowners can maximize biodiversity by promoting conservation in land use types that are typically overlooked. If industrial and residential areas are as

taxonomically and functionally diverse as urban forests, then they should be managed to preserve their ecological value.

Further research could explore ways to promote arthropod diversity in urban land use types that I did not explore in this study, such as reduced mowing, intentionally increasing plant diversity in developed areas, maintaining current greenbelt sites, and planning for greenbelt in new residential and industrial areas (Proske et al. 2022). Future studies could also expand sampling for pollinators or flying/overstory arthropods which also contribute to urban ecosystem services and consider the effect of geospatial variables at larger scales (eg. 500 meters) to see how arthropods respond to landscape-level urbanization.

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Chapter three: The abundance and diversity of scuttle flies in Prince George

3.1. INTRODUCTION

While concerns mount over declining insect abundance and diversity (Forister et al. 2019), few groups remain as species-rich, but as simultaneously understudied as the scuttle fly family (Diptera: Phoridae) (Brown and Vendetti 2020; Brown 2022a). Roughly 4500 species have been described, including 1700 in the genus *Megaselia*, but true phorid richness could prove to be ten times greater (Brown and Hartop 2017; Brown 2022b; Brown 2022a).

Phorids play many ecological roles, from fungivores and scavengers to herbivores, predators (Brown and Hartop 2017), and especially parasitoids (Brown 2022b). They are also extremely common and abundant in most parts of the world and have even been collected north of the Arctic circle (Disney 2013).

Because they are species-rich, ecologically diverse, and ubiquitous, phorids make excellent model organisms for studying disturbance (Brown and Hartop 2017). They've been used to investigate the effects of different kinds of habitat modification from wildfire (Durska 2015), and forest management (Durska 2006), to urbanization (Durska 1981; McGlynn et al. 2019). Many species are also of economic interest as they can be honeybee parasites (Core et al. 2012), important for the bio-control invasive fire ants (Chen and Morrison 2021), used in forensic entomology (Alcaine-Colet et al. 2015), or serve as a model organism for biological studies (Jayakumar Pallavi et al. 2023).

Despite their importance and great potential as study subjects, phorids have been largely overlooked in research (Brown and Hartop 2017). Phorids are generally small, inconspicuous, and hard to identify. Many groups have complex or unresolved taxonomy or have only one sex described (Hartop et al. 2015; Brown 2022b). For example, in 1999, Disney reviewed more than 1000 *Megaselia pulicaria* specimens, and reclassified all except a single lectotype into different species (Disney 1999). Despite this, phorids represent an excellent opportunity for further biodiversity work, especially with the advent of DNA barcoding.

Molecular sequencing technologies have become cheaper and faster in recent decades (Bansal and Boucher 2019). At the same time, emerging online repositories like GenBank and the Barcode of Life Database (BOLD) make it possible to sequence, store, and compare genetic data from thousands of animal species. However, arthropods remain proportionately severely underrepresented and identified compared to vertebrates (Meiklejohn et al. 2019; Hotaling et al. 2021). Additionally, while sequencing capacity has risen, morphological and other taxonomic efforts have not kept up due to insufficient personnel with taxon-specific expertise. In 2015, fewer than half of the invertebrate taxa added to GenBank possessed species identifications, largely because they included unnamed records from BOLD (Page 2016).

Nevertheless, DNA barcoding remains one of the quickest and most affordable ways to quantify the biodiversity for obscure taxa, including phorids. For example, in 2019, more than 650 molecular operational taxonomic units (mOTUs) of phorids were detected from a single Malaise trap in Uganda using rapid sequencing

technology (Srivathsan et al.2019). Similarly, nearly 1500 phorid barcode index numbers (BINs) were found in Costa-Rica's Conservación Guanacaste area in 2022 (Brown 2022a). Most recently, a 2023 Indonesian study uncovered 500 genetic sequence clusters from 5034 phorid specimens in an under-surveyed national park (Chimeno et al. 2023). While barcodes do not replace morphological and other non-DNA taxonomy, they complement it as they represent a way to gain ground when dealing with dark taxa (Srivathsan et al. 2019).

Urban areas, long-regarded as impoverished habitats (Hartop et al. 2015), have largely been neglected in entomological literature save for studies focused on pests and insect disease vectors. However, as cities expand, more researchers are paying attention to how this impacts insect biodiversity (McIntyre 2009), especially in recent decades (Fenoglio et al. 2020). Phorids have proven to be very interesting focal taxa, due to their complicated relationship with urbanization. Phorids are most prevalent in forests (Durska 1981), and many depend on large swathes of natural habitat. However, phorids are often common in cities. Many species are synanthropic urbanophiles, and have even been sampled at the tops of 1000 ft buildings (Brown and Hartop 2017).

Some of the earliest urban phorid research began in 1981, with Durska 1981. Durska surveyed public parks, residences, and the downtown area of Warsaw for phorids, discovering higher richness and abundance away from the urban core. She documented 36 species (Durska 1981) in that city. Twenty years later Disney (2001) recorded 53 *Megaselia* species from a single garden in London (Hartop et al. 2015).

In 2009, more work began to emerge in North America as Disney and Brown reported two new phorids for the Nearctic region from a California backyard (Disney and Brown 2009). In 2015, Hartop et al. described 30 new species from a Bioscan survey of 30 backyards in Los Angeles (L.A.) (Hartop et al. 2015). Further work unearthed nearly 100 species present in L.A., and the sites closest to natural areas were the most species rich (Brown and Hartop 2017). However, McGlynn et al. 2019 found that distance from natural areas had no significant effect on richness. Instead, temperature was the most important driver of phorid diversity and abundance. Further research into phorids can help us better understand how they respond to urbanization and what environmental variables drive these patterns. As phorids are an important component of urban biotic communities, understanding their assemblages can be useful for ecosystem services management and assessment.

3.2. OBJECTIVES

The main goals of this project were to

I) Inventory the phorids of an urban ecosystem in British Columbia's central interior.

II) Compare phorid abundance and richness between land use types: greenbelt, residential, industrial, and edge sites.

III) Model how underlying factors like temperature and land use type impact phorid abundance and richness.

IV) Compare these findings with other phorid records from Global Biodiversity Information Facility (GBIF) and BOLD for British Columbia.

As other studies have found that phorids appear to be more abundant and diverse near or in natural areas, I expected to collect fewer species and individuals in industrial areas.

3.3. METHODS

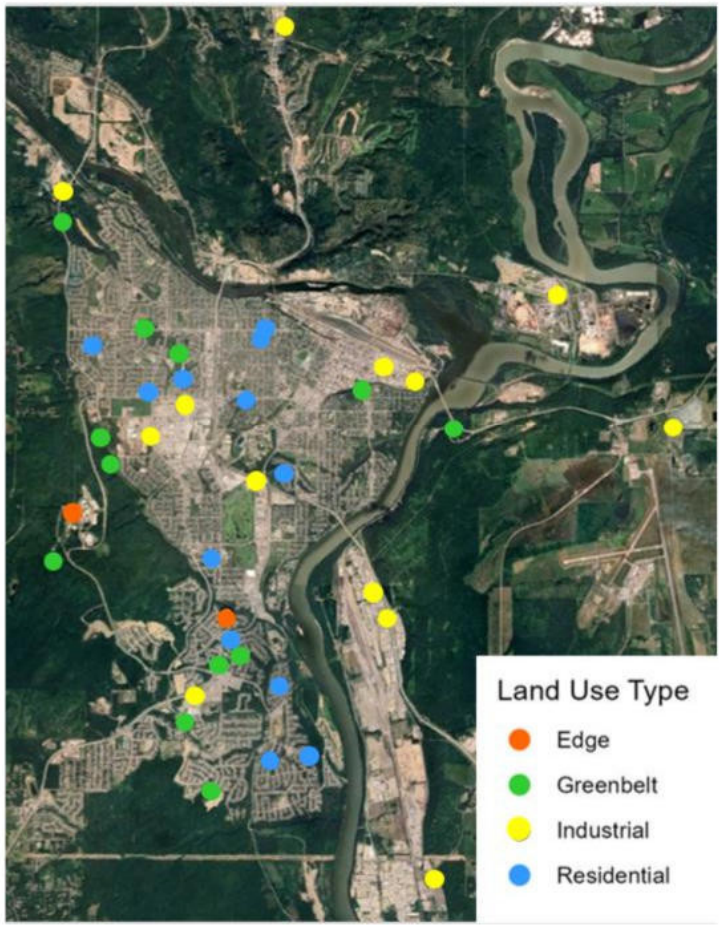
3.3.1. Study sites

This project included 30 sites that were sampled in 2022, and 12 sites that were sampled in the 2015 study described in Chapter 2 Three of the 2015 sites were resampled in 2022: Moore's Meadows, Rolling Mix Concrete, and Connaught Hill. The 2022 sites included eight residential sites, two edge sites (residences next to forests), ten industrial sites, and ten greenbelt sites. Like the 2015 sites, residences were homes with gardens in residential-zoned areas, industrial sites were businesses in industrial-zoned areas, and greenbelt sites were forested parks within city limits. The edge sites included student housing and a private residence that both bordered immediately adjacent forests. Residential and edge sites were confirmed with owners to be pesticide free. Greenbelt sites were unmanaged within their forested canopy, and most industrial sites were mown infrequently and were unlikely to be treated with pesticides.

Of the 2022 sites, G7 (Connaught Hill) involved sampling along a cliff, so one side of the cups was frequently buried. Given this, and the low trapping yields, abundance data from G7 was excluded. Site I3 (Overhang) also had all traps and temperature sensors removed after only the second collection for that site, so it was

excluded from the diversity data. All sites were within an 8km radius of each other, spread out over a 200 km^2 area.

Figure 3.1. Map of 2022 study sites. on a satellite map of Prince George from Google Earth. Point color indicates land use types. Sites (R = Residential (R1 and R3 are edge sites), G = Greenbelt, I = Industrial) are shown in the table beside.



Site	Latitude	Longitude
R1	53.89244	-122.817
R2	53.88611	-122.782
R3	53.87786	-122.778
R4	53.86733	-122.764
R5	53.85647	-122.766
R6	53.90983	-122.773
R7	53.92103	-122.768
R8	53.91319	-122.79
R9	53.91119	-122.798
R10	53.91808	-122.812
G1	53.88542	-122.821
G2	53.87147	-122.774
G3	53.86178	-122.787
G4	53.85167	-122.782
G5	53.90039	-122.807
G6	53.90528	-122.72
G7	53.91203	-122.744
G8	53.91669	-122.791
G9	53.92119	-122.799
G10	53.93692	-122.821
I1	53.86608	-122.785
I2	53.83925	-122.726
I3	53.89783	-122.771
I4	53.87742	-122.737
I5	53.90628	-122.665
I6	53.91314	-122.73
I7	53.92622	-122.694
I8	53.96736	-122.765
I9	53.94181	-122.821
I10	53.90408	-122.798

3.3.2. Sampling

For 2015 collection methods, see Chapter 2. In 2022, I collected phorids using three covered pitfall traps set in two meter transects at every site. Fewer traps were used in 2022 to ensure trap catch yields would be manageable. I filled the traps with 50% propylene glycol and began sampling in late-May for a single site (R1: UNBC Residence) and set traps in early-June for all other sites. I emptied the traps roughly every two weeks until mid-September. Each site was also equipped with a temperature sensor (Kestrel or Convergence Instruments THM sensor) which were placed in sealed cups buried in the same manner as the traps and which took readings every 30 minutes. Prior to use in the field, all of the sensors were stored together in a box for a week and their mean temperatures were compared to ensure sensor brand did not impact temperature accuracy (Wilcoxon test $p = 0.26$, $r = 0.22$).

I excluded 17 out of 190 temperature records due to sensors being disturbed, batteries dying, or erratic measurements. From these data, I took the mean, minimum, and maximum temperature across all readings for a given sampling period THM sensors record the minimum, maximum and mean temperature within a 30-minute period while Kestrels show only one temperature value. I also measured temperature variation as temperature standard deviation for a sampling period, divided by the number of readings for each period.

3.3.3. Sorting and DNA sequencing

I counted all specimens that amounted to more than half a fly – i.e. if they included at least a thorax with a head or abdomen and with wings and most legs attached for a total of 3730 flies collected in 2022. I compiled traits from phorid keys such as Borgmeier's 1964 Revision of the North American Phorid Flies Part II: The Species of the Genus *Megaselia*, Subgenus *Aphiochaeta* (Diptera, Phoridae), McAlpine's 1987 Manual of Nearctic Diptera Volume 2, and Disney's 2013 article: An unusually rich scuttle fly fauna (Diptera, Phoridae) from North of the Arctic Circle in the Kola Peninsula, N. W. Russia. Based on these traits, and other observed differences, I sorted my phorids into different morphospecies, separated by sex. Because of the large volume of specimens, I mainly sorted only a single pitfall trap from each site/sampling period from June to September 11th. Due to time constraints, and the limited number of samples that could be selected for sequencing, I counted, but did not sort or barcode additional samples taken on May 28th, June 10th, and September18th. I sorted additional traps for particularly productive sites or sampling periods, or to find more complete specimens for certain morphospecies.

I sent 380 specimens to the Centre for Biodiversity Genomics at Guelph, based upon differential morphology, for sequencing of the DNA barcode region of the CO1 gene. I made an effort to represent every morphospecies present in my samples in relation to each land use type and, as much as possible, for each site. When combined with the 2015 DNA barcode data, this amounted to 590 successfully

sequenced specimens, of which 530 were barcode compliant (at least 500 bp long with less than 1% ambiguous pairs (Bold Systems 2014).

3.3.4. mOTU count

Using the BOLD cluster sequence function, I grouped my flies into different molecular operational taxonomic units (mOTUs) to act as proxies for species identifications. I excluded all sequences less than 400 bp long, or that included stop codons or contaminants, leaving 582 sequences. The sequences were aligned with the BOLD Aligner and distances were calculated using the pairwise deletion method. This method converts genetic sequences to peptide sequences and arranges them using a Hidden Markov Model of the COI protein. It then converts the sequences them back into nucleotides, and those with less than 2.2% divergence from each other are grouped together with single linkage clustering. Those with 4.4% divergence or less may initially be included with their nearest neighbour, but further refinement with Markov clustering can either lump or split these sequences based on variation patterns. Several possibilities are considered and scored with a Silhouette index, where the highest scoring outcomes are kept (Ratnasingham and Hebert 2013).

I built species accumulation curves for all sites, and each land use type using the method “rarefaction” from the *specaccum* function in vegan (R). This method randomly subsamples a given number of individuals for each site to account for differences in numbers of individuals between collections (Hurlbert 1971; Oksanen et al. 2015). It repeats this process (permutations = 10000) to generate mean numbers

of species found per given number of individuals and their standard deviation (Oksanen et al. 2015).

I combined 2022 and 2015 sites that were resampled since they were likely to contain similar species assemblages across both years. Rarefying species richness works best when samples are random, complete, and of equal sampling effort (Hurlbert 1971). This was not the case for my data as resampled sites had the greatest sampling efforts, 2022 sites were sampled for roughly three weeks longer than 2015 sites, and different sites had different numbers of specimens sequenced. However, rarefaction is commonly used in arthropod studies to account for unequal sampling (Buddle et al. 2005). True numbers of species were estimated using the estaccumR and specpool functions from the vegan R package.

3.3.5. Abundance modelling

No temperature data were collected for 2015, so only 2022 specimens were considered in these models. Of the 570 trap collections, 16 were removed due to trap disturbance or the loss of contents, and all collections from G7 were excluded due to the landscape interfering with trap efficacy. Data from September 18th was included in models, but not in biodiversity data. Fly abundance was measured as the number of flies caught per trap, per day, by site, to account for slightly different numbers of sampling days and numbers of undisturbed traps between collections.

Using the lme4 and lmerTest packages in R, I built nine mixed effects models that predicted abundance as a function of mean temperature, temperature variation, and land use type. Minimum and maximum temperature were excluded as they

correlated strongly with mean temperature. Sites G7, and R2 were also excluded from the data, the latter due to extremely high abundance values which may have resulted from a garden, several fruit trees, and large compost pile at the site. Collection date and site were included as random intercepts in all models. For simplicity, collection dates were combined into seven sampling periods. Temperature variables were added to models as second-degree polynomial terms as I expected abundance to be low at more extreme mean temperatures, and peak at moderate temperatures.

Temperature conditions varied between land use types with greenbelt sites being the coolest and industrial sites the warmest. I expected flies in different land use types to have different temperature preferences (eg. warmer industrial sites should favour flies that can tolerate hotter temperatures), and abundances also varied greatly between land use types (highest in residential, lowest in industrial) so I modelled land use type as an intercept, and an interaction term (with and without intercepts) in different models.

I evaluated model quality and assumptions with the performance package in R, including the residuals vs fitted, homogeneity of variances, normality of residuals and random effects plots, and testing the heteroscedasticity of the data using the function *check_heteroscedasticity*. For model quality, the performance package includes indices such as R^2, intraclass correlation coefficients, weights for Aikake and Bayes Information Criterion, root mean squared error, and residual standard error. It also features an overall score calculated by rescaling all indices between zero and one, then averaging their scores for each model. I then tested the

significance of different terms using likelihood ratio tests on nested models fitted using restricted maximum likelihood.

Table 3.1. Seven sampling periods used as random intercepts in mixed models.

Sampling Period	Dates	
1	2022-06-19	2022-06-26
2	2022-07-03	2022-07-10
3	2022-07-17	2022-07-24
4	2022-07-31	2022-08-07
5	2022-08-12	2022-08-13
6	2022-08-28	2022-09-04
7	2022-09-11	2022-09-18

Table 3.2. Model equations for nine mixed effects models (Abun = Abundance). Land use type is a 4-way factorial term. In some models, land use type is an interaction term, an intercept, or excluded. Second degree polynomial terms for temperature variables are referred to as poly(temperature variable).

Models
Abun = land use type * poly (mean temperature) (interaction and intercepts)
Abun = land use type * poly (mean temperature) (interaction only)
Abun = land use type + poly (mean temperature) (no interaction)
Abun = land use type * poly (temperature variation) (interaction only)
Abun = land use type + poly(temperature variation) (no interaction)
Null model with random effects only
Abun = poly (mean temperature)
Abun = land use type
Abun = poly (temperature variation)

3.3.6. mOTU richness by land use type

I compared the richness of mOTUs by land use type using Kruskal Wallis and Dunn tests. Due to differences in sampling methods between years, I kept comparison of flies from 2022 and 2015 separate. I also explored the habitat preference of different mOTUs using a Venn diagram built with the ggvenn package and r_{pb} index from the indicspecies package (Table 5.2.2.).

3.3.7. Identifications and BINs

BOLD clusters sequences from its overall database using neighbour joining trees. Terminal clusters are assigned barcode index numbers or BINs which, like mOTUs, can act as species proxies but include sequences from public and private data from BOLD, while mOTUs in this case, were grouped using data from only this project. BINs may be split or rearranged when new 500 bp sequences are added and help refine relationships between specimens (BOLD Systems 2011).

Sequences can be compared on BOLD using the complete BOLD database which includes sequences at least 500 base pairs (bp) long or using the BOLD species database which excludes sequences without an associated species identification (BOLD Systems 2011). I wanted to know what potential species names or BINs my mOTUs belonged to. Using the Batch ID engine from BOLD, I compared sequences from my project with those from existing BINs and species names recorded in the BOLD database. I used sequences at least 400 bp long, with 400 bp of overlap. I first searched the database for matches with species identifications. In R, I filtered those results to include only 100%, 99%, or 98.5% matches, and grouped them by mOTU. I chose conservative divergence thresholds (≤1.5%) because my minimum

sequence length was short and broader matches tended to result in more species names for a single mOTU. A single specimen from this project could match with more than a hundred records from the BOLD, so I averaged the percent match at each filtration level for each unique species identification.

Most species identifications also had corresponding BINs. For those that did not, I repeated my search using the full BOLD database, and filtered results using a 98.5% match threshold. For results that matched neither species nor BIN, I would search again without a match percent threshold, or BLAST the genetic sequence on GenBank, which helped indicate specimen genus (Table 5.2.1.).

3.3.8. Phorid records in British Columbia from GBIF and BOLD

To compare these results with other species and BINs already recorded in British Columbia (BC), I extracted public records from GBIF and BOLD. On September 18th 2023, I downloaded 102302 phorid records from GBIF. I drew a polygon around British Columbia, and used the TaxonKey Phoridae, including records that were preserved and material specimens. Assuming that coordinates were recorded in the World Geodetic System 1984 (WGS 84), I assigned occurrence records to different ecoregions using the the “bcmaps” package. I excluded all observations recorded outside BC (52108 observations), and without ecoregion data (18157 observations). For sites that had no province recorded, but did have an ecoregion, I checked the locality data to confirm their location, and excluding 57 blank records. I grouped the resulting 31980 records by species.

On September 25th 2023, I downloaded 12418 records from the BOLD public database using the search terms “Phoridae British Columbia”. I excluded four records without coordinates. I plotted occurrence records in different ecoprovinces using the ggplot2, sf, and the bcmaps package in R. I compared the number of species and BIN records between GBIF, BOLD and this project. Using data from the Sub-Boreal Interior ecoprovince, I repeated the procedure.

3.4. RESULTS

3.4.1. Data Quality

Figure 3.2. shows the number of flies collected, sorted, and barcoded by site for 2022. Of the 3730 flies collected, 58% were sorted morphologically (64% for selected dates), and 9.4% were genetically sequenced (10.3% for selected dates).

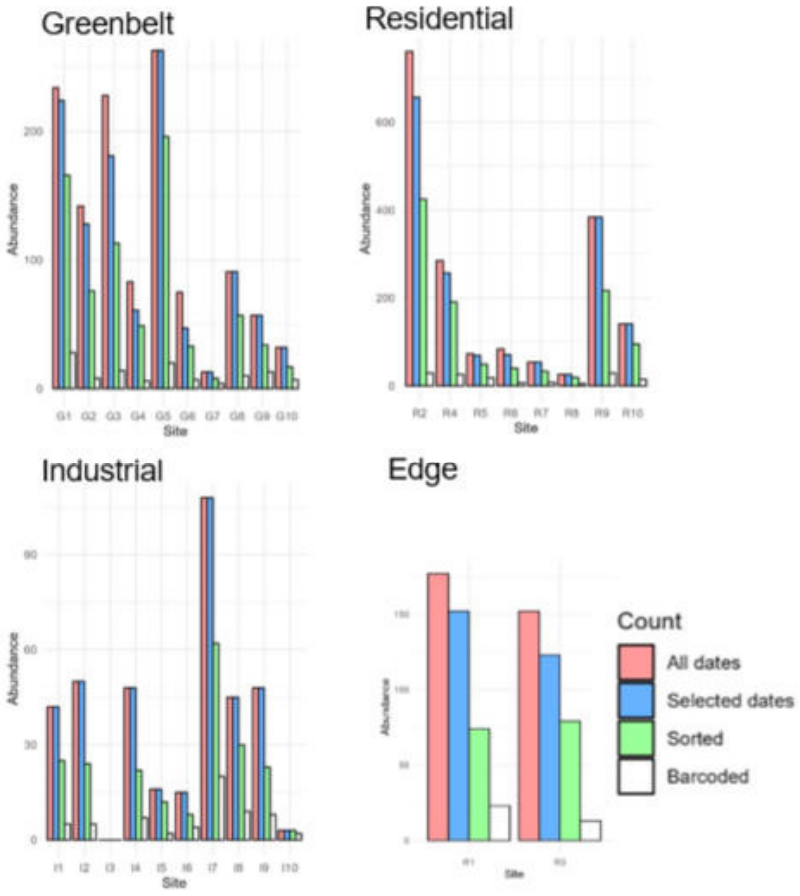


Figure 3.2. Abundance of flies by site for all dates (red), selected dates (2022-06-19 to 2022-09-11) which excluded early and late collections so that sites were comparable in their sampling effort (blue). The green and white bars show the number of flies, by site, that were morphologically sorted and the number that were DNA-barcoded, respectively.

Figure 3.3. shows the number of morphospecies, specimens barcoded, and mOTUs detected by site. On average, mOTUs estimated only 55% of the richness values per site compared to morphological sorting. Morphospecies likely represent an overestimate as male and female phorids are dimorphic, so a single species could count as two morphospecies. The number of mOTUs likely represents the most conservative estimate as only a proportion of the flies sampled could be sequenced (roughly seven specimens for every ten morphospecies estimated by site). Of the 132 morphospecies assessed to be in Prince George in this study, only seven had no recovered barcodes due to failed sequencing at the service provider.

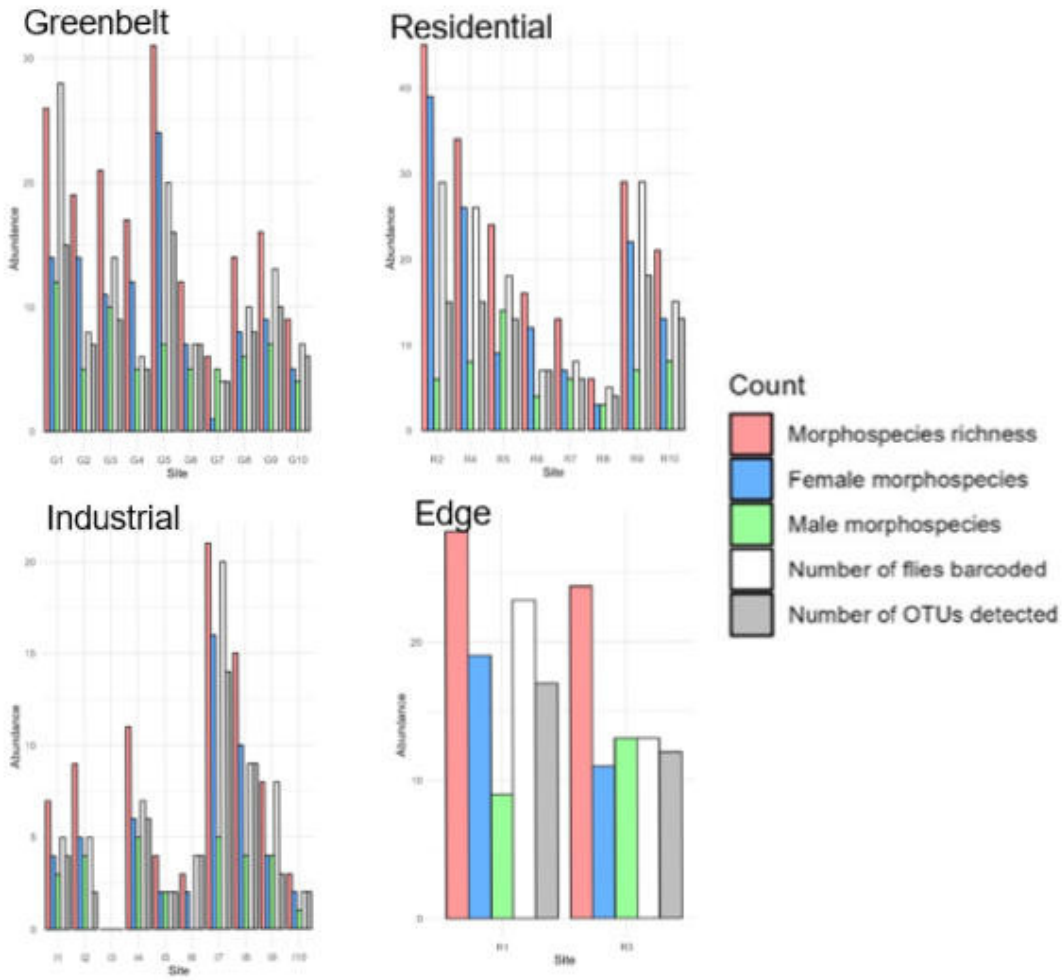


Figure 3.3. The number of all, female, and male morphospecies estimated by site, the number of specimens barcoded, and the number of mOTUs actually detected for greenbelt, residential, edge, and industrial sites land use types.

For flies collected between 2022-06-19 and 2022-09-11, when sampling methods were consistent, greenbelt, residential, and industrial sites did not differ significantly from each other in the number of samples sorted (ANOVA, df = 3, F = 2, p = 0.14), the proportion of flies sorted (ANOVA, df = 2,24, F = 0.37, p = 0.70), and the proportion of flies sequenced (ANOVA, df = 2,24, F = 1.47, p = 0.25), or the ratio of morphospecies identified per site to the number of specimens barcoded (ANOVA,

df = 2,24, F = 0.51, p = 0.61), suggesting a similar sampling effort between land use types (Table 3.3).

Table 3.3. The number of flies counted and sorted for each land use type. The mean ratio of morphospecies estimated (MSE) per specimens barcode, and the mean ratio of morphospecies estimated to the number of mOTUs detected.

Land use type	Fly count for all dates	Number of flies sorted	Mean ratio of MSE to specimens barcoded per site	Mean ratio of MSE to unique mOTUs detected
Gb	1218	749	1:0.67	1:0.53
Indus	375	209	1:0.74	1:0.61
Res	1808	1069	1:0.72	1:0.52
Edge	329	153	1:1.36	1:1.11

Flies from 2015 were sampled from fewer sites (n=12) and were not sorted to morphospecies. Most flies caught during the selected dates from chapter 2 (17 July, 24 July, 6 August, and 28 August 2015) were sent to BOLD. In 2015, more than 100 flies were caught at the Connaught Hill site, most of those belonging to *Megaselia arcticae.*

3.4.2. Richness estimates

Of the 590 flies sequenced, I detected 99 mOTUs (Figure 3.4.). Estimates (Bootstrap and Jackknife estimates respectively) suggest there could be an additional 18 ± 6 to 61 mOTUs that have not yet been detected. However, these estimates assume equal sampling effort between sites and years, which is not the case for this data. Greenbelt sites had the highest richness, followed by residential and industrial sites with 67, 45, and 28 mOTUs. Chao 1 analysis gave maximum estimates of 188 ± 60, 79, and 63 mOTUs, respectively (Table 3.4.). Edge sites were not included in these estimates as only two sites were sampled, although they proportionally were overrepresented in the barcoding data.

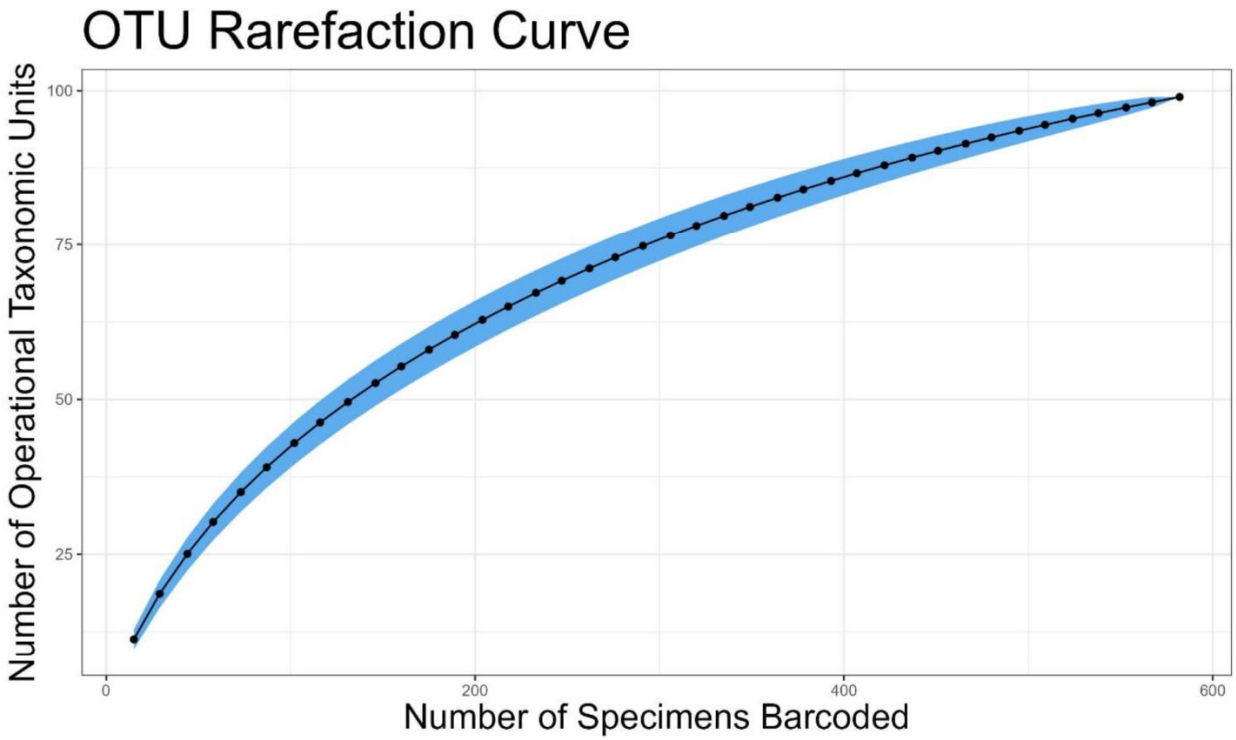


Figure 3.4. The accumulation curve of mOTUs detected from the 582 sequenced specimens across 40 sites, over two sampling years (2015 and 2022). Using the *specaccum* (method=*rarefaction*) package from vegan in R, individuals were added randomly in 10000 permutations of the data to find the mean species accumulation curve. Dots represent the mean number of mOTUs found per number of sites sampled (± one standard deviation in blue). A total 99 mOTUs were detected across the sites and sampling years.

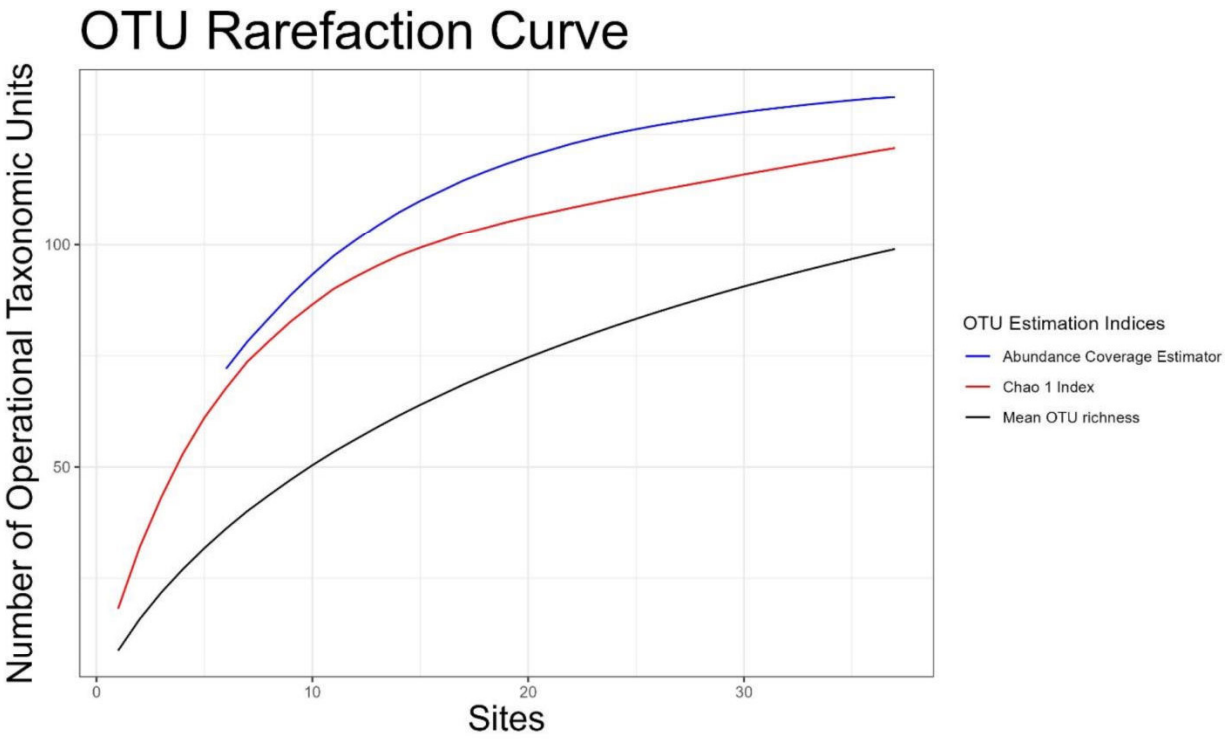


Figure 3.5. The accumulation curves of mOTUs for Prince George where the black line represents the mean mOTU richness by site, red the richness estimated by the Chao 1 index, and blue the richness estimated by the Abundance Coverage index from estimateR in vegan.

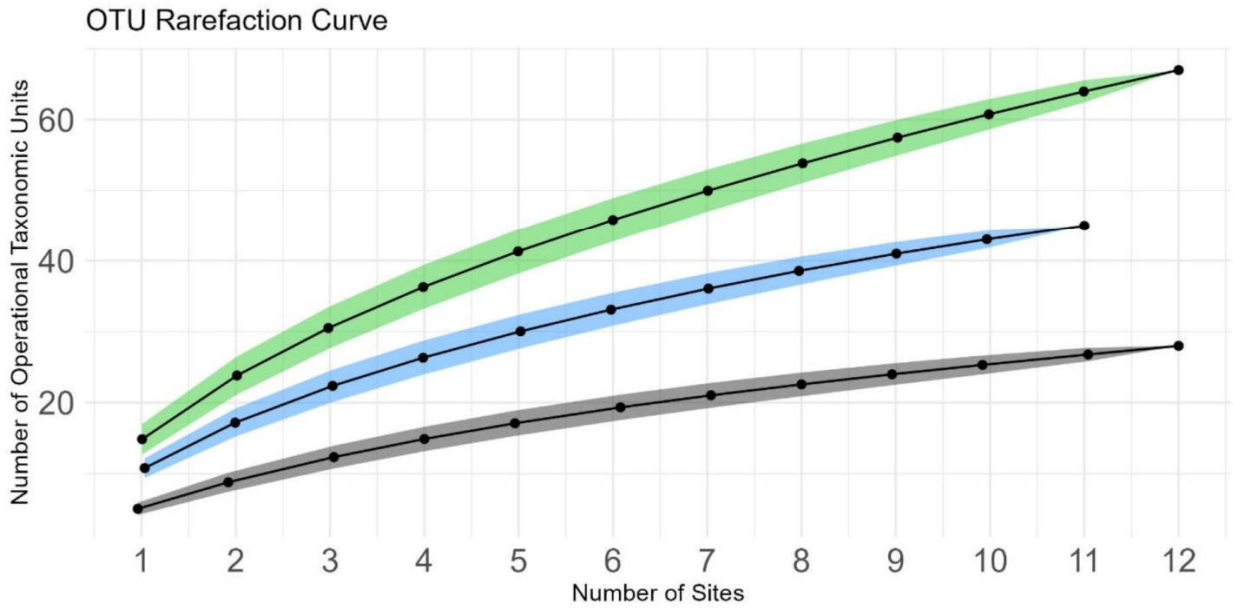


Figure 3.6. The accumulation curves of mOTUs detected in greenbelt (green), residential (blue), and industrial (gray) land use types, using the *specaccum* (method=*rarefaction*) package from vegan in R. Individuals were added randomly in 10000 permutations of the data to find the mean species accumulation curve. Dots represent the mean number of mOTUs found per number of sites sampled (± one standard deviation which is the shaded area)

Table 3.4. Estimates of mOTU richness for the regional species pool and each land use type, along with their ± one standard error for the Chao 2 index, Jackknife 1, Jackknife2, Bootstrap, Chao 1, and Abundance Coverage estimators.

Land use type	Number of sites	mOTU richness	Chao 2	Jack 1	Jack 2	Bootstrap	Chao 1	ACE
All	40	99	142 ± 18	139 ± 10	160	117 ± 6	122	133
Greenbelt	12	67	188 ± 60	106 ± 15	137	83 ± 6	110	129
Residential	11	45	71 ± 14	67 ± 10	79	55 ± 5	60	76
Industrial	12	28	57 ± 21	43 ± 7	53	34 ± 4	63	45

3.4.3. Fly abundance modelling

Phorid abundance (the number of Phoridae caught per trap per day) peaked in late July to mid August, when mean temperatures were at their highest for the summer (Figures 3.6. and 3.7.). Despite industrial sites having the highest mean temperatures, they also had the lowest trap yields, with many traps catching almost no flies throughout most of the summer. Residential, edge, and greenbelt sites were increasingly shaded and thus cooler, in that order (Figure 3.7.), but also had much higher trap yields (Figure 3.8.). The other land use types with more vegetation cover (especially tall vegetation such as trees and shrubs), generally supported greater numbers of phorids than industrial sites. Phorid abundance peaked at moderate mean temperatures – near 15 °C and decreased once temperatures exceeded 18 °C .(Figure 3.10.).Temperature variation was also much higher at industrial sites and lowest at greenbelt sites, indicating industrial site flies also had to cope with greater fluctuations in temperature (Figure 3.9.).

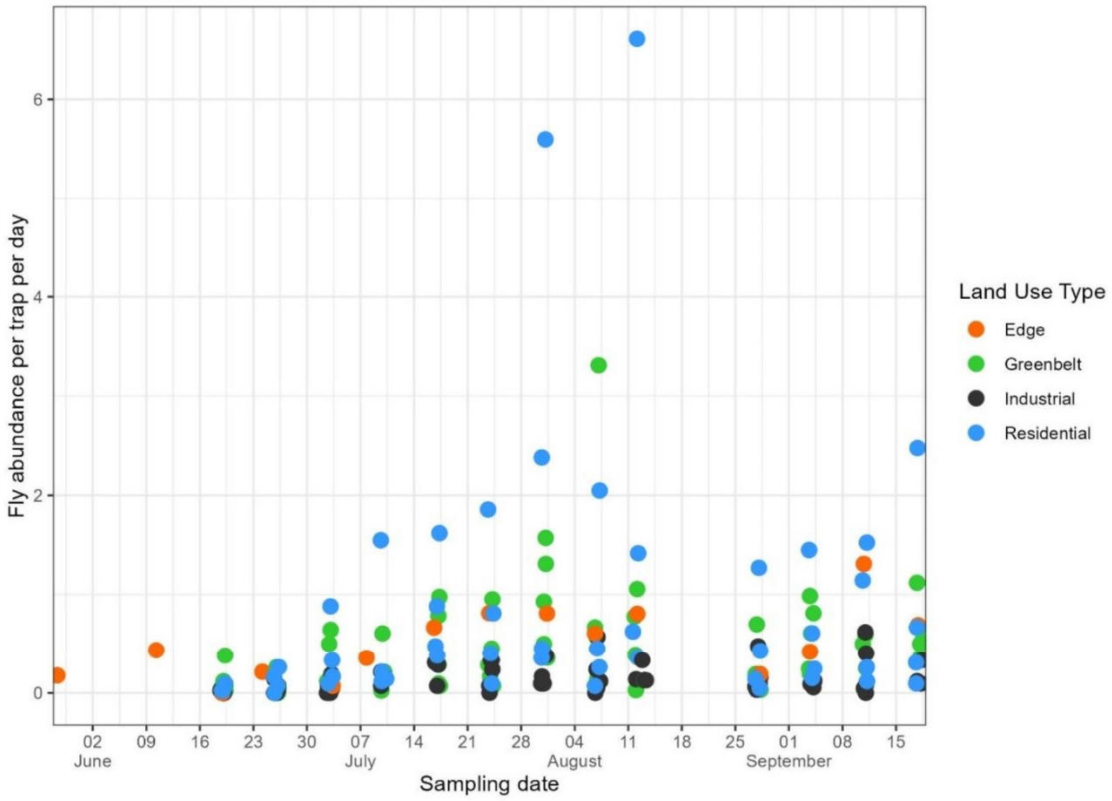


Figure 3.6. The mean number of flies caught per trap per day by collection date during the summer of 2022. Most trapping periods were two-weeks in length. Residential and greenbelt sites had the highest trap yields while industrial sites had the lowest.

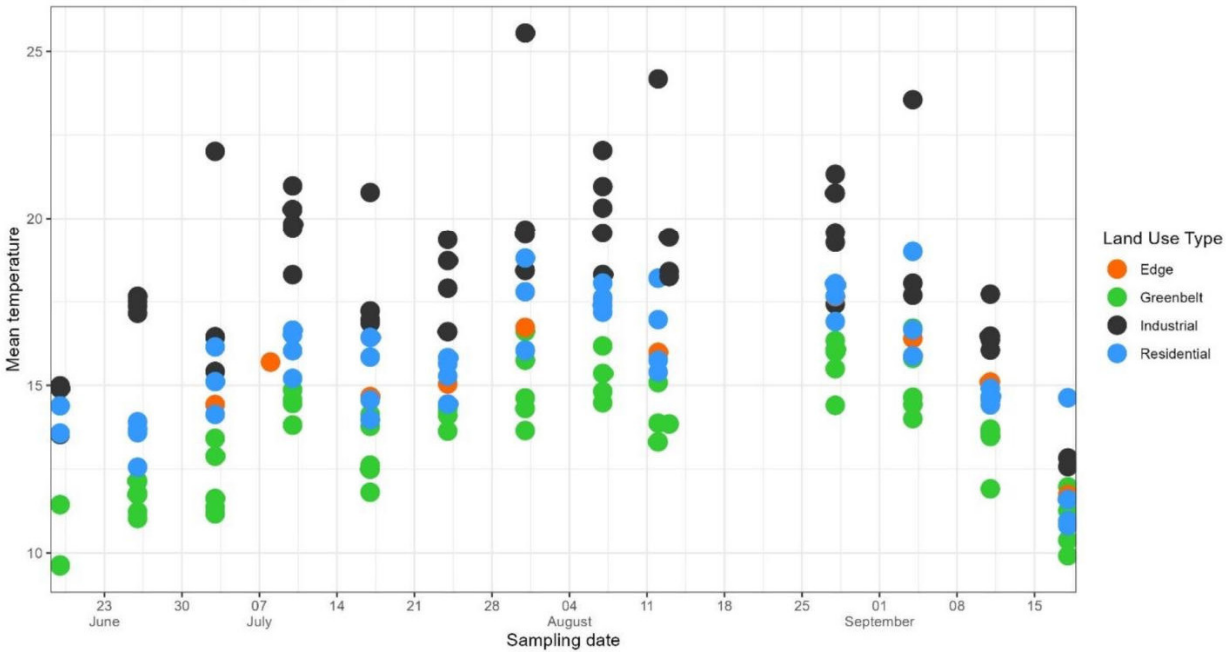


Figure 3.7. Mean temperature (°C) by date for the summer of 2022. Industrial sites were consistently the warmest while greenbelt sites were the coolest and residential and edge sites were intermediate. The temperature peaked in August for most sites.

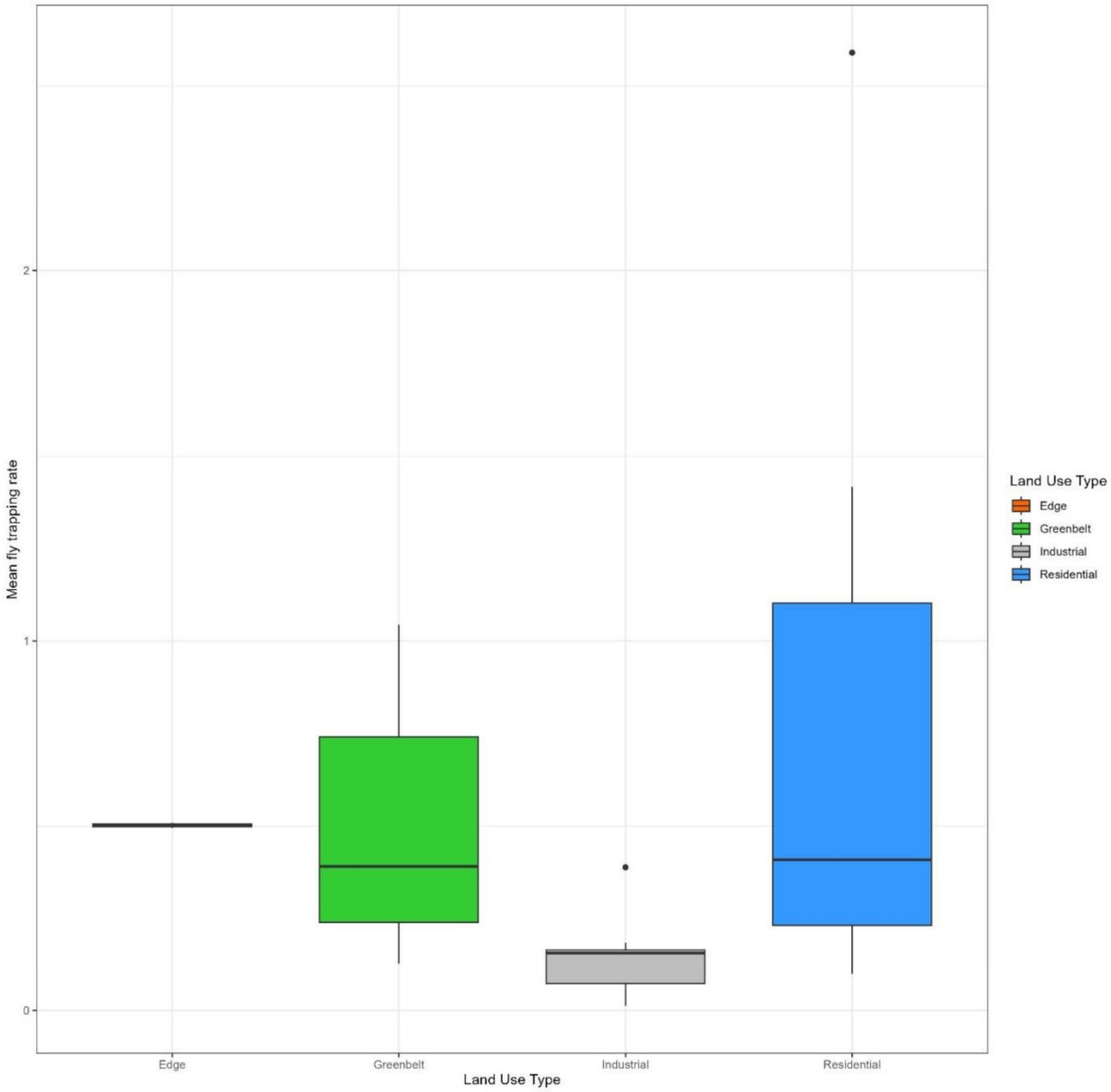


Figure 3.8. Mean fly trapping rate over the summer of 2022 by land use type. The number of flies caught per trap, per day per site was averaged over the course of the summer – excluding I3 (too few collections retrieved) and G7 (trapping rates potentially affected by trap position). Data from outside selected dates (May 28th, June 10th, and September18th) were included as their trapping rates were not very different than those from collection periods directly before, or after them (assessed visually using figure 3.6.).

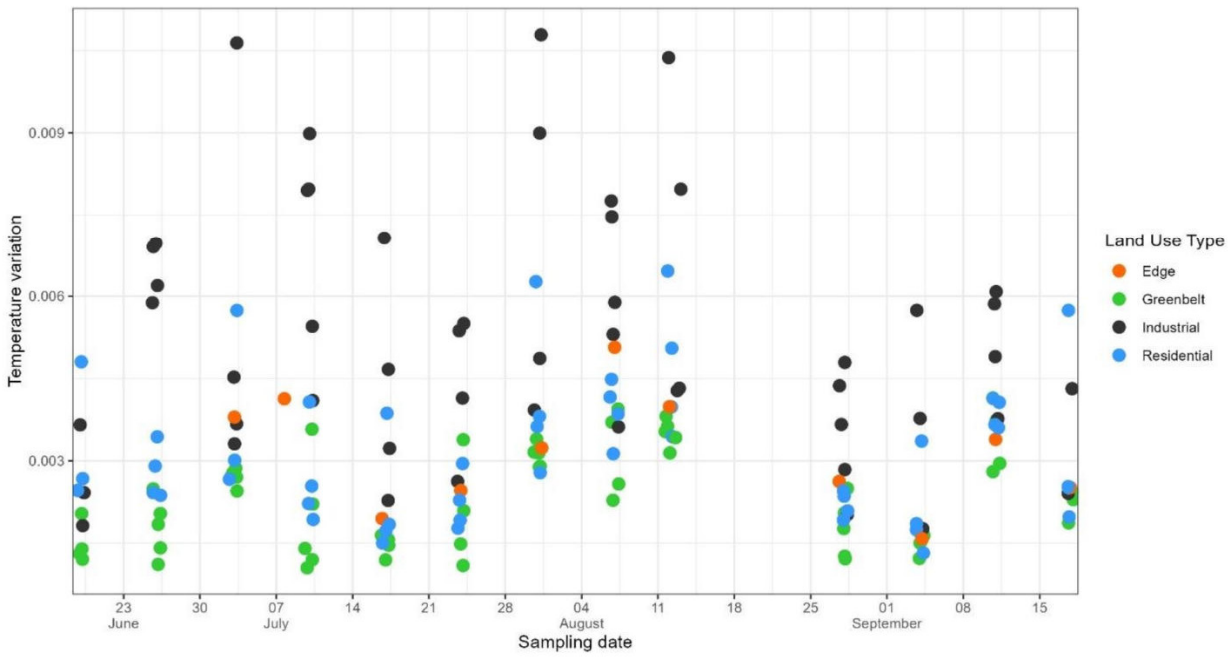


Figure 3.9. Temperature variation (temperature standard deviation/number of temperature readings) by collection dates. Industrial sites had the highest variation and greenbelt sites the lowest. Variation was highest in August, but less stable on a weekly basis than mean temperature.

Of the nine models tested for their ability to predict fly abundance, the full model including mean temperature and land use type performed best (Table 3.5.). It scored the highest performance score from the performance package and all its predictors proved significant in maximum likelihood ratio tests. The model suffers from two main weaknesses. The first is that it contains many terms, including polynomial terms which can be complex to interpret and can be highly correlated (Table 3.7.). This makes it difficult to separate model variation among different terms as those terms represent related, and non-linear relationships. The second issue is that because greenbelt sites never reached temperatures extreme enough to reduce fly abundance, the slope of the greenbelt model predicted exponential abundance

growth with increasing temperatures rather than declining with extreme heat (Table 3.12.).

When land use type was included as an intercept term rather than a slope/interaction term (Abun = land use type + mean temperature (no interaction)), the model did not predict increasing abundance with increasing temperature for greenbelt sites and contained fewer terms (Figure 3.10.). However, it was not as good at predicting abundance values and its scores were lower according to performance's index (Table 3.5.). Nevertheless, mean temperature, and land use type were both significant predictors of fly abundance, while temperature variation was not (Table 3.6.).

Table 3.5. Indices ranking the performance of nine fly abundance models, built using the compare_performance function from the performance package in R. Indices include conditional R^2 (R^2 cond.), marginal R^2 (R^2 marg.), intraclass correlation coefficient (ICC), root mean squared error (RMSE), residual standard error (RSE), corrected Aikake Information Criterion weight (AICc wt), Bayesian Information Criterion weight (BIC wt), and the performance score (Score).

Model	R^2 cond.	R^2 marg.	ICC	RMSE	RSE	AICc wt.	BIC wt.	Score
Abun = land use type * mean temperature (interaction and intercepts)	0.64	0.19	0.56	0.27	0.30	0.69	0.00	0.81
Abun = land use type * mean temperature (interaction only)	0.64	0.08	0.61	0.27	0.30	0.16	0.00	0.59
Abun = land use type + mean temperature (no interaction)	0.62	0.14	0.55	0.28	0.32	0.00	0.00	0.34
Abun = land use type * temperature variation (interaction only)	0.60	0.05	0.57	0.28	0.32	0.00	0.00	0.27
Abun = land use type + temperature variation (no interaction)	0.59	0.15	0.52	0.29	0.32	0.06	0.00	0.24
Null model with random effects only	0.56	0.00	0.56	0.29	0.32	0.01	0.85	0.21
Abun = mean temperature	0.58	0.03	0.56	0.29	0.32	0.03	0.10	0.19
Abun = land use type	0.58	0.12	0.52	0.29	0.32	0.04	0.03	0.14
Abun = temperature variation	0.56	0.03	0.54	0.30	0.33	0.00	0.02	0.05

Table 3.6. The results of likelihood ratio tests for nested sets of models fitted using restricted maximum likelihood. (Degrees of freedom= d.f., p-value = p, Abun = Abundance)

Model 1	Model 2	χ^2	d.f.	p
Null	Abun = land use type	8.63	3	0.03*
Null	Abun = poly (mean temperature)	5.90	2	0.05*
Null	Abun = poly (temperature variation)	2.31	2	0.31
Abun = land use type	Abun = land use type + poly (mean temperature)	5.62	2	0.06
Abun = land use type	Abun = land use type * poly (mean temperature) (interaction only)	14.18	5	0.01*
Abun = land use type + poly (mean temperature)	Abun = land use type * poly (mean temperature) (interaction and intercepts)	18.78	6	0.0046*
Abun = land use type * poly (mean temperature) (interaction only)	Abun = land use type * poly (mean temperature) (interaction and intercepts)	10.22	3	0.02*
Abun = land use type	Abun = land use type*poly (temperature variation) (interaction only)	3.77	5	0.58
Abun = land use type*poly (temperature variation) (interaction only)	Abun = land use type*poly (temperature variation) (interaction and intercepts)	7.01	3	0.07

Table 3.7. The variable estimates for the full model of mean temperature. (Mean Temperature = Mean. Temp., Mean Temperature 2nd degree polynomial term =Mean. Temp^2)

Variable	Estimate	s. e.	T
Intercept	0.64	0.25	2.62
Gb	0.08	0.27	0.30
Indus	-0.47	0.27	-1.73
Res	-0.01	0.27	-0.03
Mean Temp.	-0.25	0.24	-1.07
Mean Temp.^{2}	-0.24	0.23	-1.04
Gb * Mean Temp	0.91	0.28	3.26
Indus * Mean Temp	0.26	0.25	1.04
Res * Mean Temp	0.34	0.24	1.44
Gb * Mean Temp^2	0.50	0.25	2.02
Indus * Mean Temp^2	0.22	0.23	0.95
Res * Mean Temp^2	0.00	0.25	-0.02

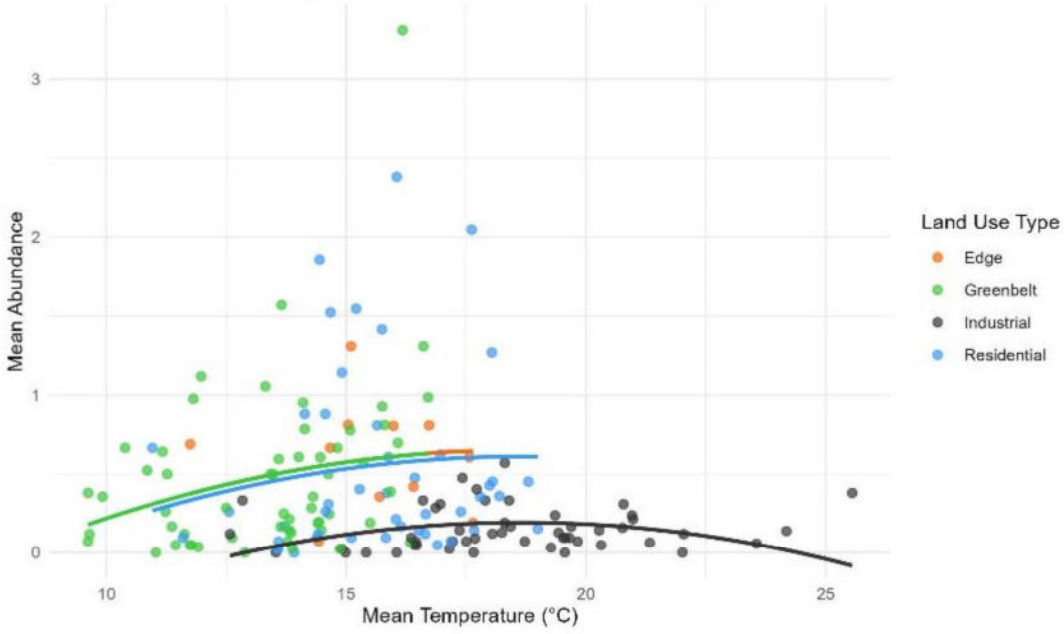


Figure 3.10. Mean fly trapping rate by mean temperature with curves representing the slope of the model with mean temperature and land use type included as an intercept. Each land use type had the same slope. Edge slope (orange) hidden by greenbelt slope (green).

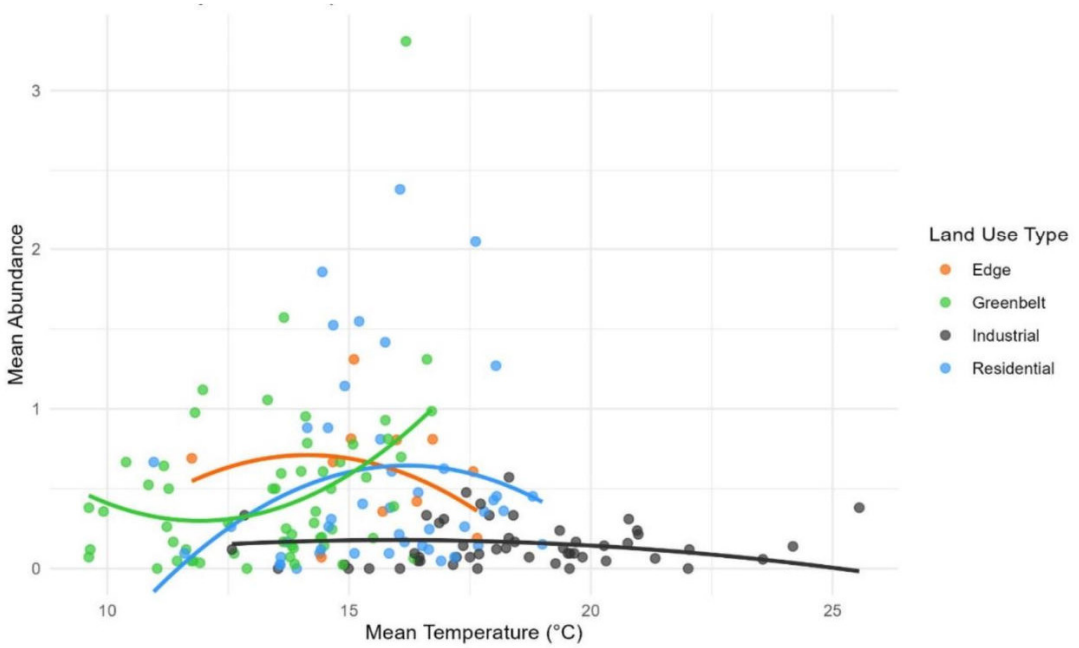


Figure 3.11. Mean fly trapping rate by mean temperature with slopes from the full model. Each land use type has its own slope and intercepts.

3.4.4. mOTU richness by land use type

mOTUs richness was significantly lower in industrial sites compared to other land use types in 2022 (Table 3.8.). Residential sites in 2015 had far fewer flies and mOTUs compared to residential sites in 2022, and significantly fewer flies compared to 2015 greenbelt sites. Edge sites had the highest number of mOTUs on average, while industrial sites generally had low richness regardless of the year of sampling (Figure 3.12.). However, edge sites had more specimens sent for barcoding per morphospecies estimated than other land use types, and fewer sites were sampled. So, while they may have high richness, flies from edges sites are overrepresented in the data and variation in richness may not have been captured by only sampling two sites. Likewise, 2022 samples were not sequenced equally or randomly. Specimens were selected maximize the number of morphospecies represented per land use

type, and site as much as possible. While greenbelt, residential, and industrial sites were comparable in the proportion of specimens sequenced per number of morphospecies identified, some sites were better represented in the data than others, and some mOTUs, especially cryptic species, may have been missed.

Table 3.8. Comparison of mOTU richness by land use type and for 2015 and 2022 at selected dates with Kruskal-Wallis and Dunn tests.

Year	Test	Comparison	Chi-sq	Z	df	p-value	adj. p-value
2015	Kruskal-Wallis	All	8.55		2	0.01	
2015	Dunn Test	Gb-Indus	8.55	1.68		0.05	0.14
2015	Dunn Test	Gb-Res	8.55	2.91		0.00	0.01*
2015	Dunn Test	Indus-Res	8.55	1.23		0.11	0.33
2022	Kruskal-Wallis	All	10.05		3	0.02	
2022	Dunn Test	Edg-Gb	10.05	1.10		0.14	0.81
2022	Dunn Test	Edg-Indus	10.05	2.37		0.01	0.05*
2022	Dunn Test	Gb-Indus	10.05	2.10		0.02	0.11
2022	Dunn Test	Edg-Res	10.05	0.73		0.23	1.00
2022	Dunn Test	Gb-Res	10.05	-0.58		0.28	1.00
2022	Dunn Test	Indus-Res	10.05	-2.61		0.00	0.03*

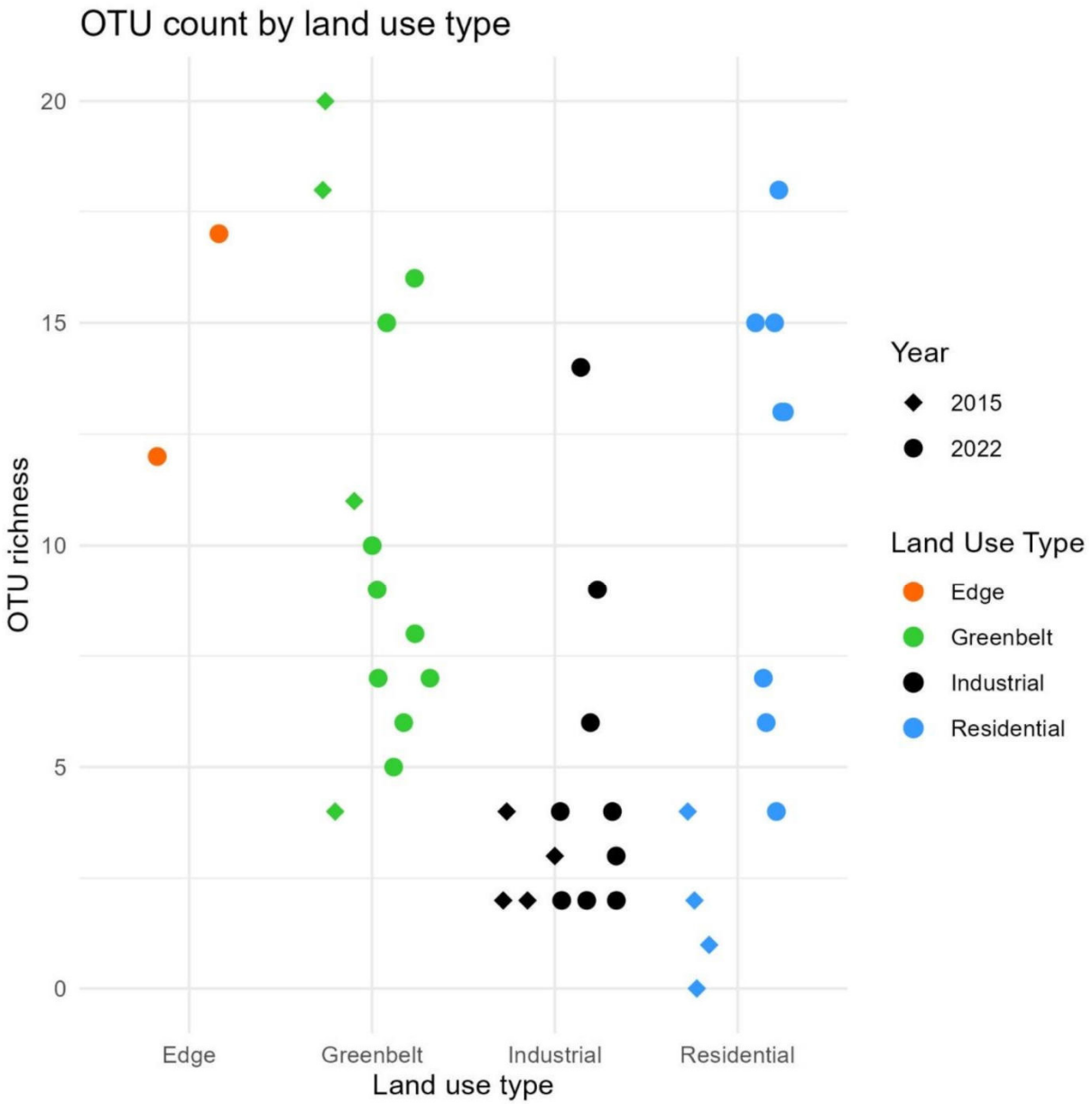


Figure 3.12. The number of mOTU detected for each site where color represents land use type and shape represents year. Industrial sites generally had low richness, edge sites, high richness and greenbelt and residential sites had high variability. Site G7 and I3 were excluded.

Greenbelt sites had the most unique mOTUs (31) – i.e., mOTUs found nowhere else – followed by residential (11), industrial (6), and edge (3) sites (Figure 3.13.). Some edge site unique mOTUs may have resulted from those sites status as effectively a combination of greenbelt and residential habitats – and only a few sites were sampled, giving a smaller species pool to draw from. mOTU overlap may increase with further sequencing. Only five mOTUs were present at all land use types, potentially indicating a high number of habitat specialists in greenbelt sites, more than forty flies found in two to three land use types, and limited number of eurytopic flies in the overall species pool when considering all habitat types. However, only mOTU-8 was significantly associated with greenbelt habitat (r_{pb}= 0.59, p = 0.01).

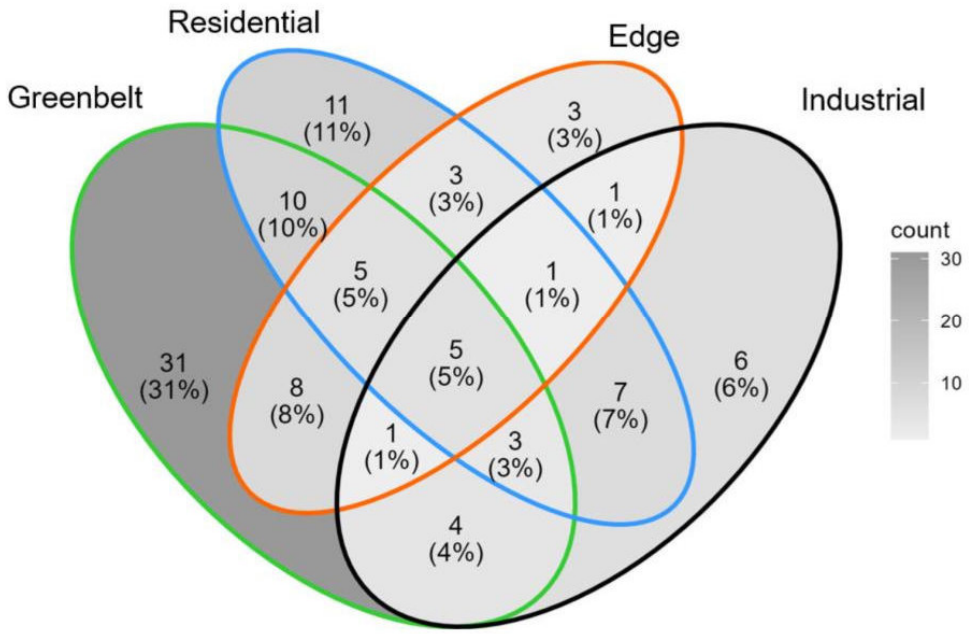


Figure 3.13. Venn diagram of mOTUs unique to and shared by land use types using sequenced flies from 2022 and 2015. Shade indicates the number of mOTUs found in each category. The figure was made using the ggvenn package in R.

3.4.5. Provincial data from GBIF and BOLD databases

By comparing gene sequences from Prince George with records from the Barcode of Life and GenBank databases, I detected 80 BINs and 31 species matches. BOLD assigned an additional 16 BINs to Prince George specimens that did not appear in the Batch ID engine search results, likely because of the conservative search criteria. Additionally, one BIN that did not appear in search results had most of its members originating from this project or matching specimens from private data that was inaccessible at the time of this writing.

Two mOTUs matched with more than one species name, and a few species names were associated in common for several different mOTUs. This is not unexpected given the current state of phorid taxonomy (Brown 2022b), and the potential for misidentifications in database records (Pentinsaari et al. 2020). When more than one species name appeared for a single mOTU, the names were excluded. Prince George specimens matched ten different genera, with the vast majority of mOTUs belonging to the hyperdiverse genus *Megaselia*.

When comparing with online databases, GBIF listed 103 species names (15 genera) and 2 BINs, while public BOLD records listed 81 species names, (11 genera), and 520 BINs. In both cases, most observations originated in southern British Columbia, concentrated around Vancouver and Victoria, leaving much of the province unexplored. Observations from GBIF and BOLD had similar rates of species identifications: 22.6 % and 25.2 %. However, 99.6 of BOLD observations had associated BINs compared to 0.9 % of observations from GBIF. When considering the Sub-Boreal Interior ecoprovince, both GBIF and BOLD listed fewer

observations than I found in my research – recording 12 species and 2 BINs, and 8 species and 37 BINs, respectively.

Table 3.9. The number of mOTUs from PG belonging to each genus. Identifications were made from morphological sorting, as well as matches on GenBank and BOLD.

Genus	Number of mOTUs
Aenigmatias	1
Beckerina	1
Diplonevra	1
Gymnophora	1
Lecanocerus	1
Megaselia	86
Metopina-group	1
Metopina	1
Phora	2
Pseudoaceton	1
Puliciphora	1

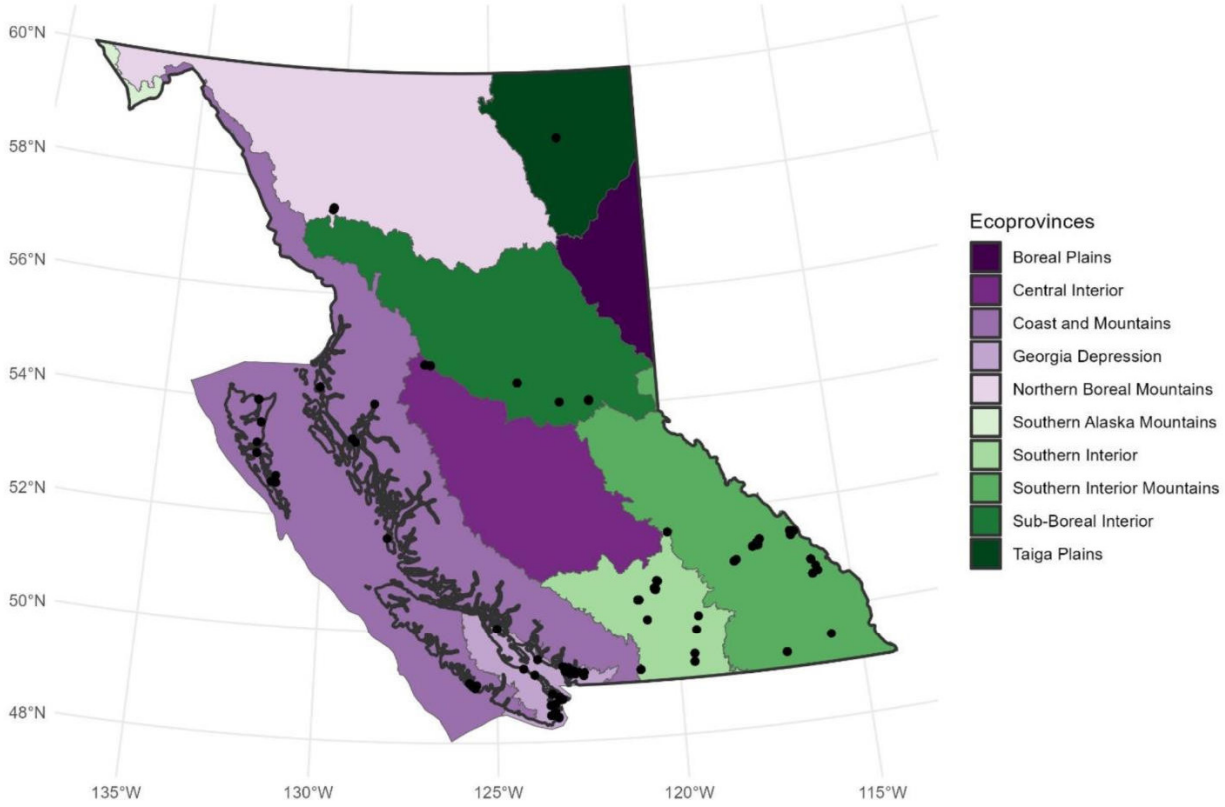
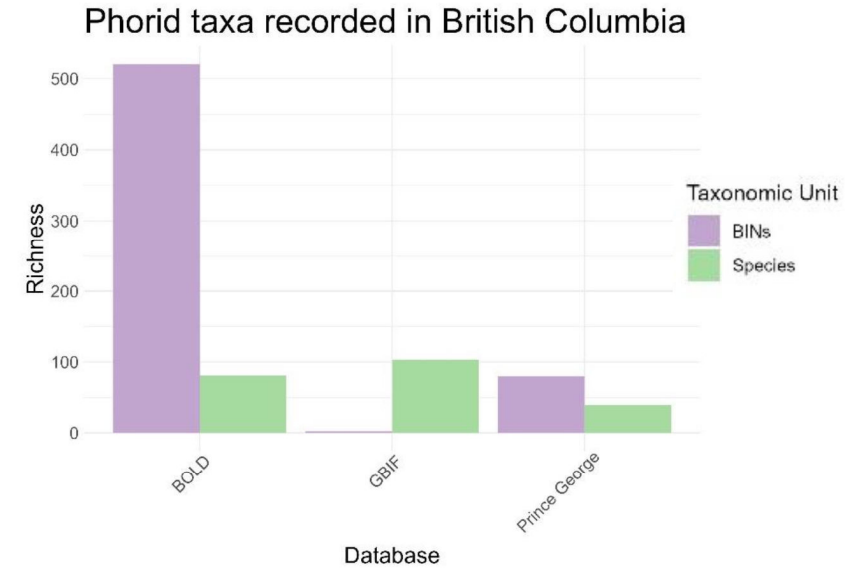


Figure 3.14. Map of 12414 phorid observations downloaded from BOLD on September 24th, 2022.This map was built using the BCmaps and sf package.



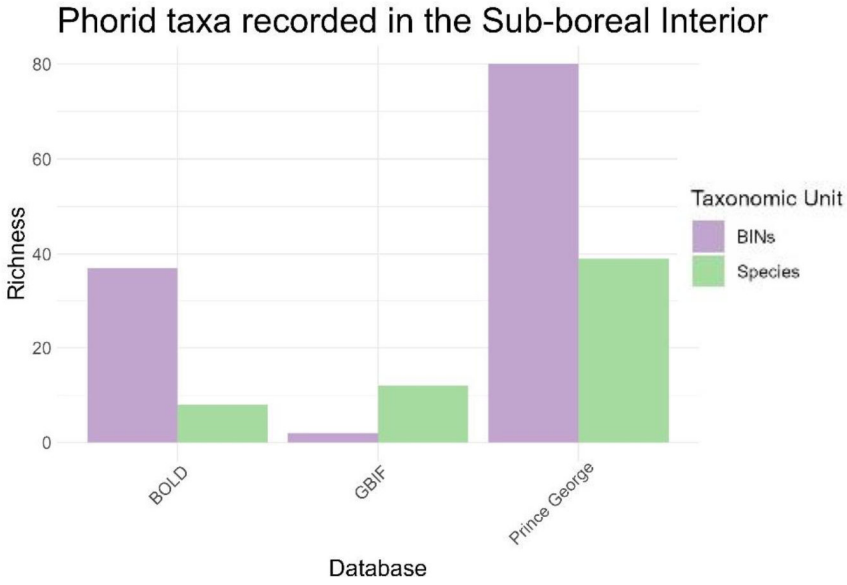


Figure 3.15. The number of species and barcode index numbers (BINs) recorded in GBIF, and the Barcode of Life public database from September 2023 for the entire province of British Columbia and BC's Sub-Boreal Interior ecoprovince specifically. Prince George refers to flies collected from this project.

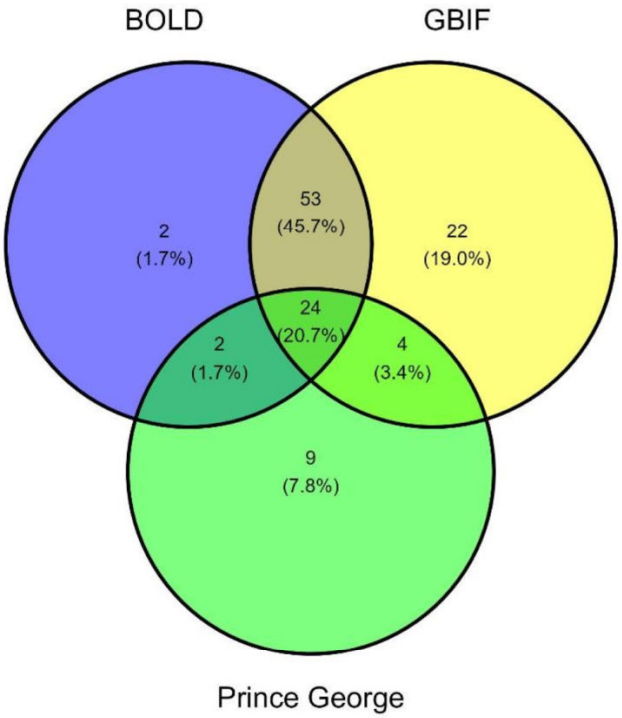


Figure 3.16. Venn diagram of species unique to and shared between GBIF, BOLD, and the Prince George project.

3.5. DISCUSSION

Prince George hosts a high diversity of phorids including 99 distinct mOTUs, with potentially another 61 mOTUs yet to be found. In tropical biodiversity hotspots, researchers have caught as many as 650 mOTUs in a single trap (Srivathsan et al. 2019). This project resembles the 2015 Los Angeles Bioscan project in scope, which also sampled 30 sites and uncovered 99 species (Brown and Hartop 2017). Yet the LA study took place at a lower latitude (~34 N) over a larger area, and caught roughly eleven times the amount of phorids using Malaise traps (Brown and Hartop 2017). Despite being less urbanized and arid than LA, its still surprising Prince George hosts similar levels of diversity. However, given that more than 60 species

were found in Russia's far north (~67°N) in one study (Disney 2013), it seems that phorid diversity can be high, even at moderate latitudes.

Industrial sites generally had poor phorid abundance and diversity, suggesting heavy urbanization does not favour phorids. Temperature is a likely explanatory factor, as industrial sites were significantly warmer and more variable than greenbelt sites, and abundance peaked at moderate temperatures typical of greenbelt sites. McGlynn et al. 2019 found that temperature had a stronger influence on phorid diversity and abundance than land cover. However, abundance may have been more affected by land use type for industrial sites as the abundance remained low across a range of temperatures, while other land use types had distinct peaks.

Phorids occupy a wide range of niches (Brown and Hartop 2017), so it is difficult to determine what factors may affect phorid abundance. However, resources like gardens, composts, fungi, and decomposing vegetation may better provide phorids with certain food resources or hosts (Durska 2015; Hartop et al. 2018). The residential site with the highest abundance (R2) also had a massive compost pile, garden, and decomposing apples at the site, which might have contributed to the high trap rates.

This may also be part of the reason industrial sites had such low richness. Richness for the 2022 flies was significantly higher in residential and edge sites compared to industrial sites. I7, the industrial site with the highest richness and abundance, also had very tall, unmown vegetation suggesting good vegetation cover could be favourable to phorids in otherwise less-suitable settings. This is consistent with Durska 1981, who found the highest phorid richness in Warsaw parks compared

to the city center, and described phorids as most common in forests, often occurring in wet soil or decaying organic matter. Greenbelts sites also had the most unique mOTUs, suggesting many phorids might be forest specialists. Notably, the 2015 residential sites had much lower abundance and significantly lower richness compared to greenbelt sites. 2015 sites had a shorter sampling period, but low richness may also be due to site specific differences, or different environmental conditions during the summer of 2015. Temporal variation should be further explored.

Prince George has a rich assemblage of phorid species, and given that many species have unknown life histories (Hartop et al. 2018; Brown 2022b), their full contribution to functional diversity goes unappreciated. Because they are species rich, diverse in their niches, and important colonizers to habitats recovering from various types of disturbance, they could also be valuable indicators of environmental health (Disney and Durska 2008). Given that one of the main differences between industrial and other land use types is vegetation cover, phorid diversity could potentially be improved at industrial sites by growing taller vegetation such as long grass or trees. Shading would also help reduce and stabilize temperature (Shiflett et al. 2017).

While GBIF and BOLD both represent extensive repositories of taxonomic records, they are far from comprehensive (Meiklejohn et al. 2019; Garcia-Rosello et al. 2023). GBIF records contained many scientific names, but most phorids in their database lacked detail to the species level. This is especially difficult as even museum specimens may be misidentified or belong to groups with unresolved

taxonomy (Disney 2002). Public records from the Barcode of life database recorded fewer scientific names, but roughly five times more identifications than GBIF in the form of Barcode Index Numbers. BINs provide a way to name and track specimens from cryptic or taxonomically complex taxa. However, BINs do not necessarily represent accurate delimitations of species, and require morphological evidence to support grouping (Young et al. 2019; Prieto et al. 2021).

Most identifications from BOLD (species and BINs) matched with what had previously been recorded for the province of BC on BOLD and GBIF. 6 BINs that appeared unique to the Prince George dataset had previously been recorded near or in BC when private records were checked. mOTUs that did not strongly match sequences from the BOLD database may belong to BINs with large intraspecific variation, require higher quality sequences, or more specimens, and more public records.

It is currently not possible to know if any mOTUs from this project represent new species (either undescribed species or species that weren't previously recorded in BC), given the lack of available data to compare specimens against (Page 2016), and the challenges of morphological sorting for this group. However, this project has helped fill in one of the geographic gaps in phorid records for the province, as BINs and species names from this project outnumbered those previously recorded in public data for BOLD and GBIF for the Sub-Boreal Interior ecoprovince. Likewise, vouchered Prince George specimens and sequences have helped quantify potential biodiversity in the area and can serve as reference for future projects.

Despite recent efforts which have uncovered unexpectedly high phorid diversity in many parts of the world (Namaki-Khameneh et al. 2021; Brown 2022a), much work remains to be done for this taxon, both in building comprehensive species records, and in untangling their taxonomy (Brown 2022a; Chimeno et al. 2023). Future work should prioritize collecting phorids in under-sampled areas, collecting DNA from holotypes and type specimens for better reference sequences (Prosser et al. 2016), and revising phorid taxonomy from both old and newly collected specimens using both morphological and genetic data (Brown 2022a; Hartop et al. 2022).

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Chapter four

SUMMARY

Despite its small geographic size, Prince George harbours a rich assemblage of ground arthropods, across several different land use types. Industrial, residential, and greenbelt areas host similar levels of taxonomic and functional diversity. If they can foster high ecological diversity, highly urbanized spaces like industrial parks and yards should be managed for their conservation value. Future studies could test ways of improving arthropod diversity such as reduced mowing, diversifying lawn plants, and increasing green space size and continuity. Simultaneously, forested areas should be protected because they harbour unique sets of species and may better support natural enemies. Many studies report the negative effects of urbanization. Given the limited scope of this project, further research should look at the long-term effects of urban development, as well as the potential for yearly variation in arthropod diversity. Nevertheless, these results suggest that cities can be biodiversity friendly and support a myriad of ecosystem services.

Prince George supports an unexpectedly high richness of phorid flies. Scuttle flies are especially abundant and diverse in greenbelt, edge, and residential sites. Temperature and land use significantly predict their abundance. Industrial areas are extremely hot and may offer fewer resources to flies. Conversely, many phorid mOTUs appear to specialize to greenbelt habitats. Because the life history of many species remains unknown, it can be hard to understand what factors drive these trends.

When looking at data from BOLD and GBIF, it is clear phorid richness has been largely unexplored in many parts of British Columbia. This project had added a suite of new datapoints to an underrepresented corner of the map, but much work remains to be done. More sampling is needed in the north and west of the province. New specimens should be vouchered, and taxonomists are needed to properly describe them and build a provincial species checklist. Although phorids prove to be a taxonomic challenge, DNA barcoding and new sampling efforts are helping us understand them better than ever before.

APPENDIX I

Tables for chapter two

Table 5.1.1. Table of OTU guild affinities. Each guild is ranked as having no (0), weak (1), moderate (2) or strong (3) affinity to each feeding guild (Herb = herbivore, Nat. En. = Natural Enemy, Decomp. = Decomposer, Fung. = Fungivore, Hon. d.f. = Honeydew feeder).

Lowest Classification	Herb.	Nat. En.	Decomp.	Fung.	Hon. d.f.
Agyneta ordinaria	0	3	0	0	0
Alydus sp.	3	0	1	0	0
Amara idahoana	3	2	0	0	0
Anoscopus sp.	3	0	0	0	0
Anthomyiidae	NA	NA	NA	NA	NA
Anystidae	0	3	0	0	0
Aphididae	3	0	0	0	0
Aphrodes sp.	3	0	0	0	0
Aphrophora sp.	3	0	0	0	0
Arganthomyza duplex	1	0	3	0	0
Atomaria sp.	0	0	0	3	0
Basalys sp.	1	3	0	0	0
Bathyphantes sp.	0	3	0	0	0
Botanophila hucketti	3	0	0	0	1
Braconidae	1	3	0	0	1
Bradysia scabricornis	1	0	3	2	0
Bradysia sp.	1	0	3	2	0
Bradysia splendida	1	0	3	2	0
Bradysia trivittata	1	0	3	2	0

Bryotropha similis	3	0	0	0	0
Camnula pellucida	3	0	0	0	0
Carabidae	NA	3	NA	NA	0
Carabus taedatus	0	3	0	0	0
Cecidomyiidae	NA	NA	NA	NA	NA
Ceratagallia sp.	3	0	0	0	0
Chaitophorus neglectus	3	0	0	0	0
Chilopoda	0	3	0	0	0
Chloropidae	NA	NA	NA	NA	NA
Chorthippus curtipennis	3	0	0	0	0
Cicadellidae	3	0	0	0	0
Cinara sp.	3	0	0	0	0
Clubionidae	0	3	0	0	0
Coccinella septempunctata	1	3	0	1	0
Collembola	NA	NA	NA	NA	NA
Conioscinella sp.	NA	NA	NA	NA	NA
Cordyla sp.	0	0	0	3	0
Corticarina cavicollis	0	0	0	3	0
Corynoptera saccata	1	0	3	2	0
Corythucha sp.	3	0	0	0	0
Cryptophagus sp.	0	0	0	3	0
Curculionidae	NA	NA	NA	NA	NA
Cybaeidae	0	3	0	0	0
Cybaeus morosus	0	3	0	0	0
Cytilus sericeus	3	0	0	0	0
Delia sp.	2	0	3	0	0
Devia prospera	0	3	1	1	0
Dinotrema sp.	1	3	0	0	1
Doratura stylata	3	0	0	0	0
Entiminae	NA	NA	NA	NA	NA
Epipsocidae	NA	NA	NA	NA	NA
Eremocoris sp.	3	0	0	0	0
Erythraeidae	0	3	0	0	0
Exitianus sp.	3	0	0	0	0
Forficula auricularia	2	1	3	0	0
Formica sp.	1	3	3	0	3
Gelis festinans	1	3	0	0	1
Geocoris sp.	1	3	0	0	0
Glocianus punctiger	3	0	0	0	0
Gnaphosidae	0	3	0	0	0
Habronattus ophrys	0	3	0	0	0
Hahniidae	0	3	0	0	0
Helina sp.	1	3	0	0	0
Heliocobia rapax	1	2	3	0	1

Henicopidae	0	3	0	0	0
Heterosilpha ramosa	0	3	3	0	0
Hybotidae	0	3	0	0	0
Hydrophoria sp.	NA	NA	NA	NA	NA
Incertella incerta	0	0	3	0	0
Lamyctes emarginatus	0	3	0	0	0
Larrinae	1	3	0	0	1
Lasius sp.	1	2	2	0	3
Leptocera sp.	0	0	3	0	0
Leptothorax sp.	1	3	3	0	1
Linyphiidae	0	3	0	0	0
Liogluta nitens	NA	NA	NA	NA	NA
Lithobiidae	0	3	0	0	0
Oedipodinae	3	0	0	0	0
Lycosidae	0	3	0	0	0
Manica sp.	1	3	3	0	1
Megaselia	NA	NA	NA	NA	NA
Melanophthalma sp.	0	0	0	3	0
Meteorus sp.	1	3	0	0	1
Myrmica sp.	1	3	3	0	2
Nearctaphis sensoriata	3	0	0	0	0
Oscinella sp.	3	0	0	0	0
Otiorhynchus sp.	3	0	0	0	0
Oxypoda	NA	NA	NA	NA	NA
Parasitidae	0	3	0	0	0
Pardosa moesta	0	3	0	0	0
Pardosa tesquorum	0	3	0	0	0
Phalangiidae	1	3	1	0	0
Philodromidae	0	3	0	0	0
Philonthus sp.	0	3	0	0	0
Phrurolithidae	0	3	0	0	0
Platygastridae	1	3	0	0	1
Pollenia pediculata	1	3	0	0	0
Polydesmidae	0	0	3	0	0
Psammotettix confinis	3	0	0	0	0
Pseudolycoriella sp.	NA	NA	NA	NA	NA
Psychidae	3	NA	NA	NA	0
Pterostichus adstrictus	0	3	0	0	0
Pterostichus carbonarius	0	3	0	0	0
Pterostichus melanarius	1	3	1	0	0
Rhopalidae	3	0	0	0	0
Sarcoptiformes	NA	NA	NA	NA	NA
Scaphinotus marginatus	0	3	0	0	0
Schizolachnus sp.	3	0	0	0	0

Sciaridae	1	0	3	2	0
Sciocoris microphthalmus	3	0	0	0	0
Sciomyzidae	0	3	1	0	1
Scotinella pugnata	0	3	0	0	0
Silphidae	NA	NA	NA	NA	NA
Siphonella sp.	1	3	0	0	0
Sitona hispidulus	3	0	0	0	0
Slaterobius insignis	3	0	0	0	0
Staphylinidae	NA	NA	NA	NA	NA
Stygnocoris sabulosus	3	0	0	0	0
Stygnocoris sp.	3	0	0	0	0
Synuchus impunctatus	3	2	0	0	0
Tachyporus sp.	1	3	0	1	0
Tenuiphantes zelatus	0	3	0	0	0
Thaumatomyia sp.	1	3	0	0	1
Thomisidae	0	3	0	0	0
Trachelipus rathkii	0	0	3	0	0
Trachyphloeus sp.	3	0	0	0	0
Trapezonotus sp.	3	0	0	0	0
Trichogramma sp.	1	3	0	0	1
Tricimba sp.	1	0	3	2	0
Trixoscelis sp.	0	0	3	0	0
Tychius sp.	3	0	0	0	0
Vespula pensylvanica	1	3	2	0	1
Xysticus benefactor	0	3	0	0	0
Xysticus montanensis	0	3	0	0	0
Zelotes sp.	0	3	0	0	0

Table 5.1.2. OTU observations by site and land use type (Gb. = Greenbelt, Ind. = Industrial, Res. = Residential).

	Gb.				Ind.				Res.			
Lowest Classification	G1	G2	G3	G4	I1	I2	I3	I4	R1	R2	R3	R4
Agyneta ordinaria	0	1	0	0	0	0	0	0	0	0	0	0
Alydus sp.	0	0	0	0	0	1	0	0	0	0	0	0
Amara idahoana	0	0	0	0	0	1	0	0	0	0	0	0
Anoscopus sp.	1	0	0	0	2	0	0	0	1	0	1	0
Anthomyiidae	0	2	0	0	7	0	0	1	0	0	0	1
Anystidae	0	1	1	0	0	0	2	0	1	0	0	1
Aphididae	1	1	0	0	22	6	2	1	3	5	1	3
Aphrodes sp.	0	0	0	0	0	0	1	0	0	0	0	0
Aphrophora sp.	0	0	0	0	0	0	0	0	1	0	0	0
Arganthomyza duplex	0	0	0	0	0	1	0	0	0	0	0	2
Atomaria sp.	0	2	0	0	1	5	0	0	0	0	0	1
Basalys sp.	1	0	1	0	0	0	0	0	0	0	0	0

Bathyphantes sp.	0	1	0	0	0	0	0	0	0	0	0	0
Botanophila hucketti	0	2	0	0	0	0	0	0	0	0	0	0
Braconidae	0	0	0	2	0	0	0	0	0	0	0	0
Bradysia scabricornis	0	0	0	0	3	0	0	0	0	0	0	1
Bradysia sp.	1	0	0	0	2	0	0	0	0	0	0	1
Bradysia splendida	0	0	0	0	2	0	0	0	0	0	0	0
Bradysia trivittata	2	0	0	0	0	0	0	0	0	0	0	0
Bryotropha similis	0	0	0	0	0	0	2	0	0	0	0	0
Camnula pellucida	0	0	0	0	0	0	0	1	0	0	0	0
Carabidae	0	0	0	0	0	0	0	0	2	1	0	1
Carabus taedatus	0	0	0	0	0	0	0	0	0	0	0	1
Cecidomyiidae	0	0	2	0	4	0	0	1	0	0	1	1
Ceratagallia sp.	0	0	0	0	0	0	0	0	1	0	0	0
Chaitophorus neglectus	1	1	0	0	0	0	0	0	0	0	0	0
Chilopoda	0	0	0	0	1	0	0	0	0	0	0	0
Chloropidae	0	0	0	0	0	0	0	0	0	0	0	2
Chorthippus curtipennis	0	0	0	0	0	0	0	0	0	0	0	2
Cicadellidae	0	0	0	0	0	0	0	0	0	0	0	1
Cinara sp.	0	0	1	0	0	0	0	0	0	0	0	0
Clubionidae	0	0	1	0	0	0	0	0	0	0	0	0
Coccinella septempunctata	0	0	0	0	1	0	0	0	0	0	0	0
Collembola	15	11	6	4	20	12	12	10	14	11	14	11
Conioscinella sp.	0	0	0	0	0	1	0	0	0	0	0	0
Cordyla sp.	0	0	0	0	0	0	0	0	0	2	0	0
Corticarina cavicollis	0	0	0	0	0	1	0	0	0	0	0	0
Corynoptera saccata	0	0	0	0	1	0	0	0	0	0	0	0
Corythucha sp.	0	0	0	1	0	0	0	0	0	0	0	0
Cryptophagus sp	0	2	0	0	0	0	0	0	0	0	0	0
Curculionidae	1	0	0	0	0	0	1	0	0	1	1	0
Cybaeidae	0	0	1	0	0	0	0	0	0	0	0	1
Cybaeus morosus	2	0	0	0	0	0	0	0	0	0	0	0
Cytilus sericeus	0	0	0	0	0	0	0	0	3	0	1	1
Delia sp.	0	0	0	0	3	0	1	2	0	0	3	1
Devia prospera	2	0	1	0	0	0	0	0	0	0	0	0
Dinotrema sp.	2	0	0	0	1	0	0	0	0	0	0	1
Doratura stylata	0	0	0	0	4	5	0	1	0	1	0	5
Entiminae	0	0	0	0	0	0	0	0	0	0	1	0
Epipsocidae	1	0	0	0	0	0	0	0	0	0	0	0
Eremocoris sp.	1	1	0	1	1	3	0	0	0	0	1	0
Erythraeidae	0	0	0	0	0	7	0	2	0	0	0	3
Exitianus sp.	0	0	0	0	0	0	0	2	0	0	0	0
Forficula auricularia	0	0	0	0	0	0	0	0	5	2	0	1
Formica sp.	3	98	563	48	3	19	206	24	173	15	106	39
Gelis festinans	0	0	0	0	0	1	0	0	0	0	0	0
Geocoris sp.	0	0	0	0	26	1	1	1	1	0	0	1
Glocianus punctiger	0	0	0	0	0	1	0	0	0	0	0	0
Gnaphosidae	0	3	1	1	8	1	0	2	0	2	1	0
Habronattus ophrys	0	0	0	0	0	0	1	0	0	0	0	0

Hahniidae	0	0	1	0	0	0	0	0	0	0	0	0
Helina sp.	0	0	0	0	0	0	1	0	0	0	0	2
Heliocobia rapax	0	0	0	0	1	0	0	0	0	0	0	0
Henicopidae	0	0	0	0	0	0	1	0	0	0	0	0
Heterosilpha ramosa	0	0	0	0	0	0	0	0	0	0	0	83
Hybotidae	0	1	0	0	0	0	0	0	0	0	1	0
Hydrophoria sp.	0	1	0	0	1	0	1	0	0	0	0	0
Incertella incerta	0	0	0	0	0	1	0	0	0	0	0	0
Lamyctes emarginatus	0	0	0	0	0	0	0	2	0	0	0	0
Larrinae	0	0	0	0	0	0	1	0	0	0	0	0
Lasius sp.	0	0	0	1	0	0	0	0	14	10	17	15
Leptocera sp.	0	0	0	0	0	1	1	1	0	0	0	0
Leptothorax sp.	0	0	1	4	1341	14	3	0	0	0	1	0
Linyphiidae	6	6	15	0	11	0	4	3	7	3	2	9
Liogluta nitens	0	0	0	0	0	0	0	0	0	1	0	0
Lithobiidae	0	0	0	0	1	0	1	0	0	0	0	0
Oedipodinae	0	0	0	0	0	0	1	1	0	0	0	0
Lycosidae	1	0	6	1	1	5	13	1	5	4	8	6
Manica sp.	1	0	0	0	0	0	2	0	0	0	0	0
Megaselia sp	14	28	3	107	3	2	4	3	0	1	0	3
Melanophthalma sp.	0	0	0	0	0	0	0	2	0	0	0	0
Meteorus sp.	0	0	0	0	0	1	0	0	0	0	0	0
Myrmica sp.	0	0	0	0	4260	0	30	11	3	6	3	0
Nearctaphis sensoriata	0	0	0	0	0	0	1	0	0	0	0	0
Oscinella sp.	0	0	0	0	1	1	0	1	0	1	3	4
Otiorhynchus sp.	0	0	0	3	0	0	2	0	0	13	0	2
Oxypoda	0	1	0	0	0	0	0	0	0	0	0	0
Parasitidae	2	1	0	0	2	1	0	0	0	0	0	14
Pardosa moesta	0	0	0	0	0	1	0	0	0	0	0	0
Pardosa tesquorum	0	0	0	0	0	0	1	0	0	0	0	0
Phalangiidae	11	5	13	73	0	4	5	0	11	1	2	11
Philodromidae	0	0	0	0	0	1	0	0	0	0	0	0
Philonthus sp.	0	0	0	0	0	0	0	0	0	0	1	27
Phrurolithidae	0	0	0	0	5	0	2	0	0	0	0	0
Platygastridae	4	3	3	4	11	0	1	1	0	2	4	2
Pollenia pediculata	0	0	0	0	0	0	0	0	0	0	0	2
Polydesmidae	1	58	4	0	3	0	0	0	0	0	0	0
Psammotettix confinis	0	0	0	0	1	0	2	2	0	0	0	0
Pseudolycoriella sp.	0	0	0	0	0	1	0	0	0	0	0	0
Psychidae	0	0	0	0	0	0	0	0	0	0	0	2
Pterostichus adstrictus	1	0	0	0	0	0	0	0	0	0	0	0
Pterostichus carbonarius	0	0	0	0	0	0	0	0	0	0	0	2
Pterostichus melanarius	54	7	0	1	0	1	0	0	3	5	0	48
Rhopalidae	0	0	0	0	0	3	0	0	0	0	0	0
Sarcoptiformes	1	0	0	0	7	0	1	0	1	0	1	1

Scaphinotus marginatus	34	0	0	0	0	0	0	0	0	0	0	0
Schizolachnus sp.	0	0	0	0	0	0	0	0	0	1	0	0
Sciaridae	1	1	0	1	5	0	1	0	1	0	0	0
Sciocoris microphthalmus	0	0	0	0	0	0	2	0	0	0	0	0
Sciomyzidae	1	0	0	0	0	0	0	0	0	0	0	0
Scotinella pugnata	0	0	0	0	4	0	1	0	0	0	0	0
Silphidae	0	0	0	0	0	0	0	0	0	0	0	10
Siphonella sp.	1	0	0	0	0	0	0	0	0	0	0	0
Sitona hispidulus	0	0	0	0	0	0	0	0	0	0	0	1
Slaterobius insignis	0	0	0	0	1	0	0	0	0	0	0	0
Staphylinidae	1	1	0	0	0	0	0	0	1	1	0	0
Stygnocoris sabulosus	1	0	0	0	0	0	0	0	0	1	0	0
Stygnocoris sp.	0	0	0	0	0	0	0	0	0	0	1	1
Synuchus impunctatus	4	0	0	0	0	0	0	0	0	0	0	0
Tachyporus sp.	1	0	1	0	0	0	0	0	0	1	1	0
Tenuiphantes zelatus	1	0	1	0	0	0	0	0	0	0	0	0
Thaumatomyia sp.	0	0	0	0	0	0	0	0	0	0	0	1
Thomisidae	0	0	0	0	1	4	0	6	0	1	0	0
Trachelipus rathkii	0	0	0	0	0	0	0	0	0	0	5	0
Trachyphloeus sp.	0	8	0	3	0	4	22	2	10	9	1	2
Trapezonotus sp.	0	0	0	0	0	1	0	0	1	0	0	0
Trichogramma sp.	0	0	0	0	2	0	0	0	0	0	0	0
Tricimba sp.	0	0	0	0	6	4	0	3	1	2	1	1
Trixoscelis sp.	0	0	0	0	0	1	0	1	0	0	0	0
Tychius sp.	0	0	0	0	1	0	0	0	1	0	0	0
Vespula pensylvanica	3	1	0	0	48	26	3	0	0	6	0	52
Xysticus benefactor	0	0	0	0	0	0	1	0	0	0	0	0
Xysticus montanensis	0	0	0	0	0	0	0	1	0	0	0	0
Zelotes sp	0	0	0	0	0	1	0	0	0	0	0	0

Table 5.1.3. The association of OTUs with different land use types. I listed OTU's habitat preference ranging from open areas (fields and grasslands) to closed (forests) as described in the literature. I tested OTU associations with different land use types using the r_{pb} correlation index from the *indicspecies* package in R which conducts permutations (n=10000) to determine whether OTUs correlate more with groups of sites than randomly generated communities. In the land use column, one indicates that OTU is positively associated with a land use type while zero indicates it is not. The variable r represents the correlation for an OTU's strongest habitat association (with a single land use type or a group of land use types), and p indicates the significance. The total number of positive associations are listed on the bottom of the table for each land use type. Species names are bolded when they have a 0.05 significance or lower.

Lowest Classification	Habitat Preference	Gb	Ind	Res	r_{pb}	p
Agyneta ordinaria	Both	1	0	0	0.43	1.00
Alydus sp.	Open	0	1	0	0.43	1.00
Amara idahoana	Open	0	1	0	0.43	1.00
Anoscopus sp.	Open	0	1	1	0.18	1.00
Anthomyiidae	Unknown	0	1	0	0.40	0.67
Anystidae	Unknown	0	1	1	0.00	1.00
Aphididae	Unknown	0	1	0	0.49	0.24
Aphrodes sp.	Open	0	1	0	0.43	1.00
Aphrophora sp.	Unknown	0	0	1	0.43	1.00
Arganthomyza duplex	Both	0	0	1	0.30	1.00
Atomaria sp.	Semi-Open	0	1	0	0.37	0.70
Basalys sp.	Unknown	1	0	0	0.63	0.27
Bathyphantes sp.	Unknown	1	0	0	0.43	1.00
Botanophila hucketti	Unknown	1	0	0	0.43	1.00
Braconidae	Unknown	1	0	0	0.43	1.00
Bradysia scabricornis	Unknown	0	1	0	0.35	1.00
Bradysia sp.	Unknown	0	1	0	0.19	1.00
Bradysia splendida	Unknown	0	1	0	0.43	1.00
Bradysia trivittata	Unknown	1	0	0	0.43	1.00
Bryotropha similis	Both	0	1	0	0.43	1.00
Camnula pellucida	Open	0	1	0	0.43	1.00
Carabidae	Unknown	0	0	1	0.76	0.05
Carabus taedatus	Both	0	0	1	0.43	1.00
Cecidomyiidae	Unknown	0	1	0	0.30	0.87
Ceratagallia sp.	Open	0	0	1	0.43	1.00
Chaitophorus neglectus	Semi-Open	1	0	0	0.63	0.28
Chilopoda	Unknown	0	1	0	0.43	1.00
Chloropidae	Unknown	0	0	1	0.43	1.00
Chorthippus curtipennis	Open	0	0	1	0.43	1.00
Cicadellidae	Unknown	0	0	1	0.43	1.00
Cinara sp.	Unknown	1	0	0	0.43	1.00

Clubionidae	Unknown	1	0	0	0.43	1.00
Coccinella septempunctata	Both	0	1	0	0.43	1.00
Collembola	Unknown	0	1	1	0.48	0.29
Conioscinella sp.	Unknown	0	1	0	0.43	1.00
Cordyla sp.	Unknown	0	0	1	0.43	1.00
Corticarina cavicollis	Open	0	1	0	0.43	1.00
Corynoptera saccata	More Closed	0	1	0	0.43	1.00
Corythucha sp.	Unknown	1	0	0	0.43	1.00
Cryptophagus sp	Closed	1	0	0	0.43	1.00
Curculionidae	Unknown	0	0	1	0.25	1.00
Cybaeidae	Unknown	1	0	1	0.32	1.00
Cybaeus morosus	Closed	1	0	0	0.43	1.00
Cytilus sericeus	Open	0	0	1	0.68	0.05
Delia sp.	Open	0	1	1	0.52	0.28
Devia prospera	More Closed	1	0	0	0.59	0.27
Dinotrema sp.	Unknown	1	0	0	0.19	1.00
Doratura stylata	Open	0	1	1	0.48	0.28
Entiminae	Open	0	0	1	0.43	1.00
Epipsocidae	Closed	1	0	0	0.43	1.00
Eremocoris sp.	Unknown	1	1	0	0.35	0.67
Erythraeidae	Unknown	0	1	0	0.43	0.49
Exitianus sp.	Open	0	1	0	0.43	1.00
Forficula auricularia	More Open	0	0	1	0.66	0.05
Formica sp.	Unknown	1	0	0	0.33	0.69
Gelis festinans	Open	0	1	0	0.43	1.00
Geocoris sp.	Open	0	1	0	0.47	0.06
Glocianus punctiger	Open	0	1	0	0.43	1.00
Gnaphosidae	Unknown	0	1	0	0.39	0.63
Habronattus ophrys	Open	0	1	0	0.43	1.00
Hahniidae	Both	1	0	0	0.43	1.00
Helina sp.	Unknown	0	1	1	0.30	1.00
Heliocobia rapax	Both	0	1	0	0.43	1.00
Henicopidae	Unknown	0	1	0	0.43	1.00
Heterosilpha ramosa	Semi-Open	0	0	1	0.43	1.00
Hybotidae	Unknown	1	0	1	0.32	1.00
Hydrophoria sp.	Both	0	1	0	0.41	0.71
Incertella incerta	Open	0	1	0	0.43	1.00
Lamyctes emarginatus	Both	0	1	0	0.43	1.00
Larrinae	Unknown	0	1	0	0.43	1.00
***Lasius* sp.**	Both	0	0	1	0.97	0.01
***Leptocera* sp.**	Both	0	1	0	0.82	0.05
Leptothorax sp.	Unknown	0	1	0	0.43	0.10
Linyphiidae	Unknown	1	0	0	0.21	0.84
Liogluta nitens	Both	0	0	1	0.43	1.00

Lithobiidae	Both	0	1	0	0.63	0.27
Oedipodinae	Open	0	1	0	0.63	0.26
Lycosidae	Both	0	1	1	0.44	0.42
Manica sp.	Both	0	1	0	0.30	1.00
***Megaselia* sp.**	Unknown	1	0	0	0.58	0.03
Melanophthalma sp.	Closed	0	1	0	0.43	1.00
Meteorus sp.	Unknown	0	1	0	0.43	1.00
***Myrmica* sp.**	Both	0	1	0	0.43	0.05
Nearctaphis sensoriata	Semi-Open	0	1	0	0.43	1.00
Oscinella sp.	Open	0	0	1	0.61	0.18
Otiorhynchus sp.	Both	0	0	1	0.41	0.65
Oxypoda	Closed	1	0	0	0.43	1.00
Parasitidae	Unknown	0	0	1	0.34	1.00
Pardosa moesta	More Open	0	1	0	0.43	1.00
Pardosa tesquorum	More Open	0	1	0	0.43	1.00
Phalangiidae	Unknown	1	0	0	0.52	0.06
Philodromidae	Open	0	1	0	0.43	1.00
Philonthus sp.	Both	0	0	1	0.44	0.27
Phrurolithidae	Unknown	0	1	0	0.57	0.27
Platygastridae	Unknown	1	1	0	0.23	0.88
Pollenia pediculata	Open	0	0	1	0.43	1.00
Polydesmidae	Unknown	1	0	0	0.46	0.10
Psammotettix confinis	Open	0	1	0	0.78	0.05
Pseudolycoriella sp.	Unknown	0	1	0	0.43	1.00
Psychidae	Unknown	0	0	1	0.43	1.00
Pterostichus adstrictus	Both	1	0	0	0.43	1.00
Pterostichus carbonarius	More Open	0	0	1	0.43	1.00
Pterostichus melanarius	More Open	1	0	1	0.37	0.36
Rhopalidae	Unknown	0	1	0	0.43	1.00
Sarcopteriformes	Unknown	0	1	0	0.38	0.88
Scaphinotus marginatus	Both	1	0	0	0.43	1.00
Schizolachnus sp.	Unknown	0	0	1	0.43	1.00
Sciaridae	Unknown	0	1	0	0.35	0.87
Sciocoris microphthalmus	Both	0	1	0	0.43	1.00
Sciomyzidae	Closed	1	0	0	0.43	1.00
Scotinella pugnata	Both	0	1	0	0.53	0.27
Silphidae	Unknown	0	0	1	0.43	1.00
Siphonella sp.	More Open	1	0	0	0.43	1.00
Sitona hispidulus	More Open	0	0	1	0.43	1.00
Slaterobius insignis	More Open	0	1	0	0.43	1.00
Staphylinidae	Unknown	1	0	1	0.50	0.43
Stygnocoris sabulosus	Semi-Open	1	0	1	0.32	1.00
Stygnocoris sp.	Unknown	0	0	1	0.63	0.27
Synuchus impunctatus	Semi-Open	1	0	0	0.43	1.00

Tachyporus sp.	Semi-Open	1	0	1	0.50	0.42
Tenuiphantes zelatus	Both	1	0	0	0.63	0.27
Thaumatomyia sp.	Open	0	0	1	0.43	1.00
Thomisidae	Unknown	0	1	0	0.66	0.11
Trachelipus rathkii	More Open	0	0	1	0.43	1.00
Trachyphloeus sp.	Open	0	1	1	0.27	0.78
Trapezonotus sp.	Open	0	1	1	0.32	1.00
Trichogramma sp.	Unknown	0	1	0	0.43	1.00
Tricimba sp.	Both	0	1	0	0.67	0.07
Trixoscelis sp.	Open	0	1	0	0.63	0.28
Tychius sp.	Open	0	1	1	0.32	1.00
Vespula pensylvanica	Both	0	1	1	0.40	0.47
Xysticus benefactor	More Open	0	1	0	0.43	1.00
Xysticus montanensis	Both	0	1	0	0.43	1.00
Zelotes sp	Both	0	1	0	0.43	1.00
Total	134	36	71	46		

Table 5.1.4. Degree of host specialization in herbivorous taxa where 1 indicates feeding within a single genus of plants. 2 within a single family, and 3 within multiple families.

Lowest Classification	Host Specialization
Alydus sp.	3
Amara idahoana	3
Anoscopus sp.	2
Aphrodes sp.	3
Aphrophora sp.	3
Bryotropha similis	3
Camnula pellucida	3
Ceratagallia sp.	3
Chaitophorus neglectus	1
Chorthippus curtipennis	2
Cinara sp.	1
Cytilus sericeus	3
Delia sp.	3
Doratura stylata	2
Eremocoris sp.	3
Exitianus sp.	3
Forficula auricularia	3
Glocianus punctiger	1
Nearctaphis sensoriata	3
Oedipodinae	3
Oscinella sp.	2
Otiorhynchus sp.	3

Psammotettix confinis	3
Psychidae	3
Schizolachnus sp.	1
Sitona hispidulus	2
Slaterobius insignis	3
Stygnocoris sabulosus	3
Stygnocoris sp.	3
Synuchus impunctatus	3
Trachyphloeus sp.	3
Trapezonotus sp.	3
Tychius sp.	2

APPENDIX. II
Tables for chapter three

Table 5.2.1. BINs and species names from the BOLD identification engine that matched OTUs from Prince George. Individual counts (Ind Cnt) represent the number of specimens belonging to each mOTU, BIN, and species search result (left to right). Percent similarity (% sim.) indicates the mean % similarity between Prince George and BOLD sequences. Match count indicates the number of BOLD sequences that matched identifications (≥ 98.5%) (BINs and species). mOTUs highlighted in red matched more than one species.

mOTUs	Ind Cnt	BIN	Ind Cnt	Lowest taxonomic identification	Ind Cnt	% sim.	Match Cnt
OTU-1	4	BOLD:ACV1885	1	*Aenigmatias*		99.8	44
OTU-2	3	BOLD:AEA0066	2	*Megaselia aequalis*	2	99.4	1
OTU-2	3	BOLD:AEA0067	2	*Megaselia giraudii*		99.8	1
OTU-3	5	BOLD:AAG3349	2	*Megaselia*		100	100
OTU-4	11	BOLD:AEU7203	3	*Megaselia brevicostalis*	3	98.7	81-82
OTU-4	11	BOLD:AEU7203	3	*Megaselia* sp:BOLD:AAG3266	3	98.7	19
OTU-4	11	BOLD:AEU7203	3	*Megaselia* sp. 40 SH-2017	1	98.7	1
OTU-5	4	BOLD:AAM9355	2	*Megaselia devia*		100	9
OTU-6	2	BOLD:AAP6420	1	*Megaselia*		100.0	100
OTU-7	4	BOLD:AAP6408	3	*Megaselia pongsaiae*	3	100	5
OTU-8	17	BOLD:ACB2325	14	*Megaselia largifrontalis*	14	100	3-101
OTU-9	58	BOLD:AAU8534	55	*Megaselia pulicaria* complex	55	100	1-101
OTU-10	8	BOLD:ACX3812	1	*Megaselia*		100.0	9
OTU-11	13	BOLD:ABV3315	5	*Megaselia nigra*		100	2
OTU-12	14	BOLD:AAU5599	13	*Megaselia crassipes*	13	100	1-62
OTU-13	15	BOLD:ADA4621	14	*Megaselia giraudii*	3	100	1
OTU-13	15	BOLD:ADA4621	14	*Megaselia lucifrons*	14	100	1-101
OTU-14	111	BOLD:ACS7008	94	*Megaselia arcticae*	94	100	2-101
OTU-15	34	BOLD:ACX6055	27	*Megaselia brevicostalis*	27	100	1-14
OTU-16	2	BOLD:ACZ4030	1	*Megaselia infraposita*	1	100	41

OTU-17	17	BOLD:ADA4916	14	*Megaselia longicostalis*	14	100	11-101
OTU-18	2	BOLD:ACB2539	1	*Megaselia hendersoni*	1		
OTU-19	2	BOLD:AAU6605	1	*Megaselia meconicera*	1	98.6	1
OTU-20	4	BOLD:ACC5889	2	*Megaselia*		100.0	48
OTU-21	7	BOLD:AAL9073	6	*Megaselia pulicaria* complex	6	100	8-101
OTU-22	10	BOLD:ACF3749	2	*Megaselia*		100	100
OTU-23	2	BOLD:AAN8687	1	*Megaselia fujiokai*	1	100	25
OTU-24	7	BOLD:AAP6413	2	*Megaselia*		99.9-'100	100
OTU-25	3	BOLD:AAL9075	3	*Megaselia lucifrons*	3	100	101
OTU-26	1	BOLD:AEV9051	1	*Megaselia*		99.6	100
OTU-27	1	BOLD:ACX1916	1	*Megaselia*		99.5	3
OTU-28	18	BOLD:AAG3274	16	*Megaselia hardingorum*	16	100	1-101
OTU-29	1	BOLD:AAP8725	1	*Megaselia*		99.7	43
OTU-30	3	BOLD:ABU5538	2	*Megaselia*		100	101
OTU-31	3	BOLD:AAG3259	2	*Megaselia longipennis*	2	99.5	1
OTU-32	9	BOLD:AAG3315	3	*Megaselia*		99.1-99.8	80-96
OTU-33	1	BOLD:AAG3310	1	*Megaselia*		99.2	100
OTU-34	8	BOLD:AEV9050	4	*Megaselia*		99.8-'100	100
OTU-35	1	BOLD:AAG3286	1	*Megaselia lombardorum*	1	99.6	100
OTU-36	2	BOLD:ACD4564	2	*Megaselia*		99.4	17
OTU-37	5	BOLD:AAU6624	3	*Megaselia spinicincta*	3	100	1
OTU-38	1	BOLD:ACB0962	1	*Megaselia citrinella*	1	100	101
OTU-39	12	BOLD:ABA6993	12	*Megaselia pleuralis*	12	100	101
OTU-40	9	BOLD:AAG3266	3	*Megaselia*		100	101
OTU-41	2			*Megaselia*			
OTU-42	1	BOLD:AAG3343	1	*Megaselia*		98.9	5
OTU-43	2	BOLD:AAG3338	1	*Lecanocerus compressiceps*	1	100	12
OTU-44	3	BOLD:AAG3238	2	*Phora*		99.8-'100	100
OTU-45	1	BOLD:ABY0932	1	*Megaselia*		99.7	78
OTU-46	3	BOLD:ACX6289	3	*Metopina galeata*	3	100	26
OTU-47	2	BOLD:AAU5646	1	*Puliciphora*		99.7	28
OTU-48	1	BOLD:AAU5624	1	*Pseudoaceton*		99.5	100
OTU-49	3	BOLD:AAG3236	3	*Diplonevra nitidula*	3	100	101
OTU-50	2	BOLD:AAP4685	1	*Megaselia*		99.7	67
OTU-51	1	BOLD:ACS2187	1	*Megaselia*		100.0	17
OTU-52	16	BOLD:AAU6533	13	*Megaselia coaetanea*	13	100	5
OTU-53	2	BOLD:AAU5652	1	*Megaselia*		99.7	13
OTU-54	2	BOLD:AAN8696	2	*Megaselia*		99.8	39
OTU-55	2	BOLD:ADP3479	2	*Megaselia rufipes*	2	100	19
OTU-56	3	BOLD:ABX8608	2	*Megaselia thomseni*	2	98.6	2-4
OTU-57	5	BOLD:ADF8082	5				
OTU-58	1	BOLD:AAL9070	1	*Megaselia longiseta*	1	100	2
OTU-59	2	BOLD:AAG3235	1	*Megaselia*		99.8	3

OTU-60	3	BOLD:AAG3304	3	*Megaselia nigriceps*	3	100	1-'100
OTU-61	1	BOLD:ACA2662	1	*Megaselia*		99.9	12
OTU-62	2	BOLD:AAM9373		*Megaselia*		99.5	23
OTU-63	3	BOLD:AAZ6701	3	*Megaselia joanneae*	3	100	8-56
OTU-64	1	BOLD:ACL8521	1	*Megaselia*		100.0	4
OTU-65	11	BOLD:AAG3356	2	*Megaselia*		100.0	100
OTU-66	1	BOLD:ABX8135	1	*Megaselia*		99.7	56
OTU-67	1	BOLD:AAG3235	1	*Megaselia*		99.9	100
OTU-68	2	BOLD:AAG3355	1	*Megaselia*		99.8	44
OTU-69	3	BOLD:ACB0987	3	*Megaselia spinigera*	3	100	53
OTU-70	1			*Megaselia*			
OTU-71	1			*Megaselia*			
OTU-72	3			*Megaselia*			
OTU-73	2			*Metopina*-group			
OTU-74	1	BOLD:ACP5869	1	*Megaselia gregaria*	1	99.3	101
OTU-75	2	BOLD:ACB0673	2	*Megaselia stoakesi*	2	100	71
OTU-76	2	BOLD:AAG3311	2	*Megaselia tecticauda*	2	100	16-101
OTU-77	4			*Megaselia*			
OTU-78	1			*Megaselia*			
OTU-79	2	BOLD:ACN5785	1	*Megaselia devia*	1	99.4	2
OTU-80	2			*Megaselia*			
OTU-81	1			*Megaselia*			
OTU-82	1			*Megaselia*			
OTU-83	1	BOLD:ABX8427	1	*Megaselia atrox*	1	99.9	101
OTU-84	1	BOLD:AAG3302	1	*Megaselia losangelensis*	1	99.4	32
OTU-85	1			*Phora*			
OTU-86	1			*Megaselia*			
OTU-87	1	BOLD:AAG3351	1	*Megaselia lutea*	1	100	36
OTU-88	1			*Megaselia*			
OTU-89	2	BOLD:AAP8118	1	*Gymnophora subarcuata*	1	100	11
OTU-90	1	BOLD:AAM9346	1	*Megaselia fungivora*	1	100	23
OTU-91	1			*Megaselia*			
OTU-92	1			*Megaselia*			
OTU-93	1			*Megaselia*			
OTU-94	19	BOLD:ACB6729	11	*Megaselia cinereifrons*	11	100	2
OTU-95	4	BOLD:ACB6729	2	*Megaselia*		99.7	68
OTU-96	3	BOLD:AAU6529	2	*Megaselia baileyae*	2	100	2
OTU-96	3	BOLD:AAU6529	2	*Megaselia pulicaria complex*	2	100	1
OTU-97	3	BOLD:AAU6529	3	*Megaselia baileyae*	3	98.7	33-34
OTU-97	3	BOLD:AAU6529	3	*Megaselia pulicaria complex*	2	98.6	1
OTU-98	1	BOLD:ACC7814	1	*Megaselia*		99.6	57
OTU-99	1	BOLD:ACC7711	1	*Megaselia*		99.9	79

Table 5.2.2. Number of phorid flies found in each land use type (Greenbelt = green, Edge = orange, Residential = blue, Industrial = gray), by year (2015 = 15, 2022 = 22) and the results of habitat associations found by the indicspecies package function *multipatt*. The r_{pb} index represents the correlation between mOTUs and groups of sites. It displays the land use type or groups of land use types that had the most significant association (p) for each mOTU. mOTUs with significant associations were bolded. The zero and one values in the right section of the table indicate no or positive associations. mOTUs that occur in all land use types are highlighted in yellow, while those that occur in only one land use type are highlighted in purple (Note: some are singletons).

mOTUs	15	22	22	15	22	15	22	Gb	Edg	Res	Ind	r_{pb}	p
OTU-1	0	0	0	2	0	1	1	0	0	1	1	0.27	0.55
OTU-2	1	0	0	0	0	0	2	1	0	0	1	0.22	0.79
OTU-3	2	3	0	0	0	0	0	1	0	0	0	0.47	0.07
OTU-4	1	1	2	0	4	0	3	0	1	0	0	0.33	0.24
OTU-5	1	0	0	0	0	1	2	0	0	0	1	0.32	0.26
OTU-6	1	1	0	0	0	0	0	1	0	0	0	0.35	0.39
OTU-7	1	0	0	0	3	0	0	0	0	1	0	0.34	0.11
OTU-8	9	8	0	0	0	0	0	1	0	0	0	0.59	0.01
OTU-9	35	8	1	0	10	2	2	1	0	0	0	0.27	0.21
OTU-10	7	0	0	0	1	0	0	1	0	0	0	0.30	0.25
OTU-11	2	0	0	0	7	1	3	0	0	1	0	0.25	0.46
OTU-12	14	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-13	3	8	1	0	3	0	0	1	0	0	0	0.38	0.12
OTU-14	81	9	2	0	14	2	3	1	0	0	0	0.24	0.62
OTU-15	0	0	0	7	9	3	15	0	0	1	1	0.48	0.03
OTU-16	1	0	1	0	0	0	0	0	1	0	0	0.47	0.11
OTU-17	5	6	1	0	5	0	0	1	1	1	0	0.39	0.08
OTU-18	1	0	0	0	1	0	0	1	0	1	0	0.19	0.78
OTU-19	1	0	1	0	0	0	0	0	1	0	0	0.47	0.11
OTU-20	2	0	1	0	0	0	1	0	1	0	0	0.24	0.60
OTU-21	2	4	1	0	0	0	0	1	1	0	0	0.47	0.02
OTU-22	5	1	0	1	0	1	2	1	0	0	0	0.25	0.49
OTU-23	0	0	0	1	0	0	1	0	0	1	1	0.19	0.78
OTU-24	3	3	0	0	1	0	0	1	0	0	0	0.42	0.07
OTU-25	1	0	0	0	1	0	1	1	0	1	1	0.07	1.00
OTU-26	0	0	0	0	0	1	0	0	0	0	1	0.24	1.00
OTU-27	1	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-28	2	2	1	0	12	0	1	0	0	1	0	0.35	0.16
OTU-29	1	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-30	2	1	0	0	0	0	0	1	0	0	0	0.43	0.09
OTU-31	2	0	0	0	1	0	0	1	0	1	0	0.18	0.79
OTU-32	4	2	2	0	1	0	0	1	1	0	0	0.40	0.09

OTU-33	1	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-34	1	5	2	0	0	0	0	1	1	0	0	0.45	0.07
OTU-35	1	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-36	2	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-37	1	0	0	0	4	0	0	0	0	1	0	0.31	0.26
OTU-38	1	0	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-39	0	0	0	0	12	0	0	0	0	1	0	0.43	0.07
OTU-40	1	7	0	0	0	0	1	1	0	0	0	0.39	0.11
OTU-41	0	0	0	1	1	0	0	0	0	1	0	0.37	0.18
OTU-42	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-43	0	1	1	0	0	0	0	0	1	0	0	0.47	0.10
OTU-44	0	2	0	0	1	0	0	1	0	1	0	0.23	0.59
OTU-45	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-46	0	0	0	0	0	0	3	0	0	0	1	0.43	0.08
OTU-47	0	0	0	0	1	0	1	0	0	1	1	0.19	0.79
OTU-48	0	0	1	0	0	0	0	0	1	0	0	0.70	0.06
OTU-49	0	0	1	0	2	0	0	0	1	1	0	0.31	0.35
OTU-50	0	1	0	0	1	0	0	1	0	1	0	0.19	0.79
OTU-51	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-52	0	0	3	0	7	0	6	0	1	1	1	0.40	0.07
OTU-53	0	1	0	0	0	0	1	1	0	0	1	0.18	1.00
OTU-54	0	0	0	0	2	0	0	0	0	1	0	0.37	0.19
OTU-55	0	0	0	0	2	0	0	0	0	1	0	0.26	0.35
OTU-56	0	0	0	0	2	0	1	0	0	1	0	0.24	0.40
OTU-57	0	0	1	0	0	0	4	0	1	0	1	0.33	0.16
OTU-58	0	0	0	0	1	0	0	0	0	1	0	0.26	0.36
OTU-59	0	2	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-60	0	0	0	0	2	0	1	0	0	1	0	0.24	0.40
OTU-61	0	0	0	0	1	0	0	0	0	1	0	0.26	0.35
OTU-62	0	0	0	0	2	0	0	0	0	1	0	0.26	0.36
OTU-63	0	0	1	0	2	0	0	0	1	1	0	0.40	0.10
OTU-64	0	0	1	0	0	0	0	0	1	0	0	0.70	0.05
OTU-65	0	7	3	0	1	0	0	1	1	0	0	0.41	0.08
OTU-66	0	0	0	0	1	0	0	0	0	1	0	0.26	0.36
OTU-67	0	0	0	0	0	0	1	0	0	0	1	0.24	1.00
OTU-68	0	1	1	0	0	0	0	0	1	0	0	0.47	0.11
OTU-69	0	0	0	0	2	0	1	0	0	1	0	0.24	0.41
OTU-70	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-71	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-72	0	0	0	0	0	0	3	0	0	0	1	0.24	1.00
OTU-73	0	2	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-74	0	0	0	0	1	0	0	0	0	1	0	0.26	0.36
OTU-75	0	1	1	0	0	0	0	0	1	0	0	0.47	0.10
OTU-76	0	0	1	0	1	0	0	0	1	0	0	0.47	0.10

OTU-77	0	1	1	0	2	0	0	0	1	0	0	0.30	0.45
OTU-78	0	0	1	0	0	0	0	0	1	0	0	0.70	0.05
OTU-79	0	0	0	0	2	0	0	0	0	1	0	0.26	0.35
OTU-80	0	2	0	0	0	0	0	1	0	0	0	0.35	0.38
OTU-81	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-82	0	0	0	0	0	0	1	0	0	0	1	0.24	1.00
OTU-83	0	0	0	0	1	0	0	0	0	1	0	0.26	0.35
OTU-84	0	0	0	0	0	0	1	0	0	0	1	0.24	1.00
OTU-85	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-86	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-87	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-88	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-89	0	2	0	0	0	0	0	1	0	0	0	0.35	0.38
OTU-90	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-91	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-92	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-93	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-94	4	4	2	0	8	1	0	1	1	1	0	0.31	0.28
OTU-95	0	3	0	0	1	0	0	1	0	0	0	0.25	0.53
OTU-96	2	0	1	0	0	0	0	1	1	0	0	0.29	0.39
OTU-97	0	2	0	0	1	0	0	1	0	1	0	0.23	0.59
OTU-98	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00
OTU-99	0	1	0	0	0	0	0	1	0	0	0	0.24	1.00