Spatial and temporal variation in pollinator communities and plant-pollinator interactions at different scales – A case study from Finland

Dissertation

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“I den blombiologiska litteraturen rörande Europas nordliga Iänder äro uppgifterna om de blombesökande insekterna i allmänhet sparsamma eller ofullständiga, särskildt beträffande de högnordiska växtarterna.”

(In the floristic literature of the northern countries of Europe, information on flower-visiting insects is generally scarce or incomplete, especially regarding the high-Nordic plant species.)

- Frans F. Silén, Blombiologiska iakttagelser i Kittilä Lappmark (1905)

Contents

Summary

The majority of wild plants and crops depend on animal pollinators for reproduction; hence, animal pollination is essential for maintaining biodiversity and ensuring food security. However, pollinators and plants currently face a variety of anthropogenic threats, including climate change. The impacts of climate change can be complex and operate at different spatial and temporal scales. For example, the effects of increasing average temperatures become only apparent over long time spans, while the increasing frequency of extreme weather events might produce changes over short time spans. The effects of climate change are also not uniformly distributed across the globe, but they are more pronounced at higher latitudes compared to the global average. Understanding the natural dynamics of plant-pollinator interactions, and the potential effects of climate change on these dynamics, at different temporal and spatial scales is therefore of great interest. However, our current understanding of plant-pollinator interactions is based predominantly on short-term data that is temporally and spatially aggregated, and underlying processes that happen at fine or broad grains may be obscured.

This dissertation consists of six chapters that contribute to our understanding of dynamics in plant and pollinator communities and their interactions, as well as the potential effects of climate change on these dynamics, at different temporal and spatial scales. Chapter 1 broadly introduces the topics of pollination, plant-pollinator interaction networks, and the threat of climate change. I present the current state of knowledge about the temporal and spatial dynamics of plant-pollinator networks in the literature and identify major gaps in our current knowledge. I also argue for the use of historical data and high latitudes as study regions to fill some of these knowledge gaps.

Chapters 2 - 5 present my original research. These four chapters are also stand-alone studies that have been published in, or submitted to, peer-reviewed scientific journals. In Chapter 2, I investigated plant and pollinator communities and their interactions at different latitudes of Finland, spanning 750 km. Specifically, I was interested in the variation of plant and pollinator richness, diversity, and composition across latitudes, dissimilarity of interactions, and in potential differences in specialization of interaction networks across these spatial distances. I found a decrease in species diversity but an increasing dominance of muscoid flies at higher latitudes, resulting in lower network specialization at the northernmost latitudes. I also found that species turnover introduced high dissimilarity in interactions, especially across latitudes, but also across sites within the same latitude.

In Chapter 3, I examined daily dynamics in pollinator communities across the 24-hour cycle during the Arctic Summer. I compared these dynamics in two climatically very different summers, including an

extreme heat summer. I found that pollinators show a robust pattern of daily foraging activity despite conditions of constant daylight in the Arctic summer. However, I also showed a marked difference in foraging activity patterns between years. In particular, flies, which are the main pollinators at high latitudes, showed strong responses in daily behavior patterns, likely as behavioral reaction to the high temperatures.

In Chapter 4, I present a unique historical dataset of plant-pollinator interactions in northern Finland, recorded by Frans Silén in the late 1900s, and I describe how I digitized and curated the dataset. The curated historical dataset is archived on a public repository and is openly accessible. At the same location where the historical dataset was collected, I resampled plant-pollinator interactions over two years. The results of the comparison between the historic and current datasets, which were collected more than a century apart, are presented in Chapter 5. I have shown that plant-pollinator interactions have changed dramatically during the last century. In particular, proportional abundance of moth and hoverfly pollinators has declined, and muscoid flies now provide large parts of the pollination service. Specialized pollinators in particular have declined disproportionately, leading to a decrease in specialization at the network level. This could potentially have a negative impact on the pollination service. In final Chapter 6, I synthesize and discuss the results of the four previous research chapters. I show how the results from these chapters contribute to our overall understanding, but I also describe their limitations. Finally, I explain the utility of my findings for future research and conservation action.

Zusammenfassung

Die meisten Wild- und Kulturpflanzen sind für ihre Fortpflanzung auf tierische Bestäuber angewiesen, demnach ist die Bestäubung durch Tiere von entscheidender Bedeutung für die Erhaltung der biologischen Vielfalt und die Gewährleistung der Ernährungssicherheit. Bestäuber und Pflanzen sind jedoch einer Vielzahl von anthropogenen Bedrohungen ausgesetzt, darunter auch dem Klimawandel. Die Auswirkungen des Klimawandels können vielfältig sein und auf verschiedenen räumlichen und zeitlichen Skalen wirken. So sind die Auswirkungen steigender Durchschnittstemperaturen nur auf langen Zeitskalen erkennbar, während die zunehmende Häufigkeit extremer Wetterereignisse zu Veränderungen in kurzen Zeiträumen führt. Auch räumlich sind die Auswirkungen des Klimawandels nicht einheitlich, sondern sind in höheren Breitengraden bereits stärker spürbar als in vielen anderen Teilen der Welt. Gerade deshalb ist es wichtig, die natürlichen Dynamiken der Beziehungen zwischen Pflanzen und Bestäubern - und die möglichen Auswirkungen des Klimawandels darauf - auf verschiedenen zeitlichen und räumlichen Skalen zu untersuchen. Gegenwärtig basiert unser Verständnis der Beziehungen zwischen Pflanzen und Bestäubern jedoch überwiegend auf zeitlich und räumlich aggregierten Daten, deshalb bleiben zugrundeliegende Prozesse, die auf feineren Skalen ablaufen, oft verschleiert.

Diese Dissertation besteht aus sechs Kapiteln, die zu unserem Verständnis der Dynamiken von Pflanzen-Bestäuber-Gemeinschaften und deren Interaktionen, sowie zu den möglichen Auswirkungen des Klimawandels auf diese Dynamik auf verschiedenen zeitlichen und räumlichen Skalen beitragen. Kapitel eins bietet eine umfassende Einführung in die Thematik der Bestäubung, der Interaktionsnetzwerke zwischen Pflanzen und Bestäubern und der Bedrohungen durch den Klimawandel. Ich stelle den aktuellen Wissensstand in der Literatur über die zeitliche und räumliche Dynamik von Pflanzen-Bestäuber-Netzwerken dar und zeige Lücken in unserem derzeitigen Wissen auf. Ich plädiere auch für den Nutzen historischer Daten und hoher Breitengrade als Studienregionen, um einige dieser Wissenslücken zu schließen.

In den Kapiteln zwei bis fünf stelle ich meine eigene Forschung vor. Bei diesen vier Kapiteln handelt es sich um eigenständige Veröffentlichungen, die bereits in wissenschaftlichen Fachzeitschriften mit Peer-Review veröffentlicht, oder zur Veröffentlichung eingereicht wurden. In Kapitel zwei untersuchte ich Pflanzen- und Bestäubergemeinschaften und ihre Interaktionen in verschiedenen Breitengraden Finnlands, mit einer räumlichen Spanne von insgesamt 750 km. Insbesondere interessierte ich mich für potentielle Variationen in der Artenvielfalt und -zusammensetzung von Pflanzen- und

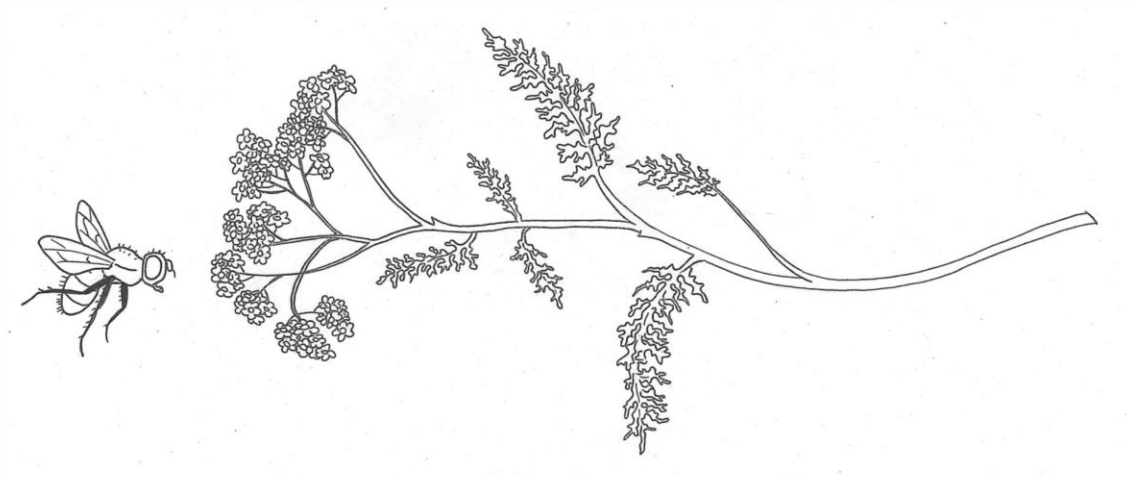
Bestäubergemeinschaften, und für mögliche Unterschiede in Interaktionen und in der Spezialisierung von Interaktionsnetzwerken über die räumlichen Entfernungen hinweg. Ich stellte fest, dass die Artenvielfalt in höheren Breitengraden abnahm, aber die Dominanz der Fliegen zunahm, was zu einer geringeren Spezialisierung der Netzwerke in den nördlichsten Breitengraden führte. Außerdem stellte ich fest, dass die Interaktionen aufgrund einer Fluktuation von Arten sehr unterschiedlich waren, insbesondere zwischen den Breitengraden, aber auch zwischen den verschiedenen Studienstandorten innerhalb desselben Breitengrades.

In Kapitel drei untersuchte ich die Dynamiken der Bestäubergemeinschaften während des 24-Stunden-Zyklus im Arktischen Sommer. Ich verglich außerdem diese Dynamiken in zwei klimatisch sehr unterschiedlichen Sommern, einer davon ein extremer Hitzesommer. Ich stellte fest, dass die Bestäuber trotz des konstanten Tageslichts im Arktischen Sommer ein robustes Muster der täglichen Nahrungssuche aufweisen. Ich zeigte jedoch einen deutlichen Unterschied in den Aktivitätsmustern zwischen den Jahren. Insbesondere Fliegen, die in hohen Breitengraden die wichtigsten Bestäuber sind, zeigten starke Reaktionen im täglichen Verhaltensmuster, was wahrscheinlich auf ein verändertes Verhalten aufgrund der Hitze zurückzuführen ist.

In Kapitel vier präsentiere ich einen historischen Datensatz über die Interaktionen zwischen Pflanzen und Bestäubern in Nordfinnland, der von Frans Silén in den späten 1900er Jahren aufgezeichnet wurde. Ich beschreibe, wie der Datensatz digitalisiert und kuratiert wurde. Der kuratierte historische Datensatz ist nun öffentlich archiviert und frei zugänglich. An demselben Standort, von dem der historische Datensatz stammt, habe ich eine erneute Datenaufnahme der Interaktionen zwischen Pflanzen und Bestäubern durchgeführt. Die Ergebnisse des Vergleichs zwischen den beiden Datensätzen, die mehr als ein Jahrhundert auseinanderliegen, werden in Kapitel 5 vorgestellt. Ich habe gezeigt, dass sich die Interaktionen zwischen Pflanzen und Bestäubern im letzten Jahrhundert drastisch verändert haben. Insbesondere die Häufigkeit von Nachtfaltern und Schwebfliegen hat proportional abgenommen, während Fliegen vom Genus *Thricops* heutzutage vermehrt die Blüten besuchen. Insbesondere spezialisierte Bestäuber sind überproportional zurückgegangen, was zu einem Rückgang der Spezialisierung auf der Netzwerkebene führte. Dies könnte sich negativ auf die Bestäubungsleistung auswirken. Im sechsten und letzten Kapitel fasse ich die Ergebnisse der vier Forschungskapitel zusammen und diskutiere sie. Ich zeige auf, wie die Ergebnisse aus den Forschungskapiteln zu unserem Gesamtverständnis beitragen, beschreibe aber auch ihre Grenzen. Abschließend erkläre ich den Nutzen meiner Ergebnisse für künftige Forschungs- und Naturschutzmaßnahmen.

Chapter 1

General Introduction



1.1. Pollination – a vital process

Insects account for 75-90% of the world´s animal species (Erwin, 2004; Gaston, 1991; Grimaldi and Engel, 2005; Stork et al., 2015). They are found all over the world and are the most numerous, biomass-rich and diverse group of animals (Grimaldi and Engel, 2005). Because of this prevalence, insects form the basic framework of terrestrial ecosystems. Individual organisms interact with one another in numerous ways and through the interactions of insects with their environment and with other organisms, a range of fundamental ecological functions is realized. For example, mutualistic interactions between plants and insect pollinators can result in pollination. It is estimated that 87.5% of wild plant species rely on animal pollination for reproduction (Ollerton et al., 2011). Thus, pollination is crucial for maintaining the biodiversity of native plant species (Garibaldi et al., 2013; Klein et al., 2007; Memmott et al., 2004). This in turn benefits a wide range of other organisms, as plants provide food, habitat and numerous other ecosystem functions such as the circulation of nutrients, uptake and storage of carbon, or release of oxygen. Animal pollinators are also crucial for human food security, as they contribute to the pollination of more than 75% of the world's important crops (Klein et al., 2007) and are thus of immense economic value (Gallai et al., 2009; Lautenbach et al., 2012).

1.2 Plant-pollinator interaction networks – blueprints of the architecture of pollination

Historically, plant-insect interactions were often regarded in isolation and were described as highly specialized relationships resulting from co-evolution between one plant and one insect species. One famous example stems from an orchid species from Madagascar - *Angraecum sesquipedale*, now referred to as Darwin´s orchid - whose nectar tube measures an impressive 30 cm. Charles Darwin predicted that the orchid should be pollinated by an insect that has mouthparts to match the length of the Orchid’s nectar tube (Arditti et al., 2012; Darwin, 1862). No such insect was known from Madagascar at that time, but four decades after Darwin´s prediction, a moth with the matching physiological features was discovered (Rothschild and Jordan, 1903). However, when researchers started examining pollination in a community context (Herrera, 1996; Jordano, 1987; Waser et al., 1996), it became clear that such extreme specialization is more the exception than the rule. Nowadays we know that pollinators typically visit multiple plant species, and plant species are in turn visited by various different pollinator species, thereby forming a complex network of interactions (Bascompte et al., 2003; Memmott, 1999; Vázquez and Aizen, 2003; Vázquez and Simberloff, 2002).

Studying interaction networks is of great interest, as they provide a way to organize and quantify the structure of a community beyond simply identifying the presence and abundance of species. Furthermore, descriptive network properties can provide information on robustness (the ability of a community to withstand change after disturbance) and resilience (the ability of a community to recover after disturbance), or the maintenance of biodiversity and the provision of ecosystem services in a community (Memmott et al., 2004; Stouffer and Bascompte, 2011; Thébault and Fontaine, 2010). Network properties can be calculated on the level of the whole network, but also on the level of individual species in the network (Dormann et al., 2021). Commonly reported network-level properties include nestedness (Bascompte et al., 2003), modularity (Olesen et al., 2007) and specialization (Blüthgen et al., 2006).

In a nested network, the core group of common generalized pollinators interact with a wide range of generalized as well as specialized plant species, while specialist pollinators interact with a subset of the generalized plant species (Bascompte et al., 2003). Nestedness reportedly promotes stability in networks, as there is a high redundancy of interactions, and random species loss will not lead to cascading extinctions of interaction partners (Fortuna and Bascompte, 2006; Memmott et al., 2004). Modularity describes the presence of distinct subgroups ("modules") in a network, in which species interact with each other more than with species from other modules (Olesen et al., 2007). Modularity is also proposed to stabilize a network, as perturbations do not cascade into other modules(Grilli et al., 2016; Olesen et al., 2007).

Specialization measures the extent to which species in the network restrict their choice of partners to a subset of all available partners (Blüthgen et al., 2006). Highly generalized networks are better able to maintain their structure and services in the face of perturbation, as interactions involving generalist species tend to be highly redundant (Brosi, 2016; Elmqvist et al., 2003; Waser et al., 1996) and more persistent in time and space (Resasco et al., 2021). On the other hand, generalized pollinators usually carry and deliver a lower proportion of conspecific pollen (pollen from other individuals of the same species) and therefore provide a poorer pollination service (Ashman et al., 2020; Waser and Ollerton, 2006).

Typically, mutualistic networks share a similar, non-random structure, even across different habitats and irrespective of species make-up. For example, mutualistic networks tend to be nested and modular and have a skewed distribution of interactions (i.e. a few common generalist species are involved in a large number of interactions, while most species have fewer interactions) (Montoya et al., 2006; Vázquez et al., 2022). These properties increase the stability of networks. However, there are concerns that in the face of severe disturbance a tipping point may be reached once common generalist species disappear, beyond which the network may collapse (Fortuna and Bascompte, 2006; Memmott et al., 2004; Potts et al., 2010). Hence, ongoing evidence of marked declines in insect abundance and diversity (Biesmeijer et al., 2006; Hallmann et al., 2017; Klink et al., 2020; Potts et al., 2016b, 2010; Seibold et al., 2019) are rising global concern.

1.3 Spatio-temporal variation in networks, and the importance of scale

The probability of an interaction to occur depends first and foremost on the spatiotemporal overlap between interaction partners, but also a range of other factors, including species abundance, environmental conditions (e.g. temperature, light availability or wind speed), and morphology, phenology and behavior of species (CaraDonna et al., 2021; Peralta et al., 2020; Vázquez et al., 2022). For example, abundant species are more likely to encounter each other, increasing the likelihood of interaction. Matching morphological traits of the interaction partners (e.g. length of a plant´s floral nectar tube and length of an insect´s mouth parts) can increase the feeding rewards obtained by a pollinator and thus increase the frequency of interaction through pollinator preference (Peralta et al., 2020).

The identity of species and their interactions are not static, but can vary considerably over time and space (Alarcón et al., 2008; Brosi and Briggs, 2013; CaraDonna and Waser, 2020; Dupont et al., 2009; Olesen et al., 2008; Petanidou et al., 2008; Trøjelsgaard and Olesen, 2016). Variation in interactions emerges when an interaction is gained or lost due to changes in the presence or absence of species in a community (“species turnover”), or because existing species change their interaction partners (“interaction rewiring”) (CaraDonna et al., 2021). The underlying drivers of species gain, loss, and change in frequency of interactions, however vary across temporal and spatial scales (CaraDonna et al., 2021). For example, at fine temporal scales spanning minutes to hours, activity or inactivity of species determine if interactions form or dissolve. Environmental conditions, determine a physiological window of activity for plants and pollinators (Stone et al., 1999) and within this window, other local factors, such as level of competition, predation and availability of resources, influence if a pollinator forms an interaction with a plant (CaraDonna et al., 2021; Schwarz et al., 2021; Vázquez et al., 2022). Currently, our understanding of interaction networks is predominantly based on data collected during the day that is then aggregated over weeks, seasons or years (CaraDonna et al., 2021), therefore underlying processes shaping communities at fine grains can be masked.

At broader temporal scales spanning several years to decades, the presence, absence or abundance of species is driven by population dynamics, interannual climate variation, local or global species extirpation, and new arrival of species through invasion or range expansion. While interannual variation in interactions often appears to influence network properties only weakly (Chacoff et al., 2018; Petanidou et al., 2008), at scales ranging from decades to centuries, network structure may be dramatically reshaped through continued shifts in interactions (CaraDonna et al., 2021). However, empirical evidence on temporal changes spanning decades or centuries is largely absent, as the vast majority of studies on ecological interaction networks consider short time scales, typically 1-4 years (CaraDonna et al., 2021).

1.4 Historical data: Opportunities and challenges

Historical documents and museum collections can help bridge this knowledge gap, as they provide information that allow reconstruction of diversity and composition of plant and pollinator communities and plant-pollinator interaction networks (Burkle et al., 2013; Rakosy et al., 2022). Furthermore, historical data can improve our understanding of mechanisms driving variation in interactions over long time. For instance, information on the phenology of species can be an indicator for potential phenological mismatch that could lead to a shift in interactions (Burkle et al., 2013; Rakosy et al., 2022), or resampling historical datasets can help link effects of human stressors to changes in network structure. To date, only a handful of studies have investigated network variation over long time intervals using historical data, finding high degrees of interaction rewiring (Burkle et al., 2013), disproportionate loss of specialist species (Jacquemin et al., 2020) and an increasingly important role of exotic species (Mathiasson and Rehan, 2020).

Despite the opportunities that historical data provide, there are also challenges that come with working with historic data. For example, it requires careful consideration of potential methodological or taxonomic biases of the collector, or missing or incomplete information, such as lack of quantitative information or an underrepresentation of common species (Rakosy et al., 2022). Most of these challenges can be overcome by careful planning of resampling strategies or the use of statistical tools. Hence, historic data can provide unprecedented insights into long-term changes in plant-pollinator interaction. This is particularly important due to rapidly advancing anthropogenic global change. To tease apart the effects of human stressors, we need to understand the baseline fluctuations of species and the networks they are involved in, at different spatial and temporal scales. Furthermore, comparisons over long time scales made possible by historical data are necessary to quantify the rate of change in interactions, and to investigate responses to shifts in species abundance and diversity due to human stressors that take a long time to transpire, such as climate warming.

1.5 Human stressors as threats to pollination

A series of multifaceted anthropogenic stressors remain the main drivers for biodiversity decline, from land-use change, increased use of agrochemicals, invasion of non-native species and the spread of pathogens to climate change (e.g. Hegland *et al.*, 2009; Stout and Morales, 2009; Winfree *et al.*, 2009; Cameron *et al.*, 2011; Potts, Imperatriz-Fonseca, *et al.*, 2016). These stressors differ in their biotic and abiotic nature as well as in their spatial and temporal scales of impact, and they rarely act in isolation. Climate change is probably the most geographically prevalent factor and is most likely to act in conjunction with other stressors (Halsch et al., 2021; Kühsel and Blüthgen, 2015; Pecl et al., 2017; Scheffers et al., 2016). Impacts of climate change on insect communities have the potential to be substantial, even surpassing the importance of habitat loss (Bowler et al., 2017; Halsch et al., 2021; Thomas et al., 2004; Urban, 2015).

Climate change does not only encompass long-term gradual changes in average weather conditions (e.g. global warming), but also shifts in maxima and minima of conditions and changes in frequency and strength of extreme weather events (IPCC, 2001; Jentsch et al., 2007). Furthermore, climate change is not evenly distributed across the globe (IPCC, 2014), and regions at higher latitudes and elevations experience the most severe increases in temperature (Post et al., 2009). Thus, climate change is a multifaceted phenomenon acting at different temporal and spatial scales, and the responses of plant and insect communities are as of yet poorly understood but likely to be manifold (Halsch et al., 2021). For instance, on a short term, extreme events such as heatwaves or droughts may affect the behavior of pollinators, or alter local resource availability in plant species, for instance through lower production of nectar (Arroyo et al., 2020; Descamps et al., 2021). However, it remains unclear if this potentially links to changes in network structure, and due to the stochastic nature of extreme weather events, not many studies so far have studied such potential effects.

In the long term, climate change may shift previously suitable climatic conditions in time and space. This in turn can cause shifts in phenology and geographical ranges of pollinators and/or the plants associated with them, potentially leading to temporal and spatial mismatches between interaction partners (Burkle et al., 2013). Species with limited abilities to track climatic changes, e.g. due to limited mobility or high specialization in habitat or dietary requirements, are likely to be particularly affected. However, the literature on long-term responses of insect populations and plant pollinator interactions to climate and other human stressors is taxonomically and spatially incomplete.

1.6 Major knowledge gaps

Despite the ever growing literature, there remain a number of major gaps and biases in our present understanding of plant-pollinator interactions.

Taxonomic biases: As bees are considered to be the most important pollinators globally (Hung et al., 2018; Rader et al., 2016), large parts of the pollination literature have focussed on this taxonomic group. However, responses of pollinators to human stressors can differ among functional and taxonomic groups. This highlights the need to include all pollinator groups in pollination network studies (Doré et al., 2021; Orford et al., 2015).

Temporal biases: Most data on plant-pollinator interactions cover one or a few years (CaraDonna et al., 2021) and data are typically aggregated over seasons or years. Therefore, long-term patterns in plant-pollinator interactions remain largely unknown and short term mechanistic processes might be obscured by data aggregation.

Spatial biases: Our knowledge on plant-pollinator interactions is not evenly distributed across space, but comes mainly from Western Europe and North America, while tropical and high latitude regions remain underrepresented (Bennett et al., 2018; Knight et al., 2018; Ollerton, 2017). This is concerning, as tropics tend to have very high species richness, and high latitudes are disproportionally affected by climate change. Even within Europe and North America, the major part of data and literature focus on temperate regions. For example, the plant-pollinator networks presented in this thesis are the first to be published from Finland (Bennett et al., 2018).

1.7 High latitudes offer a good model system

High latitude regions offer a good model system to address many of the previously raised knowledge gaps. First, high latitudes can provide a spatial way to examine effects of climate change. Polar amplification describes the phenomenon that warming near the poles has progressed much faster in recent decades than in the rest of the world. Estimates range from double to four times the rate of warming compared to the global average (Rantanen et al., 2022). Therefore, the effects of global warming are likely to be particularly pronounced at high latitudes, and the impacts now observed at high latitudes are likely to be harbingers of future changes in many other regions of the world. On the other hand, other drivers of global change, such as land-use change and agricultural intensification often play a less important role at high latitudes compared to other regions (Sala et al., 2000).

Second, flies are ranked second after bees in terms of global pollinator importance, and at high latitudes, they are particularly abundant and are known to be important pollinators (Kevan, 1972; Pont, 1993). As our knowledge on the impacts of global change on non-bee pollinators remains scarce, there is a need to collect more data from regions where non-bee insects are the dominant pollinators.

Third, biodiversity generally decreases with increasing latitude (MacArthur, 1972; Pianka, 1966). Hence, the relatively species poor fauna and flora of high latitude regions are simplified and more easily traceable (Olesen and Jordano, 2002) compared to the typically highly complex interaction networks from other regions of the world (Evans et al., 2013; Fontaine et al., 2011). The limited species numbers and short growing season also facilitate the task of adequately sampling species communities and their interactions. Therefore, high latitude regions may provide a suitable model system for understanding the links between network structure and functioning. Furthermore, important predictors of insect activity, such as temperature and light availability, are less variable across the diel cycle during the Arctic summers. These particular environmental conditions allow for many interesting questions related to physiological and behavioral adaptations of Arctic insects, such as the diurnal activity patterns of pollinators.

1.8 Aims of this thesis

In this dissertation, I aimed to bridge some of these knowledge gaps by investigating how pollinator communities and plant-pollinator interactions vary across a latitudinal gradient and two different temporal scales at a high latitude site. Over the summers 2018 and 2019, I collected an extensive dataset on plant-pollinator interactions in Finland. Sampling sites were located in three different regions across Finland (Kittilä, Pudasjärvi and Lammi), situated along a latitudinal gradient spanning 750 km (Figure 1).

Figure 1: Location of the different sampling sites throughout Finland.

First, I quantified how plant-pollinator communities and their interactions vary across three locations along a latitudinal gradient at a national scale (Chapter 2). Here, I expected that latitudinal change in climate will dramatically influence plant-pollinator interactions, due to the loss of species that are not cold-adapted from the higher latitude locations. Second, focussing on Kittilä, a high latitude site located 120 km north of the Arctic Circle, I investigated diel-scale dynamics of pollinators during the polar day and across two climatically very different years (Chapter 3). Here, I expected that pollinators will be most active during mid-day, when temperatures are warmest. However, extreme heat might shift diel-scale patterns. Third, to understand changes across very long temporal scales, I digitized and curated a unique historic data set on plant-pollinators interactions from Kittilä, my high latitude site (Chapter 4). The historic dataset was collected by Frans F. Silén in the late 1800s, and contains spatially and temporally explicit observations of interactions involving four orders of pollinators. I compared historic and current data to investigate changes in the plant-pollinator interaction network across two time points spanning 120 years (Chapter 5). Here, I expected that highly specialized pollinators might be more vulnerable to extinction through time and that climate change might have resulted in pollinators immigrating from lower latitudes into this high latitude site through time. In Chapter 6, I synthesize my key findings and place them in a broader context. Furthermore, I discuss the limitations of my research and the future implications of my findings for the field of pollination ecology and species conservation.

My dissertation aims to fill knowledge gaps on the role of climate on plant-pollinator networks by tackling the problem from a variety of different spatio-temporal scales (Figure 2). At the largest spatial grain, I examine plant-pollinator interaction changes across sites nested in three locations along a latitudinal gradient (Lammi, Pudasjärvi, and Kittilä). The detailed observations at the smallest temporal grain and the historical recollections that allowed me to quantify change at the largest temporal grain all took place at a smaller spatial grain, at locations within the site of Kittilä.

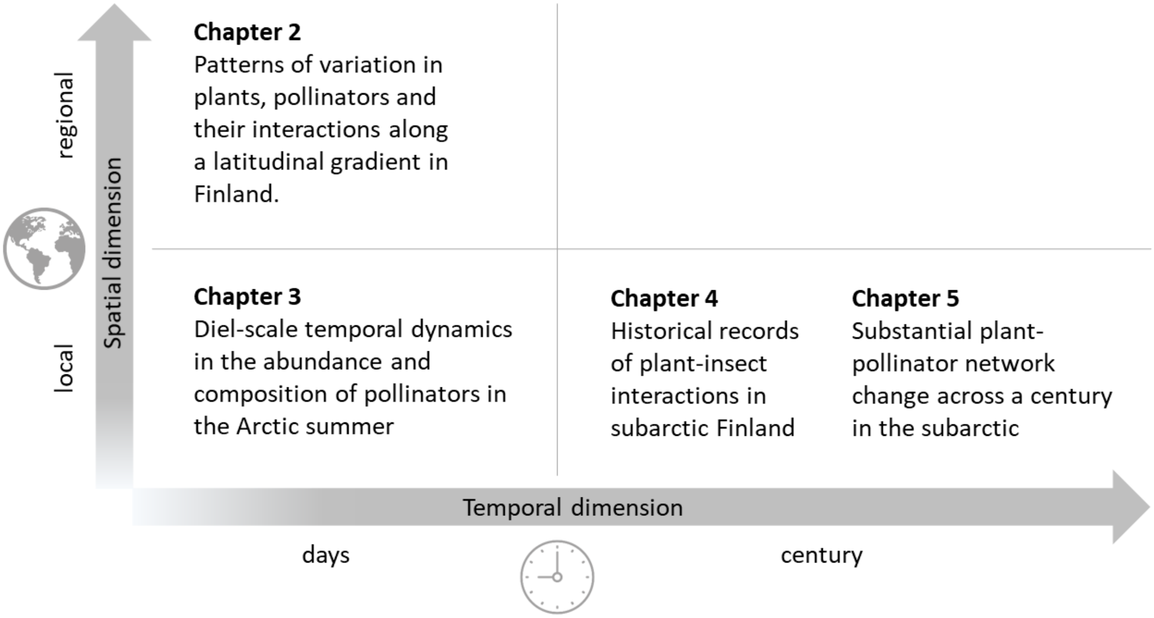
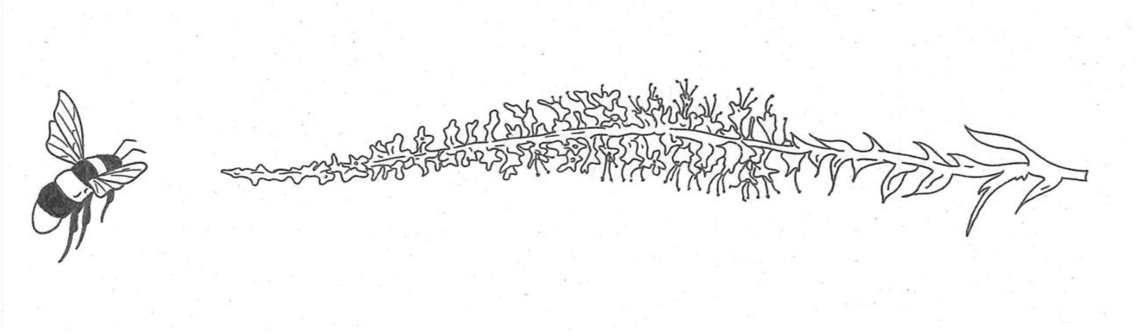


Figure 2: Schematic overview of the spatial and temporal grains of the different research chapters in this thesis.

Chapter 2



Patterns of variation in plants, pollinators and their interactions along a latitudinal gradient in Finland

Leana Zoller & Tiffany M. Knight

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Patterns of variation in plants, pollinators and their interactions along a latitudinal gradient in Finland

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Abstract:

Understanding the distribution of biodiversity along environmental gradients has long been an important endeavor for scientists, but latitudinal patterns in species interactions remain less explored. We collected data on plant-pollinator interactions at three different latitudes in Finland and examined patterns of alpha- and beta diversity of plants, pollinators, and their interactions, as well as patterns of specialization of plant-pollinator networks across latitudes. Our results show that plant and pollinator diversity, as well as network-level specialization, generally decreased towards higher latitudes, and that flies became more dominant in the north. The dissimilarity of plant-pollinator interactions across latitudes was greater than across sites within latitudes, but site-to-site heterogeneity at small spatial scales was also very important in shaping communities and species interactions. Our results highlight the importance of local studies to provide a foundation for future research on variation in plant and pollinator communities and their interactions across space and time.

Keywords: boreal**,** subarctic, bipartite, beta-diversity, community composition

Introduction

Biodiversity is not uniformly distributed across the Earth, and understanding the distribution of biodiversity and the factors that determine it has long been a key question in ecological research. One of the most striking patterns in global biodiversity distribution is the general decline in species richness towards higher latitudes and elevations (Gaston and Blackburn, 2000; Hillebrand, 2004; Jablonski et al., 2017; Kerkhoff et al., 2014; Pianka, 1966; Rahbek, 2005; Rohde, 1992). The mechanisms underlying this latitudinal diversity gradient are still a topic of debate, and many potential explanatory factors have been put forward, such as temperature, climate stability, available energy or the strength of biotic interactions. Generally, all these factors decrease towards higher latitudes (Belmaker and Jetz, 2015; Brown, 2014; Fine, 2015; Jablonski et al., 2017; Mittelbach et al., 2007; Pianka, 1966; Rohde, 1992) For example, at high latitudes, climatic conditions are typically colder and more variable than those at lower latitudes, and the decrease in species diversity towards the poles might be due to fewer species being able to physiologically tolerate these conditions (Kearns, 1992; Totland, 1994).

The spatial distribution patterns of insect pollinators vary across orders (Devoto et al., 2005; Kearns, 1992; Müller, 1880); hymenopterans are generally more abundant in warmer and dryer conditions found at lower elevations and latitudes (Arroyo et al., 1982; Devoto et al., 2005; Lázaro et al., 2008; Müller, 1880), whereas dipterans are the prevailing pollinators at high latitudes (Elberling and Olesen, 1999; Kearns, 1992; Kevan, 1972; Tiusanen et al., 2016). The success of flies in harsh environments might be related to their low energy requirements compared to bees and butterflies, their ability to effectively use microhabitats for thermoregulation, or the flexibility that many species of flies have in their adult and larval food and habitat requirements (Kearns, 1992). In lower elevations and latitudes, the abundance and diversity of plants is lower, and plant species with disk flowers are more dominant (Pellissier et al., 2010). These conditions favor generalist pollinators, as generalists are more able to meet their foraging energy requirements when flower resources are less abundant (Carvell et al., 2011) and disk flowers grant access to a wide range of pollinators, including those with short proboscises, like flies (Olesen et al., 2007; Pellissier et al., 2010).

While latitudinal patterns have been extensively documented at a single trophic level, they remain less explored for interactions among species. However, through interactions between species, a range of fundamental ecological functions and ecosystem services are realized (Hagen et al., 2012; Tylianakis et al., 2010). A notable example is the ecosystem service of pollination. An estimated 87.5% of all plant species rely on animal pollinators for reproduction (Ollerton et al., 2011), including more than 75% of the world´s most important crop species (Klein et al., 2007). Variation in interactions across environmental gradients can be quantified by interaction beta-diversity, which in turn can be decomposed into partitions of species turnover (changes in the presence or absence of species in a community) and interaction rewiring (reassembly of interactions among co-occurring species) (Poisot et al., 2012). Analyzing beta-diversity and it´s components can advance our understanding of causes generating spatiotemporal interaction dissimilarity. For example, species turnover is expected if climate environment filtering of species is the mechanism responsible for interaction turnover across latitudes, whereas interaction rewiring is expected if animals must change their foraging to meet their energy requirements at high elevations.

Quantifying and comparing the magnitude of interaction dissimilarity in relation to geographic distance can help identify the relevant spatial grains of interaction dissimilarity. If several sites are sampled at each latitude band, then it is possible to ask whether interaction turnover across latitudes is greater than the change across sites within a latitude. It has been suggested that latitude creates a strong environmental gradient, and thus that beta diversity of species should be greater across latitudes than within sites at a similar latitude (Hillebrand, 2004), and thus a similar pattern might be expected for interaction dissimilarity. Alternatively, there may be a high heterogeneity in natural and anthropogenic factors across small spatial scales, such as soil moisture, topography or land cover type, which might be of overwhelming importance in shaping dissimilarity in interactions.

In this study, we investigate patterns in alpha- and beta-diversity of plants, pollinators and their interactions, as well as patterns in specialization of plant-pollinator networks across 12 sites, four in each of three locations at different latitudes spanning 750 km in Finland. Specifically, we ask (1) how does richness, diversity and composition of plants and pollinators change across three locations in Finland? (2) How dissimilar are plant-pollinator interactions across sites within a location and across locations, and is this dissimilarity attributed more to nestedness or to turnover? And (3), how does network level specialization change across the three locations? We hypothesize that the richness, diversity and species composition is dissimilar across locations, with lower diversity and a dominance of fly pollinators and generalized floral forms at higher latitudes. Further, we expect that the interaction dissimilarity across locations is higher than the dissimilarity across sites within a location, and that interaction rewiring would contribute more to dissimilarity within locations, while species turnover would be more important with increasing latitudinal distance. Finally, we expected network specialization to be lower at higher latitudes. Studies like ours that consider latitudinal gradients and include high latitude sites are relevant to understanding the potential effects of climate change. Further, because high latitude locations are experiencing more rapid climate change, baseline studies on interactions are needed that set up the possibility for future research across latitude and time.

Methods

Sampling area and dates: The study was conducted in June and July of 2019 in three locations across Finland, spanning a total distance of 750 km: In Northern Finland in the surroundings of the village Kittilä (henceforth referred to as “North”), in Central Finland near the municipality Pudasjärvi (henceforth called “Center”) and in Southern Finland in the proximity of the village Lammi (henceforth referred to as “South”). Most regions in Finland are dominated by forest, while artificial areas make up only a small percentage of land cover. Urban regions are concentrated in Southern Finland, and croplands are also most common in Southern and Southwestern Finland, as climatic conditions and soil are more favorable compared to the Eastern and Northern Finland (Kivinen et al., 2006). There is a latitudinal gradient in temperature and precipitation, with Northern Finland being on average colder and dryer than the South. In the summer of 2019, the mean summer temperature and precipitation were 12.5°C and 151.9 mm in Kittilä, 14.7°C and 145.7 mm in Pudasjärvi (region Oulu) and 16.2° and 137.1 mm in Lammi (region Hämeenlinna) (FMI, 2023).

Site selection: In each of the three locations (Kittilä, Pudasjärvi and Lammi), we selected four sites that represented common habitats in the respective region, were non-densely forested and contained flowering herbaceous plant species. In Northern Finland, agriculture is sparse, and open habitats with herbaceous plants are usually found in transitional woodland/shrub. In Southern Finland on the other hand, there is proportionally more arable land. Hence, we have included more sites classified as transitional woodland/shrub in the North, while we have included more sited classified as arable land in the South. Even though land cover classification differed across the selected sites, we ensured that there is an overlap in vegetation across the sites and locations. Multiple common and abundant plant species were present at all locations, for example *Achillea millefolium*, *Chamaenerion angustifolium*, *Filipendula ulmaria* and *Ranunculaus acris*.

Data collection: On each of the 12 sites, we established several 30x2 m transects, with the distance between two transects being at least 20 meters. To ensure that each of the sites was sampled as completely as possible, the amount of transects and sampling rounds per transect were adapted according to the size of a site. In Northern Finland, areas that are not covered by forest are sparse and patches with herbaceous plants tend to be small, hence not many transects were required to adequately sample a site. A total of 8 transects were established in northern Finland (four sites each containing two transects), and each transect was sampled four times within four weeks, resulting in

32 sampling rounds. In central Finland, open patches are typically larger, therefore, more transects were established per site. We established a total of 12 transects (four sites each containing 3 transects) and each transect was sampled twice within one week, resulting in a total of 24 sampling rounds. In southern Finland, again more transects were required to adequately sample a typical site. A total of 36 transects were established (three sites containing 10 transects and one site containing 6 transects), whereby each transect was sampled once within one week, resulting in a total of 36 sampling rounds (See Table 1 for an overview of the sites, transects and sampling effort in each location). For analyses, data of all transects at a site were aggregated.

Table 1: Information on location, land cover and sampling effort for the 12 study sites

location	site	coordinates	elevation (m)	Corine land cover 2018	No. of transects	sampling effort (min)
North (Kittilä)	K1	67.684**N** 24.857E	177	Transitional woodland/shrub	2	120
	K2	67.590N 24.946E	186	Transitional woodland/shrub	2	120
	K3	67.666N 24.893E	180	Non-irrigated arable land	2	120
	K4	67.655N 24.919E	176	Transitional woodland/shrub	2	120
Center (Pudasjärvi)	PJ1	65.375N 26.917E	111	Transitional woodland/shrub	3	90
	PJ2	65.350N 26.733E	111	Non-irrigated arable land	3	90
	PJ3	65.284N 26.540E	103	Arable land	3	90
	PJ4	65.265N 26.734E	110	Transitional woodland/shrub	3	90
South (Lammi)	L1	61.055N 25.042E	122	Arable land	10	150
	L2	61.215N 25.118E	136	Non-irrigated arable land	8	120
	L3	61.062N 25.042E	141	Non-irrigated arable land	10	150
	L4	61.119N 24.940E	112	Transitional woodland/shrub	10	150

During one sampling round, we walked along a transect for a 15-minute observation period (excluding handling time) and recorded all active flower visitors and the plant species on which they were observed. Heretofore, we consider pollinators to be active flower visitors in the orders

Diptera, Hymenoptera or Lepidoptera, that intentionally moved on a flower thereby coming into contact with the reproductive organs of the flower. Here, we refer to flower visitors and pollinators synonymously, although we realize that not all flower visitors are equally efficient pollinators. If possible, pollinator species were identified in the field. When direct identification was not possible, the specimens were collected for later identification in the lab using a hand net. 45.7% of all insect species were identified to species level, 53.0 % to genus level (mainly non-syrphid Diptera), and 1.3 % to family or order level. Furthermore, we surveyed the flowering vegetation along each transect by identifying all the flowering plant species and recording the number of floral units. A floral unit was defined as a single flower or collection of flowers (e.g. an umbel), within which a pollinator can walk, but between which it flies (Baldock et al., 2015; Carvalheiro et al., 2008). All statistical analyses and indices were computed using the highest level of taxonomic resolution available for plants and pollinators.

Statistical Analysis:

All statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020), and all figures were produced using the *ggplot2* package (Wickham, 2016). Prior to all ANOVA, we identified extreme outliers in the data, checked variables for normal distribution by means of QQplot and Shapiro-Wilk test of normality (*shapiro_test* in package *rstatix*) (Kassambara, 2021), and computed Levene´s test for homogeneity of variance across groups (*levene_test* from package *rstatix*), to ensure that assumptions for performing ANOVA were fulfilled. If these assumptions were not met, we used non-parametric Kruskal-Wallis rank sum tests instead (*kruskal_test from rstatix)*. If ANOVA or Kruskal-Wallis rank sum test indicated a significant difference, we proceeded to perform post-hoc Tukey test (*tukey_hsd* from *rstatix* package), or post-hoc Dunn´s Test of Multiple Comparisons (*dunn_test* from *rstatix* package, p-values adjusted using the Benjamini-Hochberg method) respectively.

Sampling coverage: Differences in sampling effort, method, by site or over time can affect the proportion of plants, pollinators or interactions that have been observed, therefore compromising the comparability of ecological network analyses (Petanidou et al., 2008). Due to the differences in sampling effort across locations in our study, it was therefore important to check if sampling coverage (i.e. the observed species/interactions in relation to the estimated total number of species/interactions in a network (Chao and Jost, 2012)) of plants, pollinators and interactions was comparable across sites and locations. We calculated sample coverage at each site using the *iNEXT* function from package *iNEXT* (Hsieh and Chao, 2020), and tested if mean sampling coverage differed across locations using ANOVA.

Estimated richness and diversity: Observed number of species in biodiversity samples is known to be an underestimation of the true species richness, and asymptotic estimators of species richness provide a robust way to compare sites and locations (Chao et al., 2014). We calculated the estimated richness and Shannon diversity (asymptotic diversity estimates for Hill numbers of order $q = 0$ and $q = 1$), for plant and pollinator species at each site using the *iNEXT* function. Then, we compared mean estimated species richness and Shannon diversity across locations using ANOVA (Fig. 1).

Community composition and relative abundance: To visualize the distances of plant and pollinator assemblages across sites and locations, we used non-metric multi-dimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity index, using *metaMDS* from *vegan* package (Fig. 2) (Oksanen et al., 2020). To statistically test for differences in the assemblage of plant and pollinator species across locations, we performed a permutational multivariate analysis of variance (PERMANOVA) using *adonis* from package *vegan.* We tested significance using 999 permutations, and used Bray-Curtis dissimilarity as distance metric. PERMANOVA works with the assumption that the dispersion of the data among groups is equal, and unequal variance among groups can therefore cause false positive results. To ensure that our ANOVA results are reliable, we therefore tested whether on ore more groups is more variable than the others using *permutest* from package *vegan*. If the PERMANOVA indicated significance, we performed pairwise post-hoc tests using *pairwise.adonis* from *pairwise.adonis* package (p-values adjusted using the Benjamini-Hochberg method) (Martinez Arbizu, 2020). To further explore differences in plant and pollinator assemblages across locations, we calculated and visualized the proportional abundance of plant and pollinator functional groups at the three locations (Fig. 3).

Beta-diversity of interactions and turnover and nestedness components: We were interested in whether dissimilarity was higher across locations than across sites within locations. For this, we first calculated pairwise overall interaction dissimilarity between all 12 sites (β_{WN}), as well as the two additive partitions of dissimilarity (β_{OS} and β_{ST}) using *betalinkr* implemented in the package *bipartite* (Dormann et al., 2021). β_{OS} describes the dissimilarity of interactions established between species shared between two sites, and β_{ST} represents the dissimilarity of interactions due to species turnover (Poisot et al., 2012); All results of pairwise comparisons are listed in Supporting Table 1). We then compared the means of $\beta_{WN,} \beta_{OS}$ *and* β_{ST} within and between locations, and also for each pairwise location comparison. We tested for significant differences across locations using Kruskal-Wallis rank sum tests.

Network level specialization: We visualized the bipartite interaction networks for each location using *plotweb* from package *bipartite*. We then calculated and visualized network-level specialization (*H2´*) for each of the three locations (data was pooled across the four sites of each location). The *H2´* metric is insensitive to the number of species in the network, but to further ensure that the metric is comparable across the locations with different interaction sample sizes, we bootstrapped *H2´* 1000 times for each location using *boot_networklevel* in the package *bootstrapnet* (Stefan and Knight, 2021).

Results

In total, we observed 1922 pollinator individuals belonging to 40 families and 156 species. Due to the different sampling effort across regions, we first calculated and compared sampling coverage across locations to ensure that potential sampling bias was not affecting the validity of our results. Sampling coverage of pollinators ranged from 76.7% (site L1 in the South), to 94.3% (site P1 in the Center), and did not significantly differ across locations. Sampling coverage of plants was >99% at all sites. Sampling coverage of interactions ranged from 63.4%, (site L1 in the South) to 90.6% (site P4 in the Center), and was significantly lower in the South compared to the Center (ANOVA: F = 8.993, p = 0.007, Tukey´s post hoc test, adjusted p = 0.006).

Estimated richness and diversity: The estimated pollinator species richness did not significantly differ across locations (ANOVA: F = 1.713, p = 0.234; Fig. 1a), but the estimated Shannon diversity of pollinators was significantly different across locations (ANOVA: F = 6.367, P = 0.019), with the diversity in the South being significantly higher than in the Center (Tukey´s post-hoc test: adjusted p = 0.02), and a trend that the diversity is higher in the South than in the North (Tukey´s post-hoc test: adjusted p = 0.058) (Fig. 1c). Furthermore, we counted a total of 122397 flowering units, belonging to 24 plant families and 97 plant species. The estimated richness of plant species differed significantly across locations (ANOVA: F = 43.371, p < 0.001), being significantly higher in the South compared to two more northern locations (Tukey´s post-hoc test: adjusted p < 0.001 for both pairwise comparisons) (Fig. 1b). Similarly, the estimated Shannon diversity of plants was significantly different across locations (ANOVA: F = 11.601, p = 0.003), with the South harboring more diversity than the North and Center (Tukey´s post-hoc test: adjusted p = 0.005 and 0.008 respectively) (Fig. 1 d).

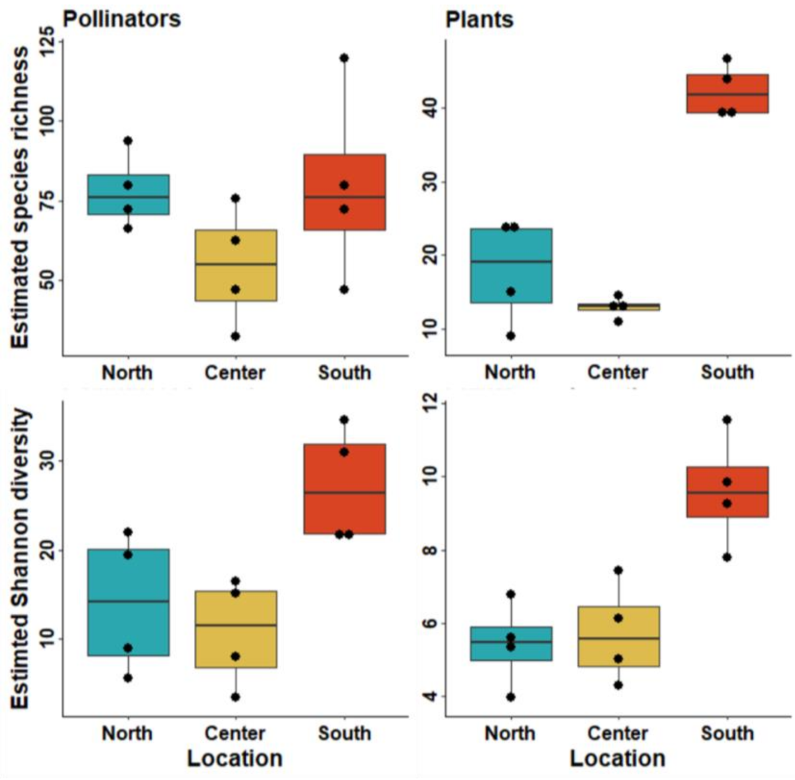

Figure 3: Estimated species richness and Shannon diversity of plants and pollinators in three locations at different latitudes in Finland. Diversity metrics were compared using ANOVA based on the means of 4 sites sampled at each location.

Proportional abundances and community composition: Considering all locations combined, the most common pollinator groups were flies (68.83% of all individuals, specifically, 49.43% muscoid flies, 12.23% hoverflies and 7.18% other flies), bees and wasps (27.73%, specifically 24.97% bumblebees, 0.94% solitary bees, 0.1 % honeybees and 1.72% other Hymenoptera), and moths and butterflies (3.43%, specifically, 2.34% butterflies and 1.09% moths). The most abundant and common pollinators were flies from the genus *Thricops*, (42.4% of all observations). The most common plant family was Asteraceae, and the most common type of floral form was disk flowers with nectar ± hidden. The community composition of pollinators and plants was significantly different across locations (PERMANOVA: Pollinators: F = 1.979, R^2 = 0.305, p = 0.014; plants: F = 2.230, R^2 = 0.331, p = 0.002). The groups did not have significantly different spreads, suggesting that the PERMANOVA results are reliable. Pairwise post-hoc testing revealed that the pollinator composition is significantly different in the South compared to the other locations (Pairwise PERMANOVA: North vs South: F = 2.344, R^2 = 0.281, adjusted p = 0.045; Center vs South: F =

2.006, $R^2 = 0.251$, adjusted $p = 0.045$), while there was no significant difference between North and Center (Fig. 2a). Comparably, plant species composition was significantly different in the South compared to the Center (Pairwise PERMANOVA: F = 2.733, $R^2 = 0.313$, adjusted $p = 0.045$ and the North (Pairwise PERMANOVA: F = 2.268, $R^2 = 0.274$, adjusted $p = 0.045$) (Fig. 2b).

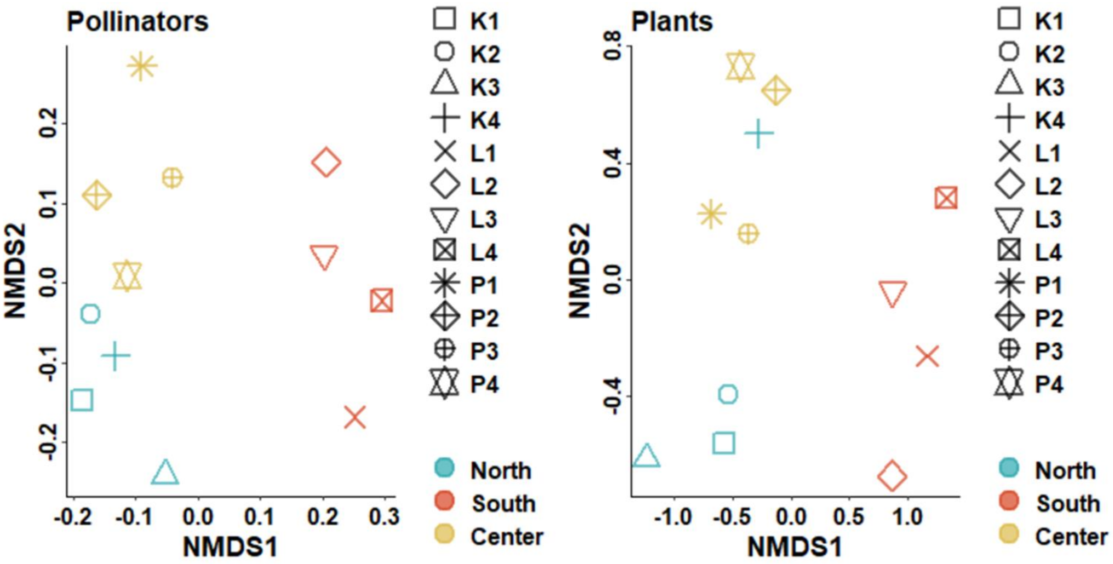

Figure 4: Non-metric multidimensional scaling ordination (NMDS) visualizing Bray Curtis dissimilarity distances of pollinator and plant communities across sites (symbols) and locations (colors).

Relative abundance of pollinator families changed across the three locations. In the North, muscoid flies and hoverflies were particularly dominant, while in the Center and South bumblebees were relatively more abundant (Fig. 3a). The relative abundances of plant families and floral form types also changed along the locations. In the North, plants with disk flowers were the most dominant. In the Center, there was a higher relative abundance of plant species with lip flowers, while in the South, plants with flag blossoms made up the largest proportion (Fig. 3b).

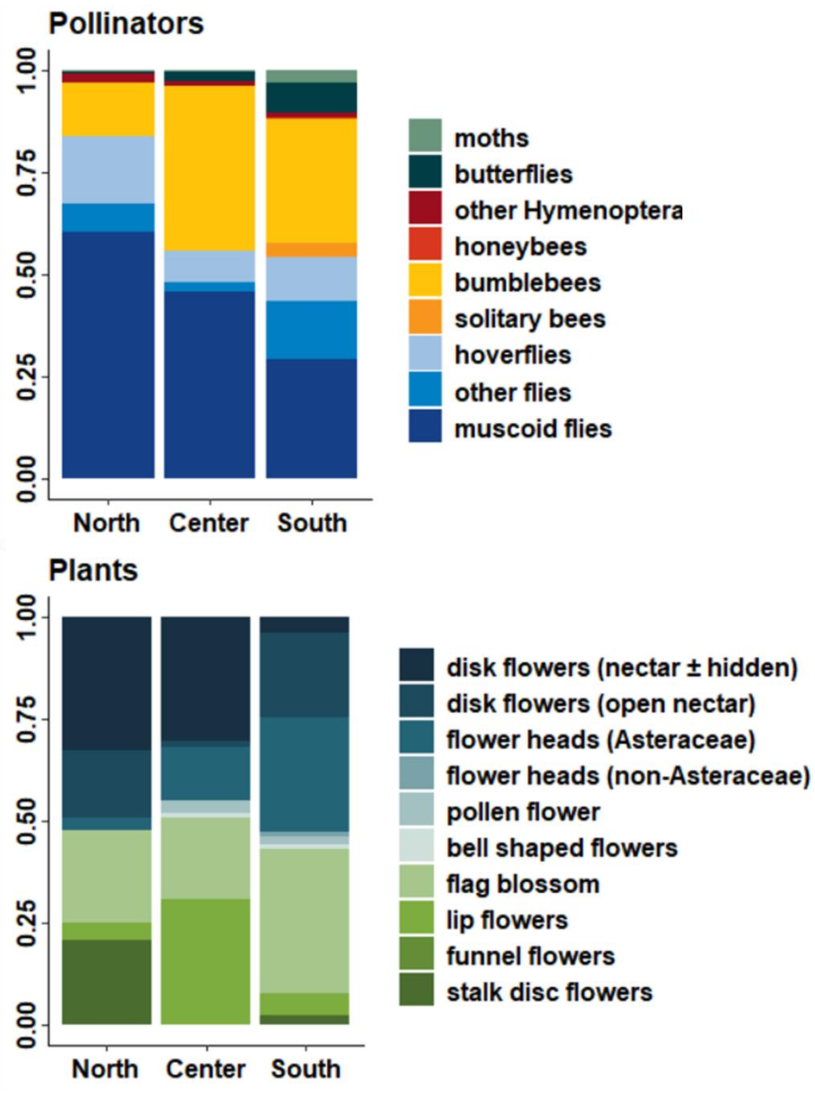

Figure 5: Proportional composition of pollinator taxonomic groups and plant floral forms across locations. Flies are the dominating pollinators in the North, while bumblebees become proportionally more abundant towards the South. In the North, plants with disk flowers are proportionally most abundant. In the Center, lip flowers were proportionally more abundant that at the two other sites, and in the South, flag blossoms made up the largest proportion of the floral forms.

Beta-diversity of interactions and turnover and nestedness components: Mean β_{WN} of interactions was significantly higher across pairwise sites between locations than across sites within locations (Kruskal-Wallis test: p = 0.008). Overall, most of the dissimilarity was due to the component related to species turnover. The rewiring component β_{OS} was significantly higher across sites within locations (Kruskal-Wallis test: p = 0.001), while the species turnover component β_{ST} was significantly higher across sites between locations (Kruskal-Wallis test: $p < 0.001$) (Supporting Fig. 1, Supporting Table 1).

This pattern became more nuanced when considering the identity of the pairwise comparisons. Across-location dissimilarities comparing sites in the South to those in the other two locations (N-S and C-S) were significantly higher than comparing North and Center sites (N-C). Within the South (S-S), we detected dissimilarities across sites that were as high as the across-location differences (C-S and N-S). In contrast, the dissimilarity across sites within the Northern (N-N) and Center (C-C) locations was lower than the dissimilarity between these locations and the South (N-S, C-S) (Fig. 4a, Supporting Table 2). The dissimilarity between sites in the South compared with sites in the North (N-S) and Center (C-S), was explained by components related to species turnover to a significantly higher degree than in the other pairwise comparisons, apart from within-location dissimilarity in the South (S-S). Related to this, the dissimilarity component related to rewiring explained a significantly lower proportion in these comparisons (Fig. 4b-c, Supporting Table 2).

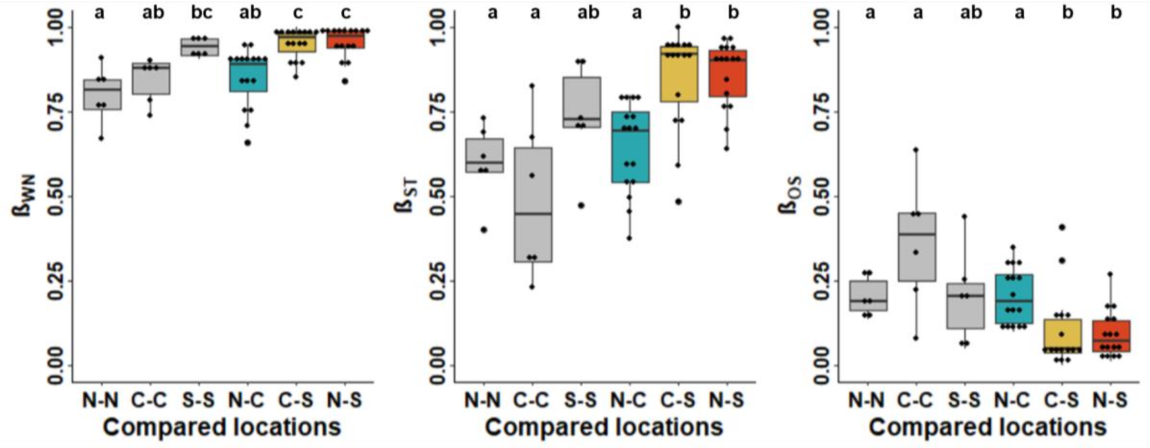

Figure 6: Boxplots of overall interaction dissimilarity (β_{WN}) and the partitions related to species turnover (β_{ST}) and interaction rewiring (β_{OS}) for all pairwise location comparisons. Groups with shared letters are not statistically significant from each other.

Interaction networks and network level specialization: We visualized the plant-pollinator interaction networks at each location (Fig. 5) and quantified the network-level specialization (*H2´*). When comparing network-level specialization (*H2´*), we found that the network in the North was the most generalized, followed by the network in the South. The Center network was the most specialized (Fig. 6).

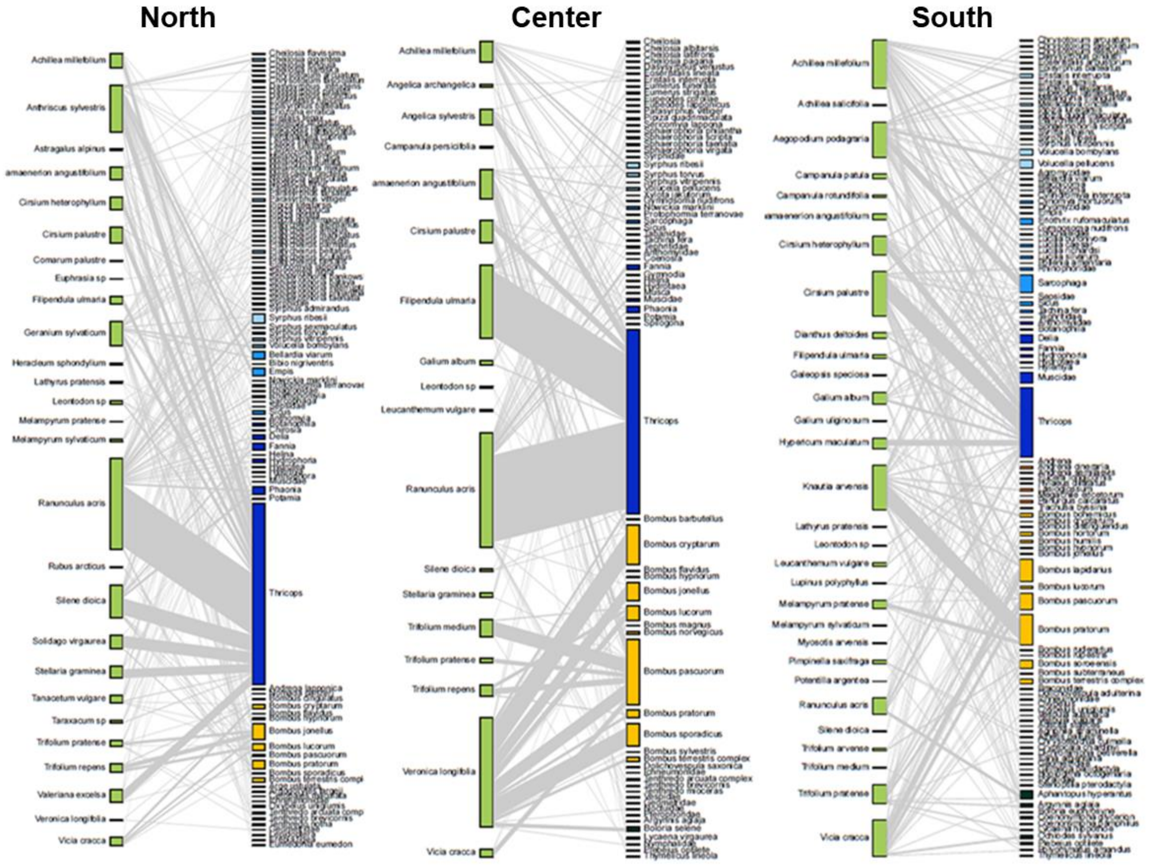

Figure 5: Plant pollinator interaction networks for the three sampled locations. Green boxes to the left of each network represent the plant species, the boxes to the right of each network represent the pollinator species, and the lines between them indicate the weighted interactions. Pollinators are sorted according to functional groups using the same colors as in Fig. 3.

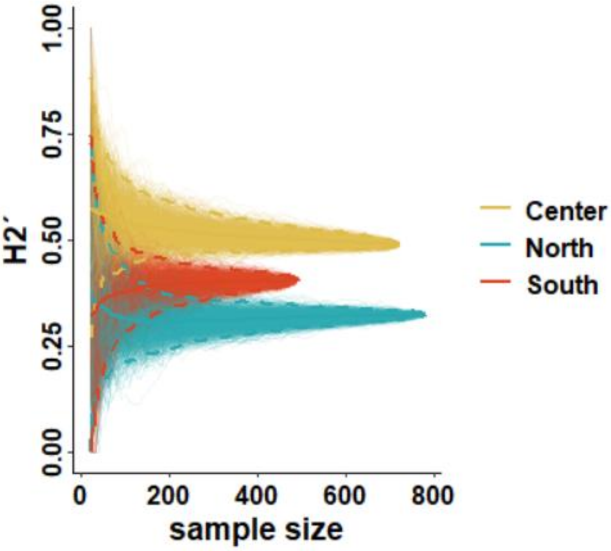

Figure 6: Bootstrapped network-level specialization (*H2´*) of networks at the three study locations (data pooled across sites). Dashed lines are 95% confidence intervals.

Discussion

We found that species richness, diversity and composition of pollinators differed significantly across locations at three different latitudes. As expected, species diversity was lowest in the North and included a larger proportion of flies. Also as expected, plant-pollinator interaction turnover was larger across latitudes than across sites within latitudes. However, these patterns were not as dramatic as expected, and some pairwise comparisons of sites across latitudes were not statistically distinguishable from pairwise comparisons of sites within a latitude. These results suggest that site-to-site heterogeneity at small spatial scales is very important for shaping communities and species interactions, and in some cases can be as strong as heterogeneity across latitudes. Dissimilarity was mainly driven by species turnover, both across sites within locations as well as across locations. Finally, as hypothesized, network specialization was lowest in the North. However, against our expectations, we found network specialization to be highest in the Center, and not in the South.

Plant community composition was significantly different in the South compared to the North and Center (Fig. 2), and estimated plant richness was significantly higher in the South (Fig. 1). Between North and Center, we detected no statistically significant difference in the community composition. This is likely because the most common flowering plant species found in the North have broad distributions and are not restricted to cold biomes. In the North, 65% of all floral units belonged to the plant species *Ranunculus acris* (26.8%), *Anthriscus sylvestris* (13.46%), *Silene dioca* (9.62%), and *Geranium sylvaticum* (11.94%). In the Center, 67% of all floral units belonged to only three plant species, *Veronica longifolia* (26.85%), *Ranunculus acris* (23.59%) and *Trifolium hybridum* (6.7%). In the South, the plant species *Achillea millefolium*, *Vicia cracca*, and *Trifolium pratense* were the most prominent (15.4%, 13.02% and 11.14% of floral units, respectively).

As expected, pollinators in the North were less diverse and more fly-dominated compared to the Center and South locations (Fig. 1). In the North, flies, in particular muscid flies of the genus *Thricops*, were the dominant flower visitors and were involved in 52.56% of all interactions. *Bombus jonellus* was the second most frequent visitor, but with only 4.62% of all visits, it was far less frequent than *Thricops*. All other pollinators were responsible for less than 3% of visits each (Fig. 5a). In the Center, *Thricops* was also the most frequent pollinator, and was involved in 41.91% of all interactions. Additionally, several bumblebees were frequent flower visitors, such as *Bombus pascuorum* (14.8% of visits), *B.cryptarum* (8.99% of all visits,), or *B.sporadicus* (5.26% of all visits) (Fig. 5b). In the South, *Thricops* were still the prevalent flower visitors, but with 20.73% markedly less so than in the North and Center. Similarly to the Center, several bumblebees were frequent flower visitors, including *Bombus pratorum* (9.15% of all visits), *B.lapidarius* (6.71% of visits), and flies of the genus *Sarcophaga* (5.2% of all visits) (Fig. 5c). Our results confirm the lower species diversity and prevalence of flies at higher latitudes that has already been previously proposed in multiple contexts (Jablonski et al., 2017; Kevan, 1972; Pianka, 1966; Tiusanen et al., 2016) and might be due to weaker environmental filters in lower latitudes allowing for more species (Kearns, 1992; Totland, 1994). However, for pollinators it has to be noted that many non-syrphid flies were not taxonomically resolved to species level; hence, it could be that there is a higher species diversity of flies in the North that is masked by our taxonomic resolution.

Contrary to our hypotheses, we did not find more generalized floral forms towards the North. In the North, *Ranunculus acris* was our most common plant species, and its flower is considered more specialized (stalk disk with hidden nectar) because scales cover the nectary. Floral forms that hide the nectary are thought to have evolved to exclude ineffective visitors and therefore increase visitation and pollen transfer by effective visitors. There is contrasting evidence in the literature for the idea that generalized floral forms are favored in colder biomes. For example, Pellissier et al. (2010) found an increase of generalized floral forms towards higher altitudes in the Alps, while Junker and Larue-Kontić (2018) did not detect any trend of in floral traits with altitude. It is also unclear if how well these broad categories of floral forms determine pollination syndromes (Fenster et al., 2004; Wang et al., 2020), particularly at high latitudes where the overall strength of biotic interactions might be lower (Rosas-Guerrero et al., 2014; Wang et al., 2020). In our study, *Ranunculus acris* was able to attract a diversity of pollinators, such as *Thricops* muscoid flies and hoverflies such as *Syrphus ribesii*, but also bumblebees such as *Bombus jonellus*, solitary bees such as *Panurgus calcaratus* or butterflies such as *Plebejus optilete*.

Site-to site turnover in interactions was high across sites within locations (Fig. 4). In part, this might be explained by our study design, which purposely sampled different grassland types at each latitude, including transitional woodland/shrub areas, and different types of arable land. Despite this, we still expected the effect of latitude to be stronger, as the latitudinal gradient was substantial, spanning 750km, and 3.7°C change in mean summer temperature in the year of sampling. The observed dissimilarity in interactions was mainly explained by species turnover, both within sites and across sites. This suggest that, even at a local scale, heterogeneous grasslands can support a diverse range of insect pollinators, thus the conservation of these habitats is of great importance for safeguarding the ecosystem service of pollination (Motivans Švara et al., 2021).

Network level specialization was lowest in the North as expected, likely due to the dominant role of the highly generalist *Thricops* flies (Fig. 5a). The Network in the Center exhibited the most specialization, even more so than in the South. This appears to be due to the dominance of interactions between a few abundant species in the community, such as the bumblebee species *B. pascuorum*, *B. caryptarum*, *B. sporadicus* and *B. jonellus* interacting with *Veronica longifolia*, and the exclusiveness of these interactions likely results in high apparent specialization (Fig. 5b). The same bumblebee species were present in the North and South, where they interacted with a wider range of plant species. These results highlight that species that are typically considered generalists can be locally specialized.

In complementary studies located at our North location, we demonstrate that the specialization of networks is also not static in time (Zoller et al., 2023) and that several common pollinator-dependent plant species currently do not have their reproduction limited by pollen (Koch et al., 2020). Network level specialization decreased over the past 120 years, and this is attributed to a disproportionate loss of specialist species. Such shifts towards generalization could lead to lower pollinator services, if the generalist pollinators deliver more heterospecific pollen (Ashman and Arceo-Gómez, 2013). However, at this time, the reproductive success of plant species in our northernmost study region were not observed to be limited by pollen receipt (Koch et al., 2020), suggesting that the common generalist fly visitors are providing adequate pollination services (Giménez-Benavides et al., 2007). Both of these studies highlight the importance of local studies to create a baseline for future research on variation in plant and pollinator communities and their interactions across space and time.

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Leana Zoller: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **Tiffany M. Knight:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (equal).

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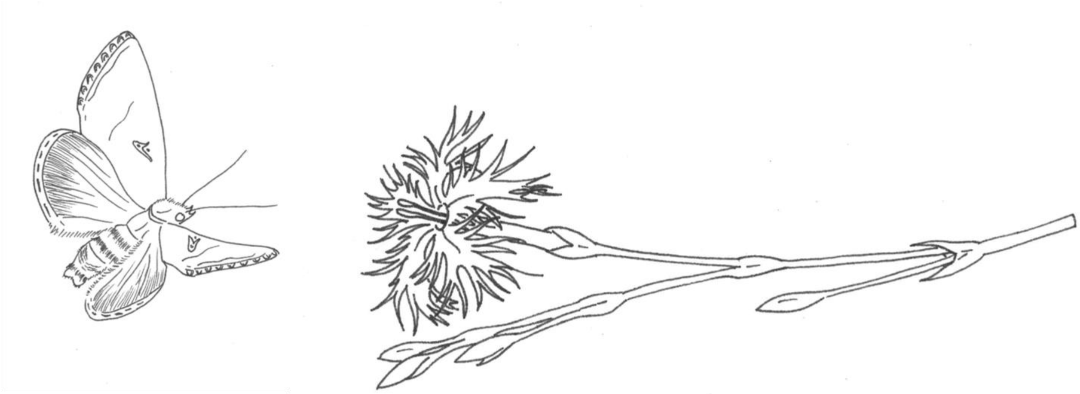
Conflict of interest

The authors declare that they have no conflict of interest.

Chapter 3



Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer

Leana Zoller, Joanne M. Bennett, Tiffany M. Knight

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Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer

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Our understanding of how pollinator activity varies over short temporal scales is limited because most research on pollination is based on data collected during the day that is then aggregated at a larger temporal scale. To understand how environmental factors affect plant–pollinator interactions, it is critical that studies include the entire diel cycle to examine patterns and processes that cause temporal variations. Further, there is little information from the Arctic, where environmental conditions that influence pollinator activity (e.g. temperature and solar radiation), are less variable across the diel cycle during the summer compared to locations from lower latitudes. We quantified abundance, composition and foraging activity of a pollinator community in Finnish Lapland at a diel scale over two summers, one of which was an extreme heat year. Pollinators showed a robust pattern in daily foraging activity, with peak activity during the day, less to no activity at night, and an absence of typically night active Lepidoptera. Abundance and composition of pollinators differed significantly between the years, possibly in response to the extreme heat in one of the years, which may particularly harm muscid flies. Our results showing strong diel and interannual abundance patterns for several taxa of pollinators in the Arctic summer have important implications for our understanding of temporal dynamics of plant–pollinator interactions.

Approximately 90% of angiosperms depend on animal pollination to some extent, making pollination a vital ecosystem service for the maintenance of plants[1]. The abundance and composition of pollinators, and thus the services they provide, are known to change across space and time. In order to understand and predict how environmental factors influence plant–pollinator interactions, it is critical that studies examine the patterns and processes that cause spatial and temporal variation[2]. Studies documenting pollinator communities are often based on data aggregated at large temporal scales, typically across weeks or entire seasons[3]. However, pollinator abundance and composition can vary considerably, even over short periods of time, such as a 24-h period[4]. Understanding fluctuations in pollinator abundance and composition on a 24-h temporal grain is of great importance because pollinator behaviour on a diel scale can affect the pollination success of plants. For example, plant reproductive output is higher when pollinator visitation and plant diel patterns (e.g. timing of anthesis, stigma receptivity or production of floral resources) are synchronised[5]. Hence, activity of pollinators during the daily cycle can provide a mechanistic understanding of the processes that take place at broader temporal scales. Currently, our understanding of diel patterns in the abundance and composition of pollinators is limited by a lack of nocturnal observations[4], and a lack of information from high latitude locations in which summers experience constant daylight.

The diel foraging activity patterns of anthophilous insects are affected by factors which vary throughout the day. These factors include biotic ones, such as availability of plant resources[6], predation and competition[5,7], as well as abiotic factors. Temperature, solar radiation and wind speed are the most important abiotic factors determining insect activity[5,8,9]. Butterflies for example derive their body heat almost exclusively through absorbing direct sunlight, hence their activity largely depends on solar radiation[8,10]. Wind speed influences insect activity, since high wind speeds increase convective cooling and can cause navigation problems, especially for small animals[11].

Abiotic factors that determine insect activity vary with latitude. In the Arctic Summer, a typical 24-h period has lower variation in both solar radiation and temperature compared to lower latitudes. There have not been

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Abiotic factors	July 2018	July 2019	t	df	p
Monthly mean temperature (°C)	19.5	13.4			
Temperature anomaly (°C)	+ 5.4	− 0.7			
Max. sampling temperature	31.5	20.5			
Min. sampling temperature	11.7	5.6			
Mean temperature (°C)	22.7	12.5	8.400	72.225	**<0.001**
Mean global solar radiation (W/m²)	1.319	197.78	1.246	77.531	0.216
Mean wind speed (m/s)	1.57	1.60	0.100	73.479	0.921

Table 1. Abiotic factors for the month of July in our two sampling years. The data are provided by the Finnish meteorological Institute (FMI) and were recorded at the nearest available weather station to our site. Degrees of freedom (df), t- and p-values from t-tests comparing the mean values of air temperature, global solar radiation and wind speed recorded during our samplings across years are presented. Significant effects are printed in bold.

any Arctic studies examining how the abundance and composition of pollinator communities change across the 24-h time period. However, it is known that some groups still have diel activity cycles. For example, bumblebees do not utilize the entire 24-h period for foraging during the Arctic summer, even though abiotic conditions, such as temperature and brightness, should allow them to do so. Instead they express a robust diurnal rhythm[12] due to their intrinsic biological clocks[5, 13]. Flower visiting flies observed in south-western Norway show peak flower visitation activity during noon and no activity during the night[9]. Similarly, moths retain a distinct diel periodicity during the Arctic summer and are active at night, despite the ambient light being at levels that would inhibit activity in their relatives from lower latitudes[14]. This leads us to the expectation that we will find changes in foraging activity across the 24 h, even in the Arctic Summer.

Temperature is the most important determinant of activity of flying insects in the Arctic[15], but to date, little is known about thermal tolerances of specific genera or species of Arctic pollinators. The primary orders of pollinators at high latitudes are Diptera, Hymenoptera and Lepidoptera, and the primary families are muscid flies (family Muscidae), syrphid flies (family Syrphidae) and Apidae (mainly represented through the genus Bombus). In recent review of thermal tolerances of 2133 organisms, none on these families were represented[16]. However, it has been proposed that flies in Arctic Alaska have a temperature optimum of around 13 °C and might be particularly sensitive to increased temperatures[17]. We expect that orders and families of pollinators might differ in their diel activity patterns, possibly due to differences in temperature sensitivity. But due to limited thermal tolerance information, we cannot make any more specific hypotheses.

During the peak flowering period in two Arctic summers we assessed the abundance and community composition and foraging activity of pollinators across a 24-h cycle. Specifically, we sampled the pollinator community in Lapland, 120 km north of the Arctic Circle. We predicted that the abundance, composition and activity of pollinators would change across the 24-h cycle, and that the abundance of pollinators would be highest in the middle of the day when temperatures are also high. We were fortunate to sample two very different years, one with temperature close to baseline conditions for the region and another that represents a mean temperature anomaly of over + 5 °C[18].

Results

Abiotic factors. July 2018 was the hottest July in Finland since the records began in the early twentieth century[19]. Lapland experienced an unprecedented mean temperature anomaly of + 5 °C from the 1981 to 2010 July average of 14.1 °C[18]. Comparatively, temperatures in 2019 were close to average (Table 1). The mean temperature during the 2018 sampling rounds was significantly higher than in 2019. Means of other abiotic factors considered to influence pollinator activity (i.e., wind speed, global solar radiation) did not significantly differ between the two sampling years (Table 1, Supplementary Fig. S1). The mean density of flowering units (number of flowers or inflorescences observed per 30 × 2 transect) did not differ between the years (in 2018 = 3204, in 2019 = 2491; t = 0.391, p = 0.698), but there were differences in the identities of the seven most visited plant species across the years (Supplementary Fig. S2, Supplementary Table S1).

Abundance and composition of pollinators. Across both sampling years we observed 1581 flower visitors from 19 families on 20 plant species. Ten families were observed in 2018, two of them exclusively. Sixteen families were recorded in 2019, nine of them exclusively. In both sampling years, Diptera was the most abundant order (58.57% of observations in 2018 and 55.89% in 2019), while Lepidoptera was the least abundant (3.72% and 1.52% respectively, Table 2). On the family level, Syrphidae represented 30.96% of total observations (52.85% of Diptera) in 2018 and 36.12% of all observations (64.63% of Diptera) in 2019, making them the most abundant Diptera family in both years. Muscidae made up 24.81% of all observations (42.36% of Diptera) in 2018, making them the second most abundant Diptera family in that year. In 2019, Muscidae represented 4.56% of all observations (8.16% of Diptera). Anthomyiidae made up 6.4% of all observations in 2019 (11.56% of Diptera), making them the second most abundant Diptera family in that year, while in 2018, they made up 1.97% of all observations (3.37% of Diptera). Apidae was the most abundant hymenoptera family in both 2018 and 2019, representing 37.63% of all observations in 2018 (99.8% of Hymenoptera) and 29.29% in 2019 (68.75% of

	Absolute abundance					Relative abundance of families within order		Relative abundance of taxa within year		Relative difference in abundance between years
Taxon	**2018**	**2019**	**t**	**df**	**p**	**2018**	**2019**	**2018**	**2019**	**2018–2019**
All taxa	**1318**	**263**	4.47	44.75	**< 0.001**					− 66.72
Diptera	**772**	**147**	3.97	27.15	**< 0.001**			**58.57**	**55.89**	**− 2.68**
Syrphidae	408	95	5.23	7.29	**0.001**	52.85	64.63	30.96	36.12	+ 5.16
Muscidae	327	12	9.40	6.43	**< 0.001**	42.36	8.16	24.81	4.56	− 20.25
Anthomyiidae	26	17	0.68	5.19	0.524	3.37	11.56	1.97	6.46	+ 4.49
Hymenoptera	**497**	**112**	3.07	6.09	**0.021**			**37.71**	**42.59**	**+ 4.88**
Apidae	496	77	7.13	6.44	**< 0.001**	99.8	68.75	37.63	29.28	− 8.35
Tenthredinidae	0	20	–	–		0	17.86	0	7.60	+ 7.60
Lepidoptera	**49**	**4**	2.27	7.31	0.056			**3.72**	**1.52**	**− 2.20**
Nymphalidae	47	1	–	–	–	95.92	25	3.57	0.38	− 3.19

Table 2. Absolute and relative abundances, as well as the interannual relative difference in total abundance, for three orders of pollinators and the most abundant families within each order. Absolute abundance refers to the total number of observed individuals in each taxon. Relative abundance of families within orders describes the percentage of a family within the order. Relative abundance of taxa within a year represents the percentage of each taxon in relation to all observed individuals in a year. Only families of which at least 10 individuals were recorded are presented. Degrees of freedom (df), t- and p-values from the t-tests comparing the mean abundance of each taxon in 2018 and 2019 are presented. Significant effects are printed in bold.

Hymenoptera, Table 2, Fig. 1). Overall abundance of pollinators was 66.7% higher in 2018 (the record hot year) compared to 2019, and the abundance of most families differed significantly between the two sampling years (Table 2). Muscidae experienced the strongest change in relative abundance, with 20.25% lower abundance in 2019 compared to 2018 (Fig. 1, Table 2). The community composition was significantly different between the two sampling years (PERMANOVA: $F = 14.869$, $R^2 = 0.667$, $p = 0.01$, Supplementary Fig. S3).

Diel foraging activity. Both Diptera and Hymenoptera exhibited a robust pattern of diel foraging activity, with peak activity during the day. We observed few individuals of Lepidoptera (Table 2) and almost all were observed during the day. The activity patterns of Diptera and Hymenoptera differed significantly from each other in 2018 ($W = 11.733$, $p < 0.001$) but not in 2019 ($W = 0.3019$, $p = 0.5366$). In 2018, the diel activity pattern of Diptera and Hymenoptera followed a bimodal distribution, with the largest peak at 07:30 and a smaller peak at 19:30. Between 07:30 and 19:30 there was a sharp drop in foraging activity, which was steeper in Diptera than Hymenoptera. Activity of both Diptera and Hymenoptera in 2018 was lowest at 01:30, but never dropped to zero (Fig. 2). Wald tests comparing activity at subsequent sampling times are provided in Supplementary Table S2. The abundance of Syrphidae and Muscidae followed the same pattern as the activity on the order level (Fig. 3).

In 2019, the diel foraging activity of both Diptera and Hymenoptera followed a unimodal distribution, with peak activity in both orders between 10:30 and 16:30. Between 22:30 and 07:30 the foraging activity dropped to near zero or zero (Fig. 2). At the family level, Syrphidae abundance showed a unimodal pattern, with peak abundance around solar noon and no observations between 22:30 and 04:30. Muscidae were recorded only between 10:30 and 16:30 (Fig. 3). The overlap in foraging activity patterns was greater across different taxa in the same sampling year (overlap-index between Diptera and Hymenoptera in 2018: $dhat4 = 0.803$ and in 2019: $daht4 = 0.915$) than within the same taxa across the sampling years (Diptera: $dhat4 = 0.429$; Hymenoptera: $dhat4 = 0.706$). The abundance of pollinators was significantly explained by hour of sampling and temperature (Table 3). Abundance of pollinators showed the expected hump-shaped relationship with temperature, although we note that all high temperature data were observed in 2018 (Table 3, Supplementary Fig. S4).

Discussion

We found evidence for robust patterns in diel foraging activity for the most common pollinator orders, and across the two most abundant families of Diptera, Syrphidae and Muscidae. Peak foraging activity occurred during the day, with less to no activity during the night. The abiotic conditions at night during our sampling would allow for foraging (*Bombus terrestris* workers for example have been observed foraging at temperatures as low as 3 °C[20]). There is also no obvious change in floral resource availability from day to night (i.e., flowers on our transect did not close at night, however, we note that we did not measure the availability of floral rewards, which could vary between day and night). The most likely explanation is, that pollinators focus their foraging activity on the times when temperatures are close to their thermal optima.

Our observations contrast with the findings of a study conducted at a 24-h grain in the Swiss Alps, where insect visitation rate never dropped to zero and moths were abundant nocturnal flower visitors[4]. During the Arctic summer, moths retain a distinct diel periodicity and are active at night[14]. Historical observations made in our study region in July 1896–1897 also show the presence of multiple species of noctuid moths (family Noctuidae) interacting with the moth-pollinated plant *Silene vulgaris*[21]. Despite projections suggesting the abundance of moths and butterflies will increase at high latitudes under climate change[22] and the high abundance of *S.*

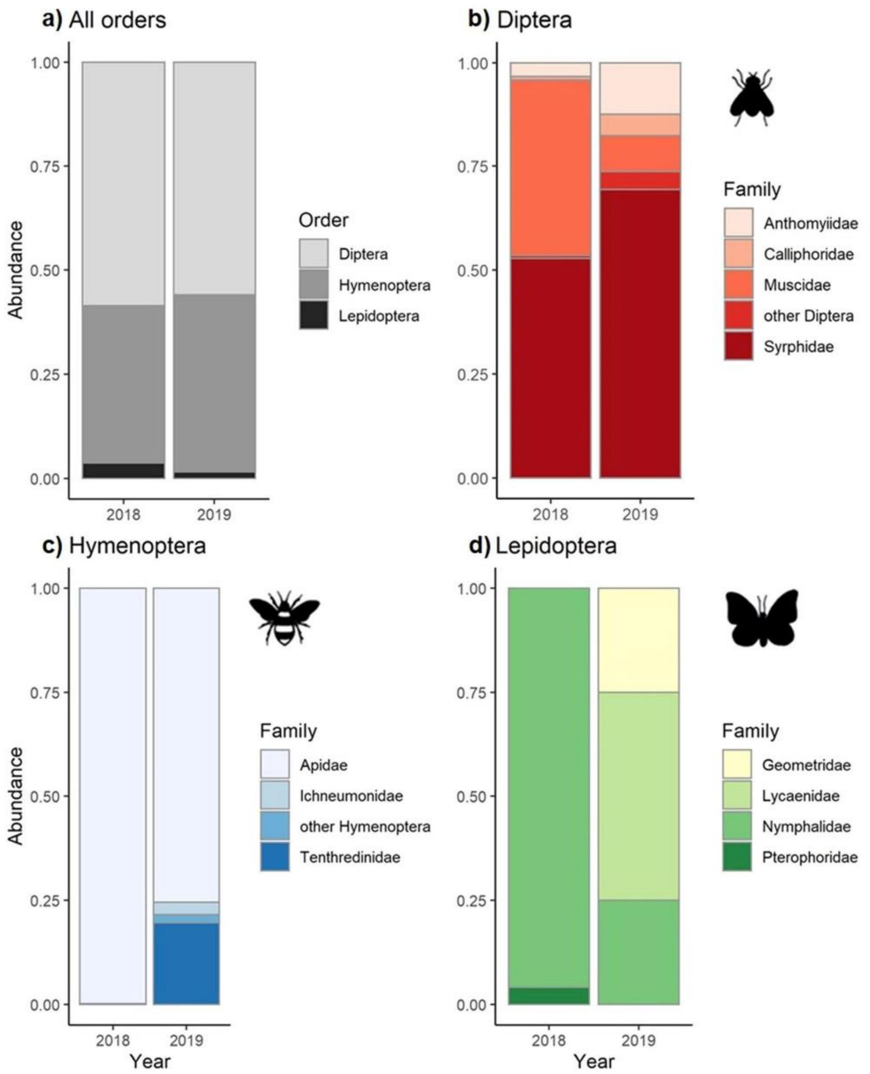

Figure 1. Relative abundance of pollinators for the two sampling years 2018 and 2019. (**a**) Relative abundance of the orders Diptera, Hymenoptera and Lepidoptera. (**b**) Relative abundance of each family among the Diptera. (**c**) Relative abundance of each family among the Hymenoptera and (**d**) relative abundance of each family among the Lepidoptera.

vulgaris at our site, we observed only few Lepidoptera and no Noctuidae. At this point, we are not able to present a satisfying explanation for this.

We found a marked difference in diel foraging activity patterns across years. In the average temperature year, activity was highest during noon. This unimodal pattern found in the average temperature year is in line with other observations on diel flower visitor activity in the Scandinavian mountains[9]. In the high temperature year on the other hand, pollinator activity drastically dropped around noon. This decline in activity in the hottest part of the day in 2018 is likely explained by the extreme temperatures, as temperature significantly explained pollinator abundance in our model. Anthophilous insects often cease their foraging activity during the warmest times of day to seek out cooler microhabitats and avoid overheating[23] and these behavioral changes are known to have fitness costs[23]. In contrast to 2019, the foraging activity of both Diptera and Hymenoptera in 2018 never ceased completely at night. Hence, it is possible that warmer temperatures and more frequent temperature

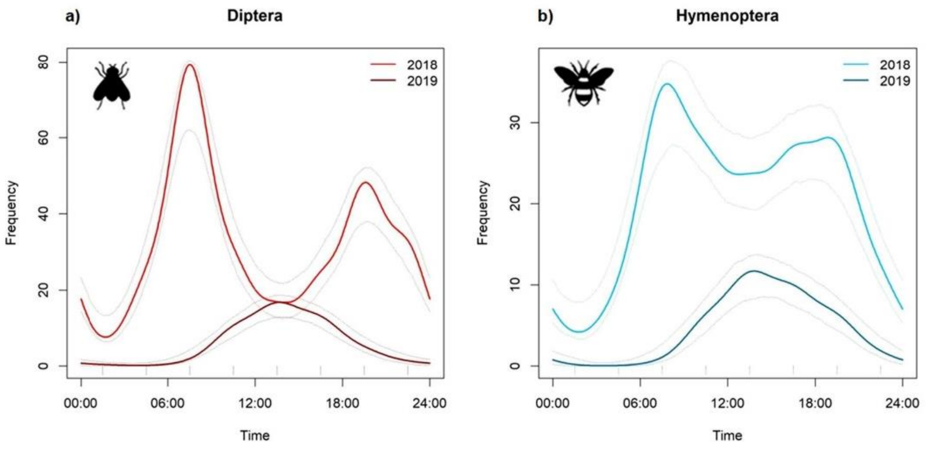

Figure 2. Activity patterns of the two most abundant orders of pollinators. Curves represent fitted circular kernel distributions of (**a**) Diptera and (**b**) Hymenoptera across the diel cycle and for the two sampling years 2018 and 2019. Dashed lines represent bootstrapped 95% confidence intervals of the activity models.

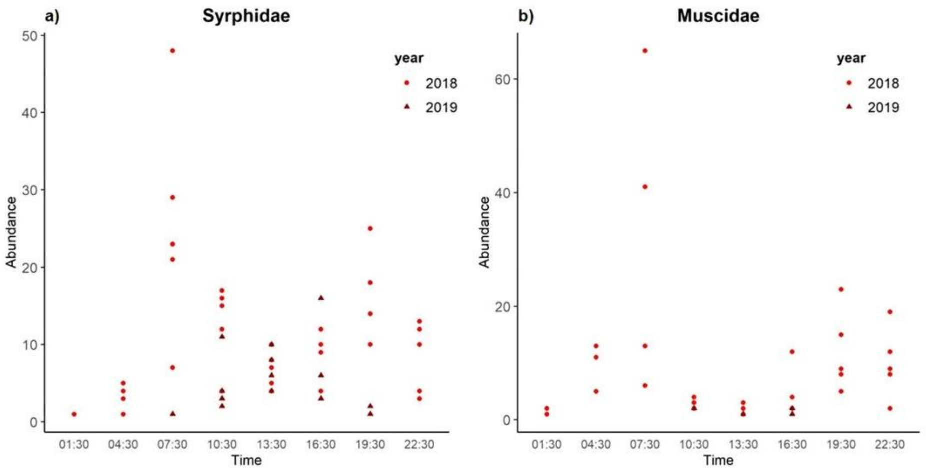

Figure 3. Abundance across the 24-h cycle of the two most abundant Diptera families (**a**) Syrphidae and (**b**) Muscidae in the years 2018 and 2019.

	Estimate	SE	z-value	p-value
Intercept	0.753	0.087	8.702	< **0.001**
Sine (sampling hour)	0.689	0.033	20.651	< **0.001**
Cosine (sampling hour)	0.006	0.028	0.214	0.83
Temperature^2	0.117	0.004	29.985	< **0.001**

Table 3. The effect of hour of sampling and temperature on the abundance of pollinators. Significant effects are printed in bold.

extremes due to climate change could potentially lead to novel diel activity patterns. As extreme temperatures inhibit pollinator activity around noon, diurnal pollinators might be forced to shift activity to night time to compensate for the lost foraging window.

We found significant differences in abundance and composition of most pollinator families across the sampling years. Flower visitors were 67% less abundant in 2019, the year following record heat year 2018. Diptera displayed the lowest interannual overlap in diel activity and flies, especially muscid flies, also underwent a large interannual decrease in abundance. Insect populations are highly dynamic[24, 25] and our results could reflect normal interannual variation. Alternatively, our results could suggest that pollinators, particularly flies, in our system are climate sensitive. The higher abundance of flies in 2018 could reflect benefits of the heat, allowing improved growth, activity and reproduction of organisms that are usually cold-limited[8]. Conversely, the low abundance in 2019 might results from population declines in response to the physiological and behavioral stress from the 2018 heatwave on flies. Several insect species, such as flour beetles and honey bees, have been shown to suffer from heavily reduced male reproductive success when exposed to heatwave conditions[26, 27]. Organisms at high latitudes or altitudes may be particularly vulnerable when temperatures exceed their thermal optima during a heatwave. For example, a bumblebee species occurring at low altitudes can tolerate air temperatures of up to 5° warmer than those occurring at high altitudes[28]. Further, our results could reflect differences in phenology and resource availability across the years. Changes in the identity of the seven most visited plant species across the years indicate that it is possible that the plant community might have been in an advanced phenological stage in 2018 compared to 2019. Plant resources are known to change in composition and concentration in response to high temperatures[29, 30].

In many Alpine and Arctic areas, muscid flies have been identified as the most common flower visitors[31] and key pollinators for certain plant species[32]. Despite this, Muscidae remain largely understudied. Globally, there are over 5000 accepted species of Muscidae[33] and over 300 of these are present in Finland[34]. However, none of these species have been assessed by the IUCN red list for extinction threat[34]. Recently, concerns have been raised about the declining numbers of muscid flies in Arctic areas and the potential to impair ecosystem services[17, 25, 35]. More research is needed investigating the thermal sensitivity and the longer-term temporal fluctuations of muscid flies.

Most pollination studies do not assess nocturnal pollinators and thus do not look for trends that might inform on patterns of their decline. Our temporal sampling is designed for sampling nocturnal pollinators, and their absence is concerning given known historical records[21]. The absence of moths might have potential implications for the pollination of plant species and highlights the need for future work in pollination ecology to incorporate pollinators across all 24 h. To establish if this is a general problem that should be of conservation concern, other locations with baseline data should be sampled for diel patterns in nocturnal pollinators.

To our knowledge, our study is the first to address patterns of diel foraging activity of pollinators on a community level in the Arctic summer and our results contribute to the growing knowledge of pollination in the Arctic. There is a need for long term observations of pollinators, plants and their interactions at high latitude sites, especially because climate change in these regions is progressing particularly rapidly[36]. Furthermore, there is a need for experimental data to assess consequences of changing plant–pollinator interactions for plant reproduction (i.e. pollen limitation), as our understanding of the extent and magnitude of pollen limitation at high latitudes is currently limited[37] (but see[38, 39]).

Conclusion

Here, we show evidence of strong temporal variation at two temporal grains in an Arctic ecosystem. Despite the constant daylight and warm temperatures in the Arctic summer, we find robust diel foraging activity patterns for several taxa of pollinators. Further, there were significant differences between years in the abundance, composition and diel activity patterns of pollinators, likely in response to extreme heat in 2018. Diptera and especially muscid flies, which are important pollinators in the Arctic, showed stark differences in activity between years and much lower abundance in the year following the extreme heat event. This potential sensitivity of muscid flies and the absence of nocturnal Lepidoptera observed here raise conservation concerns not only for these groups, but also for the plant species that rely on them for reproduction.

Methods

Sampling location and dates.

Data collection took place between 10 and 20 July in 2018 and 09 and 18 July in 2019, in the proximity of the town of Kittilä, Finland (67.655465°N, 24.912411°E, 178 m), located ~ 120 km north of the Arctic Circle. From May 29 until July 16 the sun does not set in Kittilä, and civil twilight only occurs before May 6 and after August 8. The landscape around Kittilä is dominated by boreal forest and has low human population density, few invasive plant species and little agricultural land use. A transect was established on a ruderal meadow selected to contain both typically day and night pollinated plant species. In both sampling years, we performed a vegetation survey along the transect. Abundant plant species included *Tanacetum vulgare* (Asteraceae), *Heracleum sphondylium* (Apiaceae), *Trifolium pratense* (Fabaceae) (diurnally pollinated) and *Silene vulgaris* (Caryophyllaceae) (nocturnally pollinated[40]). Flowering plant species richness was similar in the two sampling years (species totals n = 19 in 2018 and n = 18 in 2019). For the seven most visited plant species of each sampling year, we obtained data on flowering season using the database BiolFlor[41].

Data collection.

During 15 min observation periods (excluding handling time), all active flower visitors along a 30 × 2 m transect were observed. An active flower visitor was defined as any individual belonging to the orders Diptera, Hymenoptera or Lepidoptera that intentionally moved on a flower thereby touching the reproductive organs of the flower. Here, we refer to flower visitors and pollinators synonymously, although we realize that not all flower visitors are efficient pollinators. If possible, pollinator species were identified in the field. When direct identification was not possible, the specimens were collected by net for later identification in the lab. All individuals were identified to at least family level. The transect was sampled every 3 h over a 24-h cycle, starting at 01:30 (EEST) (astronomical midnight, sun at lowest point), resulting in eight sampling rounds per

24-h cycle. Sampling took place on days with favourable weather (no rain, low wind), if possible on consecutive days, to minimize the effects of seasonal turnover. The data collection was repeated for 5 full 24-h cycles in each year. Abiotic factors with potential impact on pollinator activity, namely global solar radiation (the total short-wave radiation from the sky falling onto a horizontal surface on the ground, including direct solar radiation and diffuse radiation), air temperature and wind speed were obtained in an hourly interval for the entire sampling period from the nearest weather station. Specifically, wind speed and air temperature were obtained from Kittilä kirkonkylä (67.65210°N, 24.90162°E; 181 masl) and global solar radiation from Sodankylä Tähtelä (67.36663°N, 26.62901°E; 179 masl)[42]. Kittilä kirkonkylä is located around 600 m from our sampling site, while Sodankylä Tähtelä is located 80 km from our sampling site. Sodankylä Tähtelä is at a similar latitude and thus the daily rhythmicity of solar radiation is comparable to our sampling site. However, we note that this might not be close enough to capture temporal variation in solar radiation due to could cover.

Statistical analysis. All statistical analyses were conducted in R version 3.6.0[43].

Abiotic conditions across years. We performed t-tests (using *t.test* from the R-package *stats*[43]) to compare the mean values of abiotic factors (temperature, global solar radiation and wind speed) recorded during our sampling times between years (sample size of each abiotic factor in each year: n = 40: 5 days × 8 sampling rounds).

Abundance and community composition. We compared the mean abundances of our focal pollinator taxa, as well as the number of floral units along the transect between sampling years using t-tests (*t.test* from package *stats*). To estimate ecological dissimilarity of the pollinator community of each sampling day we calculated the Jaccard similarity index[44] and the Bray–Curtis dissimilarity index[45] using the package *vegan*[46]. To visualize pollinator assemblages between years, we used a non-metric multi-dimensional scaling (NMDS) ordination based on Jaccard similarity index and Bray–Curtis dissimilarity index using *metaMDS* from the *vegan* package. We performed a permutational multivariate analysis of variance (PERMANOVA) (using *adonis* from package *vegan*) to statistically test if the community composition differed between the sampling years.

Pollinator activity. We compared the activity of pollinators across the 24-h cycle using the package *activity*[47]. To fit activity models to our observation data for the most abundant pollinator orders (Diptera and Hymenoptera) we used the function *fitact.* The *fitact* function fits a kernel density to observational data from radian time of day and estimates the activity level from the resulting circular kernel distribution, which is a nonparametric representation of the probability density function of a random variable. Since our observations were not made continuously, but rather in 3 h-intervals, we adjusted the kernel bandwidth in each model to smoothen the circular kernel distribution. The bandwidth value was chosen by visually checking the best fit of the circular kernel distribution to our data. Confidence limits were generated by bootstrapping the fitted distribution 1000 iterations. The fitted circular kernel distributions and confidence intervals were plotted using *plot.actmod*. To estimate the overlap of the diel activity patterns, we calculated the dhat4 overlap index between the fitted circular kernel distributions (see[48]) using *ovl4*. Overlap was estimated within each taxon between the sampling years, as well as across taxa within the same sampling year. We tested for the statistical difference between the activity level estimates of Diptera and Hymenoptera using *compareAct*. To test for the statistical difference in activity levels at our sampling times we used *compareTimes*. *CompareAct* and *compareTimes* perform Wald tests (see[49]) to test for the statistical difference between two or more activity level estimates. Lepidoptera were excluded from these analyses due to low sample size. For the two most abundant Diptera families (Muscidae and Syrphidae), we present raw data on abundance across the 24-h cycle, since the low sample size did not allow us to reliably fit activity models to the data.

Effects of abiotic factors on pollinator abundance. Due to concerns of collinearity of the abiotic factors and time of day, we first determined the correlation coefficients between the different abiotic factors and time of day. To account for cyclical nature of time of day, we transformed hour of sampling to radian and performed circular-linear correlations (*circlin.cor* from package *Directional*[50]. Collinearity of predictor variables can inflate the variance of regression parameters and potentially lead to a wrong identification of relevant predictors in a statistical model. If correlation coefficients between predictor variables are > 0.7, collinearity begins to severely distort model estimation[51]. In our case, the correlation coefficient between time of day and global solar radiation exceeded 0.7 (Supplementary Table S3), thus we excluded global solar radiation as a predictor variable. We also did not include wind speed as predictor variable, since our observations of wind speed were all in a narrow range between one and two meters per second. We proceeded to perform a regression analysis, specifically, we ran a generalised linear model assuming a Poisson distribution (using *glm* from package *stats*), including pollinator abundance as response variable and temperature and hour of sampling as explanatory variables. In order to account for the circular nature of time of day, the variable hour of sampling was transformed to radian and included in the model as function of the sine and cosine. Due to the expected hump-shaped relationship between temperature and pollinator abundance, temperature was fitted as a quadratic function. We note that all temperature values between the vertex and maximum of the parabola are from the year 2018 (Supplementary Fig. S4).

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

L.Z. and T.K. conceived the ideas and designed methodology; L.Z. and T.K. collected the data; L.Z. analysed the data; L.Z. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Competing interests

The authors declare no competing interests.

Additional information

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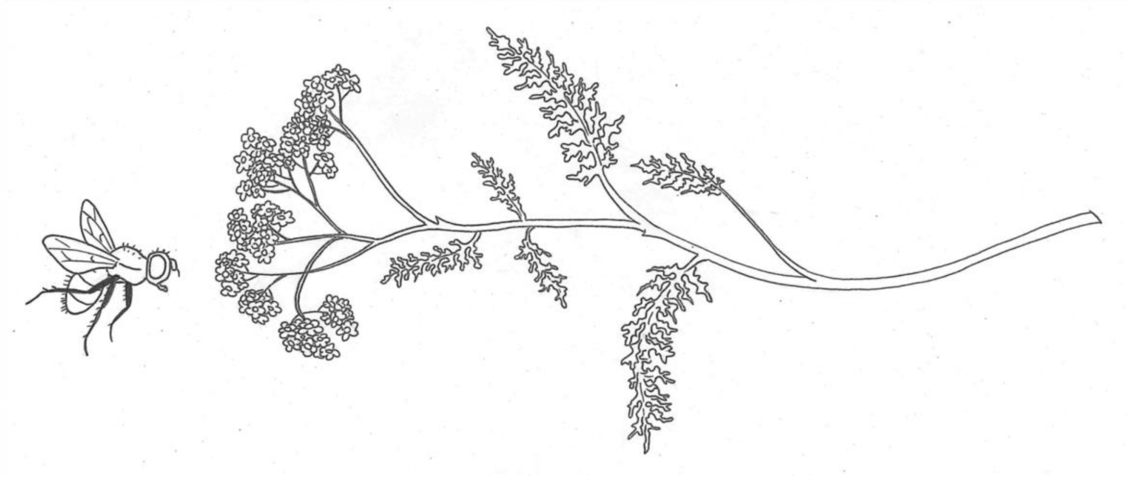
Chapter 4



Historical records of plant-insect interactions in subarctic Finland

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Historical records of plant-insect interactions in subarctic Finland

Leana Zoller[1,2*] and Tiffany M. Knight[1,2,3]

Abstract

Objectives Historical ecological records document the diversity and composition of communities decades or centuries ago. They can provide a valuable benchmark for comparisons with modern communities. Historical datasets on plant-animal interactions allow for modern comparisons that examine the stability of species and interaction networks over long periods of time and in response to anthropogenic change. Here we present a curated dataset of interactions between plants and insects in subarctic Finland, generated from digitizing a historical document from the late 19th century and updating the taxonomy using currently accepted nomenclature.

Data description The resulting dataset contains 654 records of plant-insect interactions observed during the years 1895–1900, and includes 498 unique interactions between 86 plant species and 173 insect taxa. Syrphidae, Apidae and Muscidae were the insect families involved in most interactions, and interactions were most observed with the plant species *Angelica archangelica*, *Salix caprea*, and *Chaerophyllum prescottii*. Interaction data are available as csv-file and provide a valuable resource on plant-insect interactions over 120 years ago in a high latitude ecosystem that is undergoing rapid climate change.

Keywords Pollination, Climate change, Decade, Long-term, Plant-pollinator interactions, Interaction network

Objective

The rapid degradation of natural ecosystems in the Anthropocene [1, 2] highlights the increasing need for conservation actions that preserve life-sustaining ecosystem functions and services [3]. Pollination is a vital ecosystem service as most angiosperm plants, including many crops, rely on animal pollination for sexual reproduction [4, 5]. There have been recent observations of declines of pollinators and the plants they are associated with [6], driven by intensive agriculture, pesticides, the spread of invasive species and pathogens, and climate change [7]. It may take decades or centuries for the full effects of these drivers on plant-pollinator interactions to be realized, and short-term studies may therefore underestimate their effects. Currently, our knowledge on temporal and spatial changes in plant-pollinator interactions is limited, as the vast majority of studies documenting plant-pollinator interactions encompass only one or a few years of the present [8] and come from North America and Western Europe [9].

One way to bridge this knowledge gap is through the use of historical records on plant-pollinator interactions. Historical datasets documenting these interactions (i.e. insects coming into contact with the reproductive organs of flowers) are rare, but provide unique opportunities to

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examine long-term changes in pollinator communities and the structure of plant-pollinator networks, enabling many modern research questions in pollination ecology. Data from arctic and subarctic regions are particularly valuable, because these regions are experiencing more rapid climate change compared to the global average [10] and understudied flies are the most important pollinators there [11, 12]. Here, we present a digitized and curated dataset on plant-insect interactions in subarctic Finland derived from a historical document.

Data description

During six years, between May and August of the years 1895–1900, Frans Silén documented interactions between plants and insects in Kittilä, Finland and published these observations in the naturalist journal Meddelanden af Societas pro Fauna et Flora Fennica [13]. Kittilä is located ~ 120 km north of the Arctic Circle in a boreal biome (67.66 Lat.; 24.89 Long.). Silén's original publication consists of a list of 654 records of 86 plant species visited by a total of 173 insect taxa, resulting in 498 unique interactions.

In a first step, all of Silén's original records were manually digitized. Each unique plant-insect interaction per site and date was entered as a new row of data (hereafter referred to as 'record'). Full verbatim taxonomic species names of plants and pollinators (as originally stated in the historical document), verbatim locality and date (year, month and day) were included. Additional information on insect sex (i.e. m/f), insect behaviour (e.g. nectar sucking) and categorical abundance (e.g. "scarce", "many") was available for many records. Some records in the historic document contained additional comments or field notes which were also included in the dataset. In a second step, verbatim taxonomic plant and insect names were updated to currently accepted names and added to the interaction dataset. Each unique verbatim taxonomic name was cross-checked with the GBIF Backbone Taxonomy and/or Finnish species checklists and, if necessary, the taxonomic name was updated to the currently accepted name (according to the GBIF Backbone taxonomy). Additionally, we extracted information on order, family, and genus of each taxon. When verbatim taxonomic names could not be resolved to a valid taxon using the GBIF Backbone Taxonomy and checklists, we manually researched taxonomic revisions of the verbatim taxa in other databases, publications or checklists. When the verbatim species names could not be resolved to any currently valid species, the next finest available resolution (genus, family or order), was recorded. Further, we verified if the derived species have previously been reported from Finland using the online portal (laji.fi) of the Finnish Biodiversity Information Facility (FinBIF). Verbatim taxonomic names with corresponding updated names, sources for the new names, and information of occurrence in Finland as well as the GBIF identifiers of each taxon are provided for plants and insects in two supplementary data files [14] (Table 1).

Table 1 Overview of data files/data sets

Label	Name of data file/data set	File types (file extension)	Data repository and identifier (DOI or accession number)
Data set 1	Historical records of plant-insect interactions in subarctic Finland		figshare: https://doi.org/10.6084/m9.figshare.c.5828663.v4 [15]
Data file 1	InteractionData_Silen.csv	csv-file	figshare: https://doi.org/10.6084/m9.figshare.19130474.v4 [16]
Data file 2	Supplementary data files for: Historical records of plant-insect interactions in subarctic Finland	csv-files	figshare: https://doi.org/10.6084/m9.figshare.19130501.v2 [14]

After cross-checking taxonomic names, 153 insect taxa were resolved to species level (94.34% of records), 13 to genus (2.60% of records), six to family (2.14% of records) and one to order level (0.92% of records). All plant species could be resolved to species level. The recorded insect species belong to four orders (Diptera, Hymenoptera, Lepidoptera and Coleoptera) and include 88 genera in 30 families. The most frequently recorded insect families were Syrphidae, Apidae and Muscidae and the most frequently recorded genera were *Bombus, Platycheirus* and *Thricops.* Salicacea, Apiaceae and Asteracea were the most frequently recorded plant families, and in particular the plant species *Angelica archangelica, Salix caprea*, and *Chaerophyllum prescottii.*

Limitations

As important and valuable as historical data are, working with them often presents significant challenges and limitations. A thorough examination of the potential limitations, and methods to minimize them, is therefore required. The main limitations of the dataset presented here are that methodology, sampling effort and sampling conditions (e.g. time of day, weather) are incompletely described in the historical source. For example, it is not known whether the observation of flower visitors was conducted using standardized methods or if it was done opportunistically. It is also unclear what the sampling effort was for each plant species and whether it was comparable for all plant species. However, potential biases introduced by these limitations can be minimized by using appropriate resampling methods and statistical measures. For example, using a combination different

resampling approaches (i.e. individual-based and plot-based sampling) can minimize methodological biases, and standardizing data by number of individuals or sampling completeness can minimize biases due to differences in sampling effort.

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Authors' contributions
TMK and LZ conceived the ideas and designed the methodology; LZ led the data digitization; LZ led the writing of the manuscript. TMK contributed critically to the drafts and gave her final approval for publication. Both authors read and approved the final manuscript.

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Data Availability
The data described in this Data note can be freely and openly accessed on figshare under https://doi.org/10.6084/m9.figshare.c.5828663.v4 [14–16]. Please see Table 1 for details and links to the data.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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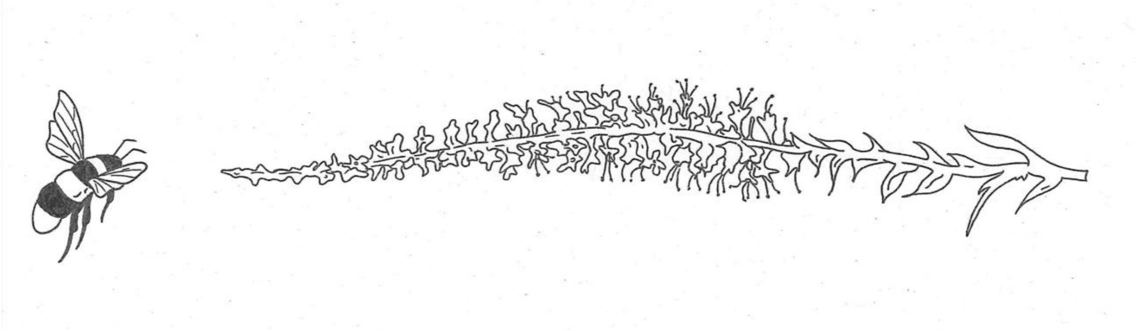
Chapter 5



Plant-pollinator network change across a century in the subarctic

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Plant–pollinator network change across a century in the subarctic

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Animal-mediated pollination is a vital ecosystem service to crops and wild plants, and long-term stability of plant–pollinator interactions is therefore crucial for maintaining plant biodiversity and food security. However, it is unknown how the composition of pollinators and the structure of pollinator interactions have changed across longer time spans relevant to examining responses to human activities such as climate change. We resampled an historical dataset of plant–pollinator interactions across several orders of pollinating insects in a subarctic location in Finland that has already experienced substantial climate warming but little land use change. Our results reveal a dramatic turnover in pollinator species and rewiring of plant–pollinator interactions, with only 7% of the interactions shared across time points. The relative abundance of moth and hoverfly pollinators declined between time points, whereas muscoid flies, a group for which little is known regarding conservation status and responses to climate, became more common. Specialist pollinators disproportionately declined, leading to a decrease in network-level specialization, which could have harmful consequences for pollination services. Our results exemplify the changes in plant–pollinator networks that might be expected in other regions as climate change progresses.

Mutualistic interactions between plants and their pollinators provide a fundamental ecosystem service of immense ecological and economic value[1,2] as most angiosperms depend on animal pollination for sexual reproduction[3,4]. Recent observations showing parallel declines of insect pollinators and their associated plants are alarming[5,6]. Plant–pollinator interactions depend on the distribution, abundance, phenology, physiology and behaviour of all species involved and consequently they may be particularly susceptible to change in response to increasing human pressures, such as climate and land use change[7,8]. The robustness of an interaction network to perturbations has been theoretically shown to be related to its structure, such as the degree of generalism (for example, refs. [9–11]). Highly generalized networks are more able to maintain their structure and services in the face of perturbations due to the high redundancy of interactions[12–14]. However, plants pollinated by specialists receive a higher quality of service, as the exclusiveness of these visitors results in the delivery of pollen from other individuals of the same species[15,16].

Plants and pollinators interact with each other on the basis of both their functional traits and their relative abundance, as species that are more common are more likely to be encountered. Trait matching is critical to pollination services, as some flowers are more effectively pollinated by bees, whereas others rely more on hoverflies, moths or other taxonomic groups[17]. Thus, stabilizing the composition of species and their interactions across space and time is crucial to safeguard the ecosystem service of pollination. To date, no studies have examined temporal patterns of plant–pollinator interactions across multiple functional groups of pollinators and across time horizons that are relevant to global change responses (decades or centuries), as most

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studies on pollinator networks only cover one or a few years of the present[18]. Thus, it is largely unclear whether plant–pollinator interactions have been stable over decades and centuries or whether the species and interaction network structures observed today have emerged more recently. The few studies quantifying network change over longer time periods have focused on single taxonomic groups (bee pollinators), noting local extinctions of native bee species[19], disproportionate losses of specialist species[19,20] and expanding interactions with exotic bee species[21]. These findings are attributed to the dramatic increase in human activity during this period. These long-term studies are all from temperate North America and western Europe, where most of our knowledge on network structure comes from and where pollinator communities are bee dominated[22,23]. Although non-bee pollinating insects make a major contribution to pollinator services globally[24], we have little knowledge regarding long-term trends in non-bee pollinators. There is a need for more studies from high-latitude ecosystems, which are currently experiencing large temperature variability and an increase in mean temperature much greater than the global average, and where bees are not the dominant pollinators[25].

While bees are considered the most numerous and important pollinators globally[24,26], at high latitudes flies often outnumber bees[27] and are considered the most important pollinators[28,29]. Anthophilic flies are diverse in their ecology but many species have more general larval and adult diets and more flexible breeding site preferences than do bee pollinators[30,31]. Therefore, flies may be more robust to environmental change than are other pollinator groups. This leads to the hypothesis that high-latitude regions might become more dominated by flies through time and that plants would become more dependent on fly pollinators (measured by species-level network indices such as the Pollination Service Index (PSI)). Alternatively, as the climate warms, bee species that were thermally excluded from high-latitude locations might successfully colonize, leading to increases in the relative abundance of bees. Species that are mobile and diet generalists should most easily persist in changing high-latitude environments and expand their ranges from lower to higher latitudes (for example, refs. [32,33]). Thus, we expect in general that high-latitude regions will have more generalist pollinators in the present than in the past, leading to a decrease in network-level specialization through time.

Given the distinct features of pollination in arctic and subarctic biomes, there is a need for information on long-term changes in pollinator composition and network structure in these regions. By using a unique historical dataset, we were able to examine changes in pollinator composition and plant–pollinator network structure over more than a century in Lapland, Finland.

Results and discussion

From 1895 to 1900, Frans Silén recorded insect visitors to plants near Kittilä, Finland[34] (Extended Data Fig. 1a–c). Kittilä is situated 120 km north of the Arctic Circle with little agricultural activity and low human density (Extended Data Fig. 1d,e). As most high northern locations, the area is experiencing rapid climate warming (Extended Data Fig. 2). We revisited the study area in 2018 and 2019 and re-collected data on Silén's best-sampled plant species, which represent several floral phenotypes that are expected to attract different compositions of pollinators. To make fair comparisons across time periods, much attention was paid to controlling for differences in sampling effort and sampling completeness between the historical and present datasets (Methods). We investigated differences in pollinator composition, pollinator network structure and the importance of different pollinator taxonomic groups to the network structure between time periods and we quantified to what degree dissimilarities in network structure are driven by components related to turnover of pollinator species (for example, loss of specialists or gains in generalists) or changes in the interactions of persisting species.

Composition of pollinators across time periods

Across 17 well-sampled plant species, we observed substantial shifts in the composition of pollinator taxonomic groups between the two time periods. Hoverflies (family Syrphidae), muscoid flies (families Muscidae, Anthomyiidae, Fanniidae and Scatophagidae), bumblebees (family Apidae, genus *Bombus*) and moths (families Noctuidae, Geometridae and Pterophoridae) were the four most abundant taxonomic groups of pollinators in our system. Hoverflies and moths were proportionally more abundant in the past, while muscoid flies and bumblebees were proportionally more abundant in the present (Fig. 1a). Assemblages of pollinators visiting a plant species were significantly dissimilar across time periods (analyses of similarities (ANOSIM): global $R = 0.40$, $P < 0.001$, Fig. 1b) but not across years within a time period (years in past—ANOSIM: global $R = 0.02$, $P = 0.28$; years in present—ANOSIM: global $R = -0.02$, $P = 0.59$). In the past, assemblages of pollinators visiting a plant species were significantly different across plant floral forms (ANOSIM: global $R = 0.29$, $P < 0.001$) but in the present this was not the case (ANOSIM: global $R = 0.05$, $P = 0.34$). These results persisted when we repeated the analysis excluding two outliers.

Particularly in the present, plant species were very similar in their visitation partners, irrespective of their floral form. The occurrence of many individuals of the same generalist species (as is the case in our system with muscoid flies of the genus *Thricops*) and the loss of specialists can result in a high degree of similarity in visitation partners across different plant species[35]. Plant species with specialized pollination systems, such as the typically nocturnally pollinated stalk-disc species *Dianthus superbus*[36] and *Silene vulgaris*[37] (Fig. 1c,d), have the greatest potential to receive altered pollination service from changes in pollinator composition. Only pollinators with a long proboscis can access the nectar reward of their tubular flowers while making contact with the reproductive parts of the flower. In the past, noctuid moth species such as *Syngrapha interrogationis*, *Plusia festucae* and *Autographa macrogamma* were observed visiting one or both of these plant species exclusively. Thus, they probably transported a high proportion of conspecific pollen, which is necessary for plant reproductive success[38,39]. In the present, visitors included mainly muscoid flies and hoverflies, which tend to have short mouthparts, hence it is unclear if they can effectively pollinate the flowers. Further, several plant species with more generalized floral forms, such as disk flowers, shifted from receiving visits from more hoverflies in the past to more muscoid flies in the present. Mean pollen loads carried by hoverflies and muscoid flies are comparable[40] but probably there are large differences between individual species. For example, the hoverfly *Volucella bombylans* is a large and hairy bumblebee mimic that was the main visitor of *Rubus arcticus* and *Geranium sylvaticum* (Fig. 1e,f) in the past. Hairiness of the face and pollen deposition are positively related[41,42], hence *V. bombylans* could possibly be a more efficient pollinator than the species of hoverflies and muscoid flies that visited the plants in the present.

Network structure and specialization

The interactions between plants and pollinators were highly dissimilar between time periods (Table 1). Only 7% of all observed interactions were present in both time periods (41 out of 601 unique interactions). Of the original interactions, 31% (41 of 132 unique interactions in the past) were persistent over time (Fig. 2). The contemporary network was distinctly more generalized (lower $H2'$) in its network structure than was the past network (Fig. 3). Highly generalized networks are considered to be resilient to perturbations and have a high network stability, as the high redundancy of interactions can buffer against loss of species[12,13]. To date, only a few experimental and observational studies have related structural network properties to the reproductive success of plants[22,43–45]. On one hand, generalized pollinators are expected to provide poorer pollination services compared to specialists because they carry and deliver less conspecific pollen to a plant species per visit[15,16]. On the other hand, there is also evidence that new and

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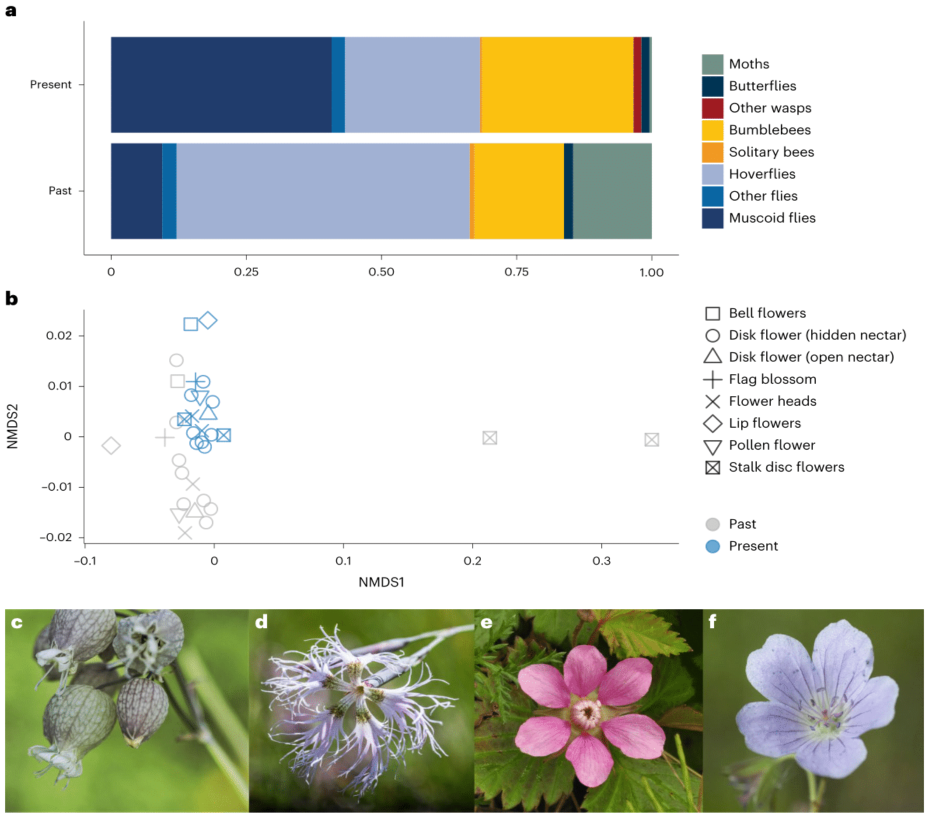

Fig. 1 | Changes in pollinator community composition across time points. a, Proportional composition of pollinator taxonomic groups in the past ($n = 899$) and present ($n = 2,657$). The largest changes in proportional abundance were observed in muscoid flies (+33.03%), hoverflies (−30.6%), moths (−13.9%) and bumblebees (+11.55%). **b**, Non-metric multidimensional scaling ordination (NMDS) visualizing dissimilarity distances of pollinator communities observed visiting plant species across time periods ($n = 17$) and plant floral forms ($n = 8$). **c**,**d**, Photos of *Silene vulgaris* (**c**) and *Dianthus superbus* (**d**), two plant species with stalk-disc flowers. **e**,**f**, Photos of *Rubus arcticus* (**e**) and *Geranium sylvaticum* (**f**), two plant species with disc flowers with hidden nectar. (All photos © L.Z).

Table 1 | Dissimilarity of interaction networks across time periods (β_{WN}) and its cumulative partitions related to rewiring (β_{OS}) and species turnover (β_{ST})

Taxa	β_{WN}	β_{OS}	β_{ST}
Full network	0.917	0.621	0.296
All flies	0.929	0.684	0.246
Hoverflies only	0.871	0.470	0.401
Bees	0.841	0.494	0.348
Butterflies and moths	1.000	0.037	0.963

generalized pollinators can sometimes have positive effects on plant reproductive output[46].

Higher generalization of a network over time can arise through two mechanisms. First, species turnover can lead to higher generalization if specialized pollinators are exiting and/or more generalized pollinators are entering the network over time. Second, interaction rewiring can result in higher generalization if persisting pollinator species engage in more interactions by becoming more abundant and/or by broadening their diet. Our results show that overall network dissimilarity (β_{WN}) in our system can be explained both by components tied to species turnover (β_{ST}) and by rewiring (β_{OS}) (Table 1). We find that changes in pollinator relative abundance were negatively associated with their specialization (d') (lm: slope = −0.88 (s.e. = 0.35), $F_{1,47} = 6.349$, $P = 0.015$, $r = 0.119$, $n = 47$; Fig. 3). As with other historical datasets on flower visiting insects (for example, ref. [19]), data on plant community composition were not collected and therefore we cannot explicitly consider how changes in the relative abundance of plant species may have contributed to the observed patterns. While we considered only plant species that persisted through time, it is possible that more generalized plants or plants with fly pollination syndromes have increased in relative abundance and that such changes contributed to the change in network structure through time.

Taxonomic subnetworks

Patterns of increasing network-level generalization and high dissimilarity of networks across time periods persisted when analysing subnetworks of separate pollinator taxonomic groups (Fig. 4a–d and Table 1) but the components related to turnover and rewiring underlying these

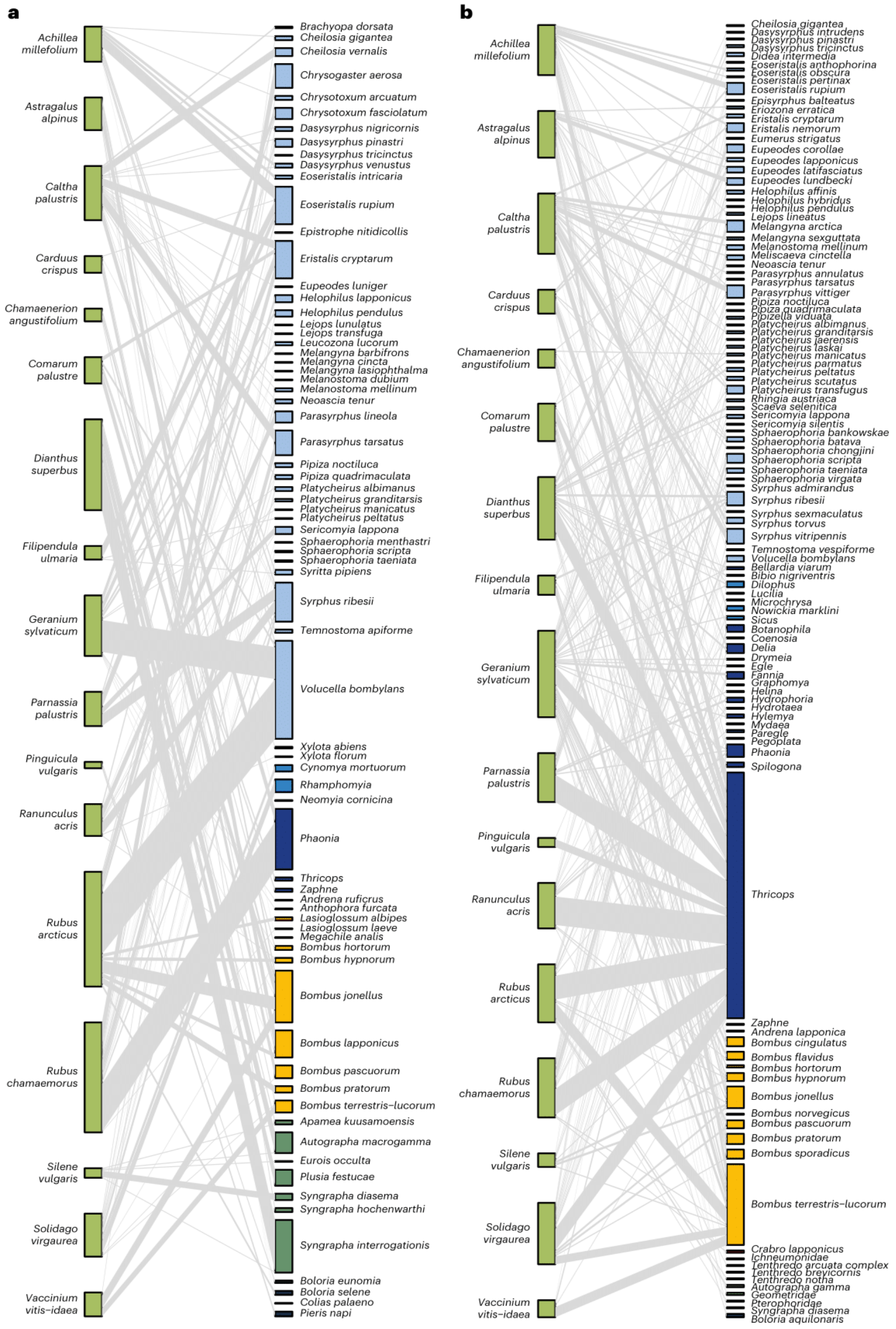

Fig. 2 | Weighted plant–pollinator interaction networks. a,b, Constructed using Silén´s data from the years 1895–1900 (**a**) and data from resampling in the years 2018–2019 (**b**). The rectangles represent plant species (left) and pollinators (right) and the connecting lines represent the weighted interactions among species. Colours of pollinators indicate the taxonomic group as in Fig. 1a. For improved visibility, the present network was rarefied to include the same number of interactions per plant species as the past network ($n = 631$ interactions).

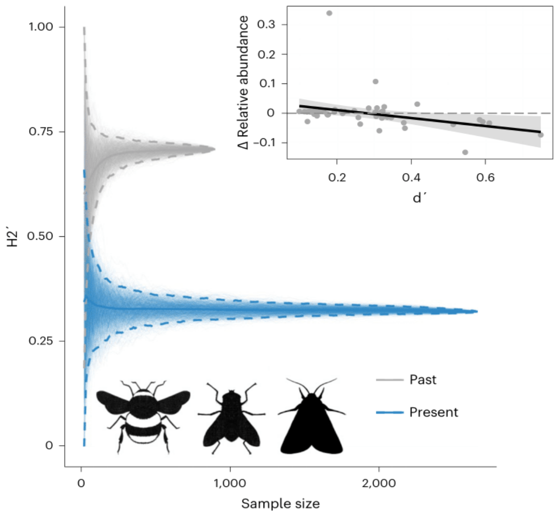

Fig. 3 | Network-wide specialization index (H2´) for the past and present networks and linear trend of species-level specialization (*d*´) and change in relative abundance. Network-wide specialization index (H2´) for the past and present networks are shown, with the linear trend between species-level specialization (*d*´) and change in relative abundance shown in the insert. Each thin line in the main figure represents H2´ calculated in one of 1,000 iterations, while the thick solid line represents the mean H2´ of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. In the insert figure, the black line represents the simple linear regression fit to data points (grey dots) and the grey shaded area represents the 95% confidence interval. Insect icons drawn by L.Z. Data from all pollinator taxa are included ($n = 219$). There was higher sampling effort and more interactions sampled in the present ($n = 899$ in the past; $n = 2657$ in the present), however, at a standardized sample size of interactions, H2´ was distinctively higher in the past. The regression model indicates that more specialized taxa (higher *d*´) underwent a larger negative change in abundance between time periods. Only species observed >10 times ($n = 49$) were included in the regression analysis, making the result robust, as specialization of rarely observed species tends to be overestimated.

patterns differ between taxonomic groups. In a subnetwork including all flies (muscoid flies, hoverflies and other flies), high dissimilarity of interactions between time periods was primarily due to the rewiring of interactions of persisting species (β_{OS}). However, as most of the non-hoverfly flies in our dataset are resolved to genus level, the role of species turnover might be underestimated. Therefore, we also analysed a subnetwork including only hoverflies, all of which are resolved to species level. When considering only hoverflies, the dissimilarity of interactions was explained in similar parts by β_{ST} (component tied to species turnover) and β_{OS} (interaction rewiring of persisting species). Of the persisting fly species, highly generalized taxa such as muscoid flies of the genus *Thricops* are involved in more links and a higher frequency of interactions now than in the past. More specialized taxa such as the hoverfly *Volucella bombylans* are involved in fewer interactions now (lm: slope = −0.49 (s.e. = 0.23), $F_{1,32} = 4.715$, $P = 0.0374$, $r = 0.128$, $n = 34$; Fig. 4b), either due to their lower abundance in the present or because they have become more specialized over time. Plants are more likely to encounter pollinators that are in high relative abundance and thus the rewiring of plants towards generalized flies might be due primarily to the increase in the relative abundance of these taxa[47,48]. Alternatively, persistent generalist flies might also have been able to broaden their diet over time, which might be expected if they are released from competition with other pollinating taxa that have declined through time[49].

In bees, a rewiring of persistent taxa was only slightly more important than the component tied to species turnover in explaining the dissimilarity of networks across time periods (Table 1). Unlike in flies there was no trend with regards to specialization and change in relative abundance between time periods (lm: slope = −0.45 (s.e. = 0.35), $F_{1,8} = 1.61$, $P = 0.240$, $r = 0.1675$, $n = 10$; Fig. 4a). While some generalized bumblebees, such as the highly generalized *Bombus terrestris-lucorum*-group increased in the number of interactions they were involved in, other generalized species, such as *B. jonellus*, decreased. Our species turnover results included observations of several bumblebee species in the present that were not recorded in the historical data ($n = 7$ in past, $n = 13$ in present), for instance *B. quadricolor*, which in Fennoscandia typically has a more southern distribution[50]. Globally, many bumblebee species have declined in range and abundance over the last century[51,52]. Thus, our finding that bumblebees have remained relatively stable over time in our study region is cause for optimism.

Contrary to the other pollinator orders, butterflies and moths may experience dramatic species loss, regardless of specialization (Fig. 4c). We refrain from formal tests, as few species of butterflies and moths were present in our community even in the past, limiting our explanatory power. However, in the past, moths showed high values of PSI (Fig. 5), indicating that these pollinators were of high importance for the specialized plants they interacted with.

Conclusion

Muscoid flies now provide large parts of the pollination service previously performed by moths and hoverflies in our system. It is not clear how efficient these flower visitors are in pollinating the plants that they visit. An important area of future research is to examine patterns of pollen deposition and the influences of pollinator taxa on plant reproduction. Our network indices are currently based on patterns of visitation and these are known to differ when pollen transport is considered rather than visitation[53,54]. The PSI, for example, cannot incorporate many mechanisms such as individual foraging fidelity that will influence patterns of pollen transport and ultimately plant reproductive success.

Two recent studies provide optimistic results suggesting that plants might maintain their reproductive success in the face of changing pollinator services. A study on eight plant species in our region, including *D. superbus* and *G. sylvaticum*, did not find evidence that plant reproduction is currently limited by pollen receipt[55]. Further, ref. [46] found that a *Silene* species with a nocturnal pollination syndrome had high reproductive success even when visited primarily by generalized diurnal pollinators. Muscoid flies have proven to be a robust group so far in our region and have increased in their relative abundance. However, it is possible that these flies will not continue to maintain their populations in the future, as previous studies found that in the high arctic, abundances of muscoid flies have been rapidly declining in recent years due to climate warming[56,57]. Such future declines could pose a threat to pollination also in our subarctic region.

Our research provides a comprehensive examination of long-term changes in interactions involving several pollinator taxonomic groups, which produces key findings that are likely to be of general relevance and points to important knowledge gaps that need to be addressed in future ecological research. All of the previous long-term studies focused exclusively on bees but the most dramatic changes in relative abundances we observed were in fly and moth pollinators. As land use change has been minimal over time but climate warming has advanced in this region, climate change is a possible mechanism that might explain the dramatic patterns we observe. Thus, our study may be a harbinger of what to expect in other regions as climate change progresses. However, we cannot directly isolate the role of climate change, as this unique study lacks replication along a gradient of climate change. While we worked diligently to make a fair comparison with the historic data,

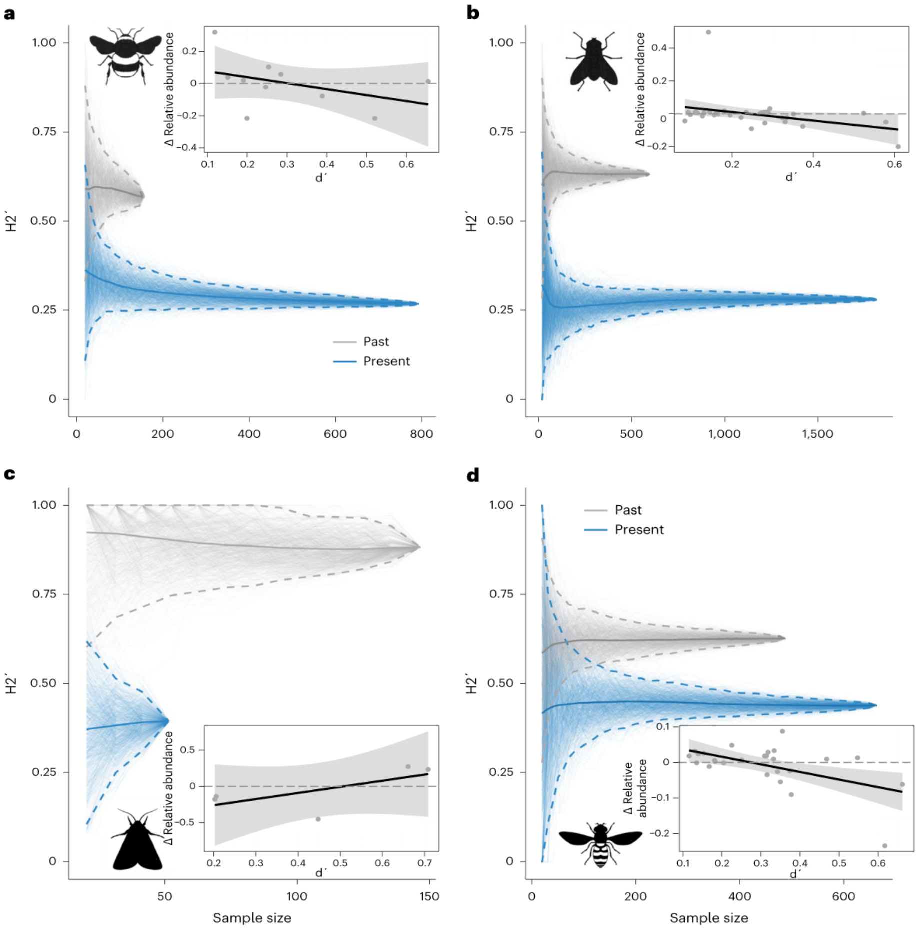

Fig. 4 | Network-wide specialization index (H2´) for the past and present networks and linear trends of species-level specialization (*d*´) and change in relative abundance for separate subsets of taxa. Network-wide specialization index (H2´) for the past and present networks of separate subsets of taxa are shown, with linear trends between species-level specialization (*d*´) and change in relative abundance given for these same subsets (inserts). Each thin line in the main figures represents H2´ calculated in one of 1,000 iterations, while the thick solid lines represent the mean H2´ of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. In the insert figures, black lines represent the simple linear regression fit to data points (grey dots) and the grey shaded areas represent the 95% confidence interval. Insect icons drawn by L.Z. **a**–**d**, Subsets include bees, wasps and bumblebees (**a**), all flies (**b**), butterflies and moths (**c**) and hoverflies (**d**). All subsets show the same pattern of higher generalization in the present (higher H2´) at standardized sample sizes of interactions. In flies, more generalized taxa are experiencing a significantly higher negative change in relative abundance and this pattern is primarily due to the hoverflies. Only species observed >10 times were included in the regression analysis ($n = 10$ for bees, wasps and bumblebees, $n = 34$ for all flies, $n = 5$ for butterflies and moths and $n = 27$ for hoverflies), making the result robust, as specialization of rarely observed species tends to be overestimated.

we cannot completely rule out the possibility that differences in biases in the collection of insects by our team and the historic collector also contribute to the observed pattern.

More studies are needed to assess the degree to which our results are specific to the subarctic context, where fly pollinators are known to be relatively more abundant and to be more important pollinators (for example, high altitude and latitude ecosystems). While an increasing number of studies are using museum collections to examine trends in bees across longer time intervals[58,59], these approaches are currently under-used, in particular for examining non-bee pollinators (but see ref. [60]) and plant–pollinator interaction networks[61]. Further, basic ecological research on the biogeography, abundance trends and threats to and ecosystem services provided by several understudied pollinator groups (for example muscoid flies, hoverflies and moths) is urgently needed to understand and forecast pollination. Research is also needed to link the structures of networks with the ecosystem services they provide, so that we can link the results of this study and others like it to threat assessments for plants.

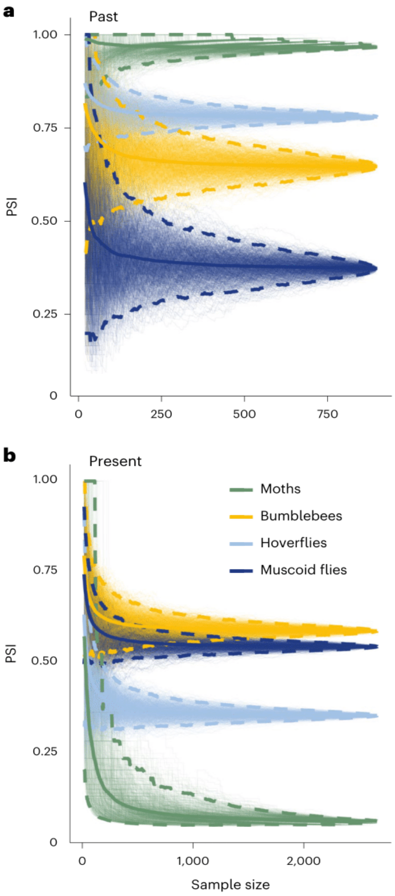

Fig. 5 | Values of the species-level metric PSI and 95% bootstrap confidence intervals. Each thin line represents PSI calculated in one of 1,000 iterations, while the thick solid lines represent the mean PSI of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. PSI takes into account the dependencies of the pollinators as well as the plants. High values of PSI indicate that the pollinator visits frequently and is specialized, whereas low values occur for pollinators that are uncommon and/or are unlikely to deliver conspecific pollen. **a**, In the past, moths showed a PSI of almost one, followed by hoverflies, bumblebees and muscoid flies. **b**, In the present, the PSI of moths dropped to nearly zero due to their low abundances, while abundant groups, such as muscoid flies, increased their PSI.

Methods

Data acquisition

Historic dataset. Between 1895 and 1900, Frans Silén recorded the interactions between plants and pollinators in the area of Kittilä. Kittilä is situated in Lapland, Finland, 120 km north of the Arctic Circle in a boreal biome. While Silén did not provide any information or description of the region, a travel book written by Cutcliffe Hyne, based upon his trip through Arctic Lapland in the summer of 1896, describes Kittilä to be a cluster of farms, with fields of barley and rye between the houses and herds of cows grazing beside the roadway[62].

Silén's aim was to observe as complete a set of insects visiting a focal plant species as possible[34], making his dataset a valuable benchmark for studying changes in plant–pollinator interactions. Silén classified focal plant species according to Knuth's 'Handbuch der Blütenbiologie'[63] (for example, as 'bumblebee flower' or 'syrphid flower'). However, he recorded insect visitors that did not necessarily fit into these categories, for example, he observed hoverflies visiting bumblebee flowers or butterflies and solitary bees visiting syrphid flowers. This minimizes probability of potential taxonomic biases. Silén's dataset was collected during 6 years but the individual plant species represented in it were typically observed for only 1–3 years (Supplementary Table 1). In his publication, Silén states that most of the observations were made in the vicinity of Kittilä village, from where his excursions extended about a mile to the north and as far south. One sampling location is exactly specified in Silén's records (the churchyard of Kittilä), while all other sampling sites are described approximately (for example, 'Kittilä town' or 'Aakenusjoki', a river close to Kittilä). While for most observations no time of day was recorded, Silén noted that certain typically night-pollinated plant species (*D. superbus* and *S. vulgaris*) were observed around midnight.

We updated the taxonomic nomenclature of plants and pollinators to match currently accepted taxonomic names. We have made our digitization and curation of the complete historical data, along with detailed descriptions of the data, openly available[64,65]. The historical dataset also contained information on the behaviour of the pollinator (for example, 'consuming pollen' and 'collecting nectar') and the quantity of interactions (in discrete groups, for example 'several' and 'very numerous') between plants and pollinators at a particular site and date. We assigned numerical quantities to the discrete quantitative groups. We used two different estimates, one conservative (for example, very numerous = 15 visits) and one generous (for example, very numerous = 100 visits, Supplementary Table 2) and found that our decisions for this numerical quantity did not significantly influence our results (Supplementary Table 3 and Supplementary Figs. 1–5). All the results presented in the main text are based on the conservative estimate. The information of the behaviour of pollinators indicates that Silén only recorded flower visitors that were engaging with the reproductive organs of the plant. One record for which the behaviour of the visitor was described as 'sleeping' was excluded from the dataset.

Contemporary dataset. In June and July of 2018 and 2019 we resampled plant–pollinator interactions in Kittilä. The one precisely known sampling site, the Kittilä churchyard, was resampled. To search for additional potential sites, we first used satellite imagery to locate non-dense forested and potentially accessible areas in the vicinity of the approximate historical locations described by Silén. For example, one of the approximate historical locations was the river Aakenusjoki, so we included accessible sites along the riverbank. We detected 20 potential sites, which we then visited and conducted rapid vegetation surveys to determine if they contained any of Silén's herbaceous plant species. Seven of the visited sites contained many of the species well represented in the historical dataset, hence they were selected as our additional study sites. All sites ($n = 8$) were located within a 6 km radius around the town centre of Kittilä in a range of habitats, including meadows, birch-dominated forests, ruderal areas, sandy riparian habitats and bogs. Generally, the sites are near-natural, as the region is characterized by low human population density, few invasive plant species and little agricultural land use (Extended Data Fig. 1d,e). On each site, two $30 \times 2\ \mathrm{m}^2$ transects were established. Along each transect, all flower visitors actively contacting the reproductive organs of a flower were recorded during 15-min observation periods (excluding handling time). Here, we synonymously refer to these flower visitors as pollinators, although we acknowledge that not all flower visitors are effective pollinators. Permits for field collections were obtained from the Lapland Centre for Economic Development, Transport and the Environment. Each site was sampled four times on separate days every year (except for one site in 2018 that was only sampled on one day and was mown afterwards and one site that was sampled five times in 2019). This resulted in a total of 1,860 min of transect-based observation. In addition to the transect sampling, targeted observations were made on plant species that were well represented in the historic data. The total observation time for each focal plant species is specified in Supplementary Table 1. Generally, sampling took place at times of the day in which pollinators under midnight sun conditions are most active (hours 7:00–21:00)[66]. We sampled each site at different times of day (both mornings and afternoons) and sampling took always place in favourable weather (no rain and no strong wind). The plant species that were observed by Silén during night-time (*D. superbus* and *S. vulgaris*) were also observed mainly at night in our study.

Statistical analyses

All statistical analyses were conducted in R v.4.0.3 (ref. [67]).

Comparability of datasets. For Silén´s dataset, no detailed methodological descriptions or estimates of sampling effort were available. We investigated possible differences in sampling between historic and contemporary datasets before other analyses to ensure that sampling effort did not affect our results. For the 30 plant species observed in both time periods, we noted the number of observation days and the number of interactions and calculated sampling coverage using the package iNEXT[68]. Only observations on plant species fulfilling following three criteria were included in the final dataset: (1) observed on at least 2 days in each time period, (2) at least five observed interactions in each time period and (3) sampling coverage is at least 60% in each time period. Seventeen plant species fulfilled these criteria and were included in the final dataset (Supplementary Table 4). Pollinator taxonomic resolution was included in the final dataset as the finest possible common resolution across both time periods (species level, 59.82%; genus level, 39.44%; family level, 0.74%). This high proportion of taxonomic resolution at the genus level is largely introduced by muscoid flies, and in particular by the high number of *Thricops* in the present dataset, which are identified at the genus level. In the historical dataset, *Thricops* is represented by only one observation, therefore higher taxonomic resolution in the present dataset would not have been of great additional informational value. Outside of the muscoid flies, 96.8% of all individuals were resolved to species level. For simplicity, we here refer to the highest common taxonomic resolution as species. For all plant species represented in the final dataset, we extracted information on floral form (classified after Kugler) from the database biolflor[69]. As the historical dataset contains categorical rather than quantitative information on insect abundances, we focused on analyses that use relative abundances and refrain from analyses that are sensitive to absolute abundances (for example, species richness analyses, which are sensitive to absolute abundance because of the nonlinear relationship between number of individuals and the number of species).

Change in temperature over time. To provide context for our study on the magnitude of temperature change between time periods, data on interpolated gridded values of mean monthly temperature in Kittilä from the years 1895 to 2019 were obtained from the Finnish Meteorological Institute. We calculated the yearly mean vegetation period temperature by averaging the mean monthly temperatures of the months April to September. To examine trends of change in mean vegetation period temperature across years, we performed a linear regression (using lm in the stats package[67]; Extended Data Fig. 2).

Composition of pollinators across time periods. To investigate potential shifts in pollinator assemblages across time periods, we calculated and plotted the proportional abundance of pollinator groups observed on the 17 focal plants in each time period (Fig. 1a). To visualize the distances of pollinator assemblages visiting a focal plant species across time periods, we used non-metric multidimensional scaling ordination based on Morisita–Horn index using metaMDS from package vegan[70] (Fig. 1b). The Morisita–Horn index was chosen because it is not strongly sensitive to species richness and sample size[71]. To do so, we built an interaction matrix, with rows representing the plant species per time period, columns representing pollinator species and the value in the cells indicating the interaction frequency between plants and pollinators (pooled across years within a time period). To statistically test for differences in the assemblage of pollinators visiting a focal plant species between time periods, we performed ANOSIM. The ANOSIM test statistic (global *R*) is a comparative measure of the mean ranked dissimilarities within and between a priori defined groups. In our case, the dissimilarities of an assemblage of pollinators of a plant species are ranked and the mean ranked dissimilarities are then compared within and between time periods. A global *R*-value close to 1 indicates that replicates within a group (time period) are more similar to each other than to any replicates from different groups, while a global *R* of 0 implies no segregation into groups. The significance of the global *R* is determined by permuting the membership of objects in the groups.

Pollinator communities are known to exhibit high interannual variability and thus it was important to also test if the composition of pollinators visiting a plant species was significantly different across the years within a time period. For this, we constructed interaction matrices containing frequencies of interactions separately for each year within a time period and tested if assemblages of pollinators visiting a focal plant species are significantly dissimilar across sampling years within one time period using ANOSIM. Further, we tested if the pollinator assemblages visiting a plant species within each time period were significantly different across floral forms using ANOSIM. All ANOSIM analyses were performed using the anosim function from package vegan[70] and corroborated by 9,999 permutations.

Network structure and specialization. We visualized plant–pollinator interaction networks for both time periods using plotweb in the package bipartite[72] (Fig. 2). Network-level specialization (H2′) was calculated for the full network using the networklevel function in bipartite. H2′ is a metric that is not sensitive to the number of species in the network[73]. To further ensure that differences in the sample size of interactions between time periods did not influence the results, we bootstrapped the value of H2′ 1,000 times for each time period using boot_networklevel in bootstrapnet[74] (Fig. 3). To investigate whether specialist species are more prone to decline, we calculated *d*´ for each species using specieslevel in bipartite (Supplementary Data 1), on the basis of data pooled across both time periods. Value *d*´ is a scale invariant metric that measures specialization of each species on the basis of its discrimination from a random selection of partners[73]. It has to be noted, however, that in both time periods, the focus was on sampling particular plant species and the result might not be easily contrasted to other studies that sample uneven communities in plots or transects[73]. Only species for which a total of >10 individuals were observed (22.37% of records, see Extended Data Fig. 3 for a histogram of the frequency of observations for all species) were considered because rare species in networks often appear to be more specialized than they really are. However, rare species also tend to be more specialized than common species and, thus, finding an effect even when naturally rare species are excluded suggests that our results are robust. We then ran linear regressions to assess whether change in relative abundance across time periods depended on *d*´ (Fig. 3). To test whether particular taxonomic groups drive potential changes in H2′, we repeated the analyses on four subsets of the data including only: (1) bees, wasps and bumblebees (order Hymenoptera), (2) all flies (order Diptera), (3) butterflies and moths (order Lepidoptera) and (4) hoverflies (family Syrphidae) (Fig. 4). The subset containing only hoverflies was included to further clarify mechanisms within the diverse order of flies. We chose hoverflies rather than muscoid flies because all hoverflies were taxonomically resolved to species level and our explanatory power was not limited by low observations in the past, as was the case for muscoid flies.

Dissimilarity of interaction networks. Dissimilarity in plant–pollinator interaction networks can originate through changes in interactions between shared species or through turnover of species (plants and pollinators) involved in the network[75]. Using the function betalinkr, implemented in the bipartite package, we calculated dissimilarity of all interactions in the network between time periods (β_{WN}) and the two additive partitions of dissimilarity, β_{OS} and β_{ST}. β_{OS} describes the component calculated from the dissimilarity of interactions between shared species, that is interaction rewiring, while β_{ST} represents the component that cannot be calculated from the dissimilarity of interactions between shared species (relative rewiring to overall dissimilarity which, all non-turnover mechanisms being accounted for in the decomposition, can be explained by turnover mechanisms[76]). We calculated network dissimilarity and its two components for the full dataset and for four subsets of the data including only (1) bees, wasps and bumblebees, (2) all flies, (3) butterflies and moths and (4) hoverflies (Table 1).

Roles of different taxa in the network. Across time, the role and importance of specific pollinators for the plant species in the network might change. We investigated this by calculating the PSI[77], for the four most common pollinator groups and for both time periods using specieslevel in bipartite. PSI is based on the idea that a pollinator is more important for a plant species when it is common and specialized. Rare pollinators will encounter, and therefore pollinate, a flower less frequently and generalists may deliver a large proportion of heterospecific pollen per visit[77]. Hence, this quantitative metric can be used to describe the importance of the group in providing pollination services based on its abundance and specialization in the network. Specifically, a low PSI indicates that, theoretically, a pollinator is irrelevant to all plant species either because it is very rare or because it is highly generalized and will deliver mostly heterospecific pollen to a plant. A high PSI indicates that a pollinator is of high relevance, either because it is very common or because it is a specialist delivering a large proportion of conspecific pollen to a plant specialized on the pollinator[77]. The metric was bootstrapped 1,000 times (gg_specieslevel_web_by_web in bootstrapnet) to ensure comparability across the two differently sized networks (Fig. 5).

In addition to using the full dataset (all 17 plant species), we re-ran all of the analyses using subsets of only the six best-sampled plants (*Achillea millefolium, Comarum palustre, Dianthus superbus, Geranium sylvaticum, Rubus arcticus* and *Solidago virgaurea*) and of only plants that had a higher frequency of interactions in the past than in the present time period (*Caltha palustris, Dianthus superbus, Rubus arcticus, Rubus chamaemorus* and *Vaccinium vitis-idaea*). We found that none of our main findings changed when using only these subsets. This gives us confidence that our patterns are robust to sampling differences across plant species and time periods.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

We published a description of the full historical data[64] and have made the data openly available on figshare (https://doi.org/10.6084/m9.figshare.c.5828663.v4)[65]. The subset of historical data and current data used in this work are freely available from GitHub (https://github.com/LeanaZ/Dramatic-plant-pollinator-network-change-across-more-than-a-century-in-the-subarctic). Information on location and accessibility of preserved insect specimens can be requested from the authors. The Biolflor database can be accessed via https://wiki.ufz.de/biolflor/index.jsp.

Code availability

The R code used for main analyses in this work is available from GitHub (https://github.com/LeanaZ/Dramatic-plant-pollinator-network-change-across-more-than-a-century-in-the-subarctic).

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Author contributions

T.M.K., J.B. and L.Z. conceived the ideas and designed the methodology. L.Z. and T.M.K. collected the data. L.Z. led the formal analysis and visualization of the data. L.Z. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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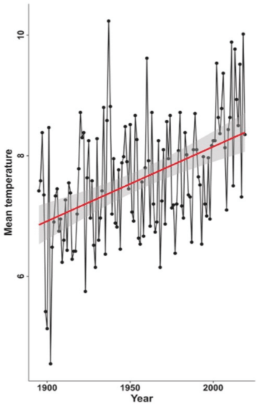
Extended Data Fig. 1 | Background on collection of the historical dataset and the study region. a, Location of the study region Kittilä, Lapland, Finland. Kittilä is situated ~120 km north of the Arctic Circle. **b**, Portrait of Frans F. Silén, who recorded plant–pollinator interactions in Kittilä in the years 1895–1900 (_. F. _qvist, Haparanda. *Metsänhoitaja Frans Johan Frithiof Silén* (Forester Frans Johan Frithiof Silén). Photo licensed under CC BY 4.0). **c**, A fly specimen collected by F. Silén in Kittilä; many specimens from his research are stored in the Finnish Museum of Natural History (© L. Zoller). **d-e**, Photos of the landscape near Kittilä in **d**, the year 1932 (Mikkola, Erkki. *Panoraama Kittilästä: Kumputunturi Jeesiörovan Pohjoislaidalta* (Panorama of Kittilä: Kumputunturi from the northern slope of Jeesiörova). Photo licensed under CC BY 4.0) and **e**, the year 2018 (© L. Zoller). Both photos show the view towards the fell 'Kumputunturi'. The village of Kittilä lies just outside the photographic frame on the left.



Extended Data Fig. 2 | Linear regression of mean vegetation period temperatures over the years 1895–2019. Black circles indicate annual mean vegetation period temperatures. The relationship was tested using a simple linear model. The red line depicts the regression line and the grey shaded area indicates the 95% confidence interval. Mean vegetation period temperature significantly increased by 1.53 °C across 124 years (two-tailed t-test, no adjustment for multiple comparisons: $F_{1,123} = 29.78$, $P > 0 .001$, r = 0.1949).

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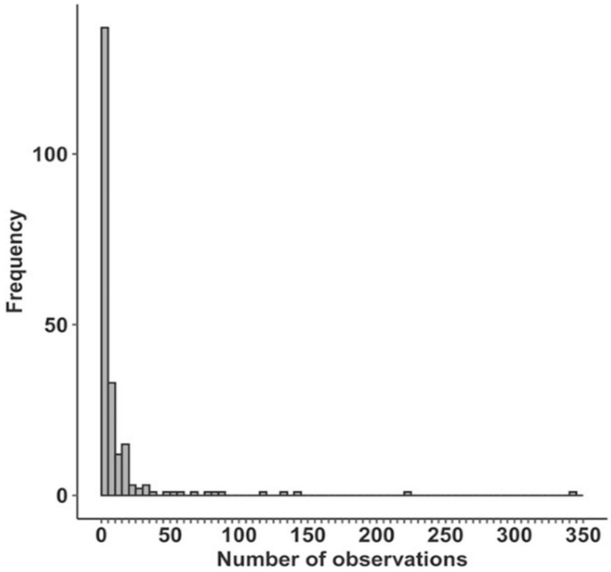

Extended Data Fig. 3 | Histogram showing the frequency of observations of pollinator species. Observations of pollinators are pooled across time periods, for the past observations, conservative numerical estimates were assumed. For better visibility, one species with 917 observations (*Thricops*) was excluded from the histogram. Only species with >10 observations (22.37% of species) were used in regressions of change in relative abundance and species specialization (*d´*).

Chapter 6

General Discussion

6.1 Synopsis

Pollination is of immense ecological and economic importance, and increasing evidence of declines in pollinators and their associated plants due to human stressors is a cause for concern. Interactions between plants and pollinators can be presented as networks whose properties can provide information about the robustness or resilience of communities. Because the occurrence of an interaction depends on a number of factors, plant-pollinator interactions are highly variable in time and space. To adequately understand and ultimately predict the effects of human stressors on the ecosystem service of pollination, it is critical to quantify patterns and understand the potential processes that result in plant-pollinator interaction variation across space and time. However, our current understanding of variation among plants, pollinators, and their interactions has gaps. For example, most research considers patterns across seasons or a few years. Examining network change at different time periods within a day provides valuable information about how pollinator activity changes due to weather, cloud cover and other factors. Examining network change across longer time intervals, such as across decades or a century, provides important insight into the potential effects of drivers such as land use and climate change. However, research across long time horizons is sparse because obtaining appropriate data to study these time scales can be difficult. In addition, our current knowledge is focused on a few taxonomic groups (e.g., bees, butterflies, and syrphid flies), while little is known about other groups, such as non-syrphid flies. Finally, the current literature is spatially biased, with tropical and high latitude regions underrepresented. High latitude systems are important areas for research on plant-pollinator interactions because climate change is progressing more rapidly compared to lower latitudes, and thus findings from high latitudes could provide early information about the patterns to expect for the rest of the world as climate change progresses.

In this dissertation, I address the aforementioned knowledge gaps by examining patterns of variation in the composition of pollinators, plants, and their interactions across different spatial and temporal scales at a high latitude site, and by addressing the potential role of climate change as a driver. I have collected an extensive dataset spanning three locations along a latitudinal gradient in Finland (Chapter 2). At the northernmost location, Kittilä, I examined pollinator community change at two different temporal grains (24-hours and 120 years), first by collecting data across the entire 24-hour cycle (Chapter 3) and second by digitizing and processing a historical dataset of plant-pollinator interactions at the same site dating back over 120 years (Chapters 4 and 5).

In Chapter 2, I show that species richness and community composition changed across three locations along a latitudinal gradient. I confirm the generality of the diversity-latitude gradient at regional scales, as well as the increasing dominance of fly pollinators and a general decrease in network specialization at higher latitudes. Furthermore, I show that beta diversity of interactions was high across latitudes, with species turnover being the main driver of this pattern, but also that dissimilarity of interactions can vary considerably at local scales. The results obtained in Chapter 3 show that patterns in daily foraging activity of pollinators during the polar day were robust. However, there were substantial differences in activity patterns between two climatically contrasting years, with particularly strong responses in fly behavior to changing environmental conditions (i.e. high temperatures). In Chapter 4, I present the process of digitizing and curating a historical dataset collected by Frans F. Silén and advocate for the value of historical data. Finally, in Chapter 5, I find that interaction networks changed dramatically over two time points more than 120 years apart. In particular, muscoid flies became more abundant over time, while specialized species declined disproportionately.

6.2 Discussion

Across the different research chapters, I found great variation in species diversity and composition and in the structure of interaction networks across space and time. In my study system, I found that interactions involving highly generalized muscoid flies persisted over large geographic distances and over a time span of more than a century. These results suggest that flies are providing a constant pollination service across highly variable environments. It is well documented in the literature that most interactions are highly variable over space and time, with only few interactions persisting (Aizen et al., 2012; Carstensen et al., 2014; Chacoff et al., 2018; Dupont et al., 2009). For example, Chacoff et al. (2018) found that few interactions occurred consistently over six years, and Aizen et al. (2012) detected few shared interactions across spatially isolated hills.

The few interactions that persist across time or space generally involve common generalist species (Aizen et al., 2012; Chacoff et al., 2018; Resasco et al., 2021). Because of their flexibility in diet or nesting requirements, generalist species are generally better able to persist in a wide range of environmental conditions, and have more potential interaction partners than species with narrower tolerances (Resasco et al., 2021). Generalists are integral to network stability, and communities dominated by generalists are more robust, with many theoretical studies showing that there are fewer secondary extinctions in response to species loss (Dunne et al., 2002; Lever et al., 2014; Memmott et al., 2004; Thébault and Fontaine, 2010).

I found in my research that the network property of specialization changed over time and space, and I found a pattern of higher generalization of networks in the modern time period and at higher latitudes. This is likely due to the prevalence of highly generalized muscoid flies in the present and in the north and the disproportionate decline of specialized species across time. This is contrasting to studies that report, that despite high variability in species composition and identity of interactions, structural properties of networks tend to remain relatively unchanged (Alarcón et al., 2008; CaraDonna et al., 2021; Dupont et al., 2009; Miele et al., 2020). However, network structure is likely to remain stable over shorter timespans, but over longer temporal distances, network structure is predicted to change significantly (CaraDonna et al., 2021). Less diversity and greater generalization of species are also predicted in more variable and less predictable environments (Optimal Foraging Theory (MacArthur and Pianka, 1966)), and in response to human stressors (Doré et al., 2021). Although generalists are integral to network stability, higher generalism could negatively affect pollination service. Generalist pollinators are considered less effective because they deliver an increased proportion of heterospecific pollen to plant stigmas (Aizen and Feinsinger, 2003; Waser and Ollerton, 2006). On evolutionary time scales, differences in network specialization could influence the co-evolutionary dynamics of pollinators and their associated plant species. For example, specialists may have a higher rate of diversification because host switching can lead to rapid reproductive isolation (Kay and Sargent, 2009). Therefore, loss of specialists could also mean loss of unique ecological interactions and co-evolutionary pathways (Aizen et al., 2012).

Thus, both specialist and generalist species are integral to the ecosystem service of pollination. Specialists are particularly at risk of decline (Burkle et al., 2013; Jacquemin et al., 2020), and thus, many conservation strategies are primarily focused on helping these taxa. Conservation efforts tend to ignore common and widespread species such as flies (Kearns, 2001; Orford et al., 2015). As these taxa are currently performing a large portion of pollination services, it is important for future conservation research to know more about their threat status. Because ecological requirements may differ between different insect groups, such as flies and bees (Kearns, 2001), flies may not benefit from measures taken for bees. I have shown that in Kittilä, the northernmost of my study locations, where flies play a particularly important role, there was an increase in the relative abundance of flies during the last century. However. I also showed that a heatwave disproportionately affected the foraging behavior of flies, thus they may be particularly vulnerable to the effects of climate change. It is likely that as climate change progresses, the suitable habitat of the typically cold-adapted fly pollinators will decrease (Larson et al., 2001). A dramatic decline in flies has already been noted in the high Arctic (Tiusanen et al., 2016).

While flies are of particular importance at high latitudes and altitudes (Arroyo et al., 1982; Kearns, 1992; Kevan, 1972; Lefebvre et al., 2018; Tiusanen et al., 2016), they are also ubiquitous in many other ecosystems. The flowers of over 1100 species of plants from 172 families are reportedly visited by flies, – no doubt an underestimate of the actual number, as the authors themselves note (Inouye et al., 2015). Flies are also important in agricultural systems (Orford et al., 2015) and they are integral pollinators of numerous crops and plants around the world, such as cocoa, mango, oil seed rape, and onion (Dag, 2009; Kaufmann, 1975; Rader et al., 2009; Saeed et al., 2008; Thompson et al., 2021). Dipterans are generally considered less sensitive to human stressors (Doré et al., 2021), and may be less sensitive to agricultural practices (Orford et al., 2015). However, it is possible that any declines have been overlooked, and further studies are needed to assess their vulnerability. Given the current decline in pollinators, along with large unknowns, such as the effects of climate change, it is time to better understand the role of lesser-known pollinator groups and to consider community dynamics and potential threats at multiple scales.

6.3 Limitations

I have often discussed the link between the observed patterns and climate change in the research chapters of this thesis, and it is possible that the patterns we observed are due to climate change, which has been dramatic in my study region. However, it remains to be mentioned that the patterns presented are descriptive in nature, and the data do not allow us to draw definitive conclusions about the causal factors of the observed patterns. In general, this is difficult in network studies with large temporal and spatial distances because so many environmental factors correlate with space and time. It is a major task of future studies to disentangle the effects of different drivers of network variation, such as land-use change or aspects of climate change. Moreover, it is unknown how generalizable my results are to other regions of the world, such as the Southern Hemisphere (Pauw and Stanway, 2015).

My thesis considered how the structure of visitation networks varied across space and time, but I did not measure pollen transport or plant reproductive success, and so the consequences of changing visitation structure on the ecosystem service of pollination is not known. I expect that plants in more generalized visitation networks might receive lower quality services if visiting pollinators deliver mostly heterospecific pollen (Ashman et al., 2020), but I did not empirically confirm whether this occurs in my system. Most studies that measure plant-pollinator interactions across space and time do not consider pollen transport and plant reproductive success because it labor-intensive to do this across many networks (Arceo-Gómez et al., 2019; Ashman et al., 2020; Bennett et al., 2020).

Sampling interactions among plant pollinators is also labor intensive, and thus no network study has complete information about all interactions that occur in a defined spatial and temporal grain. Spatiotemporal overlap and abundance of interacting species are the most important determinants of interaction patterns, thus interactions are more likely to be detected in species that occur at higher abundances (Chacoff et al., 2018).

Disentangling sampling effects from biological processes in network studies remains an important challenge (CaraDonna et al., 2021; Vázquez et al., 2009). Sampling artifacts can arise from a variety of sources, including insufficient sampling effort, broad taxonomic resolution, unequal probabilities of species detection, or sampling methods (Vázquez et al., 2009), and they can cause significant changes in observed interactions and in network metrics (Blüthgen et al., 2008; Chacoff et al., 2012; Dormann et al., 2017; Fründ et al., 2016; Jordano, 2016; Nielsen and Bascompte, 2007; Schwarz et al., 2020). Such sampling effects can be remedied by achieving the highest possible sample completeness, however this is not always possible to control, for example, when working with historical data. Then, sampling effects can be mitigated by standardizing the data in terms of sample size, method, or effort to allow comparisons across different systems, and by using network metrics that are insensitive to sampling effort (Gibson et al., 2011; Rakosy et al., 2022; Vázquez et al., 2009).

6.4 Future implications

This dissertation has highlighted the important role of common and generalist species, such as muscoid flies, and I suggest that more effort should be invested in the future in understanding their conservation status. For example, globally, there are over 5000 described species of flies in the family Muscidae (Merritt et al., 2009), but only two species are currently listed on the IUCN Red List - one of which is categorized as data deficient. Furthermore, very little is known about their physiology, such as their critical thermal thresholds, making it virtually impossible to predict the effects of climate change on them. This highlights the need for future basic research on distribution, abundance and physiology of flies, and for pollination studies to take a multitaxa approach and include pollinators other than bees and butterflies. Furthermore, common and widespread species should not be ignored in biodiversity conservation efforts.

Plant-pollinator interactions involve both visitation and pollen transport. Methodology for quantifying visitation involves observing and/or collecting pollinators in the field and identifying them to species using microscopy, as I did for this thesis. Pollen transport is rarely quantified in a next step, but when it is, it is typically done by identifying pollen on insects using microscopy (e.g. de Manincor et al., 2020). Pollen identification is time consuming and requires expert knowledge in palynology. However, automated methods, for example using flow cytometry and machine learning (Dunker et al., 2021) might accelerate the speed of this data collection, and make this pollen transport a more feasible response variable to measure in the future.

Although not part of this dissertation, I supervised an MSc student on a project to investigate pollen limitation - the insufficient reception of compatible pollen - in eight plant species at my northernmost study region. Surprisingly, none of the pollinator-dependent plant species were found to be pollen-limited (Koch et al., 2020). These insights have been valuable for providing a more complete understanding of the state of the pollination service at this study site. Relating structure and functionality of pollination networks is something that has rarely been attempted so far (Ballantyne et al., 2015; Ferrero et al., 2013; Kaiser-Bunbury et al., 2010), and future work would benefit from adding a functional perspective to better understand changes in plant-pollinator interactions.

Spatial variation in plant and pollinator communities and their interactions have been well studied at different spatial scales, and in many different geographic regions, and the insights of these studies have often been reviewed and synthesized (e.g. Doré et al., 2021; Hagen et al., 2012; McCabe and Cobb, 2021; Trøjelsgaard and Olesen, 2016; Tscharntke and Brandl, 2004; Tylianakis and Morris, 2017; Vizentin-Bugoni et al., 2018). Temporal variation has been less well studied, and the use of historical data in ecological studies remains underutilized (Rakosy et al., 2022). As historical documents and museum collections become more digitized, historical data will become more available and more researchers are likely to study long temporal trends in plant-pollinator interactions. This provides an opportunity to synthesize patterns of variation over long periods of time and to determine the generality of the patterns described in Chapter 5.

6.5 Concluding remarks

To summarize, in this dissertation I have attempted to fill knowledge gaps about variation in plant and pollinator communities and their interactions in the context of climate change. For this, I have investigated different spatial and temporal scales. Working with historical data is time consuming and presents significant challenges, and thus there are few studies that have attempted to do this despite the recognized importance of the approach. Here, I demonstrate the importance of considering different temporal and spatial scales for understanding patterns and the potential drivers that may affect pollinator communities. Furthermore, I show that specialized, highly efficient pollinators have declined significantly, and that generalized and common species now play even more pivotal roles for network robustness. Thus, conservation threat assessments are needed for both specialists and generalists. Regarding the latter group, our knowledge is currently too limited to properly assess the threats they face, and there are virtually no conservation measures in place.

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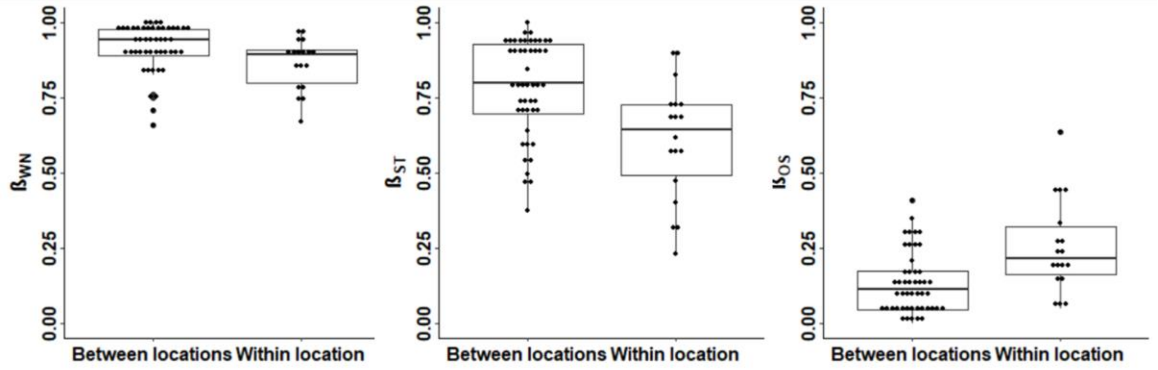
Photos taken by Leana Zoller

Appendices

Supplementary Material Chapter 2



Supporting Figure 1: Boxplots of overall interaction dissimilarity (β_{WN}) and its components related to species turnover (β_{ST}) and interaction rewiring (β_{OS}) for all pairwise site comparisons. Between location site dissimilarity (N-C, C-S, N-S) is compared to within location site dissimilarity (N-N, C-C, S-S).

Supporting Table 1: Beta-diversity of interactions and turnover and nestedness components: β_S describes the dissimilarity in the species composition of communities and β_{WN} describes the overall interaction dissimilarity. β_{OS} and β_{ST} are the two additive partition of β_{WN} , with β_{OS} describing the dissimilarity of interactions established between shared species, and β_{ST} the dissimilarity of interactions related to species turnover.

sites compared	localities compared	type of comparison	*βS*	*βOS*	*βWN*	*βST*
K1-K2	N-N	within location	0.508	0.2	0.783	0.583
K1-K3	N-N	within location	0.668	0.155	0.845	0.69
K1-K4	N-N	within location	0.63	0.134	0.751	0.616
K1-P1	N-P	between location	0.861	0.119	0.901	0.782
K1-P2	N-P	between location	0.635	0.152	0.75	0.598
K1-P3	N-P	between location	0.738	0.252	0.946	0.693
K1-P4	N-P	between location	0.388	0.286	0.659	0.373
K1-L1	N-L	between location	0.764	0.083	0.884	0.801
K1-L2	N-L	between location	0.849	0.055	0.974	0.92
K1-L3	N-L	between location	0.71	0.265	0.918	0.654
K1-L4	N-L	between location	0.906	0.097	0.986	0.889
K2-K3	N-N	within location	0.533	0.267	0.669	0.402
K2-K4	N-N	within location	0.678	0.277	0.845	0.568
K2-P1	N-P	between location	0.843	0.098	0.909	0.811
K2-P2	N-P	between location	0.715	0.114	0.826	0.712
K2-P3	N-P	between location	0.626	0.297	0.852	0.555
K2-P4	N-P	between location	0.568	0.15	0.841	0.691
K2-L1	N-L	between location	0.798	0.129	0.975	0.846
K2-L2	N-L	between location	0.831	0.031	0.957	0.926
K2-L3	N-L	between location	0.654	0.129	0.84	0.711
K2-L4	N-L	between location	0.844	0.151	0.962	0.811
K3-K4	N-N	within location	0.72	0.178	0.907	0.729
K3-P1	N-P	between location	0.867	0.126	0.917	0.791
K3-P2	N-P	between location	0.771	0.097	0.891	0.794
K3-P3	N-P	between location	0.742	0.206	0.944	0.738
K3-P4	N-P	between location	0.738	0.171	0.899	0.728
K3-L1	N-L	between location	0.811	0.061	0.977	0.916
K3-L2	N-L	between location	0.867	0.01	0.977	0.967
K3-L3	N-L	between location	0.745	0.043	0.942	0.899
K3-L4	N-L	between location	0.909	0.036	0.99	0.954
K4-P1	N-P	between location	0.759	0.318	0.904	0.586
K4-P2	N-P	between location	0.483	0.255	0.709	0.454
K4-P3	N-P	between location	0.635	0.348	0.891	0.543
K4-P4	N-P	between location	0.651	0.264	0.76	0.496
K4-L1	N-L	between location	0.824	0.038	1	0.963
K4-L2	N-L	between location	0.845	0.056	1	0.944
K4-L3	N-L	between location	0.668	0.168	0.929	0.761

K4-L4	N-L	between location	0.831	0.094	1	0.906
P1-P2	P-P	within location	0.746	0.079	0.903	0.824
P1-P3	P-P	within location	0.562	0.451	0.783	0.332
P1-P4	P-P	within location	0.809	0.634	0.863	0.229
P1-L1	P-L	between location	0.906	0.05	0.992	0.942
P1-L2	P-L	between location	0.895	0.088	0.994	0.905
P1-L3	P-L	between location	0.827	0.035	0.935	0.9
P1-L4	P-L	between location	0.879	0	1	1
P2-P3	P-P	within location	0.634	0.221	0.894	0.673
P2-P4	P-P	within location	0.631	0.439	0.738	0.299
P2-L1	P-L	between location	0.773	0.029	0.975	0.946
P2-L2	P-L	between location	0.801	0.034	0.967	0.933
P2-L3	P-L	between location	0.682	0.31	0.899	0.589
P2-L4	P-L	between location	0.729	0.163	0.888	0.725
P3-P4	P-P	within location	0.729	0.334	0.893	0.559
P3-L1	P-L	between location	0.808	0.036	0.992	0.955
P3-L2	P-L	between location	0.802	0.056	0.966	0.909
P3-L3	P-L	between location	0.646	0.131	0.853	0.722
P3-L4	P-L	between location	0.733	0.15	0.95	0.8
P4-L1	P-L	between location	0.828	0.035	0.977	0.943
P4-L2	P-L	between location	0.87	0.024	0.969	0.945
P4-L3	P-L	between location	0.689	0.398	0.89	0.492
P4-L4	P-L	between location	0.924	0.044	0.973	0.929
L1-L2	L-L	within location	0.738	0.203	0.933	0.731
L1-L3	L-L	within location	0.746	0.077	0.968	0.89
L1-L4	L-L	within location	0.75	0.207	0.904	0.697
L2-L3	L-L	within location	0.804	0.251	0.972	0.721
L2-L4	L-L	within location	0.784	0.05	0.956	0.906
L3-L4	L-L	within location	0.599	0.437	0.908	0.471
K1-K2	N-N	within location	0.508	0.2	0.783	0.583
K1-K3	N-N	within location	0.668	0.155	0.845	0.69
K1-K4	N-N	within location	0.63	0.134	0.751	0.616
K1-P1	N-P	between location	0.861	0.119	0.901	0.782
K1-P2	N-P	between location	0.635	0.152	0.75	0.598
K1-P3	N-P	between location	0.738	0.252	0.946	0.693
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K1-L1	N-L	between location	0.764	0.083	0.884	0.801
K1-L2	N-L	between location	0.849	0.055	0.974	0.92
K1-L3	N-L	between location	0.71	0.265	0.918	0.654
K1-L4	N-L	between location	0.906	0.097	0.986	0.889
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K2-P2	N-P	between location	0.715	0.114	0.826	0.712
K2-P3	N-P	between location	0.626	0.297	0.852	0.555

K2-P4	N-P	between location	0.568	0.15	0.841	0.691
K2-L1	N-L	between location	0.798	0.129	0.975	0.846
K2-L2	N-L	between location	0.831	0.031	0.957	0.926
K2-L3	N-L	between location	0.654	0.129	0.84	0.711
K2-L4	N-L	between location	0.844	0.151	0.962	0.811
K3-K4	N-N	within location	0.72	0.178	0.907	0.729
K3-P1	N-P	between location	0.867	0.126	0.917	0.791
K3-P2	N-P	between location	0.771	0.097	0.891	0.794
K3-P3	N-P	between location	0.742	0.206	0.944	0.738
K3-P4	N-P	between location	0.738	0.171	0.899	0.728
K3-L1	N-L	between location	0.811	0.061	0.977	0.916
K3-L2	N-L	between location	0.867	0.01	0.977	0.967
K3-L3	N-L	between location	0.745	0.043	0.942	0.899
K3-L4	N-L	between location	0.909	0.036	0.99	0.954
K4-P1	N-P	between location	0.759	0.318	0.904	0.586
K4-P2	N-P	between location	0.483	0.255	0.709	0.454
K4-P3	N-P	between location	0.635	0.348	0.891	0.543
K4-P4	N-P	between location	0.651	0.264	0.76	0.496
K4-L1	N-L	between location	0.824	0.038	1	0.963
K4-L2	N-L	between location	0.845	0.056	1	0.944
K4-L3	N-L	between location	0.668	0.168	0.929	0.761
K4-L4	N-L	between location	0.831	0.094	1	0.906
P1-P2	P-P	within location	0.746	0.079	0.903	0.824
P1-P3	P-P	within location	0.562	0.451	0.783	0.332
P1-P4	P-P	within location	0.809	0.634	0.863	0.229
P1-L1	P-L	between location	0.906	0.05	0.992	0.942
P1-L2	P-L	between location	0.895	0.088	0.994	0.905
P1-L3	P-L	between location	0.827	0.035	0.935	0.9
P1-L4	P-L	between location	0.879	0	1	1
P2-P3	P-P	within location	0.634	0.221	0.894	0.673
P2-P4	P-P	within location	0.631	0.439	0.738	0.299
P2-L1	P-L	between location	0.773	0.029	0.975	0.946
P2-L2	P-L	between location	0.801	0.034	0.967	0.933
P2-L3	P-L	between location	0.682	0.31	0.899	0.589
P2-L4	P-L	between location	0.729	0.163	0.888	0.725
P3-P4	P-P	within location	0.729	0.334	0.893	0.559
P3-L1	P-L	between location	0.808	0.036	0.992	0.955
P3-L2	P-L	between location	0.802	0.056	0.966	0.909
P3-L3	P-L	between location	0.646	0.131	0.853	0.722
P3-L4	P-L	between location	0.733	0.15	0.95	0.8
P4-L1	P-L	between location	0.828	0.035	0.977	0.943
P4-L2	P-L	between location	0.87	0.024	0.969	0.945
P4-L3	P-L	between location	0.689	0.398	0.89	0.492
P4-L4	P-L	between location	0.924	0.044	0.973	0.929
L1-L2	L-L	within location	0.738	0.203	0.933	0.731

L1-L3	L-L	within location	0.746	0.077	0.968	0.89
L1-L4	L-L	within location	0.75	0.207	0.904	0.697
L2-L3	L-L	within location	0.804	0.251	0.972	0.721
L2-L4	L-L	within location	0.784	0.05	0.956	0.906
L3-L4	L-L	within location	0.599	0.437	0.908	0.471

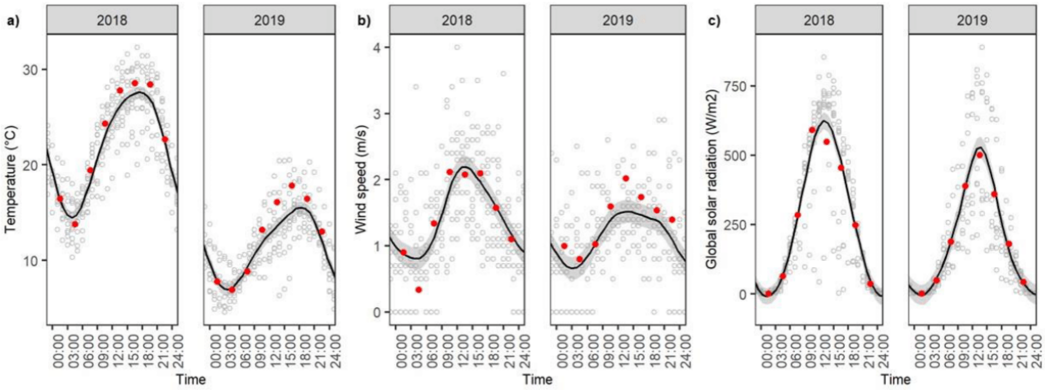
Supporting Table 2: Dunn´s test result and statistics of comparisons of β_{WN}, β_{ST} and β_{OS}

β_{WN}

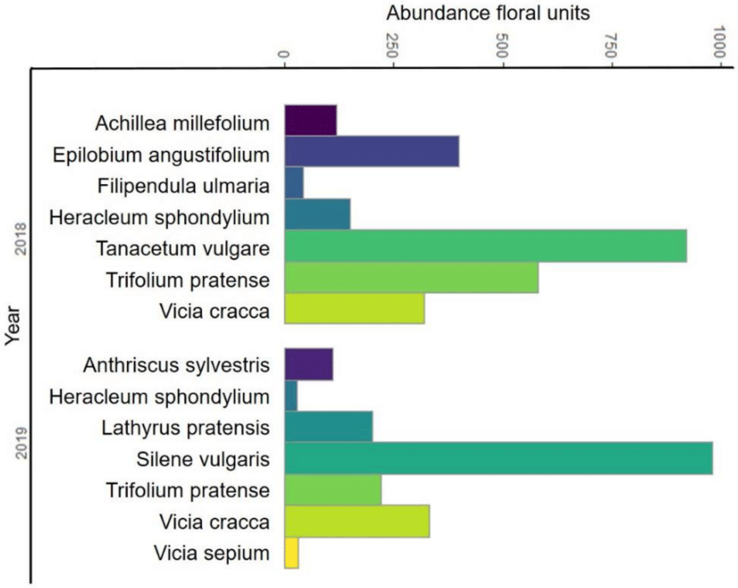
group1	group2	statistic	adjusted p-value	
C-C	C-S	2.949	0.008	**
C-C	N-C	0.313	0.754	ns
C-C	N-N	-0.466	0.740	ns
C-C	N-S	3.214	0.004	**
C-C	S-S	2.030	0.071	ns
C-S	N-C	-3.569	0.002	**
C-S	N-N	-3.511	0.002	**
C-S	N-S	0.360	0.754	ns
C-S	S-S	-0.500	0.740	ns
N-C	N-N	-0.875	0.572	ns
N-C	N-S	3.928	0.001	**
N-C	S-S	2.136	0.061	ns
N-N	N-S	3.776	0.001	**
N-N	S-S	2.497	0.027	*
N-S	S-S	-0.765	0.606	ns
β_{ST}				
C-C	C-S	3.596	0.001	**
C-C	N-C	0.977	0.442	ns
C-C	N-N	0.331	0.794	ns
C-C	N-S	3.616	0.001	**
C-C	S-S	1.57	0.191	ns
C-S	N-C	-3.545	0.001	**
C-S	N-N	-3.197	0.003	**
C-S	N-S	0.028	0.978	ns
C-S	S-S	-1.691	0.170	ns
N-C	N-N	-0.578	0.650	ns
N-C	N-S	3.573	0.001	**
N-C	S-S	0.927	0.442	ns
N-N	N-S	3.21	0.003	**
N-N	S-S	1.248	0.318	ns
N-S	S-S	-1.712	0.170	ns
β_{OS}				
C-C	C-S	-3.611	0.005	**
C-C	N-C	-1.210	0.339	ns
C-C	N-N	-0.857	0.534	ns
C-C	N-S	-3.407	0.005	**
C-C	S-S	-1.293	0.327	ns
C-S	N-C	3.251	0.006	**
C-S	N-N	2.578	0.030	*
C-S	N-S	0.276	0.838	ns
C-S	S-S	2.052	0.086	ns
N-C	N-N	0.177	0.860	ns
N-C	N-S	-2.974	0.011	*
N-C	S-S	-0.349	0.838	ns
N-N	N-S	-2.374	0.044	*
N-N	S-S	-0.436	0.828	ns
N-S	S-S	1.848	0.121	ns

Supplementary Material Chapter 3

Supplementary figures and tables



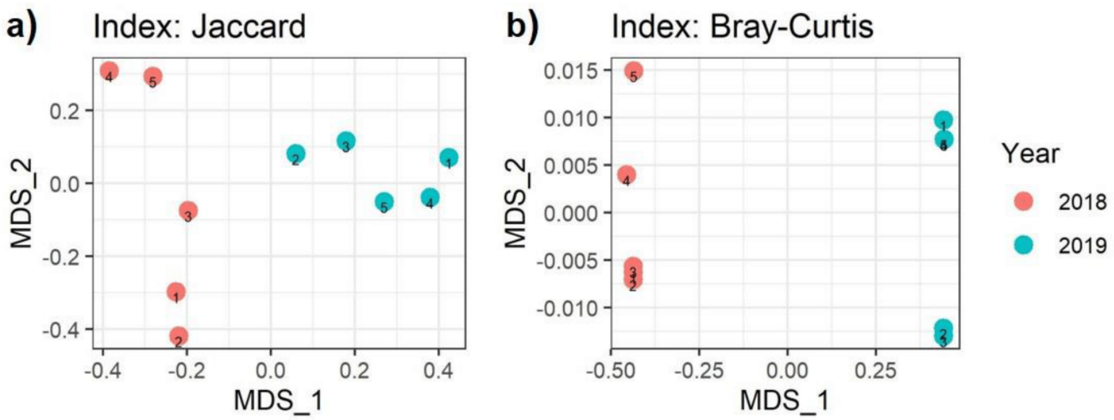
Supplementary Figure S1. *Abiotic factors **a)** temperature, **b)** wind speed and **c)** global solar radiation over the diel cycle in the years 2018 and 2019. Red points depict the mean of values measured at the beginning of each sampling round. Grey circles indicate hourly measurements during our entire sampling period. The black line depicts the loess regression fitted through the hourly data points. Raw data were obtained from the Finnish Meteorological institute (FMI). Measures of temperature and wind speed stem from the weather station Kittilä kirkonkylä and measures of global solar radiation were taken at the weather station Sodankylä Tähtelä.*



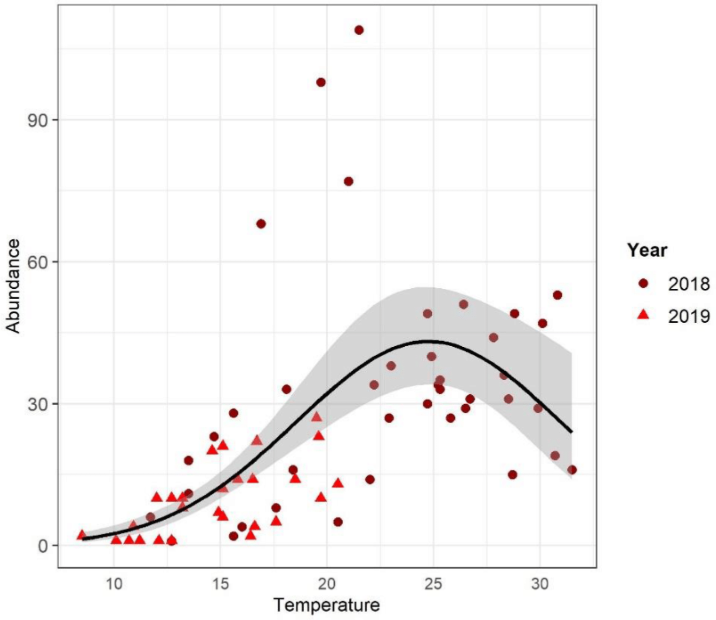
Supplementary Figure S2. *Identity and abundance of floral units (number of flowers or inflorescences pre 30x2 m transect) of the seven most visited plant species in the years 2018 and 2019.*

Supplementary Table S1. *The most visited plant species in 2018 and/or 2019 and information about their flowering season. Plant species with the earliest start of flowering (May) were only on the list of most visited species in the year 2019, whereas those with the latest start of flowering (July) were only on the list of most visited species in the year 2018 (source: Database BiolFlor).*

Plant species	flowering season	year most visited
Achillea millefolium	June – Oct.	2018
Anthriscus sylvestris	May – Aug.	2019
Epilobium angustifolium	July – Aug.	2018
Filipendula ulmaria	June – Aug.	2018
Heracleum sphondylium	June – Sept.	2018, 2019
Lathyrus paratensis	June – Aug.	2019
Silene vulagris	May- Sept.	2019
Tanacetum vulgare	July – Sept.	2018
Trifolium pratense	June – Sept.	2018, 2019
Vicia cracca	June – Aug.	2018, 2019
Vicia sepium	May - June	2019



***Supplementary Figure S3**. Visualization of non-metric multidimensional scaling (NMDS) ordination based on **a)** Jaccard similarity index and **b)** Bray-Curtis dissimilarity index of the pollinator assemblages in the years 2018 and 2019. Each point represents one of the five 24-hour sampling cycles.*



***Supplementary Figure S4**. Relationship between abundance of pollinators and temperature. The quadratic function is fit using all data. The years are color-coded in the figure to illustrate that high temperature observations come only from year 2018.*

Supplementary Table S2. *Results of wald-tests pairwise comparing activity models at subsequent sampling times (01:30, 04:30, 07:30, 10:30, 13:30, 16:30, 19:30 and 22:30) for the orders Diptera and Hymenoptera in the two sampling years 2018 and 2019. Significant values are printed in bold.*

Diptera 2018

Time	Difference	SE	W	p
01:30-04:30	-0.0910	0.0172	27.972	**<0.001**
04:30-07:30	-0.2627	0.0271	94.001	**<0.001**
07:30-10:30	0.2366	0.0279	71.900	**<0.001**
10:30-13.30	0.0718	0.0198	13.166	**<0.001**
13:30-16:30	-0.0396	0.0180	4.812	**0.028**
16:30-19:30	-0.1152	0.0228	25.542	**<0.001**
19:30-22:30	0.0752	0.0237	10.041	**0.0015**
Diptera 2019				
01:30-04:30	0.0062	0.0098	0.397	0.529
04:30-07:30	-0.0469	0.0191	6.024	**0.014**
07:30-10:30	-0.2269	0.0374	36.913	**<0.001**
10:30-13.30	-0.1562	0.0501	9.712	**0.002**
13:30-16:30	0.092	0.052	3.128	0.077
16:30-19:30	0.2074	0.0437	22.515	**<0.001**
19:30-22:30	0.0988	0.0299	10.894	**<0.001**

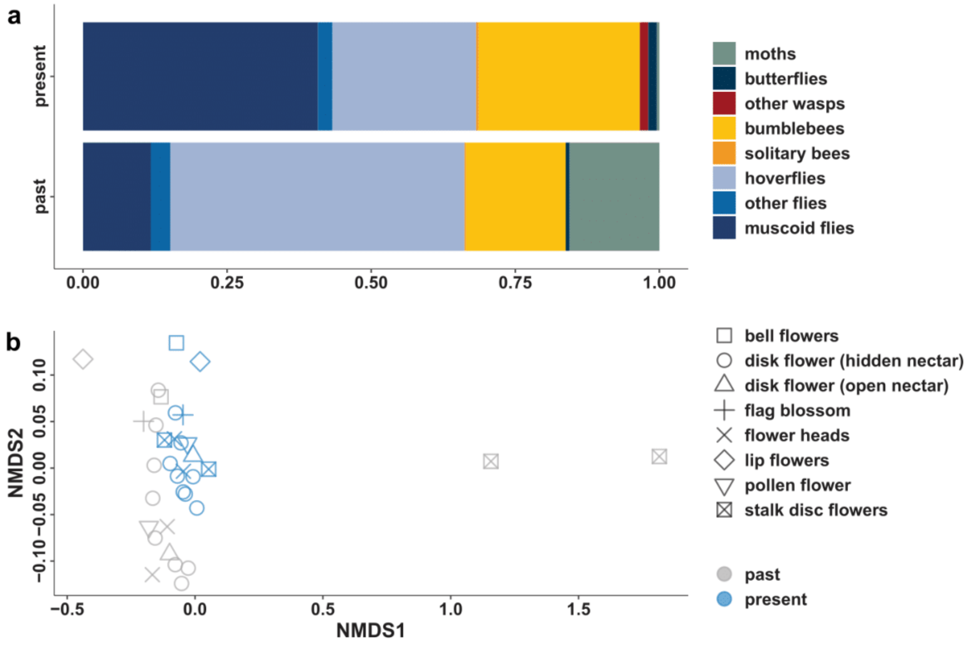
Hymenoptera 2018

Time	Difference	SE	W	p
01:30-04:30	-0.0522	0.0153	11,602	**<0,001**
04:30-07:30	-0.1788	0.0249	51,411	**<0,001**
07:30-10:30	0.0533	0.0274	3,777	0,052
10:30-13.30	0.0283	0.0244	1,350	0,245
13:30-16:30	-0.0261	0.0244	1,141	0,285
16:30-19:30	-0.0029	0.0246	0,004	0,907
19:30-22:30	0.1150	0.0220	27,356	**<0,001**
Hymenoptera 2019				
01:30-04:30	0.0044	0.0099	0.193	0.66
04:30-07:30	-0.0353	0.0196	3.238	0.072
07:30-10:30	-0.1827	0.0404	20.483	**<0.001**
10:30-13.30	-0.1765	0.0586	9.077	**0.003**
13:30-16:30	0.0549	0.0613	0.802	0.37
16:30-19:30	0.1202	0.0537	5.011	**0.025**
19:30-22:30	0.1572	0.0422	13.844	**<0.001**

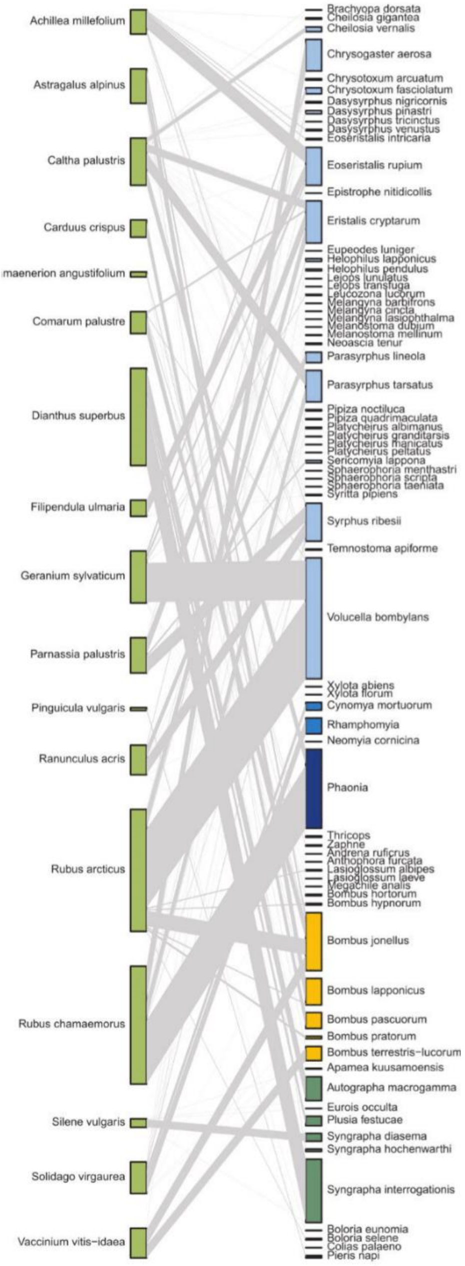
Supplementary Table S3. *R^2 and R values obtained by running correlations between radian time of day and abiotic factors air temperature, global solar radiation and wind speed.*

Variables	R^2	R
radian time –air temperature	0.241	0.491
radian time – solar radiation	0.580	0.761
radian time – wind speed	0.211	0.459

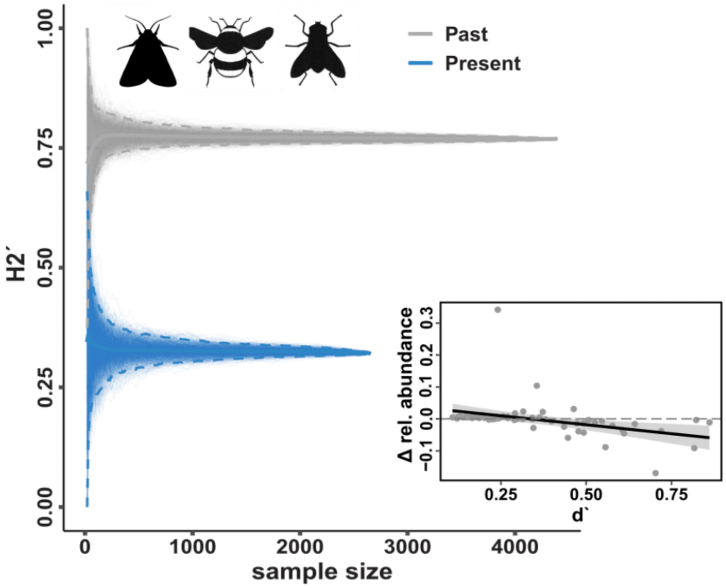
Supplementary Material Chapter 5



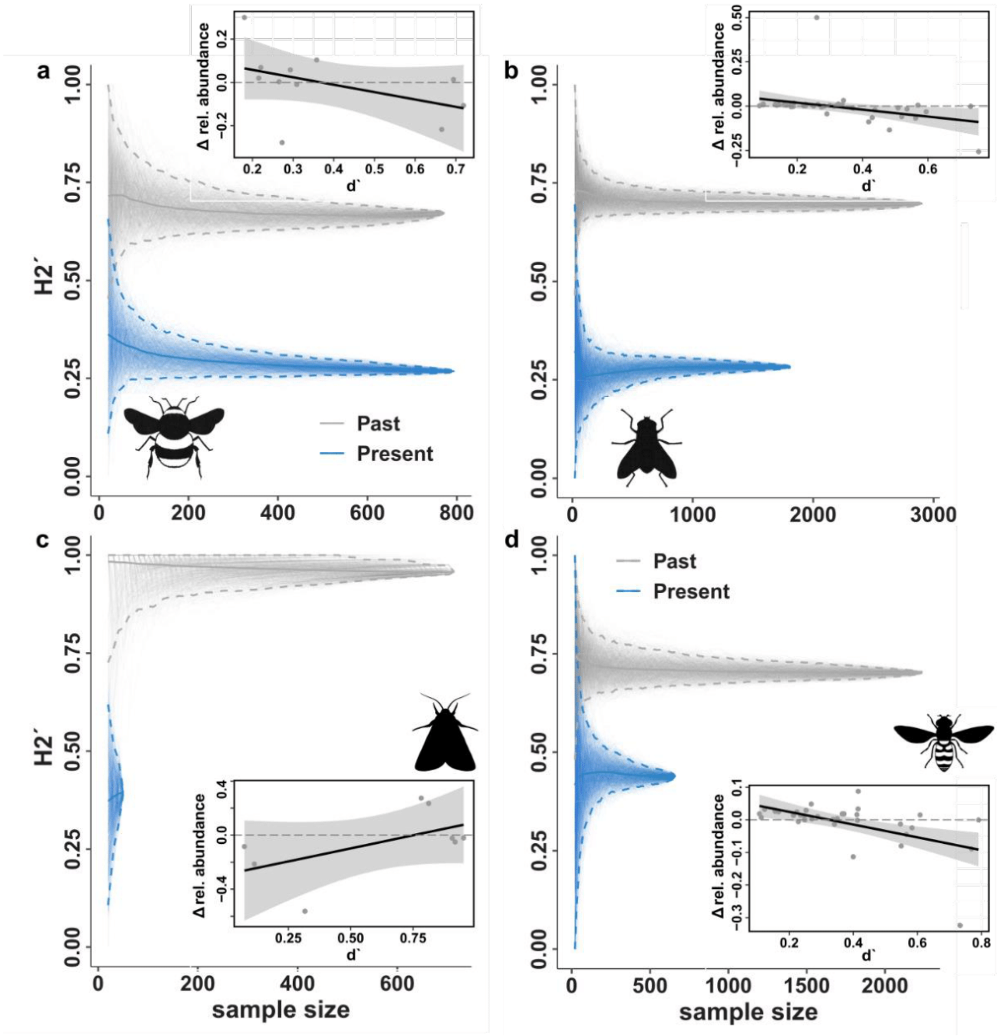
Supplementary Fig. 1. Changes in pollinator community composition across time periods using a generous numerical estimate of past pollinator abundance. a, Proportional composition of the most abundant groups of pollinators in the past and present using a generous numerical estimate of abundance from the historical data (*n* = 4393 in the past, *n* = 2657 in the present). Using a generous estimate caused only minute changes in the relative abundance of muscoid flies, solitary bees and butterflies compared to using the conservative estimate. **b,** NMDS-ordination visualizing distances of pollinator communities visiting a plant species across time periods and plant floral forms using a generous numerical estimate of pollinator abundance. Congruent with the results using a conservative estimate (presented in the main text), pollinator communities were significantly dissimilar between time periods (ANOSIM: *global* $R = 0.37$, $P < 0.001$).



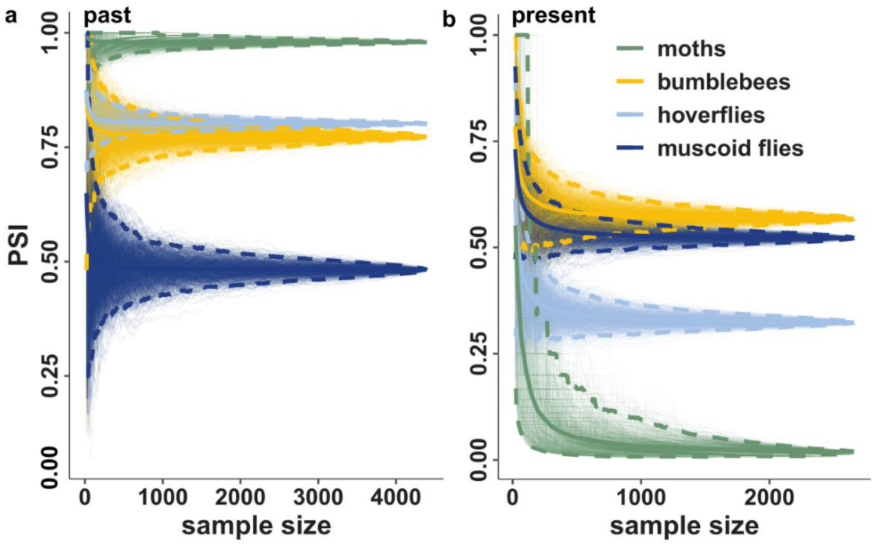
Supplementary Fig. 2. Past plant-pollinator interaction network using a generous numerical estimate of past pollinator abundance. The rectangles represent plant species (left) and pollinators (right) and the connecting lines represent the weighted interactions among species (*n* = 4393 interactions). Colors of pollinators indicate the taxonomic group as defined in Supplementary Fig. 1a.



Supplementary Fig. 3. Network-wide specialization index (*H2´*) for the past and present networks, as well as linear trends of species level-specialization (*d´*) and change in relative abundance (insert figure) using generous numerical estimate of past pollinator abundance. Each thin line in the main figure represents *H2´*calculated in one of 1000 iterations, while the thick solid line represents the mean *H2´* of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. In the insert figure, the black line represents the simple linear regression fit to data points (grey dots) and the grey shaded area represents the 95% confidence interval. Data from all pollinator taxa are included. Using a generous numerical abundance estimate for the past data results in a higher number of interactions in the past (*n* = 4394) compared to the present (*n* = 2657). At a standardized sample size of interactions however, specialization was distinctively higher in the past (higher *H2´*). The regression model indicates that pollinator taxa that underwent a larger negative change in abundance were more specialized (higher *d´*), also when using a generous estimate of pollinator abundance (*n* = 61). These results are congruent with the results presented in the main text that were obtained using a conservative numerical estimate of abundance.



Supplementary Fig. 4. Bootstrapped network-wide specialization index (*H2´*) for the past and present networks and linear trends of species level-specialization (*d´*) and change in relative abundance (insert figures) for separate subsets of taxa using a generous numerical estimate of past pollinator abundance. Each thin line in the main figures represents *H2´* calculated in one of 1000 iterations, while the thick solid lines represent the mean *H2´* of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. In the insert figures, black lines represent the simple linear regression fit to data points (grey dots) and the grey shaded areas represent the 95% confidence interval. Subsets of data used in the networks include: **a,** bees, wasps and bumblebees (*n* = 11), **b,** all flies (*n* = 42), **c,** butterflies and moths (*n* = 8) and **d,** hoverflies (*n* = 34). All subsets show distinctly lower specialization in the present (lower *H2´*) at standardized sample sizes of interactions. In flies and hoverflies, we found significant negative relationships between *d´* and change in relative abundance. These results are congruent with the results presented in the main text that were obtained using a conservative abundance estimate.



Supplementary Fig. 5. Pollination Service Index (*PSI*) for four relevant pollinator groups (bumblebees, hoverflies, moths and muscoid flies) using a generous numerical estimate of past pollinator abundance. Each thin line represents PSI calculated in one of 1000 iterations, while the thick solid lines represent the mean PSI of all iterations. Dashed lines indicate the 95% bootstrap confidence intervals. **a,** depicts results obtained using past data and **b,** present data. The results obtained using a generous numerical abundance estimate are congruent to the ones obtained using a conservative abundance estimate presented in the main text.

Supplementary Table 1. Overview of the number of sampling years per time period and the present sampling effort for the 17 plant species included in the final dataset. For the two plant species that were typically observed at night, the night sampling effort is included in brackets.

plant species	**time period**	**No. years sampled**	**total observation time (min)**
Achillea millefolium	past	1	
	present	2	2295
Astragalus alpinus	past	4	
	present	2	715
Caltha palustris	past	3	
	present	2	345
Carduus crispus	past	2	
	present	1	420
Chamaenerion angustifolium	past	1	
	present	2	1005
Comarum palustre	past	3	
	present	2	470
Dianthus superbus	past	4	
	present	2	480 (420)
Filipendula ulmaria	past	2	
	present	2	310
Geranium sylvaticum	past	3	
	present	2	800
Parnassia palustris	past	1	
	present	1	545
Pinguicula vulgaris	past	1	
	present	1	300
Ranunculus acris	past	3	
	present	2	1715
Rubus arcticus	past	2	
	present	2	520
Rubus chamaemorus	past	2	
	present	2	450
Silene vulgaris	past	2	
	present	2	1115 (700)
Solidago virgaurea	past	3	
	present	2	1320
Vaccinium vitis-idaea	past	2	
	present	2	345

Supplementary Table 2. Different numerical values of pollinator abundance estimated from Silén's original categorical description. All analyses were conducted with both estimates to ensure that our estimated values did not influence the results. Results from the conservative numerical estimate are presented in the main text, and very similar results obtained using the generous numerical estimates are presented in Supplementary Figs. 1-5.

original categorical quantity	**conservative numerical estimate**	**generous numerical estimate**
one	1	1
two	2	2
three	3	3
three or four	3	3
scarce	4	8
sparingly	4	8
sporadic	4	8
some	5	15
several	5	15
many	6	30
numerous	8	50
countless bunches	10	80
quite numerous	10	80
very numerous	15	100
total pollinators observed	899	4393

Supplementary Table 3. Sensitivity analysis: Results of the statistical tests presented in the main text, but using generous instead of conservative estimates of abundance for the past. All results that were significant and not significant in the main text were similarly classified as significant and not significant using the generous estimates of abundance from the past. Two-tailed t-tests, with no adjustment for multiple comparisons, were used to test significances of linear regression slopes.

	explanatory variable	*global R*			*P-value*
ANOSIM	**time period**	**0.37**			**>0.001**
	floral form past	**0.29**			**>0.001**
	floral form present	0.05			0.34
	years in past	0.02			0.28
	years in present	-0.02			0.59
	explanatory variable		*F*	*r*	*P-value*
linear regression (lm)	**_d´_ full network**		**$F_{1,59} = 10.36$**	**0.1366**	**0.002**
	_d´_ all flies		**$F_{1,40} = 6.072$**	**0.1318**	**0.018**
	d´ bees		$F_{1,9} = 2.295$	0.2032	0.164
	d´ moths and butterflies		$F_{1,5} = 2.656$	0.3068	0.154
	_d´_ hoverflies		**$F_{1,32} = 13.03$**	**0.2893**	**0.001**

Supplementary Table 4. Plant inclusion criteria. For each of the thirty plants species sampled in both time periods, sampling coverage and number of observed interactions (both based on a conservative numerical estimate of past pollinator abundance) as well as number of days sampled is shown for each time period. In all subsequent analyses, only plant species fulfilling following three criteria were included: (1) sampling coverage is ≥ 0.60, (2) at least five observed interactions and (3) sampled on at least two days. The seventeen plant species that were included in the final data set are printed in bold.

plant species	time period	sampling coverage	number of interactions	days of sampling	Included in final data set?
Achillea millefolium	past	0.933	44	6	**Yes**
	present	0.906	469	27	
Antennaria dioica	past	1.000	16	1	No
	present	0.368	14	5	
Astragalus alpinus	past	0.904	41	5	**Yes**
	present	0.803	76	20	
Caltha palustris	past	0.867	82	6	**Yes**
	present	0.791	57	7	
Carduus crispus	past	0.913	21	3	**Yes**
	present	0.894	132	6	
Chamaenerion angustifolium	past	1.000	16	2	**Yes**
	present	0.925	294	15	
Comarum palustre	past	1.000	33	4	**Yes**
	present	0.941	170	12	
Dactylorhiza maculata	past	0.394	6	1	No
	present	0.806	25	5	
Dianthus superbus	past	1.000	114	19	**Yes**
	present	0.842	55	9	
Filipendula ulmaria	past	0.895	17	3	**Yes**
	present	0.969	190	5	
Geranium sylvaticum	past	0.895	76	9	**Yes**
	present	0.827	185	18	
Ledum palustre	past	1.000	32	2	No
	present	0.398	11	3	
Linnaea borealis	past	0.182	4	2	No
	present	0.900	5	2	
Maianthemum bifolium	past	0.752	11	1	No
	present	0.333	3	1	
Melampyrum sylvaticum	past	0.333	3	3	No
	present	0.206	20	3	
Menyanthes trifoliata	past	0.182	4	1	No
	present	0.769	82	9	
Parnassia palustris	past	1.000	43	2	**Yes**
	present	0.887	105	5	
Pedicularis palustris	past	0.667	2	1	No
	present	0.811	26	4	
Pinguicula vulgaris	past	0.733	5	2	**Yes**
	present	0.801	9	3	
Pyrola rotundifolia	past	0.739	10	5	No
	present	0.667	2	2	
Ranunculus acris	past	0.855	41	3	**Yes**
	present	0.890	456	28	
Rubus arcticus	past	1.000	144	7	**Yes**
	present	0.865	51	10	
Rubus chamaemorus	past	0.943	139	6	**Yes**
	present	0.773	52	6	
Silene suecica	past	0.850	19	1	No

	present	0.697	29	8	
Silene vulgaris	past	0.631	13	3	**Yes**
	present	0.680	34	10	
Solidago virgaurea	past	0.853	54	8	**Yes**
	present	0.892	324	17	
Taraxacum officinale	past	0.504	24	6	No
	present	0.522	29	6	
Vaccinium oxycoccos	past	0.625	4	2	No
	present	0.834	17	8	
Vaccinium vitis-vidaea	past	1.000	30	3	**Yes**
	present	0.751	15	5	
Veronica longifolia	past	0.426	10	4	No
	present	0.829	81	13	

Author´s Contributions

Chapter 2

Leana Zoller, Tiffany M. Knight. Patterns of variation in plants, pollinators and their interactions along a latitudinal gradient in Finland (submitted).

LZ and TMK conceived the ideas and designed the methodology; LZ and TMK collected the data; LZ analyzed the data; LZ led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication. Overall contribution of LZ was 80%.

Chapter 3

Leana Zoller, Joanne M. Bennett, Tiffany M. Knight. Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. *Scientific Reports* **10**, 21187 (2020).

LZ and TMK conceived the ideas and designed the methodology; LZ and TMK collected the data; LZ analyzed the data; LZ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Overall contribution of LZ was 70%.

Chapter 4

Leana Zoller, Tiffany M. Knight. Historical records of plant-insect interactions in subarctic Finland. *BMC Research Notes* **15**, 317 (2022)

TMK and LZ conceived the ideas and designed the methodology; LZ led the data digitization; LZ led the writing of the manuscript. TMK contributed critically to the drafts and gave her final approval for publication. Both authors read and approved the final manuscript. Overall contribution of LZ was 80%.

Chapter 5

Leana Zoller, Joanne M. Bennett, Tiffany M. Knight. Plant-pollinator network change across a century in the subarctic. *Nature Ecology and Evolution* **7**, 102-112 (2023)

TMK, JB and LZ conceived the ideas and designed the methodology; LZ and TMK collected the data; LZ led the formal analysis and visualization of the data; LZ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Overall contribution of LZ was 80%.

Curriculum Vitae

Leana Zoller

MSc in Biology (with special qualification in ecology and conservation)

Languages:

- German (fluent)
- English (fluent)
- Italian (basic)
- French (basic)
- Swedish (basic)

Software skills:

- Text processing: Microsoft Word
- Presentation: Microsoft PowerPoint
- Spread sheet: Microsoft Excel
- Statistics: R
- Image editing: Adobe Lightroom, Inkscape

Work history

2022-02 - 2023-01	**Doctoral researcher (100%)** | Martin-Luther University Halle-Wittenberg, German center for integrative biodiversity research (iDiv), Leipzig, Germany Dissertation title: Spatial and temporal variation in pollinator communities and plant-pollinator interactions at different scales – A case study from Finland
2018-03 – 2022-02	**Research officer (65%)** | Martin-Luther University Halle-Wittenberg, German center for integrative biodiversity research (iDiv), Leipzig, Germany Research activity: - Planning and conducting fieldwork in Finnish Lapland, recording plant-pollinator interactions and conducting pollen limitation experiments. - Identifying insects, with a focus on fly pollinators. - Analyzing data using R, writing publications, presenting results at international conferences. - Co-supervising interns and MSc-projects. - Organization and co-teaching of a summer school on pollination ecology in Finland. - Engagement in outreach activities, e.g. Aiding in the organization of an exhibit on pollination, partaking in the Long Night of the Sciences Leipzig, giving press interviews.
2017-11 - 2018-03	**Animal attendant (100%)** | Zoo Zurich, Switzerland Tending to various animals and plants in a tropical setting.
2017-02 - 2017-10	**Internship in environmental education (100%)**| Raptorial bird station Berg am Irchel, Switzerland Guiding tours and excursions for both children and adults and tending to injured wild raptorial birds.
2016-08 - 2016-11	**Field Technician** | University of Bern, Switzerland Conducting fieldwork for a research project investigating insect migration (radar observations, insect collection, radio tracking), coordinating research projects and supervising a MSc project, maintaining facilities and equipment at the field station Col the Cou in the Swiss Alps.
2016-05 - 2016-06	**Field Assistant** | University of Bern, Switzerland Planning and conducting fieldwork for a research project investigating the effects of light pollution on pollinator communities, contributing to the experimental design, supervising interns.

CV - Leana Zoller

Leana Zoller

MSc in Biology (with special qualification in ecology and conservation)

Education

2015-01 - 2016-05 **Master of Science in Biology (with special qualification in ecology and conservation)** | University of Bern, Switzerland

Thesis title: Artificial light at night leads to a disruption of pollination of nocturnal flower visitor communities.

Research activity:
- Planning and organizing a research project and experimental design, carry out night fieldwork.
- Identification of insects, with a focus on moth pollinators.
- Statistical analysis and publication writing.
- Presentation of results at conferences.

2014-08 - 2015-01 **Erasmus Exchange Semester** | University of Uppsala, Sweden

2011-08 - 2014-08 **Bachelor of Science in Biology** | University of Bern, Switzerland

List of publications

Zoller, L., Bennett, J.M. and Knight, T.M. (2023). Plant-pollinator network change across more than a century in the subarctic. *Nature Ecology & Evolution* **7**, 102-112.

Rakosy, D., Ashman, T., Stanley, A., **Zoller, L.**, Knight, T.M. (2022). Integration of historic collections can shed light on patterns of change in plant-pollinator interactions and pollination service. *Functional Ecology* 00, 1-16.

Zoller, L. and Knight, T.M. (2022). Historical records of plant-insect interactions in subarctic Finland. *BMC Research Notes* **15**(1), 317.

Zoller, L., Bennett, J.M. and Knight, T.M. (2020). Diel-scale temporal dynamics in the abundance and composition of pollinators in the Arctic summer. *Scientific Reports*, **10**(1), 1-9.

Koch, V., **Zoller, L.**, Bennett, J.M. and Knight, T.M. (2020). Pollinator dependence but no pollen limitation for eight plants occurring north of the Arctic Circle. *Ecology and Evolution*, **10**(24), 13664-13672.

Knop, E., **Zoller, L.**, Ryser, R., Gerpe, C., Hörler, M. and Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, **548**(7666), 206-209.

Knop, E., Gerpe, C., Ryser, R., Hofmann, F., Menz, M.H., Trösch, S., Ursenbacher, S., **Zoller, L.** and Fontaine, C. (2018). Rush hours in flower visitors over a day–night cycle. *Insect Conservation and Diversity*, **11**(3), 267-275.

Leana Zoller

MSc in Biology (with special qualification in ecology and conservation)

Recent conferences, workshops and invited talks

sDiv working group sINTERVAL meeting, iDiv, Leipzig, Germany, 5-9 December 2022 (workshop participant)

26th International Congress of Entomology, Helsinki, Finland, 17-22 July 2022 (symposium organizer)

Seminar series Nature Conservation and Landscape Ecology Group, Freiburg, Germany, 18 May 2022 (invited remote seminar talk)

German Centre for Integrative Biodiversity research (iDiv) Halle –Jena-Leipzig Annual Conference, online conference, 25-26 April 2022 (organization committee)

Seminar series of the Research Center for Ecological Change (REC), Helsinki, Finland, 12 March 2021 (invited remote seminar talk)

German Centre for Integrative Biodiversity research (iDiv) Halle –Jena-Leipzig Annual Conference, Leipzig, Germany, 8-9 October 2020 (volunteer/session assistance)

49th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Münster, Germany, 9-13 September 2019 (conference talk)

German Centre for Integrative Biodiversity research (iDiv) Halle-Jena-Leipzig Annual Conference, Leipzig, Germany, 29-30 August 2019 (volunteer/session assistance)

32nd annual meeting of the Scandinavian Association of Pollination Ecologists (SCAPE), Blessington, Ireland, 18-21 October 2018 (conference talk)

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Spatial and temporal variation in pollinator communities and plant-pollinator interactions at different scales – A case study from Finland“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Leana Zoller, Halle (Saale)