Habitat heterogeneity drives plant-pollinator network diversity on the tundra of Victoria Island, Nunavut, Canada

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Table of Contents

Abstract

We often perceive the Arctic as a barren ice-covered desert, but life abounds during the short summers when 24-hour daylight fuels plants' growth and, subsequently, terrestrial arthropod populations. Though Arctic landscapes appear uniform, variations in topography, substrate composition, and water availability result in micro-scale habitat heterogeneity with different resident plant and insect species. Some of these species interact with each other to form plant-pollinator networks. Global climate change is disproportionately impacting the Arctic more than elsewhere on Earth, and this change may disrupt plant-pollinator networks. This thesis quantifies the diversity of insects, plants, and interactions and determines structural properties of plant-pollinator networks in the Canadian Arctic.

I sampled plant-pollinator networks in two distinct microhabitats of the Victoria Lowlands on Victoria Island, Nunavut: (1) rocky, xeric habitats and (2) cryosolic, mesic habitats. I observed 2,421 total interactions (65 unique pairwise interactions) between 15 insect groups (family, sub-order, or order) and 17 species of conspicuously flowering plants. Alpha, beta, and gamma diversity of insects, plants, and interactions did not differ between microhabitats. However, insect groups were more evenly distributed in xeric microhabitats. Plant and pollinator communities were compositionally, but not structurally, different. Apidae, Lepidoptera, Asteraceae, and Fabaceae were associated with xeric sites, and Psyllidae, Symphyta, *Salix* spp., and *Astragalus* spp. were associated with mesic sites. Network structure differed slightly between microhabitats: mesic sites had higher interaction strength asymmetry, nestedness, and plant vulnerability than xeric microhabitats.

This work provides a valuable snapshot of two distinct plant-pollinator networks in the Canadian Arctic and highlights the role habitat heterogeneity plays in driving landscape biodiversity. Understanding this role and documenting species interactions will be necessary for monitoring future change in the Arctic and developing conservation policies.

Résumé

Habituellement, nous percevons l’Arctique comme un désert nu recouvert de glace. Pourtant, durant les courts étés, la vie jaillit quand le jour permanent nourrit la croissance des plantes, et les populations des arthropodes terrestres explosent. Bien que les paysages arctiques paraissent uniformes, les variations topographiques, la composition des substrats, la disponibilité d’eau, entraînent l’hétérogénéité des habitats à très petite échelle, peuplés de différents insectes et plantes. Certaines de ces espèces interagissent entre elles pour former des réseaux plantes-pollinisateurs. Les changements climatiques planétaires touchent l’Artique de manière disproportionnée, plus qu’ailleurs sur la Terre. Ces changements perturberont sûrement les réseaux plantes-pollinisateurs. Cette thèse vise à quantifier la diversité des insectes, plantes, et interactions, et déterminer les propriétés structurales des réseaux plantes-pollinisateurs dans l'Arctique canadien.

J’ai échantillonné des réseaux plantes-pollinisateurs dans deux microhabitats des Victoria Lowlands sur l’île de Victoria, Nunavut: (1) habitats rocheux et xériques, (2) habitats cryosolique et mésiques. J’ai observé au total 2 471 interactions (dont 65 interactions par paires uniques) entre 15 groupes d’insectes (famille, sous-ordre, ou ordre) et 17 espèces de plantes à fleurs apparentes. Les diversités alpha, beta, et gamma des insectes, plantes et interactions ne différaient pas entre les microhabitats. Cependant, les groupes d’insectes étaient plus uniformément répartis dans les microhabitats. Les communautés de plantes et de pollinisateurs différaient en composition mais pas en structure. Apidae, Lepidoptera, Asteraceae, et Fabaceae étaient associés avec les sites xériques, et Psyllidae, Symphyta, *Salix* spp., et *Astragalus* spp. étaient associés avec des sites mésiques. La structure des réseaux changeait légèrement entre microhabitats. Ainsi, les sites mésiques avaient une force d’interaction plus asymétrique , plus d’imbrication, et des plantes plus vulnérables que les sites xériques.

Cette recherche nous procure un aperçu de deux réseaux plantes-pollinisateurs distincts au sein de l’Arctique canadien et met en lumière le rôle qu’occupe l’hétérogénéité de l’habitat dans la biodiversité d’un paysage. Comprendre ce rôle et documenter les interactions des

espèces sera nécessaire pour surveiller et enregistrer les futurs changements dans l’Arctique et dans le développement de politiques de conservations.

List of figures

List of tables

Contribution of authors

I designed the sampling protocol, collected most of the data, performed the data analysis, and wrote the original manuscript. My supervisor, Christopher Buddle, contributed to the conceptual design of this research and the sampling of the data. Jessica Gillung and Morgan Jackson provided extensive guidance on the structure of the thesis and writing. Christopher, Jessica, and Morgan all provided copious comments and edits on this thesis. I outline all other non-writing contributions in the acknowledgments section below.

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Thesis structure

I present this thesis in a traditional monograph style with nine chapters. The first chapter outlines the impetus for this work and states my research objectives, and the second chapter provides an overview of the literature of the field. Chapter 3 describes the methods used to address the research questions, and Chapter 4 presents the results of the work. Chapter 5 is a discussion of the findings of this work concerning the existing literature. Chapter 6 summarizes the work undertaken and discusses the implications of the research. Chapters 7, 8, and 9 contain the references, figures, and tables, respectively, cited in this work. I present summary tables of the data collected for flowering plants and flower-visiting insects in appendices 1 and 2, respectively.

1. Introduction

1.1 Thesis rationale

Insect pollination is the unintentional transfer of pollen from one flower to the stigma of the same flower or a conspecific flower by anthophilous insects. This pollination service is critical for the proper functioning of ecosystems as it facilitates fertilization and outcrossing of plants, thus helping maintain plant populations and structure plant communities. Insect pollination is a critical component of all ecosystems, even in the Arctic. Though often thought of as a lifeless, snowy desert, the Arctic is teeming with plants and insects, many of whom interact to form plant-pollinator networks.

Unfortunately, the Arctic is experiencing the most significant impacts of global climate change, resulting in decreasing pollinator diversity, altered flowering phenology, and shifting pollinating insect ranges (Høye et al. 2013, Kerr et al. 2015, Schmidt et al. 2017). These disruptions can destabilize plant-pollinator networks, thus weakening pollination services and corroding plant communities (Hooper et al. 2005, CaraDonna et al. 2017). As pollinator species richness drops, so too do the size, complexity, and stability of plant-pollinator networks (Cardinale et al. 2004, 2006). Plant reproductive success is also negatively impacted by declines in pollinator numbers at both the species level (Herrera 1987, Kremen et al. 2002, Klein et al. 2003) and the community level (Cardinale et al. 2002, Thebault and Loreau 2003, Fontaine et al. 2005). Conversely, greater pollinator diversity promotes plant reproductive success (Hoehn et al. 2008, Brunet 2009, Blüthgen and Klein 2011). Therefore, declines or changes in diversity within plant-pollinator networks can place plant communities at risk of deteriorating (Hooper et al. 2005).

Arctic plant communities are also changing in response to climate change. Schmidt et al. (2012) showed that increased summer temperatures in Zackenberg, Greenland, are associated with changes in the cover of various plant functional groups and plant community structure. Modelling of these plant communities indicates that changes are readily detectable two decades after warming begins (Epstein et al. 2004), and the interactions between warming, herbivory, and precipitation will restructure plant communities to favour shrubs (Yu et al.

2011). These changes in plant communities, coupled with phenological shifts, may ultimately result in pollinator communities' collapse (Burkle et al. 2016, CaraDonna et al. 2017).

Greenland is a center of Arctic plant-pollinator network research (Lundgren and Olesen 2005, Olesen et al. 2008, Tiusanen et al. 2016). Little is known about such networks in Canada except for research by Kevan (1972a, 1972b, 1973a, 1973b) and Robinson and Henry (2018). Given the relative lack of quantitative pollinator research in the Canadian High Arctic, it is unknown how these networks have changed since the 1970s or how Canadian Arctic plant-pollinator communities are currently structured.

Few researchers have explored small-scale spatial variation in Arctic plant-pollinator networks or the diversity of interactions therein. Many have described the spatial variation of plants and insects across habitat heterogeneity and some abiotic gradients (e.g. Gould and Walker 1999, Rich et al. 2013, Becker et al. 2016, Hansen et al. 2016) but not of the interactions between these groups. Olesen and Jordano (2002a) did explore global patterns of plant-pollinator networks but not the drivers of interaction diversity within the Arctic. Given that interactions between various abiotic factors produce micro-scale habitat heterogeneity, one could expect that the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961) extends to plant-pollinator networks as well. This exploration of plant-pollinator networks across different habitats lacks in the Arctic.

Though numerous researchers have explored plant-pollinator networks in lower latitudes and different contexts, this thesis quantifies such networks in a poorly studied region of the world, the Canadian Arctic Archipelago, and across an abiotic gradient.

1.2 Research objectives

My research objective is to quantify flowering plant communities, pollinating insect communities, and the plant-pollinator networks in two different microhabitats (mesic and xeric) in the Victoria Lowlands on Victoria Island, Nunavut. More specifically, I ask the following questions:

- Which insect families pollinate which conspicuously flowering plant species?

- What are the diversities of insect families, plant species, and interactions that make up Arctic plant-pollinator networks and do these differ between mesic and xeric habitats?
- What are the structural properties of Arctic plant-pollinator networks and do these differ between mesic and xeric habitats?

Answering these questions will: (a) provide fundamental new scientific knowledge about a critical ecosystem service in an understudied yet vitally important ecosystem, (b) open a window into more extensive and taxonomically complete plant-pollinator networks in the Canadian Arctic, (c) create a dataset useful for asking further questions, and (d) provide a baseline for monitoring future change in Arctic arthropods and plant-pollinator networks.

2. Literature review

2.1 The Canadian Arctic Archipelago

The Canadian Arctic, when described as the lands north of the tree line, covers 2.6 million km^2 or 26% of Canadian land. The Canadian Arctic Archipelago itself accounts for the majority of that land; it is made up of 36,563 islands covering 1.4 million km^2 and forms the longest national coastline in the world (137,329 km). The archipelago stretches 64.5° of longitude (about 2,400 km) from Cape Dyer, Baffin Island, to the western tip of Banks Island. From Akpatok Island, the archipelago spans 22.8° of latitude (about 2,540 km) northwards to Cape Columbia on Ellesmere Island.

2.2 Understanding biodiversity

Biodiversity researchers and ecologists have a slew of tools at their disposal to quantify aspects of diversity at different scales and across variable gradients. One of the earliest frameworks used to describe biodiversity trends partitioned diversity into three components: alpha, beta, and gamma (Whittaker 1972). Alpha diversity denotes the diversity at local scales (e.g. diversity at a particular site, ecosystem, or point in time) and is often reported as species richness (i.e. the absolute number of species) (Whittaker 1972). Gamma diversity is similar to alpha diversity but encompasses broader scales and is also typically reported as species richness (e.g. the number of species in a region, landscape, biome, or the number of species observed over multiple years or decades) (Whittaker 1972).

Ecologists are particularly interested in the relationship between alpha diversity and gamma diversity. Whittaker (1972) calls this relationship Beta diversity and expressed it in various ways, one of which is the ratio of alpha diversity to gamma diversity. Beta diversity can be interpreted in various ways but is generally defined as the rate, magnitude, and direction of change in species richness (Martin and Hine 2008). It can describe species turnover across space, time, or other biotic factors, between local sites, ecosystems, or points in time. Beta diversity also quantifies the magnitude of heterogeneity of species assemblages across space, time, or other abiotic factors (Tuomisto 2010). Therefore, ecologists can use beta diversity to study the importance of alpha diversity in driving regional biodiversity or the role regional diversity plays in driving alpha diversity.

Alpha and gamma diversity are often reported as an absolute number of species, a crude index that obfuscates other components of diversity (Lande 1996). To account for differences in species abundances and community structure, ecologists have developed more informative diversity indices. For example, the Shannon-Wiener diversity index (H) considers species richness and their relative abundances (Shannon 1948). Shannon's equitability index (E_H) goes a step farther and describes the distribution of individuals of the species within a community. Though these indices' power is limited, and they cannot encompass all aspects of biodiversity, they are nevertheless a useful tool for comparing communities of species (Morris et al. 2014).

2.3 Arctic biodiversity

The Arctic is far less biodiverse compared to other biomes. In an analysis of global plant biodiversity, Barthlott et al. (1996) showed that the Arctic holds less than 500 plant species per 10,000 km^2 near the tree line and less than 100 species per 10,000 km^2 in the Canadian Arctic Archipelago. Vertebrate diversity is low, with only 227 species calling the Arctic home (Payer et al. 2013). On the other hand, over 4,750 species of terrestrial and freshwater invertebrates have been recorded across the Arctic (Payer et al. 2013). Terrestrial arthropods dominate the diversity of animals in the Arctic; Danks (1993) reported over 2,000 species of spiders, mites, springtails, and insects, with many more yet to be discovered in the Canadian Arctic. The young age of current Arctic ecosystems, highly variable and extreme climatic conditions, and smaller biome surface area are some of the factors that limit biodiversity in the Arctic (Danks 1981, Currie et al. 2004, Mittelbach et al. 2007). However, the variation in these factors and the interactions between them create different micro-niches for different species and thus help promote greater species diversity (MacArthur and MacArthur 1961, Gould and Walker 1999, Hansen et al. 2016).

Current Arctic ecosystems appeared in the last 3 million years, making them geologically relatively young (Murray 1995). The characteristic tundra of the Arctic started to appear in the late Pliocene (about 3.60 to 2.58 million years ago) as the climate began to cool (Matthews, Jr. and Ovenden 1990), with localized ecosystems beginning as small disjointed areas and expanding into a panarctic belt by three million years ago (Matthews 1979). This short history and beginnings as a fractured landscape are some of the many factors hypothesized to explain the lower diversity in higher latitudes (Mittelbach et al. 2007). Additionally, a history of over 20 glaciation events over the past three million years has severely limited speciation and dispersion in the Arctic (Payer et al. 2013), thus partially explaining the low biodiversity observed today.

Arctic environments are harsh with bitterly cold winter temperatures, little precipitation, short growing seasons, low solar energy input, and high winds (Barry R.G. et al. 1981), which determines the species that can survive in the Arctic. The lack of sunlight and the short growing season hinder primary productivity, limiting plant species diversity (Currie 1991). The extreme winter cold necessitates many adaptations for plant and insect survival (Strathdee and Bale 1998), and cool summer temperatures limit the biochemical kinetics of metabolism (Allen et al. 2002). Because metabolic rates determine resource requirements, primary productivity is low, and generation time limits evolutionary rates, the low Arctic temperatures help explain the lower biodiversity in the Arctic (Rohde 1992, Allen et al. 2002). Additionally, the combination of these abiotic factors makes survival, growth, development, reproduction, and dispersal difficult for terrestrial arthropods (Downes 1962, Danks 1981, Sømme and Block 1991).

This relationship between climate and taxonomic richness has long been explored and is strongly supported by numerous studies (Currie et al. 2004), particularly in plants (Currie and Paquin 1987, O'Brien 1993, Francis and Currie 2003). Though less studied, the climate-richness relationship of terrestrial arthropods is also strongly supported (Turner et al. 1987, Kerr et al. 1998). These works illustrate the positive correlation between solar energy input and species richness (Currie et al. 2004), thus explaining the paucity of diversity near the poles.

2.4 The habitat heterogeneity hypothesis

Abiotic factors are not uniform across landscapes within a biome, and they often interact to form a mosaic of different combinations of environmental and physical characteristics. The variation in the environment consequently produces different habitats that provide refuge and resources to different organisms. This relationship between habitat heterogeneity and the presence of different species forms the basis of the Habitat Heterogeneity Hypothesis, which states: species diversity in a landscape increases as habitat heterogeneity (the number of different habitats) also increases (MacArthur and MacArthur 1961). The Habitat Heterogeneity Hypothesis has far-reaching implications for understanding drivers of beta diversity in particular. Increased habitat heterogeneity promotes specialization and spatial segregation among species to reduce competition (Cramer and Willig 2005). In turn, higher habitat heterogeneity can lead to higher beta diversity and, thus, more substantial regional gamma diversity.

The Habitat Heterogeneity Hypothesis is an integral part of ecological theory and has been used in studies of ecological succession, disturbance, and latitudinal, elevational, and moisture gradients (Cramer and Willig 2005). Research supports the hypothesis very well across habitat types, taxa, spatial scales, and many abiotic gradients (Stein et al. 2014). One of the broader applications of the Habitat Heterogeneity Hypothesis is its use in developing management plans for conservation purposes (Tews et al. 2004, Batáry et al. 2011).

2.5 Arctic plants

The Arctic flora is poorly studied even though research in the Arctic, encompassing floristic surveys, evaluating climate change impacts, long-term biological monitoring, and nutrient cycling studies, among others, has accelerated in the last 60 years (Aiken et al. 2007). The recently published Flora of the Canadian Arctic Archipelago (Aiken et al. 2007) lists only 347 species and subspecies of ferns (Polypodiophyta), fern allies (Lycopodiophyta), and flowering plants (Spermatophyta) known to occur in the Canadian Arctic.

Arctic plants tend to be long-lived, with most being perennials and maturing at a late age (Billings and Mooney 1968, Walker et al. 2006). Due to harsh climatic conditions, growth is slow and can entirely stall during years in which summers are unusually cold (Billings 1987). Research often ignores the vast variation in climatic conditions across time and space, resulting in the generalization of plants' life-history traits and reproductive strategies to a few simple models (Jónsdóttir 2011). Indeed, Arctic plants utilize various reproductive strategies: clonal growth (Jónsdóttir 2011), vegetative reproduction by rhizomes, bulbils, or layering (Billings and Mooney 1968), and sexual reproduction by self-pollination and outcrossing through wind and insect pollination (Billings and Mooney 1968). Most Arctic plants do not require insects for successful reproduction (Kevan 1972a). However, some, such as *Dryas integrifolia* Vahl, and *Saxifraga oppositifolia* L., benefit from insect pollination as it results in a higher seed set (Kevan 1972a). In contrast, others, namely *Salix arctica* Pall., *Pedicularis langsdorffii* Fisch. ex Steven, and *P. capitate* Adams, require visits from insects to ensure reproduction (Kevan 1972a). These reproductive strategies appear to be strongly associated with flowering phenology: early flowering species depend heavily on outcrossing but produce a low seed to ovule ratio, and late flowering species are highly self-compatible and guarantee pollination via self-deposition (Molau 1993).

Many abiotic factors contribute to the structuring of plant communities in the Arctic. Grime (1979) highlights that low temperatures, including temperatures below 0°C in the Arctic, sharply limit plant growth and development. Therefore, temperature structures plant communities by acting against the varied thermal limits of plants. Water availability, which is determined by snowmelt, precipitation regimes, substrate drainage, soil structure, and the amount of soil organic matter, plays an essential role in community structuring as well (Migała et al. 2014). Though water drains quickly through much of the substrate, and the ground is often dry, snow and ice melt provide moisture for plants for most of the year (Aiken et al. 2007). The timing and speed of snowmelt also have a profound impact on plant community composition and the phenological patterns of said communities (Cooper et al. 2011, Pardee et al. 2019, Kudo 2020). Körner (2003) outlines the importance of snow cover beyond being a water source during the spring melt: it also protects plants from wind abrasion and drought stress in the winter. Conversely, strongly fluctuating temperatures in the spring can result in snow cover converting to an ice layer that reduces oxygen availability for plants.

The ground of the Arctic archipelago is composed entirely of permafrost and very little to no zonal soils (Bone 1992). Unconsolidated gravel, sand, glacial till, or bare rock cover most of the land. What little soil there is has few nutrients, is coarsely textured, contains little organic material, and retains little moisture (Walker and Peters 1977). These soils are categorized as cryosols: they are frozen up to 1 m below the surface and are often waterlogged during periods of thaw. Due to the nature of the local bedrock, soils are typically highly alkaline in the Western Arctic and acidic in the Eastern Arctic (Edlund et al. 1989, Aiken et al. 2007). Of course, the chemical properties of soil, such as pH and nutrient availability, also dictate community structure (Gordon et al. 2002, Madan et al. 2007). This set of conditions make Arctic soils a poor substrate for plants and therefore limit which species can establish themselves.

These and many other abiotic factors interact to form a broad diversity of microhabitat characteristics, which in turn influence community structure at local scales (Opała-Owczarek et al. 2018). The variation in substrates between the eastern and western half also results in the presence of very different plant communities and, consequently, different phytogeographic subprovinces (Yurtsev 1994, Aiken et al. 2007). A single Arctic phytogeographic subprovince covers the western half while three subprovinces span the eastern half (Yurtsev 1994). The northern section contains the fifth subprovince but is often grouped with the eastern Arctic zones into one contiguous province (Aiken et al. 2007).

2.6 Arctic insects

Terrestrial arthropods are an essential group of organisms, particularly in the Arctic, because of the myriad ecosystem functions they perform (Danks 1992, Kim 1993, Høye and Sikes 2013). Pollination, decomposition, nutrient cycling, herbivore population control, and seed dispersal are among many of the ecosystem functions that are underpinned by the presence of terrestrial arthropods (Wilson 1987, Kim 1993). In particular, insects mediate the relationships between plants and the abiotic environment (Weisser and Siemann 2008), structure plant communities through herbivory and control of herbivores (Beckerman et al. 1997), and promote plant success by providing pollination services (Walker et al. 2006).

Insect diversity is relatively low at all taxonomic levels in the Arctic. Chernov (1995) estimates about 4,500 species found across the Arctic, representing about 0.06-0.08% of the estimated 5.5 to 7 million species of insects on Earth (Stork 2018). At the order level, the Arctic holds about half of all known insect orders, and no order holds more than 30% of all families recorded within the order (Chernov 2002, Hodkinson 2018). Species diversity within orders is even lower compared to global trends but is unevenly distributed. The most globally diverse order, beetles, is represented by only 0.1% of species in the Arctic, whereas about 1% of global fly species are found in the Arctic (Chernov 1995). Roughly 20% of Arctic insect species are endemic, with rates of endemism increasing northwards (Chernov 2002, Hodkinson 2018). Among the flies, Chernov (1996) states that about 300 species were recorded in the Canadian Arctic. Fly diversity decreases with latitude, but the share of fly species relative to all insect diversity, excluding Collembola, increases to 75% in the northern Arctic (Chernov and L.D. Penev 1993, Chernov 1996). Of the 15 largest global fly families, most are missing in the Arctic or are represented by a small number of species (Chernov 1996). The most species-rich fly families in the Arctic are Tipulidae, Chironomidae, Mycetophilidae, Empididae, Dolichopoidae, Syrphidae, and Muscidae.

Though the Arctic appears relatively uniform, it contains a rich diversity of habitats across the landscape and an equally rich diversity of microhabitats across smaller spatial scales (Downes 1964). The combined effects of abiotic factors such as moisture gradients, substrate structure, local wind speed, aspect, snow accumulation, snowmelt date, and local topology result in a mosaic of diverse microhabitats in turn structure local insect communities (Hodkinson 2018). For example, there is already ample evidence that moisture gradients structure community composition and species abundance of terrestrial carabid beetles, spiders, and chironomid midges and other nematocerous flies (Sendstad et al. 1977, Salmela 2011, Ernst and Buddle 2013, Cameron and Buddle 2017). Hodkinson (2018) summarises the effect of many other abiotic and biotic influences on insect diversity and community, such as heat accumulation, nutrient availability, disturbance, predation, and parasitism. In particular, plant species assemblages can structure insect communities via vegetation type (Schaffers et al. 2008) and dominance (Rich et al. 2013). Though there is extensive literature examining the Arctic insect fauna across various abiotic gradients, little work has been done to analyze pollinator communities and plant-pollinator interactions across abiotic gradients.

2.7 Pollination in the Arctic

Plant reproduction in the Arctic has long been thought to be limited to autogamy and apomixis. Although outcrossing via insect pollination has been observed, it was not considered necessary (Jessen 1913, Mathiesen 1921). However, ample evidence has since emerged of the importance of insect pollination for plant reproductive success (Panfilov et al. 1960, Kevan 1972a, Elberling and Olesen 1999, Larson et al. 2001). Bees, butterflies, and syrphid flies dominate pollinator communities in the low Arctic, much like in temperate regions (Hodkinson 2018). On the other hand, anthophilous flies such as Muscidae and Anthomyiidae dominate High Arctic pollinator communities(Kevan 1972a, Totland 1993, Elberling and Olesen 1999, Larson et al. 2001). Many other insects, such as parasitoid wasps, mosquitoes, and chironomid flies, are also associated with flowers (Kevan 1972a, Klein et al. 2008). However, their role in pollination within the Arctic is uncertain.

Though species diversity is low in the Arctic, plant-pollinator networks do show high complexity. Observational studies have recorded up to 456 pairwise interactions in Arctic plant-pollinator networks with rates of connectance similar or higher to those of networks in temperate regions (summarized in Olesen and Jordano 2002). When looking at the diversity of pollen found on the body of insects, Arctic plant-pollinator networks show even greater complexity and diversity of interactions (Olesen et al. 2011). Though considerable work has gone into understanding Arctic plant-pollinator networks, little of this work was done in Canada. Early studies by Peter Kevan (1972a, 1972b, 1973a, 1973b) described the basic structure of a plant-pollinator network on Ellesmere Island, Nunavut, and recorded many observations of various insect taxa being potential pollinators. More recent work in the Canadian Arctic assessed the interactions between warming, phenology, and pollination from the plants' perspective (Klady et al. 2011, Bjorkman et al. 2015, Robinson and Henry 2018).

However, all of this work was done either at Lake Hazen or Alexandra Fjord, both on Ellesmere Island, Nunavut. Also, few of these Canadian studies probed the structural properties of networks.

2.8 Understanding plant-pollinator networks

Plant-pollinator networks are systems of flowering plants and pollinating animals (denoted as nodes) that are connected by the interactions (denoted as links) between them (Jordano 1987). These networks are classified as 2-mode and bipartite because links exist solely between two distinct groups with no shared species, the plants and pollinators. However, no links exist between species within a group (Newman 2018). Though in real ecosystems, plants interact with each other just as pollinators can interact with each other, these interactions are not included in plant-pollinator network studies because the focus of the research is the pollination interaction.

Understanding plant-pollinator networks can provide insights into a myriad of ecological phenomena beyond the importance of pollination services. They help explain the effects of habitat loss on plant and insect communities (Fortuna and Bascompte 2006). They can inform management plans for the conservation of rare species (Elle et al. 2012). They provide tools for exploring patterns in and drivers of coevolution (Lomáscolo et al. 2019). Moreover, they are valuable systems for studying the evolution, patterns, and importance of specialization and generalization en ecology (Waser and Ollerton 2006).

Researchers can probe the structure of plant-pollinator networks for different properties with ecological relevance and meaning beyond that explored through network theory. Concepts such as connectance, interaction strength asymmetry, nestedness, linkage density, modularity, robustness, generality, vulnerability and extinction slopes are informative structural properties of bipartite mutualist networks.

Connectance is the ratio of realized interactions to the number of all possible interactions in a network (Gotelli and Graves 1996, Dunne et al. 2002). Maximum connectance is the product of the number of nodes in both groups (i.e. the number of plants and number of pollinators). High connectance is characteristic of complex networks in which most of all, possible interactions are observed (Blüthgen et al. 2008). Low connectance is characteristic of simple networks with few realized interactions (Blüthgen et al. 2008). Connectance can also be a descriptor of generalization in a network with higher connectance, indicating greater generalization (Lundgren and Olesen 2005). This metric provides important insights into the stability of networks, with higher connectance conferring greater stability due to greater redundancy in the network (Thebault and Fontaine 2010, Elle et al. 2012).

Interaction strength asymmetry is the apparent asymmetric dependence between two groups of interacting taxa and may be considered an indicator of specialization in a network (Bascompte et al. 2006). For example, consider a single specialist plant species that is pollinated by a single generalist insect species. The plant species is highly dependent on the insect species because it only has one pollination interaction. However, the insect species depends little on the plant species because it is a generalist and visits many other plant species. The asymmetry of a species' interactions is calculated as the average of the strength of each pairwise interaction (Vázquez et al. 2007). Interaction strength asymmetry is then calculated as the average of the interaction asymmetry scores of all species in the network (Blüthgen et al. 2007). As with connectance, greater interaction strength asymmetry is an indicator of greater network stability and species resilience (Elle et al. 2012). Specialist-generalist interactions produce strong asymmetry and provide resilience for the generalists in the face of disturbance to the specialists (Bascompte et al. 2003). Conversely, many specialist-specialist interactions reduce interaction strength asymmetry and weak species' resilience.

Nestedness refers to the degree to which specialists (taxa with few interactions) interact with generalists (taxa with many interactions, Blüthgen et al. 2008) and is denoted as temperature (*T*). High nestedness values indicate little reciprocal specialization in a network and vice versa for low nestedness values (Bascompte et al. 2003). In other words, low nestedness indicates that few specialists interact with generalists, while high nestedness indicates that many specialists interact with generalists. Understanding and quantifying nestedness can help inform predictions about species loss as habitat is lost or modified. Highly nested plant-pollinator communities, which many real networks are, contain a core set of species that may be robust to disturbances while species outside the core community are vulnerable to extirpation (Fortuna and Bascompte 2006).

Linkage density is related to connectance and is an indicator of the average specialization level (Landi et al. 2018). It, too, can signal if specialists or generalists dominate a mutualistic network.

Modularity refers to the grouping of interacting species in a network such that interactions between species within a group are more frequent than interactions between those same species and species outside the group (Newman 2003, Newman and Girvan 2004, Fortunato 2010). As an example of a highly modular network, consider a set of bee species which only interact with plants in a single family, and another set of bees, that only interact with plants in another family. Such an insect-plant network would be highly modular and contain two modules. Therefore, low modularity indicates that interactions are evenly distributed in a network, while high modularity indicates interaction clustering. Modularity plays an important role in the compartmentalization of disturbance to a network by limiting the impacts of disturbance to a single or a few modules (Thebault and Fontaine 2010). However, greater modularity concentrates the impacts of disturbance (Elle et al. 2012), and can result in greater extirpation if generalist species in modules are lost (Tylianakis et al. 2010).

Extinction slope is a measure of secondary extinction rates after losing species in one group within a network (Memmott et al. 2004). It is determined by calculating the number of secondary extinction events after simulating progressive primary extinctions, repeating the calculations and simulations many times, averaging the number of secondary extinction events, and then fitting a hyperbolic regression through the data (Dormann et al. 2009). Extinction slope is then extracted as the slope of the regression line. High extinction slopes indicate high levels of redundancy in a network and that many primary extinction events must occur to result in many secondary extinction events. The opposite is true of low extinction slopes: there is little redundancy, and few primary extinction events result in many secondary extinction events.

Network robustness is related to extinction slope in that it is calculated as the area under the extinction curve (Memmott et al. 2004). Network robustness ranges from 0, indicating a fragile network in which the extinction curve drops dramatically, to 1, indicating a robust network in which there is a slow, gradual loss of species after each extinction event.

Generality and vulnerability are related to linkage density and describe the average number of interactions of a species in one group with species in another group (Bersier et al. 2002). In a plant-pollinator network, generality refers to the average number of plants that pollinators visit, and vulnerability refers to the average number of pollinators that visit a plant.

These last network properties (extinction slope, robustness, generality, and vulnerability) are all related to each other and are valuable tools for conservation planning. Quantifying these properties and modelling the impacts of conservation actions on these properties provides data useful in determining appropriate conservation goals (Tylianakis et al. 2010)

3. Methods

3.1 Location

I conducted my research within a 10 km radius of the community of Cambridge Bay (69°06'58.8"N 105°03'28.7"W) in Nunavut, Canada (Figure 1). The community and study area are located on the southern shore of Victoria Island, adjacent to one of the arms of Cambridge Bay, a refuge along the Northwest Passage within the Arctic Ocean in Canada's territorial waters (Figure 1 inset).

Cambridge Bay has a polar climate, with average monthly temperatures never exceeding 10 °C (based on 1981-2010 data from Environment and Climate Change Canada (2020)). Winters are cold and dry with a mean daily temperature of -28.9 °C and mean monthly precipitation of 17.4 mm between November and March. Summers are short, cool, and wet with a mean daily temperature of 6.1 °C and mean monthly precipitation of 21.1 mm between June and August. Consequently, there are only 584 degree days above 0 °C and 216 degree days above 5 °C between June and August (based on 1981-2010 data from Environment and Climate Change Canada (2020)). Because summers are short, snow can persist all year long in some areas, particularly on hillsides facing north (personal observation). However, most of the landscape around the community of Cambridge Bay is snow-free from mid-June to mid-August. The extreme latitude of Cambridge Bay results in 24 hours of daylight in the summer from mid-May to late-July. Conversely, Cambridge Bay experiences very dark winters with no daylight from late-November to mid-January (Herzberg Astronomy and Astrophysics Research Centre 2020).

Victoria Island contains three major physiographic regions (Danks 1981, Ecological Stratification Working Group 1996). The Victoria lowlands cover most of the island; the Shalar mountains bisect the island in the northwest, and the Amundsen Gulf Lowlands line the southern perimeter of the island. Apart from the Shalar Mountains, Victoria Island is predominantly covered in unconsolidated glacial deposits. These deposits form large morainal hills, such as Uvayuk (formally Mount Pelly, 183 m, 69°10'15.2"N 104°42'32.3"W, Figure 1), which punctuate low undulating hills (2-10 m) that surround Cambridge Bay. There are flatter plains southwest of and below the Augusta Hills (69°06'57.7"N 105°20'19.4"W) and further west towards Tikiroaryuk (formally Long Point beach, Figure 1).

3.2 Research sites and selection process

I selected six sites each of two different microhabitat types near the roads leading away from Cambridge Bay: a drier, xeric microhabitat with a well-draining substrate and a wetter, mesic, microhabitat with a poorly-draining substrate.

In the summer of 2017, I selected six xeric sites about 75 m to 150 m southeast of the road between Cambridge Bay and Uvayuk Territorial Park, and 750 m to 1,400 m apart (Figure 1). This area is hilly (2-10 m high) with streams, rivers, and permanent, unconnected ponds between the hills. I selected sites atop hills or on the slopes of hills, such that they would be between 2,500 m^2 and 10,000 m^2 in area, faced south or south-east, and would be partially or entirely sloped up to 30° (Table 1). The substrate at the sites was made up of <1 m of carbonate/calcareous diamicton (unsorted sediment made of pebbles (6-64 mm), cobbles (64-256 mm), and boulders (>256 mm)), with minute amounts of soil between the rocks, all atop bedrock (Geological Survey of Canada 2016) (Figure 2, panel A). The flora of these sites is dominated by Prickly Saxifrage (*Saxifraga tricuspidata* Rothb.) atop the hills, Mountain Avens (*Dryas integrifolia* Vahl.) on the slopes, and willow bushes (*Salix* spp. L.) and sedges (Cyperaceae Juss.) at the base of the hills (Figure 2, panel B).

In the summer of 2018, I selected six mesic sites about 150 m to 350 m north of the road between Cambridge Bay and Tikiroaryuk, and 1,200 m to 1,600 m apart (Figure 1). The area is flat or slightly sloped (< 5°) and faces south. There were some permanent and unconnected pools of snowmelt water next to the sites. I selected sites such that they were flat and contained no stagnant water by 16 June 2018. The sites were between 900 m^2 and 3,600 m^2 in area (Table 1). They sat on 1 m to 3 m of undifferentiated marine sediments, all carbonate/calcareous diamicton, atop bedrock (Geological Survey of Canada 2016) (Figure 2, panel C). Cyperaceae dominates the flora of these sites with patches of *Salix* spp. bushes and scattered *D. integrifolia* (Figure 2, Panel D). A greater abundance of *D. integrifolia* and some legume plants (Fabaceae Lindl.) can be found in the drier areas of the sites, and a greater abundance of willow bushes can be found in wetter areas.

I selected these two microhabitat types to sample plant-pollinator networks across very different habitats and capture a visible proxy of habitat heterogeneity. The differences in moisture, substrate composition, aspect, and plant communities produce two distinct microhabitat types that are frequently found adjacent to each other across the landscape. I selected for this distinction to increase the likelihood of detecting significant differences in plant and pollinator communities and the plant-pollinator networks.

At each site, I set up one 1 m x 25 m transect to later estimate floral abundance (example: Figure 2, panel C). In mostly sloped sites, I laid transects parallel to the plane of the slope mid-way between the lowest and highest points of the sites. In flat sites, I laid the transects in the middle of the sites mid-way between the driest and wettest areas adjacent to the sites.

3.3 Sampling protocol

Though I selected sites in different years for the different habitats, I performed all the sampling in the summer of 2018. I began sampling on 22 June 2018, when the first flowers, Purple Saxifrage (*Saxifraga oppositifolia* L.), began to open. I divided the summer into ten sampling periods, each five to six days long, except for the last period, which lasted three days. Within each sampling period, I visited each site twice within the same day. When inclement weather prevented two visits in a day, I visited a site only once and again the next day. I concluded sampling on 10 August 2018, when there were no more conspicuous open flowers in the plant transects (see Table 2 for sampling schedule). I did not sample when the temperature dropped below 4 °C, the wind increased to 30 km/h, or if heavy rain or snow began to fall.

During the first visit of each sampling period at a site, I measured flower abundance by counting the number of open flowers of every flowering plant species (except grasses, sedges, and rushes) in the 1 m x 25 m transects. I recorded the abundance of 18 plant species in total (Appendix 1: Flowering plant species observations). Regarding the Asteraceae (only one species present: *Hulteniella integrifolia* (Richardson) Tzvelev), I recorded one 'open flower' per capitulum if at least one floret was open within the capitulum. For the willows (*Salix* spp., two known and two unknown species present), I recorded one 'open flower' per catkin, if at least one flower was open on a female catkin. I used the keys in the Illustrated Flora of the Canadian Arctic Archipelago (Porsild 1964) and the digital Flora of the Canadian Arctic Archipelago (Aiken et al. 2007) to identify flowering plants to species. I could not identify two morphologically distinct willows to species, so I recorded them as '*Salix* sp1.' and '*Salix* sp2.'

During each visit to a site, I observed plant-insect interactions for one hour. I recorded an interaction as occurring when I observed an insect unambiguously coming into contact with an open flower's reproductive structures. I then recorded the plant species of the interaction using the resources mentioned above to identify the plant. I also identified the insect to order, sub-order, or family when possible. For each observation, I attempted to collect the insect using an aerial net. If captured, I placed the specimens in labelled vials filled with anhydrous ethanol and then stored them in a -14 °C household freezer.

Back in the laboratory at the Lyman Entomological Museum, I sorted, dried, pinned, and identified insect specimens to the lowest taxonomic level possible. I chemically dried the flies, Hemiptera, microlepidoptera, and wasps with > 99% Hexamethyldisilazane following the protocol in Brown (1993). I washed the bumble bees (*Bombus* spp. Latreille) with warm soapy water, rinsed with cold water, partially dried them with a hairdryer, mounted them on a pin, and gently exposed their genitalia. I pinned, spread, and let air dry the large Lepidoptera.

I identified flies to family using McAlpine (1981) but recorded most acalyptrate flies as acalyptrates because identification to a lower taxonomic level was not possible. I identified the Lepidoptera as microlepidoptera (encompassing Pyralidae and Tortricidae) or otherwise to family. I identified the Hemipterans to family using Marshall (2006). I used Williams et al. (2014) to identify the bumble bees to species and recorded other Hymenoptera as "Parasitica" or Symphyta using Marshall (2006).

3.4 Data permanence and voucher specimens

I will publish a publically accessible spreadsheet containing the plant-pollinator interaction data, the floral abundance data, and the site characteristics data to the Dryad data repository (https://datadryad.org/).

All Diptera, Hymenoptera, Hemiptera, and Lepidoptera collected were dried, mounted, labelled, and deposited in the Lyman Entomological Museum at 21111 Lakeshore Dr, Sainte-Anne-de-Bellevue, Quebec H9X 3V9, Canada.

I collected multiple specimens of flowering plants, except grasses, sedges, and rushes from both mesic and xeric microhabitats. These specimens were dried and mounted on standard herbarium rag paper as voucher specimens, then deposited in the McGill University Herbarium at 21111 Lakeshore Dr, Sainte-Anne-de-Bellevue, Quebec H9X 3V9, Canada.

3.5 Diversity and community analyses

I performed diversity analyses to address the first two research questions: (1) which insects interact with which plants, and (2) what are the diversities of insects, plants, and interactions in the plant-pollinator networks? I excluded records of insects that I could not identify to family, but these records are reported in the tables of observed taxa (Appendix 2: Insect taxa observations). Since I caught few Lepidoptera, I treated them as a single taxonomic group instead of multiple families, in all analyses. I performed all data organization, cleaning, and statistical analyses in R version 3.6.1 (R Core Team 2019).

I examined diversity within the plant-pollinator communities using family diversity for insects, species diversity for plants, and pairwise interaction diversity for the networks.

I calculated alpha diversity, as an absolute number, Shannon's diversity index (H), and Shannon's equitability (E_H), for insect families recorded in interactions, flowering plant species in the transects, and pairwise interactions at each site. I calculated these indices using the *diversity* function in the *vegan* package (Oksanen et al. 2019). I then compared the mean of each of these diversity indices between microhabitat types using unpaired Student's t-tests.

Gamma diversity was similarly calculated with the same indices for each habitat type and the entire study system for insect families recorded in interactions, flowering plant species in the transects, and pairwise interactions.

I calculated Beta diversity as a Shannon index using effective species within each habitat type and across the landscape for insect families recorded in interactions, flowering plant species in the transects, and pairwise interactions.

To determine the effect of microhabitat on insects observed interacting with open flowers, on flowering plant species recorded in the transects, and on pairwise interactions, I generated site-taxa occurrence matrices and plotted the data in ordination space using the *metaMDS* function in the *vegan* package (Oksanen et al. 2019) with Bray-Curtis dissimilarity matrices of community composition inputted into the function. I plotted microhabitat centroids with 95% confidence intervals in the ordination space using the *ordiellipse* function in the *vegan* package (Oksanen et al. 2019).

3.6 Network analyses

I analyzed the plant-pollinator networks' structure to answer my third research question: What are the structural properties of plant-pollinator networks, and do these differ between mesic and xeric habitats? I modelled and analyzed the two-mode networks for each microhabitat using the *bipartite* package (Dormann et al. 2008). I imported records of insects that I had identified as Parasitica, Symphyta, Lepidoptera, or otherwise family. As with previous analyses, I treated all Lepidoptera as a single taxonomic group instead of multiple families. I imported flowering plants into the model as species or as morphospecies for the two willows I could not identify. I then calculated various descriptors of network structure (described below) for the insect-plant interaction networks in both microhabitats.

I calculated connectance as $C = L/(IJ)$, where L is the total number of interactions observed, and I and J are the number of insect taxa and flowering plant species, respectively (Gotelli and Graves 1996). Interaction strength asymmetry was calculated as the average of the interaction asymmetry scores of all species in the network (Blüthgen et al. 2007). Nestedness was calculated as a Weighted Nestedness metric based on Overlap and Decreasing Fill (WNODF, Almeida-Neto and Ulrich 2011). Linkage density was calculated as the average of vulnerability and generality scores (Bersier et al. 2002). I computed these indices using the *networklevel* function in the *bipartite* package (Dormann et al. 2009).

I calculated modularity, a measure of the strength of divisions in a network (Newman 2003), using the *computeModules* function with 1,000,000 steps in the *bipartite* package following Beckett 2016.

Using the *grouplevel* function in the *bipartite* package, I simulated the random extinction of both plants and insects in the networks over 10,000 replicates, according to Burgos et al. (2007). I then extracted the extinction slopes and calculated robustness scores for both insects and plants using the *grouplevel* function in the *bipartite* package (Dormann et al. 2009).

I calculated generality as the average number of plants that a pollinator visits, and vulnerability as the average number of pollinators that visit a plant using the *grouplevel* function in the *bipartite* package (Dormann et al. 2009) according to (Tylianakis et al. 2007).

4. Results

I observed 15 insect groups interacting with a total of 17 plant species across both microhabitats (Table 3). I collected 14 and 12 insect taxa in the mesic and xeric sites, respectively. I similarly recorded 14 and 12 flowering plant species in the mesic and xeric sites, respectively. I recorded 4,055 interactions between insects and flowering plants: 2,445 in the mesic habitat and 1,610 in the xeric habitat. Sixty-five of these records were unique pairwise interactions, with 41 recorded each in both microhabitats (Table 3). I identified the insect to family in 2,421 of those interactions.

4.1 Terrestrial arthropods

On average, there were more insect families per site in the mesic habitats than in the xeric habitats (Table 3). However, this difference was not statistically significant. Conversely, alpha diversity, measured as Shannon's diversity index (H), was higher in the xeric habitats, but, again, the difference between habitats was not significant. Similarly, there were more insect families recorded in all the mesic sites ($n = 14$) than in the xeric sites ($n = 12$) with the reverse difference in Shannon's diversity index. Notably, Shannon's equitability (E_H) indicates that the diversity of terrestrial arthropods is more evenly distributed in the xeric sites than in mesic sites (difference = 0.1555, $t = -2.6$, $df = 5.4$, $p = 0.04$, Table 3). When calculated across all sites, terrestrial arthropods diversity is not evenly distributed ($E_H = 0.46$, Table 3).

Beta diversity was similar between mesic and xeric habitats and close to zero, indicating that the microhabitats contained almost most insect families found across the landscape.

Though the diversity indices show little difference between microhabitats, their composition does differ. Muscidae make up the majority of insects observed visiting flowers (Figures 3 and 4) in both microhabitats. However, I recorded more visits by Muscidae in the mesic habitats (Figure 3) and made up a more substantial proportion of all insect visitors in the mesic habitat (Figure 4). Various other insect taxa were more common in the mesic sites than the xeric sites: Anthomyiidae, Empididae, Symphyta, and Culicidae (Figure 3). Conversely, Apidae and Chironomidae were more abundant in the xeric habitat (Figure 3).

When I plotted the insect communities of all sites on a two-dimensional ordination space (Figure 5), the communities form two distinct groups corresponding to the microhabitats studied. Figure 5 shows that Dolichopodidae, Symphyta, Psyllidae, and Scathophagidae are mostly associated with mesic habitats, while Calliphoridae, Lepidoptera, Chironomidae, and Apidae are mostly associated with xeric habitats.

4.2 Flowering plants

There were, on average, a higher number of conspicuously flowering plant species per site in the mesic habitats than in the xeric habitats (Table 3). However, this difference is not statistically significant. Similarly, alpha diversity, measured as Shannon's diversity index (H), was higher in the mesic habitat, but the difference is not significant. As with the insect taxa, I recorded more flowering plant species in all the mesic sites (n = 14) than in the xeric sites (n = 12) with a similar qualitative difference in Shannon's diversity index. Shannon's equitability (E_H) indices indicate that the diversity of flowering plant species is marginally more evenly distributed in the xeric sites than in mesic sites, though the difference is not significant.

Beta diversity was similar between mesic and xeric habitats but much higher than a value of 1, indicating that the microhabitats contained a small subset of the flowering plant species found across the landscape.

Though the diversity indices are almost identical between microhabitats, the compositions of the networks were very different. *Dryas integrifolia* is the most abundant conspicuously flowering plant species in both microhabitats but was far more abundant in the xeric sites (Figure 6). *Hedysarum boreale* Nutt., *Cassiope tetragona* D. Don, *Saxifraga oppositifolia* L., and *Oxytropis arctobia* Bunge were also much more abundant in the xeric sites. After *D. integrifolia*, the flowering plant community in the mesic sites was dominated by *Arctous rubra* (Rehder & E. H. Wilson) Nakai and various species of willows (*Salix* spp., Figure 6 and 7). In addition to these compositional differences, the xeric sites had a greater abundance of flowers of all species recorded than the mesic sites (Figure 7).

The differences in plant communities were also evident when plotted on two-dimensional ordination space (Figure 8): the communities within each site form two distinct groups corresponding to the microhabitat types with no overlap. Figure 8 shows that *Chamaenerion latifolium* L. Sweet, *Astragalus alpinus* L., *Salix arctica* Pall., and *Pedicularis capitata* are mostly associated with mesic habitats, while *O. arctobia*, *H. boreale*, *Lesquerella arctica* (Wormskjold. ex Hornem.) S. Watson, and *Hulteniella integrifolia* (Richardson) Tzvelev are mostly associated with xeric habitats.

4.3 Interactions

The number of interactions between insect families and flowering plant species, and the diversity of interactions measured as Shannon's diversity index, differed marginally between the mesic and xeric microhabitats (Table 3), with diversity greater in the mesic habitats. However, these differences are not statistically significant. Interaction diversity evenness, measured as Shannon's equitability index, was higher in the xeric habitat, but the difference between habitats is not statistically significant (Table 3). In total, I recorded 41 different interactions in each microhabitat, with 65 recorded across the landscape (Table 3).

Beta diversity was nearly identical in the mesic and xeric habitats and slightly above one (Table 3), indicating that almost all interactions in the landscape were recorded within each of the microhabitats.

The most frequently observed interaction (Muscidae with *D. integrifolia*) was recorded in both microhabitats (Figure 10). However, plotting the pairwise interactions in ordination space shows a clear grouping of sites within the same microhabitat types (Figure 9), indicating a clear distinction between the sets of interactions. The microhabitats shared many of the same pairwise interactions (β = 0.89, Table 3), but their proportion in each microhabitat differs significantly (Figure 10). Consequently, the structure of the set of interactions results in the difference between microhabitats seen in Figure 9.

4.4 Plant-pollinator networks

Connectance was similar between the mesic (C = 0.2929) and xeric (C = 0.244) microhabitats (Table 4), indicating that about 29% and 24% of all possible pairwise interactions were observed in the mesic and xeric microhabitats, respectively.

Interaction strength asymmetry differed between the microhabitats sampled. The negative interaction strength asymmetry in the mesic habitat (ISA = -0.5947, Table 4) indicates that any one interaction between an insect and a flowering plant species accounts for a large proportion of all interactions an insect engages in (Figure 11). Conversely, the positive interaction strength asymmetry of the xeric network indicates that insects interact with a higher number of plant species. Therefore, a single interaction accounts for a small proportion of all interactions of that insect (Figure 11).

Nestedness, calculated as weighted nestedness based on overlap and decreasing fill (WNODF), was similar between mesic ($T = 36.5$) and xeric ($T = 33.4$) habitats. These low values indicate low specialization asymmetry. That is, few specialists interact with generalists in these networks. Therefore, these networks comprise primarily generalists interacting with other generalists (Figure 12).

Linkage density was also similar across microhabitats (Table 4) but relatively low (D_{mesic} = 2.045, D_{xeric} = 2.163), indicating a small number of average links per species in the network. Within the mesic microhabitat, insect visitors had fewer links on average than the flowering species they visited (Figure 11). Conversely, insect visitors have more links than flowering plant species in the xeric microhabitat (Figure 11).

The extinction slope of insects and plants in the mesic sites was similar: 2.645 and 2.516, respectively (Table 4). This similarity indicates that the extinction of species in one level, either an insect taxon or plant species, will result in a larger number of extinctions in the other level in both microhabitats. On the other hand, the extinction slope of the insects (2.125) is lower than the plant species (2.705) in the xeric microhabitat. This difference indicates a greater reliance on the plants by the insects and is visible by the singleton interactions of various plant species in the xeric microhabitat (Figure 11).

Because robustness is calculated as the area under an extinction curve, the pattern observed in the robustness of the insect taxa and flowering plant species follows the pattern of the extinction slopes. Higher slopes, as seen in the insects and plants in the mesic habitat, and in the plants in the xeric habitat, indicate higher robustness. Therefore, the set of interactions between insects and plants results in robust networks from the perspective of the insects (Table 4). However, the robustness of insects is low in the xeric habitat (R = 0.6726, Table 4), indicating the dependency of insects on plants.

Generality is greater for insects in the xeric habitat (1.733) than in the mesic habitat (1.474, Table 4). Here, generality indicates the average number of plant species interacting with any given insect taxon. Figures 11 and 12 show that, indeed, insects interact with a higher number of plant species in the xeric habitat.

Vulnerability indicates the average number of insect taxa that interact with any given plant species. Vulnerability scores are very similar between mesic (2.615) and xeric (2.593) habitats.

Computing modules in both networks show the presence of four major modules or interaction groupings in both the mesic and xeric habitats (Figure 13). Though not identical, some modules in the networks share similar composition. In both microhabitats, there is a module containing Anthomyiidae and Empididae that interact with a *Salix* spp. Syrphidae and Muscidae are likewise found paired in modules in both microhabitat types, albeit the plants associated with the modules differ across microhabitats. Various plant species in the family Fabaceae (such as *A. alpinus*, *H. boreale*, *O. maydellianna*, and *O. arctobia*) are grouped in similar modules containing Apidae.

5. Discussion

The main objectives of my research were to describe the insect pollination community and quantify the plant-pollinator networks in two microhabitats on the Victoria Lowlands of the Canadian Arctic Archipelago. I found little difference in the structural diversity of insect families, plant species, and interactions across mesic and xeric microhabitats (Table 3). However, I did observe significant differences in community composition in the insect families, plant species, and plant-pollinator interactions between the microhabitats (Figures 5, 8, and 9). There were few structural differences in the plant-pollinator networks, but the sets of interactions in both microhabitats were considerably different (Figure 11). Though I detected few structural differences in diversity or the plant-pollinator networks, the compositional differences between microhabitats illustrate the importance of landscape heterogeneity in driving total biodiversity in plant-pollinator networks in the Victoria Lowlands. Therefore, examining species interactions at multiple spatial scales with different approaches and toolsets is necessary to better understand drivers of biodiversity in the Arctic. These conclusions need to be considered when developing conservation policies in the Arctic, and they provide support for the Habitat Heterogeneity Hypothesis. The data presented here also provides a high-quality dataset for monitoring the future change of plant-pollinator networks in the Canadian Arctic Archipelago.

5.1 Effect of habitat heterogeneity

The core of my research focuses on habitat heterogeneity and its impact on insects, plants, and the interactions between them. Analysis of community composition clearly shows that habitat heterogeneity has a strong effect on local biodiversity and, in turn, is an important driver of landscape biodiversity.

The composition of the insect communities in the two microhabitats differed dramatically even though diversity indices did not. Except for Muscidae, the relative abundance of insect groups were very different in the mesic and xeric habitats (Figure 4). Understanding the constituent insect groups' ecological niches and natural history can help explain some of these differences. For example, Arctic bumblebees nest in cavities in the ground, which are not readily available in mesic habitats: crevices between rocks, lemming nests (Richards 1973), and snow bunting nests (Kukal and Pattie 1988). This nesting site preference explains why I observed bumblebees mostly in the xeric sites: the ground was rocky with many sheltered cavities and lots of evidence of lemming burrows (personal observation). Another example of the explanatory power of natural history is the interaction between sawflies and their host plants. Of their many preferred host plant genera, the most abundant in the Arctic is the willow (Hjältén et al. 2003). Therefore, the greater abundance of sawflies in the mesic habitats (Figure 3) is likely due to the greater abundance of willows in the mesic habitat (Figures 6 and 7). These results illustrate how different abiotic and biotic conditions in different microhabitats help shape insect communities in different ways. Therefore, habitat heterogeneity, whether defined by abiotic or biotic conditions, is a critical component that increases regional insect diversity.

As with the insect families, the community composition of plants in the two microhabitats also differed substantially even though both communities have the same number of plant species (Figure 7). The contrast in abiotic conditions, such as substrate drainage and soil structure, can help explain some of these observed differences (Migała et al. 2014). Because of the well-draining substrate and hilly topography, water availability is lowest in the xeric habitat. Therefore, the low water availability can explain why I recorded many more drought-tolerant plants such as *Saxifraga tricuspidata* in the xeric habitats (Teeri 1973). Conversely, the presence of more water in the mesic habitats supports more drought-intolerant plants such as willows (Bliss 1960). Other abiotic factors that differ between microhabitats, such as nutrient availability and soil temperature, also impact the composition of plant communities, but not the structure (Bliss 1960, Billings 1987, Brooker and van der Wal 2003). The lower abundance of conspicuously flowering plants in the mesic habitats can be partly explained by their intolerance of saturated soil and the dominance of sedges (Cyperaceae), which do tolerate saturated soils and are often associated with wetlands (Mishra et al. 2015).

Interaction diversity did not differ across microhabitats (Table 3), but the composition of interactions did vary (Figures 10 and 11). The observed differences in the composition of pairwise interactions are a natural result given the presence and absence of different plant species and flower-visiting insect groups across the microhabitats. That is not to say, however, that the presence of species solely dictates the interactions I observed. As has long been discussed in ecology (Molles and Cahill 2011), abiotic conditions are not the only drivers of diversity and species interactions. Species interactions themselves contribute to the presence and absence of species in a community (Molles and Cahill 2011). For example, plant-pollinator interactions can shape plant community assembly via filtering, facilitation, and competitive exclusion (Sargent and Ackerly 2008).

Similarly, I detected few structural differences in the plant-pollinator networks (Table 4). In particular, both networks were sparse (low connectance: not all possible interactions are realized), nested, and exhibit some bias in interaction strength. These similarities are unsurprising, given that these are characteristic properties of most plant-pollinator networks (Jordano et al. 2002). Previous work also showed that these and other network properties (modularity and centrality) vary little across space and time in plant-pollinator networks in other habitats (Dupont et al. 2009). Therefore, one might hypothesize that multiple species in different habitats fill the same topological roles and that the landscape biodiversity has some redundancy in terms of species functionality (Dupont et al. 2009). Not only are some of these properties invariant across space and time, but the numeric values of the properties are also comparable to other plant-pollinator networks in the Arctic. Olesen and Jordano (2002) summarize geographic patterns of plant-pollinator network structure and show high levels of connectance in Arctic networks, though marginally so after correcting for network size.

The differences observed in the plant, insect, and interaction assemblages (Figures 5, 8, and 9) strongly suggest that habitat and landscape heterogeneity drive the total biodiversity in plant-pollinator networks in the Victoria Lowlands. Though commonly assumed that the Arctic is a homogeneous biome (Payer et al. 2013), the data provided here is an addition to the growing body of literature showing otherwise (e.g. Shaver et al. 1996, Beckerman et al. 1997, Gould and Walker 1999, Jia et al. 2006, Becker et al. 2016). It is well established that Arctic terrestrial arthropod communities vary across space and that landscape heterogeneity drives total biodiversity (Bowden and Buddle 2010a, 2010b, Rich et al. 2013, Hansen et al. 2016). The same is true of plants (Gould and Walker 1999, Becker et al. 2016). In turn, this biodiversity pattern within the Arctic is congruent with the long-accepted Habitat Heterogeneity Hypothesis stating that species diversity increases with increasing habitat heterogeneity (MacArthur and MacArthur 1961).

I also explored the impacts of habitat heterogeneity on insects, plants, and their interactions using various diversity metrics at different spatial scales. Diversity metrics, such as absolute richness and Shannon's diversity, did not differ between microhabitats but showed some differentiation from the landscape (Table 3). Arctic climatic conditions are very harsh and have powerful limiting effects on species diversity than other abiotic factors. Though the microclimate differs slightly between microhabitats (e.g. the xeric sites are slightly warmer), this variation is minimal and has a limited influence on species richness variation (Tedrow and Cantlon 1958). The limited heat budget in the Arctic is another constraint on species diversity that does not differ between microhabitats as it is a consequence of the amount of solar radiation input. Therefore, abiotic conditions such as cold temperatures, strong winds, little precipitation, and little solar radiation input, limit diversity across the landscape equally among different microhabitats (Billings and Mooney 1968). As Arctic climates continue to change (e.g. higher temperatures, increased precipitation), conditions across the tundra (at the scale of dozens of kilometres) will change uniformly. Therefore, the constraints on species diversity in both microhabitats will diminish equally.

The importance of habitat heterogeneity in driving landscape diversity illustrates the need to take constituent species and pairwise interactions into account when evaluating diversity and interaction networks. Ecologists have long searched for simple indices to describe species assemblages and interactions. However, some of these alpha diversity and network property indices lack nuance and are unable to show differences across space, time, or abiotic gradients (Jordano et al. 2002, Dupont et al. 2009), as is the case with the data presented here.

This discussion of plant-pollinator networks can be expanded to highlight the need to study similar mutualistic plant-animal interactions and networks in different habitats within a single biome and across zoogeographic scales. Little work on Arctic plant-pollinator networks has been done outside of Ellesmere Island, Nunavut, or the Zackenberg Valley, Greenland. Replicative work in other locations is necessary to provide support for broader conclusions and illustrate that some ecological patterns are consistently observed across larger scales. For example, this work supports the conclusion that Muscid flies are essential pollinators in the Arctic (Tiusanen et al. 2016), that Arctic plant-pollinator networks are particularly highly connected compared to such networks in lower latitudes (Olesen and Jordano 2002a), and that Arctic plant-pollinator networks have the same characteristic structural properties as such networks elsewhere in the world (Jordano et al. 2002). Given the importance of mutualistic interactions in maintaining ecosystems, future studies into networks between seed dispersers, plant defenders, and plants should look for similar patterns as highlighted here.

5.2 Muscid pollination

The results presented here clearly show that muscid flies (order Diptera, family Muscidae) are the dominant group of flower-visiting insects in both xeric and mesic microhabitats (Figure 3). Other research across the Arctic has also presented the same result indicating that muscid flies are the most important pollinators in Arctic ecosystems (Kevan 1972a, Totland 1993, Elberling and Olesen 1999, Larson et al. 2001, Tiusanen et al. 2016). In this study, the most commonly observed families of flies were: Muscidae, Syrphidae, Anthomyiidae, and Empididae. These fly families were also prominent in results reported in Elberling and Olesen (1999), Lundgren and Olesen (2005), and (Tiusanen et al. 2016), among others. This dominance of flies presented here provides further support to recent assertions that non-syrphid flies are essential providers of pollination services other than bees, butterflies, and syrphid flies (Orford et al. 2015).

5.3 Monitoring arthropod communities

The Arctic is changing faster than anywhere else in the world (ACIA 2005a), and this change is profoundly impacting Arctic ecosystems: mean annual snow cover is expected to drop up to 18% in the present century (ACIA 2005b), about half the permafrost in Canada could disappear (Smith and Burgess 2004), plant species endemic to the Canadian Arctic would see their ecological niches shrink (ACIA 2005c), and at least 11% of Arctic tundra could be replaced by boreal forest (Harding et al. 2002, Skre et al. 2002). These changes will significantly disrupt species interactions, particularly plant-pollinator interactions (Høye et al. 2013, Schmidt et al.

2016). Though this disruption may lead to the extirpation of individual species, particularly those with a small ecological niche, habitat heterogeneity may help maintain species diversity. Habitat heterogeneity has already been shown to buffer against some of the impacts of climate change (Ackerly et al. 2010, Elmendorf et al. 2012). Additionally, interactions between disruptive impacts of climate change are expected to increase habitat heterogeneity (Raynolds et al. 2014). It remains to be seen, though, if the net change in Arctic biodiversity will be positive or negative.

Though monitoring of future change will include measurements of abiotic conditions and perhaps plant communities, there is an urgent call to also monitor for terrestrial arthropods (Danks 1992, Kim 1993, Hodkinson and Jackson 2005, Timms et al. 2013a, Gillespie et al. 2020). Terrestrial arthropods form the majority of Arctic biodiversity, which makes them a key group to monitor. Such monitoring requires baseline datasets to compare to, that encompass more than species presence or community composition. Species interactions themselves are subject to environmental stresses which need to be monitored. Cirtwill et al. (2018) have already shown a high between-year variation of species roles in a plant-pollinator network in Zackenberg Valley, Greenland, and that this variation increases with species turnover. Their results imply that increased turnover in the future will result in more network rewiring and destabilization. The data presented here provide a snapshot of a plant-pollinator network in the Canadian Arctic that can be monitored across time for rewiring as predicted by Cirtwill et al. (2018).

Monitoring for future change will require high-quality data of pairwise interactions between insects and plants. Some authors stress the need for species-level identifications (Nahmani et al. 2006, Grimbacher et al. 2008). Such high-resolution data would indeed provide insights into species-level changes. However, as the data presented here illustrates, plant-pollinator networks in the Arctic are easily distinguished between microhabitats, even with insects identified to the family level (Figure 5). Therefore, the results of this work (using the diversity indices along with community composition analyses) supports the conclusions of many authors (e.g. Pik et al. 1999, Caruso and Migliorini 2006, Timms et al. 2013b) that monitoring of terrestrial arthropods for disturbance or change can be accomplished with low taxonomic resolution. This conclusion does not negate the need for species-level identifications for reaching more nuanced conclusions. Additionally, higher taxonomic resolution can provide a stronger significance of differences across space, time, or experimental treatments (Timms et al. 2013b).

The methods used to collect data on plant-pollinator interactions have a significant impact on the quality of data. Gibson et al. (2011) evaluated the inherent biases in different pollination sampling methods, namely using transects or timed observations. Each method is appropriate in different circumstances and for answering different questions. The authors conclude that timed observations (which were performed in this work) are more appropriate for research in patchy or heterogeneous environments. Timed observations were shown to detect a broader diversity of species and interactions, and when coupled with floral surveys (which were also performed in this work), provide more 'realistic' descriptions of plant-pollinator networks.

Monitoring for future change will also require that data be securely stored and available to future researchers. Hampton et al. (2013) highlight the value in making the vast quantities of ecological data easily accessible. Not only does it permit replication and comparative studies, but doing so also opens up avenues to explore big questions and to address major scientific problems. To ensure the data presented here is available for future studies, I will deposit it in the Data Dryad repository (https://datadryad.org/). Doing so will provide future researchers more data to monitor Arctic terrestrial arthropods, as called for by many authors (Danks 1992, Kim 1993, Hodkinson and Jackson 2005, Timms et al. 2013a, Gillespie et al. 2020).

Data in the form of voucher specimens are equally valuable as spreadsheets and databases. Depositing voucher specimens in long-term secure collections such as museums permits the verification of identifications (Martin 1990), is essential for repeatability in science (Knutson 1984) and allows researchers to verify the impacts of climate change on ecological communities (Dubois 2010). Turney et al. (2015) summarize many of the challenges in collecting and depositing voucher specimens and conclude that, by 2014, only 35% of papers reported depositing vouchers. To safeguard the value of the data that will be deposited in the

Data Dryad repository, I will also deposit voucher specimens of both insects and plants into the Lyman Entomological Museum and the McGill University Herbarium, respectively.

Monitoring for future change requires more complex analysis of the data than simply monitoring for species loss or introduction. The network properties highlighted here are important tools used for predicting and detecting future change. The greater levels of connectance (Figure 11) indicate that Arctic plant-pollinator networks may be more robust to disturbance as suggested by Thebault and Fontaine (2010). However, the presence of many modules (Figure 13) may result in outsized impacts on certain species, especially those at the periphery of individual modules (Tylianakis et al. 2010, Elle et al. 2012). Collecting plant-pollinator network data and tracking the network properties across time can provide evidence for these hypotheses. The use of these tools in conservation is not new, however. Cumming et al. (2010) highlighted the need for network analysis and metrics in conservation. For example, they ask what impact the creation of habitat corridors will have on ecological networks, or how will direct intervention impact disease transmission within an ecological network. The authors argue that these questions are best answered using both ecological and social network analysis, then using classic network properties to monitor ecological communities. Evaluating ecological networks with these metrics also provides a window into the impacts of conservation outside of protected areas, particularly regarding networks of terrestrial arthropods (Pryke and Samways 2012).

6. Thesis summary and conclusion

This research's principal objective was to describe Arctic plant-pollinator networks in terms of taxonomic diversity, community composition, interaction diversity, and network structure. The key questions of my research were:

- Which flower-visiting insect families interact which conspicuously flowering plant species?
- How do the diversities of flower-visiting insect families, plant species, and interactions differ across different microhabitats?
- How do the structural properties of plant-pollinator networks in different microhabitats differ from each other?

I sampled plant-pollinator networks in two microhabitats in the Victoria Lowlands of the Canadian Arctic Archipelago: a drier, xeric microhabitat with a well-draining substrate and a wetter, mesic microhabitat with a poorly-draining substrate. I observed 65 unique pairwise interactions between 15 insect families and 17 species of flowering plants. Diversity indices did not differ between microhabitats, but pollinator diversity is more evenly distributed in xeric microhabitats. The plant and pollinator communities were very compositionally different but did not differ structurally. The pairwise interactions in the plant-pollinator networks were also very different across the microhabitats, but the structure of the networks differed only marginally.

The results presented here illustrate the importance of habitat heterogeneity in driving landscape diversity and plant-pollinator network diversity – a finding of importance for Canada and other northern countries. The data also confirm previously recorded patterns in Arctic pollination systems, namely that: (1) muscid flies are the dominant pollinators in the Arctic, (2) that Arctic plant-pollinator networks possess the same structural characteristics of plant-pollinator networks elsewhere in the world, and (3) that Arctic plant-pollinator networks are highly connected. Confirmation of patterns in entirely different Arctic regions is important for progress in science for many reasons: (1) it validates the applicability of broad ecological theories in extreme climatic conditions, (2) it validates many assumptions about Arctic ecosystems based on alpine research, and (3) it validates the applicability of Arctic research for understanding future impacts of other ecosystems that are experiencing climate change more slowly.

The work presented here is not an exhaustive analysis of the data collected, and there is ample opportunity for future work with this data. Though exceptionally difficult, there is value in identifying the insect specimens to species and building more complex plant-pollinator network models. Doing so would shed further light on the level of taxonomic resolution needed to detect changes in plant-pollinator networks sufficiently. Hypotheses related to network stability in the face of species extinction or species invasion can be better tested using such complex networks.

The conclusions presented here have important implications for monitoring future change and developing conservation efforts in the Canadian Arctic Archipelago. This work provides a baseline dataset for monitoring changes in plant-pollinator networks in the Canadian Arctic as climate change continues to apply abiotic pressures on Arctic ecosystems. Combining the data presented here with natural history studies will enable us to hypothesize how Arctic plant-pollinator networks will respond to increased warming and then test those hypotheses. These data, the patterns that have emerged from them, and the hypotheses that can be elaborated from them can also inform Arctic conservation policy. In particular, the results presented here highlight the need to take the importance of landscape heterogeneity into account when developing conservation plans.

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8. Figures

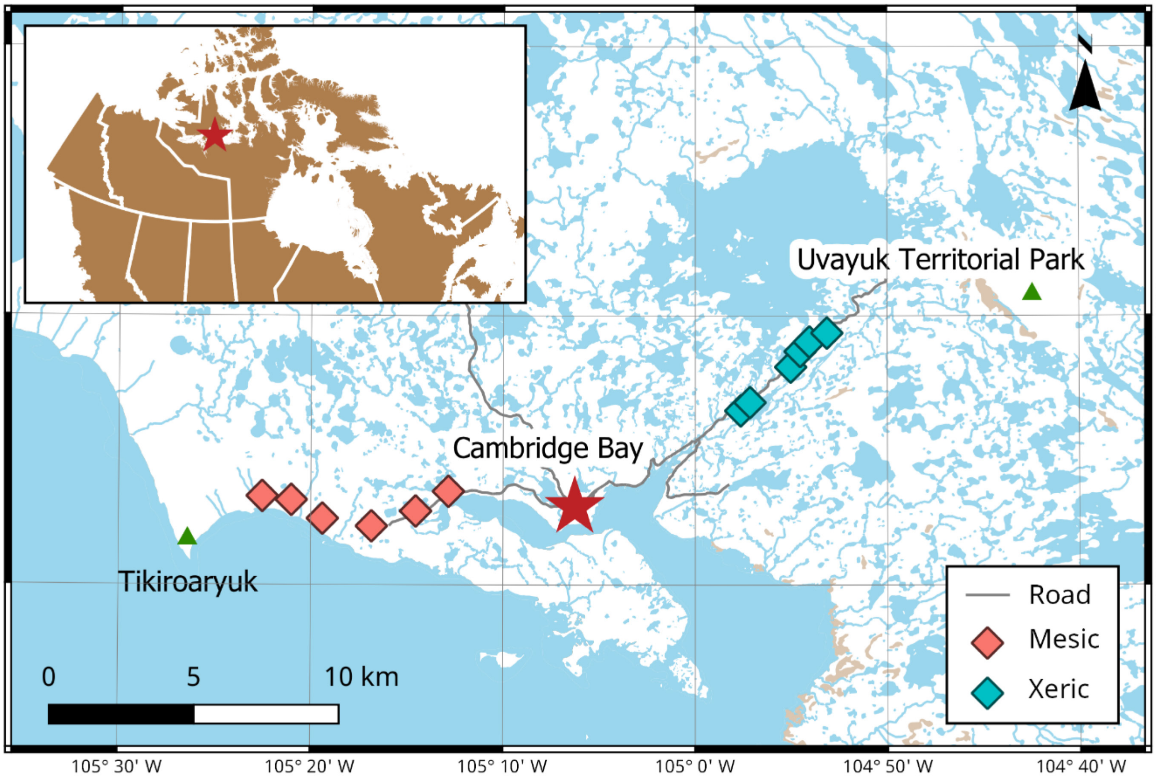

Figure 1: Location of mesic (pink diamonds) and xeric (blue diamonds) research sites in the region around the community of Cambridge Bay, Nunavut (69°07'06.5"N 105°03'18.8"W, red star). Xeric sites are located along the road between Cambridge Bay and Uvayuk (formally Mount Pelly, 69°10'15.2"N 104°42'32.3"W). Mesic sites are located along the road between Cambridge Bay and Tikiroaryuk (formally Long Point beach, 69°05'41.9"N 105°26'31.4"W).

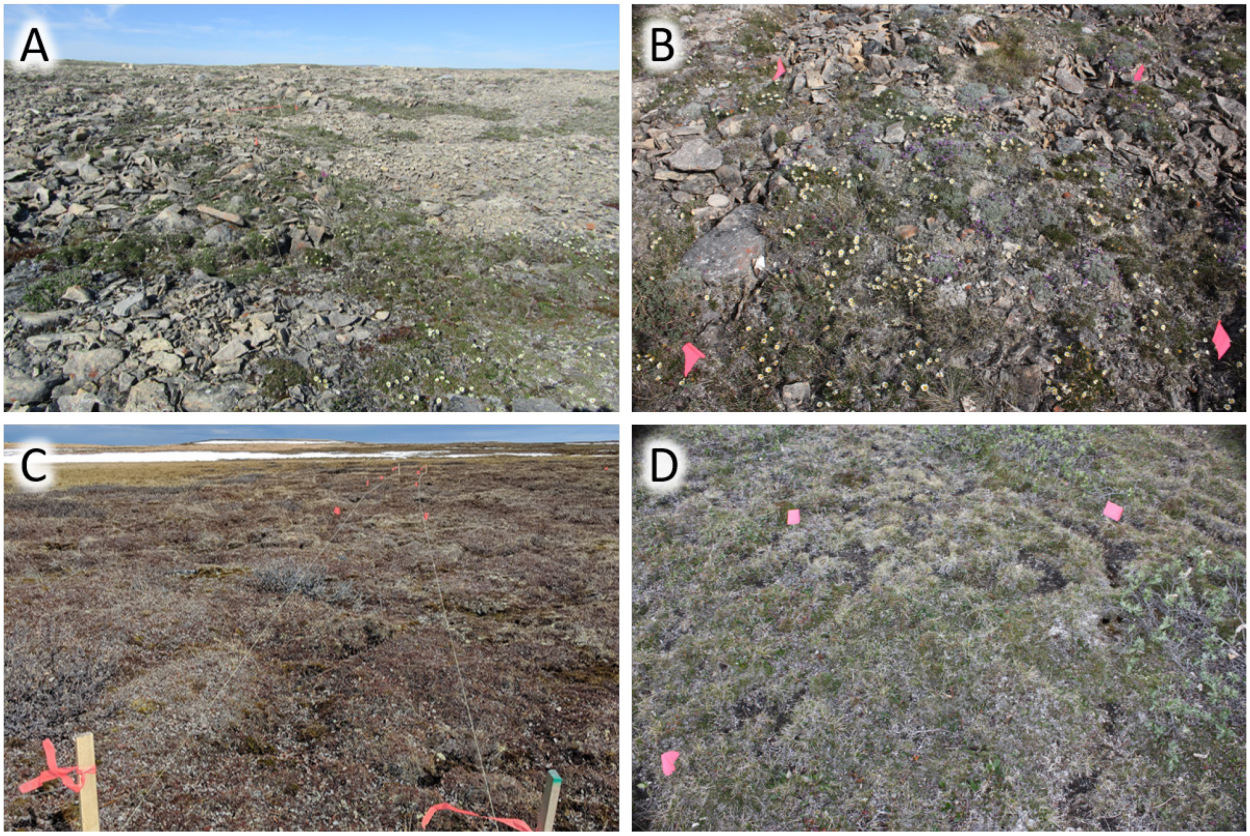

Figure 2: Representative photographs of dry, rocky, xeric microhabitat with a well-draining substrate (panel A) and wet, soil containing mesic microhabitat with a poorly-draining substrate (panel C). The flora of the xeric sites was dominated by Prickly Saxifrage (*Saxifraga tricuspidata* Rothb.) atop the hills, Mountain Avens (*Dryas integrifolia* Vahl.) on the slopes, and willow bushes (*Salix* spp. L.) and sedges (Cyperaceae) at the base of the hills (panel B). Cyperaceae dominated the flora of the mesic with patches of willow bushes and scattered *D. integrifolia* (panel D).

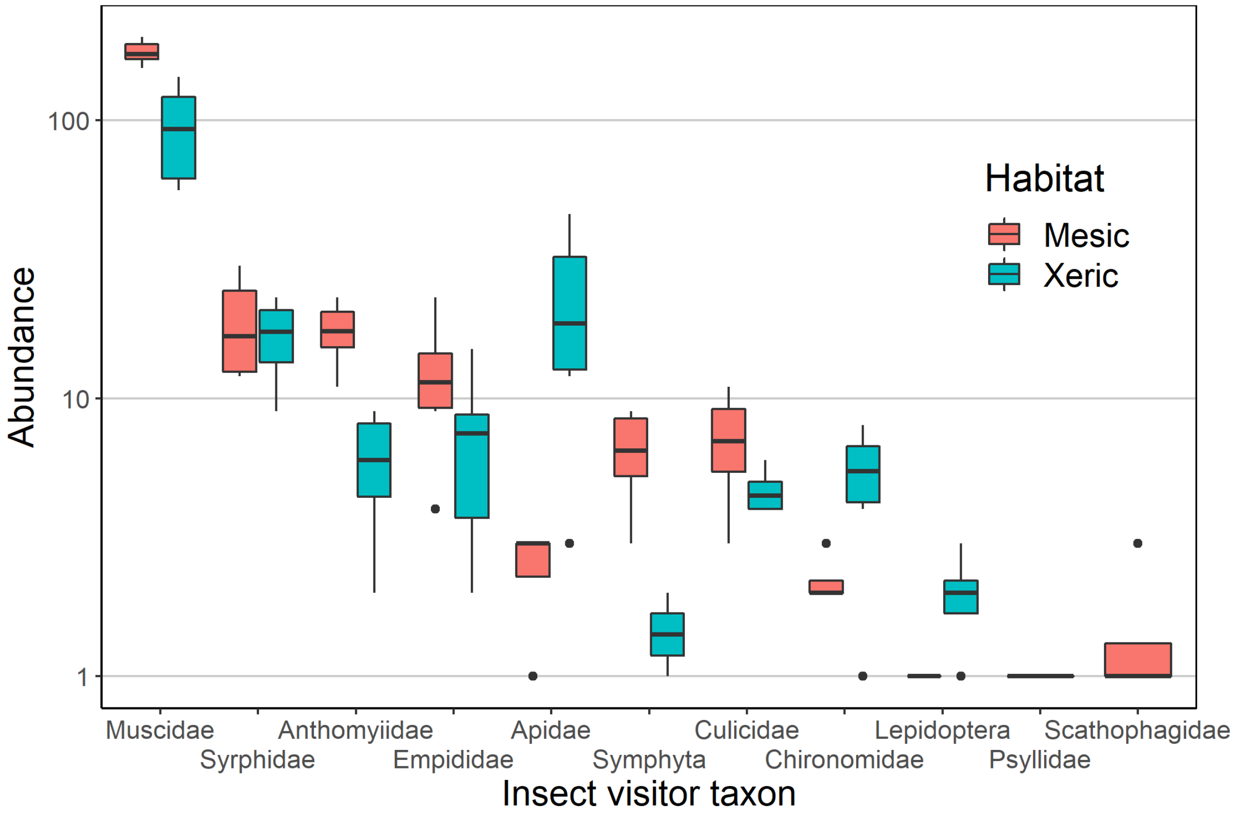

Figure 3: Abundance of insect taxa observed unambiguously interacting with the reproductive structures of conspicuously flowering plant species in mesic (pink) and xeric (blue) microhabitats. Data were pooled across all sampling periods. n = 6. Boxplot centerline indicates median values, box upper and lower bounds indicate first and third quartile, whiskers indicate values withing 1.5 x interquartile range, and points indicate values beyond 1.5 x interquartile range.

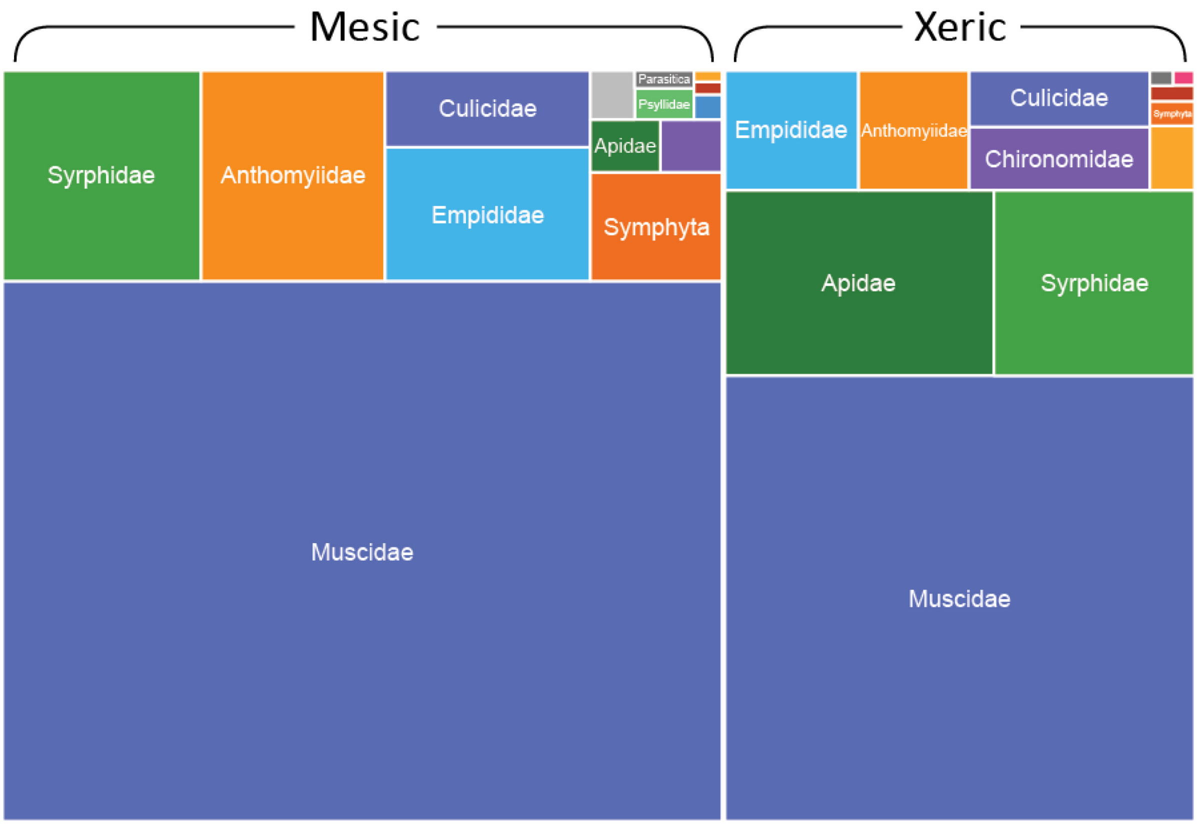

Figure 4: Relative proportion of insect taxa observed unambiguously interacting with the reproductive structures of conspicuously flowering plant species in mesic and xeric microhabitats. Data per insect taxon were pooled across all sampling periods and averaged across sites (n = 6). The area of boxes represents the relative proportion of the log10 transformed number of observations.

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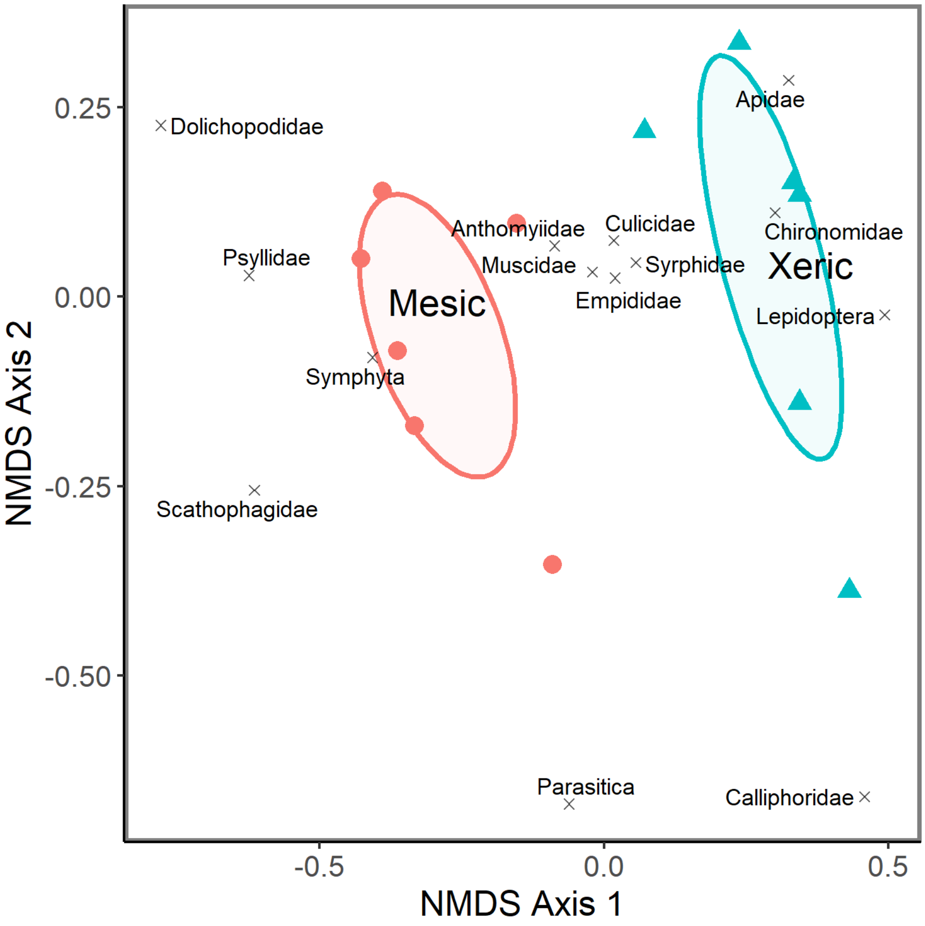


Figure 5: Non-metric multidimensional scaling (NMDS) of insect taxa observed interacting with flowering plants in mesic (pink) and xeric (blue) microhabitats. Solid circles and triangles represent mesic and xeric sites, respectively. Points closer to each other are more similar in community composition than points farther apart. Crosses denote the location of insect taxa within the multidimensional space of the insect community. Ovals represent the 95% confidence intervals from the centroid of each microhabitat.

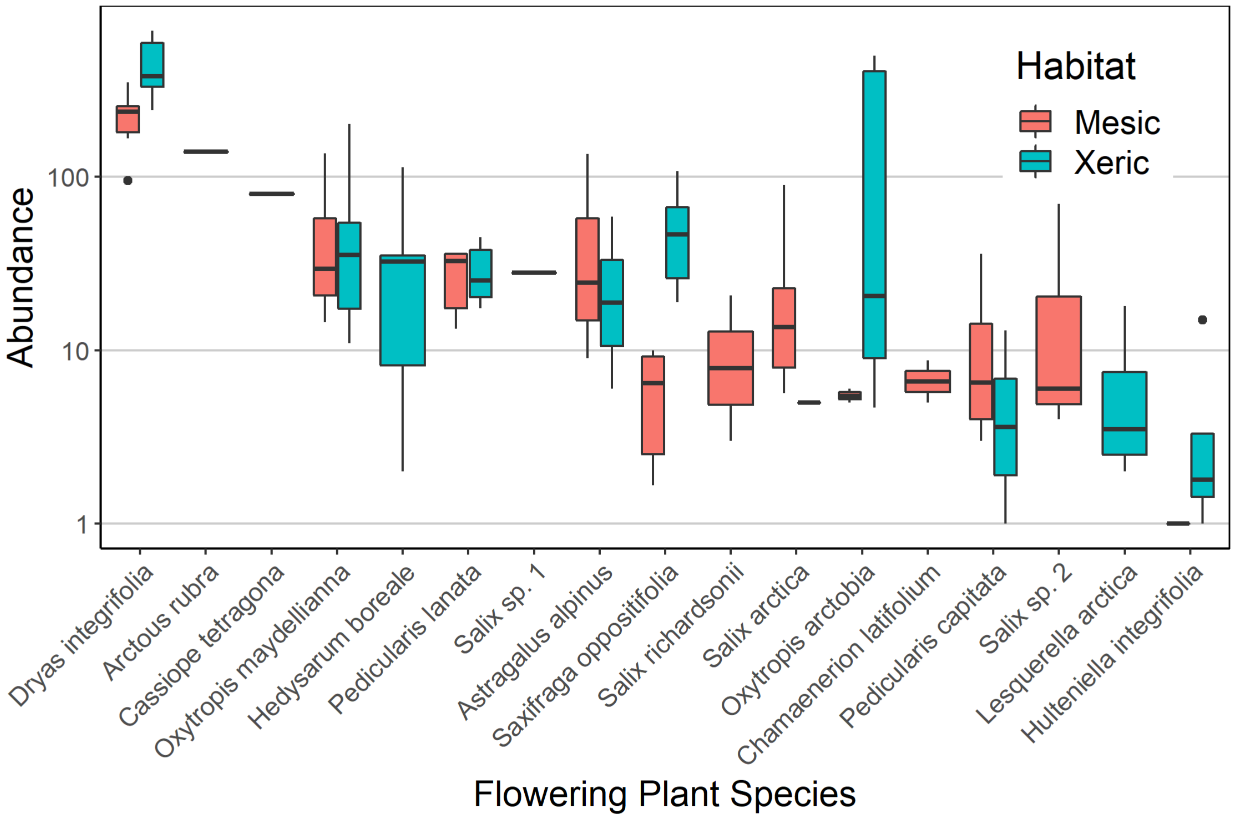


Figure 6: Abundance of conspicuously flowering plant species in mesic (pink) and xeric (blue) microhabitats. Data per flowering species were pooled across all sampling periods. n = 6. Boxplot centerline indicates median values, box upper and lower bounds indicate first and third quartile, whiskers indicate values withing 1.5 x interquartile range, and points indicate values beyond 1.5 x interquartile range.

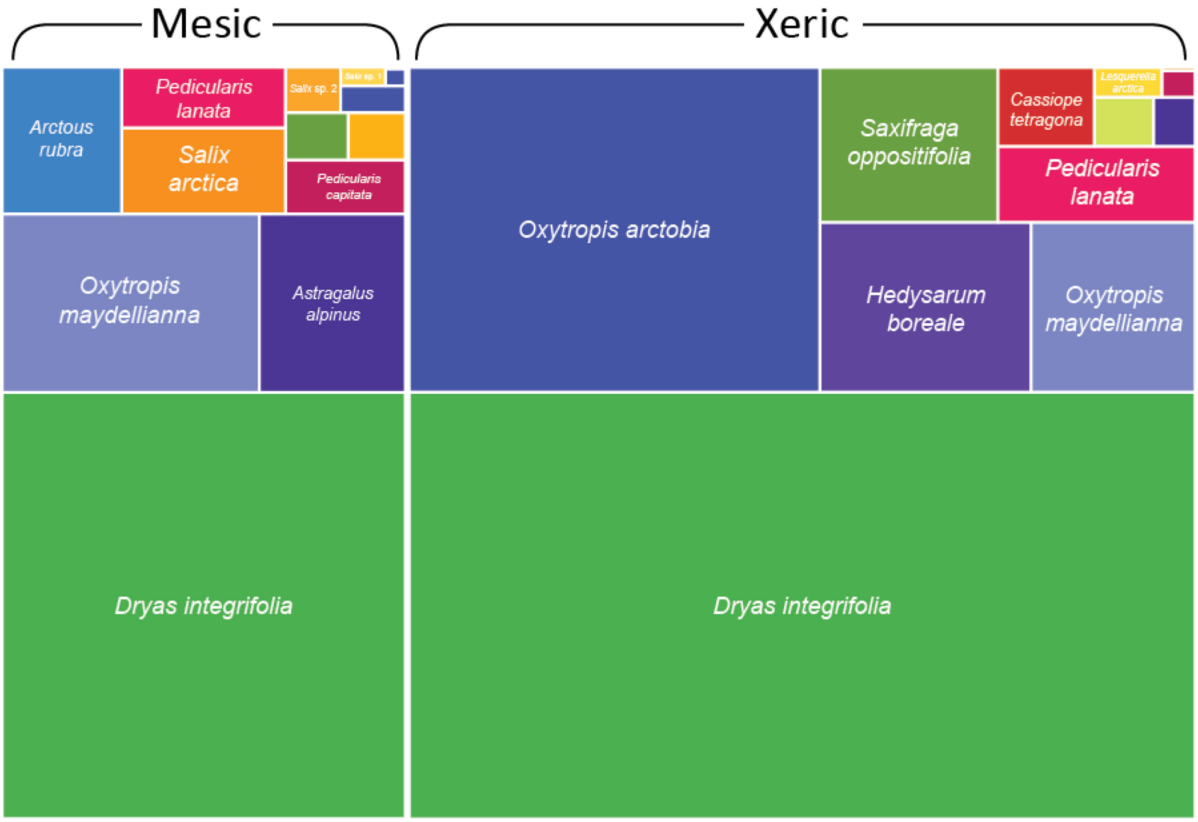


Figure 7: Relative proportion of conspicuously flowering plant species in mesic and xeric microhabitats. Data per plant species were pooled across all sampling periods and averaged across sites (n = 6). The area of boxes represents the relative proportion of the log10 transformed number of observations.

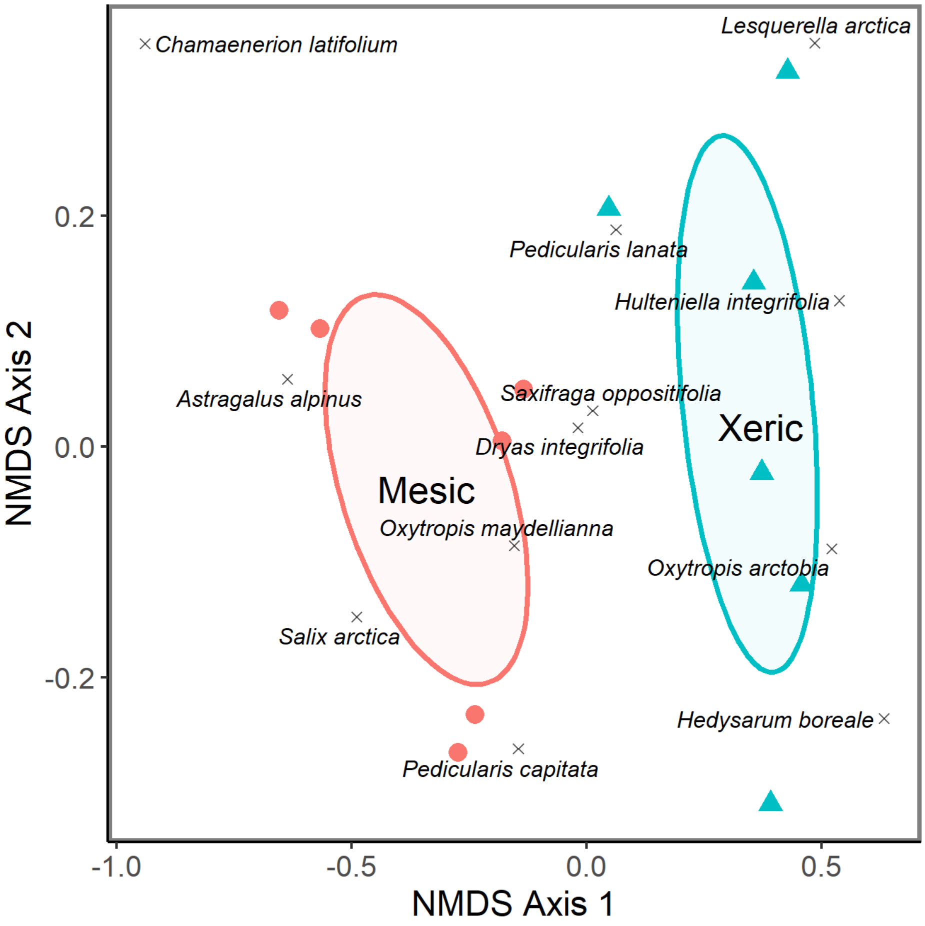


Figure 8: Non-metric multidimensional scaling (NMDS) of flowering plant species across all in mesic (pink) and xeric (blue) habitats. Solid circles and triangles represent mesic and xeric sites, respectively. Points closer to each other are more similar in community composition than points farther apart. Crosses denote the location of the ten most abundant plant species within the multidimensional space of the insect community. Ovals represent the 95% confidence intervals from the centroid of each microhabitat.

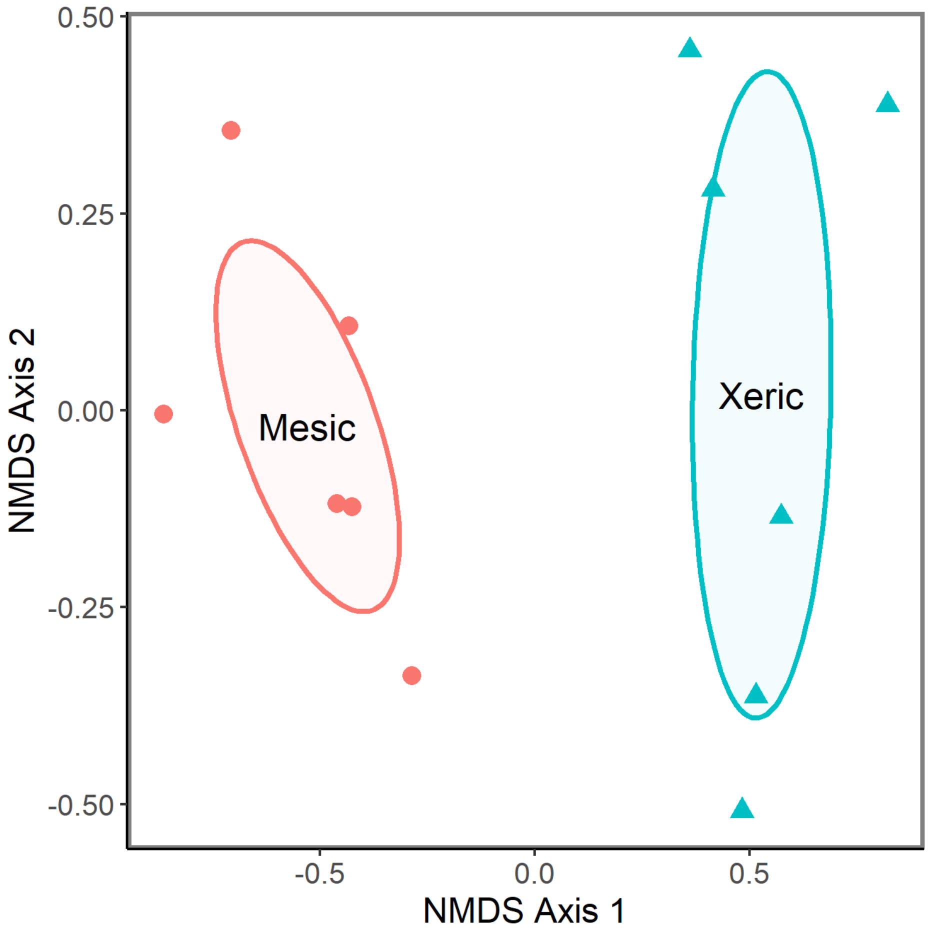


Figure 9: Non-metric multidimensional scaling (NMDS) of interactions between insect taxa and conspicuously flowering plant species across in mesic (pink) and xeric (blue) habitats. Solid circles and triangles represent mesic and xeric sites, respectively. Points closer to each other are more similar in community composition than points farther apart. Ovals represent the 95% confidence intervals from the centroid of each microhabitat.

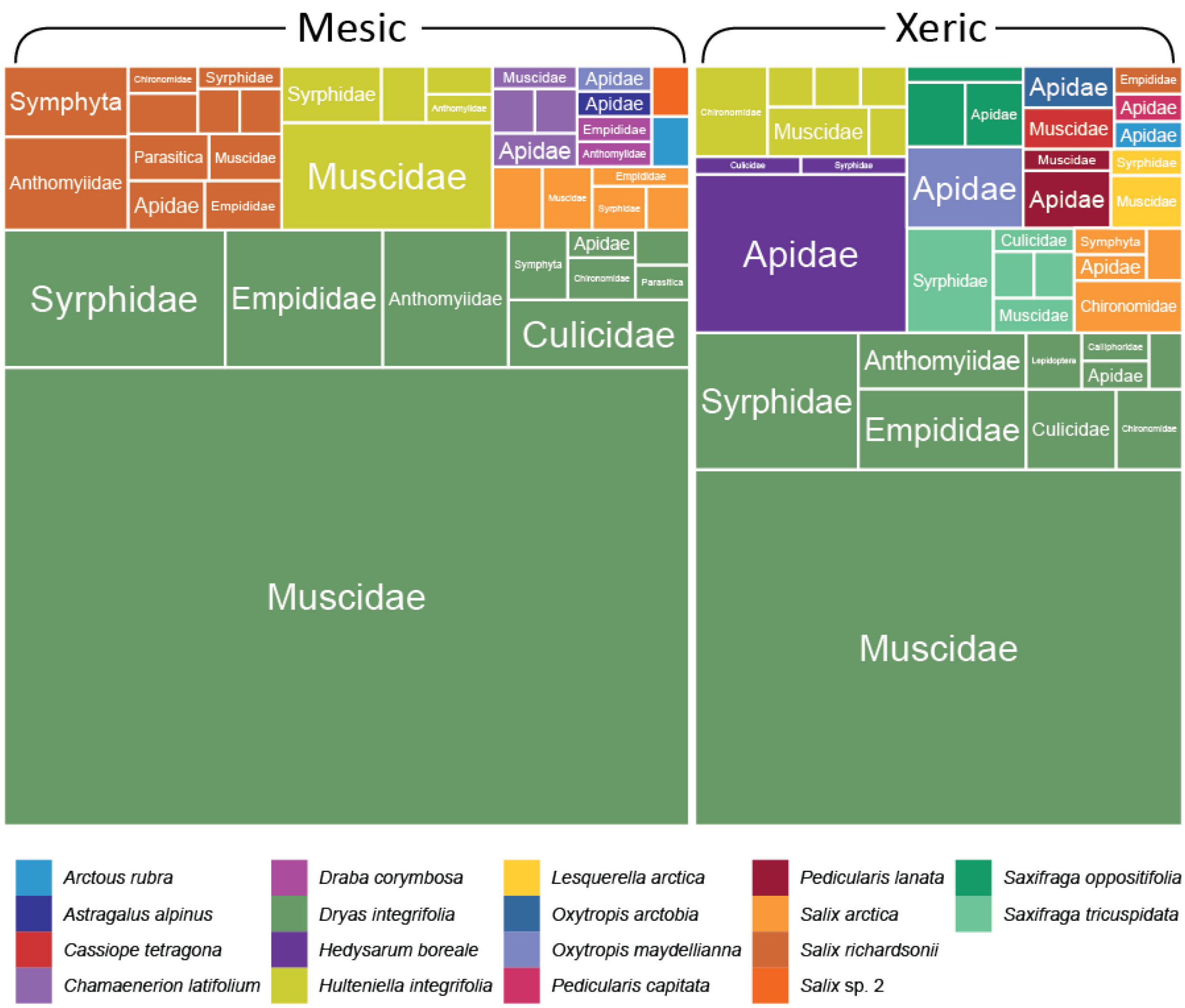


Figure 10: Relative proportion of interactions between insect taxa and conspicuously flowering plant species in mesic and xeric microhabitats. Data were pooled across all sampling periods and averaged across sites (n = 6). Boxes of the same colour denote the same species of plant but are broken down by visiting insect taxon. The area of boxes represents the relative proportion of the log10 transformed number of observations.

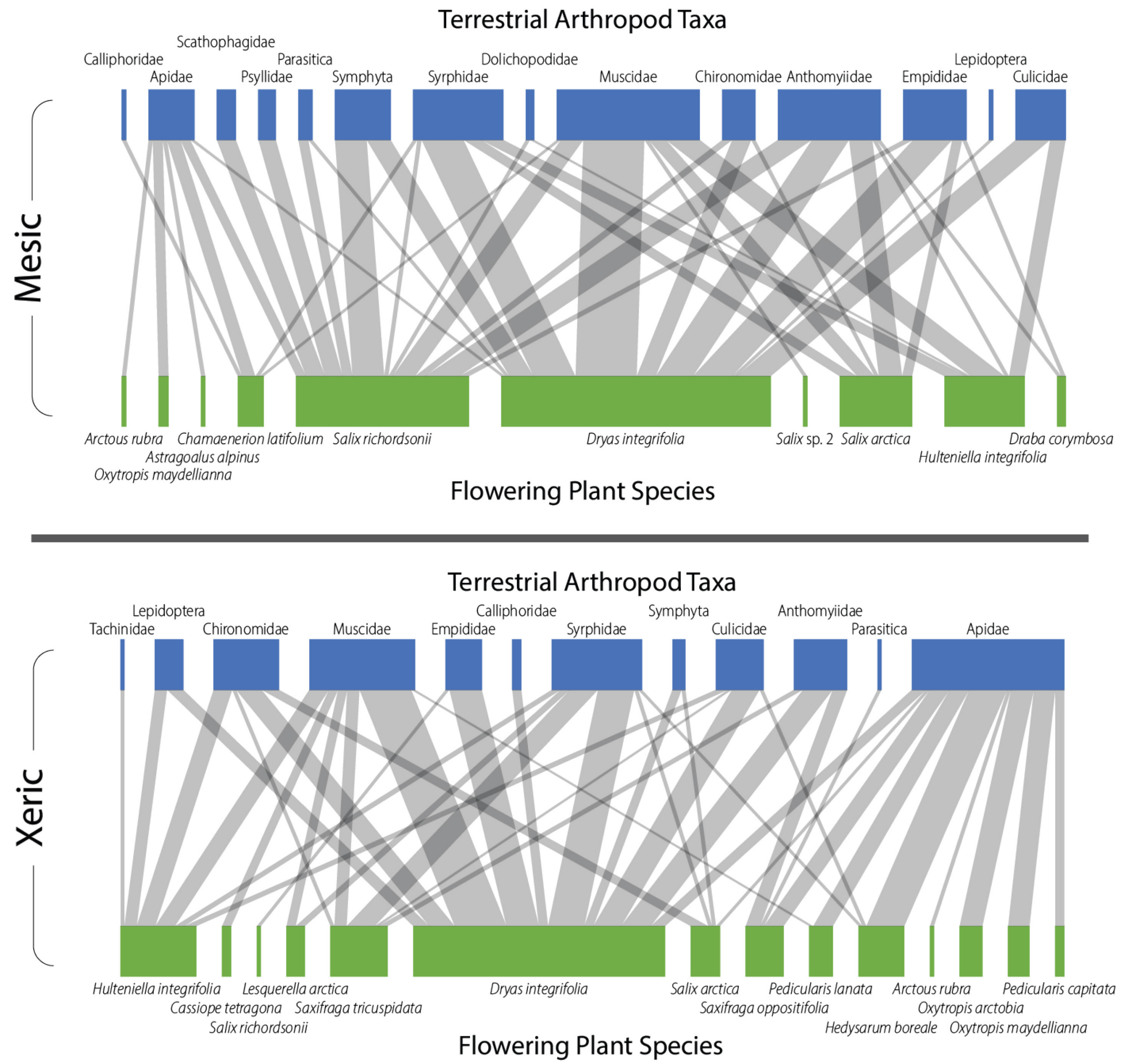


Figure 11: Interaction network structure between various insect taxa (blue, top) and flowering plant species (green, bottom) in mesic (top panel) and xeric (bottom panel) microhabitats. Width of bars for insects and plants correspond to the total number of observations recorded for each insect taxon or plant species. Width of gray trapezoids represents the number of recorded interactions between a plant species and insect taxon. Data are presented as the log10 transformed average number of each pairwise interaction across six sites.

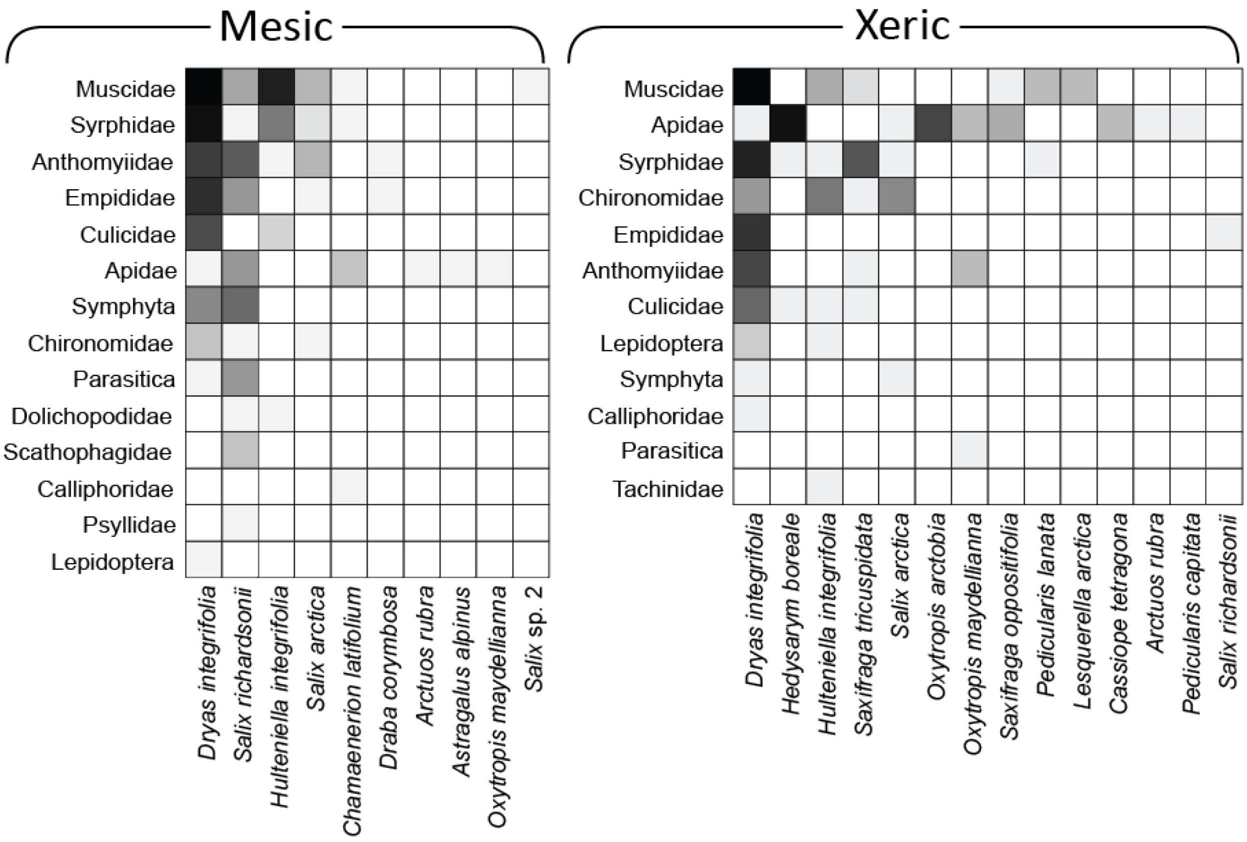


Figure 12: Adjacency matrix of interactions between insect taxa (rows) and conspicuously flowering plant species (columns) in mesic (left) and xeric (right) microhabitats. The intensity of the black cells corresponds to the log10 transformed number of each pairwise interaction averaged across six sites. Darker cells denoted a higher number of interactions, and lighter cells denote fewer interactions.

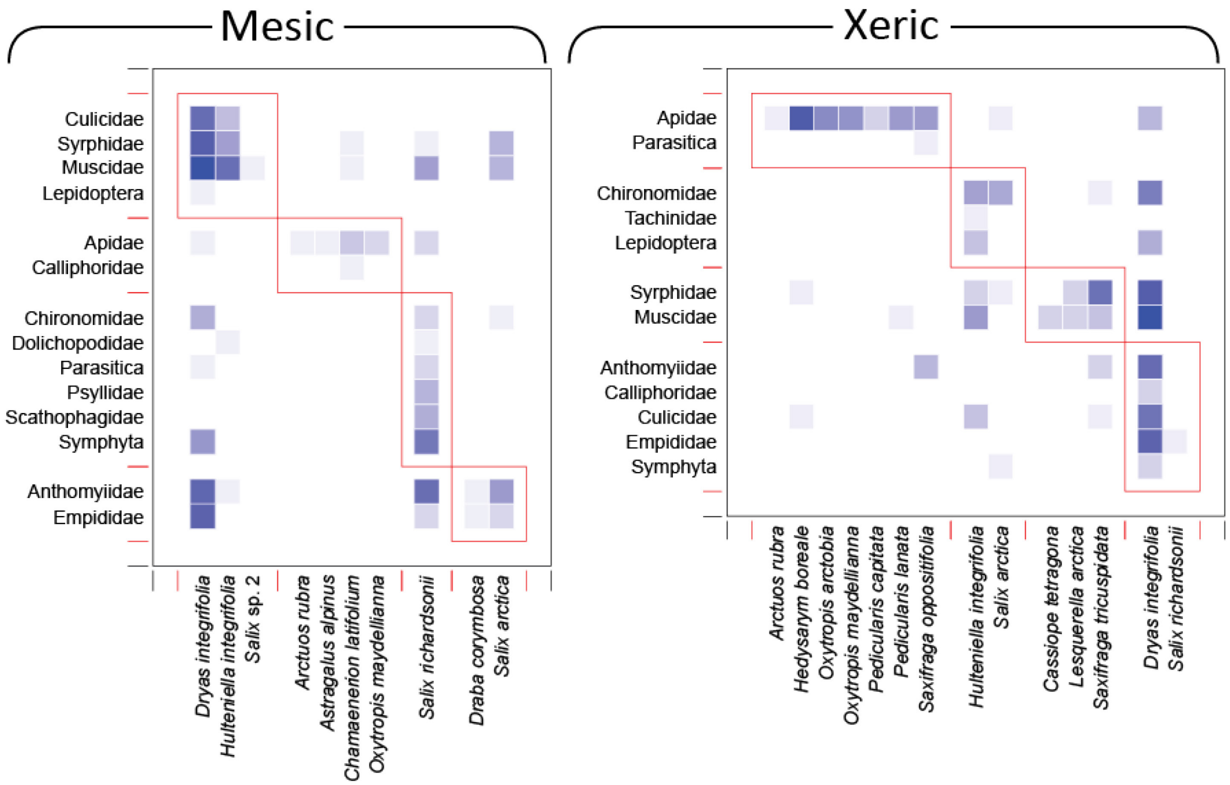


Figure 13: Adjacency matrix of interactions between insect taxa (rows) and conspicuously flowering plant species (columns) in mesic (left) and xeric (right) microhabitats with highlighted modules calculated using the algorithm in Beckett (2016) outlined in red. The intensity of coloured cells corresponds to the log10 transformed number of each pairwise interaction averaged across six sites of each microhabitat. Darker cells denote a higher number of interactions, and lighter cells denote fewer interactions.

9. Tables

Table 1: Location and topographic characteristics of mesic and xeric sites selected for this research.

ID	Habitat type	Location (decimal degrees)	Altitude (m above sea level)	Aspect	Distance from the road (m)
X01	Xeric	69.137° N 104.961° W	16	SE	220
X02	Xeric	69.14° N 104.953° W	13	E	77
X03	Xeric	69.151° N 104.917° W	18	E	54
X04	Xeric	69.156° N 104.909° W	18	S	93
X05	Xeric	69.159° N 104.901° W	14	SW	30
X06	Xeric	69.161° N 104.886° W	16	SW	119
M01	Mesic	69.112° N 105.214° W	28	N/A	148
M02	Mesic	69.106° N 105.242° W	27	N/A	132
M03	Mesic	69.102° N 105.281° W	23	N/A	276
M04	Mesic	69.104° N 105.323° W	13	N/A	251
M05	Mesic	69.11° N 105.35° W	13	N/A	335
M06	Mesic	69.111° N 105.375° W	9	N/A	146

Table 2: Sampling schedule for each site (rows) from 22 June 2018 when first open flowers began to appear on the landscape, to 10 August 2018, when there were no more conspicuous open flowers in the plant transects. The summer was divided into ten sampling periods (denoted by differently coloured columns), each five or six days long, except for the last period, which lasted three days. Within each sampling period, I visited each site twice within the same day. When inclement weather prevented two visits in a day, I visited a site only once and again the next day. Sampling was not performed when the temperature was below 4 °C, the wind was greater than 30 km/h, or if there was heavy rain or snow. X denotes I measured floral abundance and performed two interaction samples. A denotes I measured floral abundance and performed a single interaction sample in the morning. B denotes I measured floral abundance and performed a single interaction sample in the afternoon. P denotes I only measured floral abundance.

	June									July																															August									
Day	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10
X01					X						X				X				X			X						X						X						X				P				P		
X02					X						X				X				X			X						X						X						A				P				P		
X03	X					X						X				X						X						X						X					X					P				P		
X04	X					X						X				X						X					X						A	B					X					P				P		
X05	X					X					X					X					X						X						X						X					P				P		
X06	X					X					X					X					X						X						X						X					A	B			P		
M01					X					X				X					X						A	B						X			X					X					X				P	
M02					X					X				X					X						A	B						X			X					X					X				P	
M03		X								X				X				X						X								X			X					X					X				P	
M04		X								X				X				X						X								X				A						X				X			P	
M05		X						X				A	B					X						X								X				A						A				X			P	
M06		X						X				A	B					X						X								X				A						X				X			P	
	1					2						3				4					5						6						7					8					9					10		

Period

Table 3: Alpha, beta, and gamma diversity indices of insect taxa, flowering plant species, and pairwise interactions between insects and plants for mesic and xeric microhabitats and the regional landscape. Alpha diversity indices were calculated as the mean number of observations across six sites and compared with unpaired Student's t-test. Means are presented with 95% confidence intervals in square brackets. Indices in bold indicated statistically significant differences (α = 0.05).

	Alpha diversity			**Gamma diversity**			**Beta diversity**		
	Mesic	**Xeric**	**t-test**	**Mesic**	**Xeric**	**Landscape**	**Mesic**	**Xeric**	**Landscape**
Terrestrial Arthropods									
Number of Families	9.833 [8.606, 11.060]	8.667 [7.087, 10.247]	*t* = 1.5, df = 9.4, *p* = 0.2	14	12	15			
Shannon diversity index (*H*)	1.084 [1.007, 1.161]	1.343 [1.076, 1.611]	*t* = -2.4, df = 5.8, *p* = 0.06	1.11	1.39	1.28	1.03	1.04	0.9
Shannon's equitability (E_H)	**0.476** **[0.448, 0.504]**	**0.631** **[0.483, 0.780]**	***t* = -2.6, df = 5.4,** ***p* = 0.04**	0.42	0.56	0.47			
Flowering Plants									
Number of species	8.17 [6.77, 9.56]	8 [5.61, 10.39]	*t* = 0.15, df = 8.05, *p* = 0.88	14	12	17			
Shannon diversity index (*H*)	1.99 [1.85, 2.12]	1.96 [1.70, 2.22]	*t* = 0.20, df = 7.52, *p* = 0.85	2.33	2.25	2.53	1.41	1.33	0.78
Shannon's equitability (E_H)	0.95 [0.93, 0.98	0.96 [0.94, 0.98]	*t* = -0.78, df = 8.89, *p* = 0.46	0.88	0.91	0.89			
Interactions									
Number of unique interactions	19 [16.26, 21.74]	18.5 [15.87, 21.13]	*t* = 0.34, df = 9.99, *p* = 0.74	41	41	65			
Shannon diversity index (*H*)	1.37 [1.17, 1.57]	1.70 [1.31, 2.01]	*t* = -1.91, df = 7.39, *p* = 0.10	1.46	1.84	1.72	1.1	1.15	0.89
Shannon's equitability (E_H)	0.47 [0.41, 0.52]	0.58 [0.46, 0.70]	*t* = -2.24, df = 7.20, *p* = 0.06	0.39	0.49	0.41			

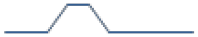
Table 4: Structural properties of plant-pollinator networks in mesic and xeric microhabitats. The two-mode networks for each microhabitat were modelled and analyzed using the *bipartite* package (Dormann et al. 2008). Network scale properties (connectance, interaction strength asymmetry, weighted nestedness based on overlap and decreasing fill (WNODF), and linkage density) were calculated using the *networklevel* function in the *bipartite* package. Insect and plant group properties (extinction slope, robustness, generality, and vulnerability) were calculated using the *grouplevel* function in the *bipartite* package.

	Habitat	
Network Property	**Mesic**	**Xeric**
Connectance	0.2929	0.244
Interaction strength asymmetry	-0.5947	0.09067
WNODF	36.5	33.4
Linkage density	2.045	2.163
Extinction slope (insects)	2.645	2.125
Extinction slope (plants)	2.516	2.705
Robustness (insects)	0.7132	0.6726
Robustness (plants)	0.7049	0.7207
Generality (insects)	1.474	1.733
Vulnerability (plants)	2.615	2.593

Appendix 1: Flowering plant species observations

Table 5: Abundance of open flowers per species recorded in 1 x 25 m transects at each site, summed across all sites, per sampling period. Phenology line plots graphically depict the proportion of open flowers per species across the growing season. The X-axis is the time from the start of the first sampling period (22 June 2018) to the end of the last sampling period (10 August 2018). Y-axes are independent across species and correspond to the ratio of open flowers at a given point in time to the number of open flowers during peak flowering of the same species (scaled from 0 to 1).

			Period										
Species	**Family**	**Total**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Phenology**
Mesic													
Saxifraga oppositifolia	Saxifragaceae	93	37	44	12								
Arctous rubra	Ericaceae	558	32	308	184	34							
Salix richardsonii	Salicaceae	86	10	39	27	10							
Salix arctica	Salicaceae	440		74	183	183							
Pedicularis lanata	Orobanchaceae	317			92	166	59						
Dryas integrifolia	Rosaceae	5415			7	836	4378	186	8				
Salix sp. 2	Salicaceae	80				80							
Oxytropis arctobia	Fabaceae	11				6	5						
Oxytropis maydellianna	Fabaceae	1440					402	680	308	40	10		
Astragalus alpinus	Fabaceae	864					137	295	224	90	73	45	
Pedicularis capitata	Orobanchaceae	203					43	116	43	1			
Salix sp. 1	Salicaceae	28					28						
Chamaenerion latifolium	Onagraceae	57						8	25	18	4	2	
Hulteniella integrifolia	Asteraceae	2							1	1			

Species	Family	Total	1	2	3	4	5	6	7	8	9	10	Phenology
Xeric													
Saxifraga oppositifolia	Saxifragaceae	868	269	455	143	1							
Pedicularis lanata	Orobanchaceae	472		9	177	190	93	3					
Dryas integrifolia	Rosaceae	10539			112	2514	7754	156	3				
Oxytropis arctobia	Fabaceae	4187			9	2120	2035	18			5		
Cassiope tetragona	Ericaceae	240				38	148	54					
Lesquerella arctica	Brassicaceae	65				25	40						
Salix arctica	Salicaceae	5				5							
Astragalus alpinus	Fabaceae	65					65						
Hedysarum boreale	Fabaceae	1118					8	652	346	67	30	15	
Oxytropis maydellianna	Fabaceae	873						560	295	18			
Pedicularis capitata	Orobanchaceae	28						22	6				
Hulteniella integrifolia	Asteraceae	91						8	22	29	21	11	

Appendix 2: Insect taxa observations

Table 6: Abundance of insects observed visiting and unambiguously coming into contact with the reproductive structures of conspicuously flowering plant species at each site, summed across all sites, per sampling period. Phenology line plots graphically depict the proportion of visits per taxon across the growing season. The X-axis is the time from the start of the first sampling period (22 June 2018) to the end of the 9th period (7 August 2018). Y-axes are independent across taxa and correspond to the ratio of visits at a given point in time to the number of visits during peak activity of the same taxon (scaled from 0 to 1).

		Period									
Insect taxa	**Total**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**Phenology**
Mesic											
Anthomyiidae	105	21	15	16	37	14	1		1		
Symphyta	39	11	14	4	8	2					
Muscidae	1054	3	4	32	313	456	199	33	12	2	
Scathophagidae	6	2	4								
Psyllidae	5	2	3								
Chironomidae	9	2		1	4		2				
Parasitica	3	2				1					
Apidae	10	1	1		1		1	3	3		
Muscoidea	2	1			1						
Syrphidae	114		2	8	52	24	11	7	9	1	
Acalypterates	3		1	2							
Dolichopodidae	2		1				1				
Empididae	74			1	26	43	4				
Culicidae	43				1	24	3	2	3	1	
Lepidoptera	1				1						
Oestroidea	1					1					
Calliphoridae	1								1		

		Period									
Insect taxa	**Total**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**Phenology**
Mesic											
Apidae	135	5	3	12	9	2	14	35	54	1	
Symphyta	3	1			2						
Chironomidae	31		6	1	8	4	4	8			
Anthomyiidae	36		4	2	2	6	3	1			
Muscidae	569		1	82	166	137	177	6			
Muscoidea	2		1			1					
Parasitica	1		1								
Syrphidae	101			6	3	16	3	18	1		
Empididae	44			1	3	1	3				
Lepidoptera	8			1		1	3	3			
Oestroidea	3			1		1	1				
Culicidae	28				12	6	6	3	1		
Calliphoridae	2				1		1				
Tachinidae	1							1