The temporal dynamics of plant-insect interactions in the Low Arctic

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Temporal patterns of plant flowering and insect activity influence plant-pollinator community structure and function, especially in seasonal environments like Arctic tundra. While plant-pollinator interactions in the High Arctic are well documented, fewer studies have addressed these interactions in the Low Arctic. We investigated baseline temporal dynamics in network structure, floral density, insect visitation, and insect pollen transfer over a single growing season in Alaska. During the summer of 2022, we routinely surveyed flowering phenology, conducted insect visitor observations, and collected insect specimens for pollen analysis at two study sites proximal to Toolik Field Station on the Alaskan North Slope. Plant-visitor networks were created for both the entire growing season and for time-slices, temporal trends in flowering, visitation, and pollen transfer were analyzed using GAMM models, and insect pollen load was compared between taxonomic groups. The cumulative plant-insect network contained 41 plant species and 28 insect families, and showed patterns of generalization and nestedness. We found strong temporal dimensions of plant flowering, insect visitation, and plant-insect interactions. Network complexity exhibited a gradual build up and decline, peaking at the beginning of July. Temporal trends in floral density differed significantly between study sites and community types. Flies (Order Diptera) maintained a constant low visitation rate throughout the season, while bumblebees and wasp (Order Hymenoptera) visitation exhibited distinct pulses. Hymenopterans also carried significantly more pollen than Dipterans, and showed a clear peak in pollen load in early June. These findings create a foundation for understanding plant-pollinator interactions over time in the Low Arctic, which is especially important given the rapid impacts of climate change on phenology and mutualistic interactions.

Key words: Arctic pollinators, visitation network, temporal dynamics, pollen load, floral density

Introduction

Phenology shapes interspecific interactions and processes such as pollination, thereby influencing fitness (Olesen et al. 2008; Forrest 2014; Valverde et al. 2015; Kudo and Cooper 2019). In seasonal environments, phenological events are controlled by numerous temporally variable environmental factors including temperature, precipitation, and light quality and quantity (Høye and Forchhammer 2008; Schmidt et al. 2016; Collins et al. 2021; Gillespie and Cooper 2021). In recent years, numerous authors have highlighted the importance of considering seasonality and temporal dynamics when investigating mutualistic interactions between plants and their insect visitors (Olesen et al. 2008; Pradal et al. 2009; Burkle and Alarcón 2011; Valverde et al. 2015; Schmidt et al. 2016; Gillespie and Cooper 2021). Authors have approached this broad challenge at both the species level (Iler et al. 2013; Kudo and Ida 2013; Kudo and Cooper 2019), and at a community level using complex network analysis (Alarcón et al. 2008; Olesen et al. 2008; Pradal et al. 2009; Rasmussen et al. 2013; Hoiss et al. 2015; Valverde et al. 2015; Robinson et al. 2018; Gillespie and Cooper 2021). The network approach has gained popularity in recent decades due to its utility in describing interactions at a community level (Jordano 1987; Olesen and Jordano 2002), which enables the quantification of standardized network attributes like nestedness (Bascompte et al. 2003; Bascompte and Jordano 2007), modularity (Olesen et al. 2007), and specialization (Bluthgen et al. 2006). These tools provide a framework for understanding community structure, composition, and change over time.

Investigations into the temporal dynamics of plant pollinator interactions are especially important in highly seasonal environments like the Arctic tundra (Høye and Forchhammer 2008; Schmidt et al. 2016; Gillespie and Cooper 2021). The Arctic experiences drastic seasonal variation throughout the year in day length, temperature, and precipitation, as well as inter-annual variation (Kankaanpää et al. 2018). This variation is especially impactful considering the disproportionate effects of climate change on Arctic ecosystems (Druckenmiller et al. 2022). Long-term climate datasets and models show that the Arctic is warming between two and four times as fast as the rest of the world due to Arctic amplification (Intergovernmental Panel on Climate Change (IPCC) 2014; Jansen et al. 2020; Rantanen et al. 2022). This rapid warming is resulting in cascading changes to virtually every part of Arctic environments, including permafrost soils (Brown and Romanovsky 2008; Schuur et al. 2008; Schuur et al. 2015), hydrological regimes (Turetsky et al. 2020; McCrystall et al. 2021), and fire cycles (Descals et al. 2022). Additionally, climate change is disproportionately increasing winter temperatures in the Arctic (Bintanja and Van der Linden 2013), resulting in earlier snowmelt (Saha et al. 2006; Cooper 2014; McCrystall et al. 2021). Combined with delays in autumn snowfall accumulation, the summer growing season is expected to increase in duration in the coming decades (Cooper 2014). Snowfall patterns are intrinsically linked with growing season duration, as snowmelt signals the start of the growing season to plants and controls flowering timing (Wipf and Rixen 2010; Rixen et al. 2022). Along with changes in mean trends, climate change may increase stochastic variation in extreme weather events (Saha et al. 2006), which will also influence seasonal patterns in the Arctic.

These environmental changes are expected to influence biotic communities in unique ways. Long-term data from warming experiments, including the International Tundra Experiment (ITEX), have found that vegetative communities across the Arctic are shifting towards an increased dominance of deciduous shrubs, outcompeting forbs and evergreen shrubs (Myers-Smith 2011; Elmendorf et al. 2012; García Criado et al. 2020; Mekonnen et al. 2021; Henry et al. 2022). Changes in plant community composition may alter floral resource availability, as forbs and evergreen shrubs are important floral resources for insects (Khorsand et al. *in review*).

In tandem with compositional changes, plant phenological shifts in the Arctic are well documented (Chapin and Shaver 1996; Wipf and Rixen 2010; Oberbauer et al. 2013; Bjorkman et al. 2015; Khorsand Rosa et al. 2015; Semenchuk et al. 2016; Collins et al. 2021). Warming treatments cause plants to leaf out and flower earlier in the season, yet these responses vary heterogeneously among regions and taxa (Oberbauer et al. 2013; Semenchuk et al. 2016; Collins et al. 2021). Phenological trends differ at a growth-form and species-level, as well as between early and late flowering species (Arft et al. 1999; Oberbauer et al. 2013; Khorsand Rosa et al. 2015). Snowmelt date and air temperature strongly predict phenological trends in early flowering species (Wipf and Rixen 2010; Oberbauer et al. 2013; Bjorkman et al. 2015), and potentially in late flowering species as well (Semenchuk et al. 2016). However, late-flowering species are often thought to respond more to day length and temperature as the growing season progresses (Oberbauer et al. 2013). Further nuancing these trends, vegetative and reproductive phenology respond differently to environmental cues, with reproductive events like flowering and fruiting shifting more than vegetative events like greening and senescence (Collins et al. 2021). The duration of growth and flowering has been shown to remain constant in some studies (Semenchuk et al. 2016), while flowering duration increased in others (Collins et al. 2021).

On a community scale, the flowering phenology of individual plant species interplays with patchy species distributions to influence landscape patterns in floral availability over the growing season. This spatial heterogeneity has been shown to increase the duration of flowering in California grasslands (Oliff-Yang and Ackerly 2020). However, in the High Arctic, the duration of community floral availability seems to be decreasing in a warming future due to forward shifts in the flowering phenology of late-flowering species (Høye et al. 2013). These landscape-level patterns in plant phenology have crucial implications for other members of Arctic communities, as plants serve as food and shelter resources for arthropods, birds, and mammals (Gauthier et al. 2011; Bjorkman et al. 2019).

One crucial biotic interaction that plant phenological changes may alter is pollination. While asexual and clonal reproduction are thought to be common in Arctic plants (Molau 1993), many Arctic plants depend on insects for pollination services and seed set (Williams and Batzli 1982; Philipp et al. 1996; Fulkerson et al. 2012; Tiusanen et al. 2016; Urbanowicz et al. 2018; Koch et al. 2020). In coastal Arctic Alaska, Williams and Batzli (1982) found that numerous *Pedicularis* species rely exclusively on queen bumblebees for seed set. At a higher latitude in Greenland where bumblebees are rare, Philipp et al. (1996) also found some *Pedicularis* species depend on insect visitors. Similarly, *Dryas spp.* in Greenland rely on muscid flies for seed set (Tiusanen et al. 2016). Even plant species that are not pollen limited, such as *Vaccinium vitis-idaea,* are still dependent on pollinators for maximum seed set (Koch et al. 2020).

Plant-insect interactions in the Arctic are not one sided, as the adult stages of many insect taxa rely on floral resources like pollen and nectar as a food source (Larson et al. 2001; Høye and Forchhamer 2008; Høye et al. 2013). The insect-visitor fauna of the High Arctic is fairly well documented from sites like Uummannaq, Greenland (Lundgren and Olesen 2005), Zackenburg, Greenland (Olesen et al. 2008), Ellesmere Island, Canada (Robinson et al. 2018), and Svalbard, Norway (Gillespie et al. 2016; Gillespie and Cooper 2021). However, fewer studies on insect pollination have been conducted in Low Arctic sites like the North Slope of Alaska (Williams and Batzli 1982, Khorsand et al. *in review*), especially in the past few decades. Across High Arctic sites, flies (Order Diptera) comprise the majority of floral visitors, while bees and wasps

(Order Hymenoptera) are uncommon compared to temperate and tropical regions (Kevan, 1972; Elberling and Olesen 1999; Lundgren and Olesen 2005). The Dipteran families Muscidae, Chironimidae, Empididae, Syrphidae, and Anthomyiidae comprise most of the High Arctic fly-visitor fauna (Elberling and Olesen 1999; Lundgren and Olesen 2005). Interestingly, High Arctic sites have few bee pollinators, with Ichneumon wasps comprising the majority of Hymenopteran visitors (Elberling and Olesen 1999; Lundgren and Olesen 2005; Gillespie et al. 2016). In contrast, eusocial bumblebees (*Bombus spp.*) comprise a larger proportion of the pollinator fauna in Low Arctic study sites such as the North Slope of Alaska (Kevan et al. 1972; Williams and Batzli 1982; Eidesen et al. 2017). Eidesen et al. (2017) suggest that bumblebee species richness may be higher in Low Arctic sites due to an increased abundance of attractive blue and purple flowers, which enabled increased colonization of those areas. Butterflies and moths (Order Lepidoptera), beetles (Order Coleoptera), thrips (Order Thysanoptera), and caddisflies (Order Trichoptera) have also been observed visiting Arctic plants, yet they are less common than the two dominant orders (Elberling and Olesen 1999). Observations of Arctic pollinators often only account for insect visitation, which may not equate to effective pollination as insect taxa vary in behavior and pollen-collection (Alarcón 2010; Ne'eman et al. 2010). To date, few studies have investigated pollen transport in the Arctic, and these have focused primarily on pollen transfer networks rather than taxonomic differences (Urbanowicz et al. 2017; Cirtwill et al. 2023). Consequently, there is an increasing need to investigate the pollen carrying capabilities of insect taxa to better understand the role of insects in Arctic plant reproduction (Alarcón 2010; Ne'eman et al. 2010; Schmidt et al. 2016; Cirtwill et al. 2023).

Arctic insect taxa have variable life histories (Høye and Forchhammer 2008) and thus, may differ in their responses to climate change. As Arctic insects often live in environments near their lower thermal tolerances (Deutsch et al. 2008; Høye 2020), warming temperatures may decrease metabolic restrictions and increase insect activity (Deutsch et al. 2008; Asmus et al. 2018; Høye 2020). Climate change may also impact insect population dynamics. Long-term insect monitoring out of Zackenburg, Greenland has found non-linear and taxa-specific population trends over the last few decades in tandem with background climate variation (Høye et al. 2021). Høye et al. (2021) also observed increasing numbers of a small proportion of species, indicating potential insect community homogenization as forecasted by Vasiliev and Greenwood (2021).

Insects also respond to a changing climate by shifting their phenology, primarily the timing of emergence (Høye et al. 2007; Høye and Forchhammer 2008). Data from the High Arctic suggest that snowmelt date best predicts insect emergence in several key Dipteran families, while air temperature is less important (Høye and Forchhammer 2008). This corroborates temperate studies like Kudo and Cooper (2019) that highlight the role of snowmelt timing in controlling bumblebee emergence. Another biotic factor that influences insect phenology at a taxa-level is food resource availability (Robinson et al. 2018). Insects that rely on pollen and nectar for all developmental phases, like bees, are more reliant on flowering timing than insects that feed on detritus, meat, or vegetation during early life history stages (Høye and Forchhammer 2008; Robinson et al. 2018). Consequently, bees have been shown to maintain tight phenological synchrony with their feeding plants (Bartomeus et al. 2011). In contrast, High Arctic Dipteran diversity has been shown to not respond to floral availability, likely because flies do not rely on floral resources during their larval stages (Robinson et al. 2018). On an insect community scale, differing phenological drivers and life histories may result in unique temporal dynamics of insect activity.

At a community level, Arctic plant pollinator networks are highly generalized and exhibit strong temporal dynamics (Lundgren and Olesen 2005; Olesen et al. 2008; Pradal et al. 2009; Gillespie and Cooper 2021). Arctic plant-insect visitor communities exhibit low species diversity, as expected given their high latitude (Callaghan et al. 2004). Investigations into temporal dynamics in Arctic plant-pollinator networks reveal that both species abundance and phenophase-length predict a species' number of partners, with the most abundant and long-flowering/foraging species being the most generalized (Olesen et al. 2008). This partially supports the neutrality hypothesis of species interactions, which asserts that species abundance is the primary driver of interactions, rather than factors like floral morphology (Vázquez et al. 2007; Krishna et al. 2008; Vázquez et al. 2009). Seasonally, Arctic networks exhibit a gradual increase in network complexity throughout the growing season, followed by either an abrupt collapse due to cold temperatures, snowfall, and shortening days (Pradal et al. 2009; Semenchuk et al. 2016), or a gradual decrease in complexity due to senescence and insect inactivity (Gillespie and Cooper 2021). These temporal dynamics are also driven by rapid turnover of species within the growing season, as many species have very short phenophases of only a few weeks (Olesen et al. 2008; Cirtwill et al. 2018). While there is also high turnover in insect species composition between years (Cirtwill et al. 2018), network structure seems to remain stable over these time frames (Olesen et al. 2008). These findings indicate that high generalization may buffer individual species from changes in community composition, as new species can fill the functional roles of old species in the network (Gillespie and Cooper 2021).

Both the timing and duration of plant flowering, as well as the active foraging period of insects, can influence the strength of interactions between trophic levels. At a basic level, plants must be flowering while insects are active for potential interactions to occur. A complete asynchrony between trophic levels can result in forbidden links, or interactions that cannot occur due to timing differences (Olesen et al. 2011). A complete or partial temporal mismatch between mutualistic partners is also known as phenological mismatch or asynchrony (Hegland et al. 2009), and has garnered significant attention in recent years as a possible outcome of climate change due to its potential impacts on both plants and pollinators (Schmidt et al. 2016; Gérard et al. 2020). While theoretically plausible, researchers have predominately been unsuccessful in empirically demonstrating plant-pollinator phenological mismatch (Forrest 2015; Gérard et al. 2020; Gillespie and Cooper 2021). Those that have been able to provide evidence for phenological mismatch have often focused on pairwise interactions between species, rather than entire communities (Kudo and Ida 2013; Kudo and Cooper 2015). Reductions in pollinator services due to differences in bumblebee spring emergence and spring ephemeral flowering have been shown to decrease plant seed set at a species-level (Kudo and Ida 2013; Kudo and Cooper 2019). Moreover, declines in floral resources for some insects due to a shortening of the growing season may contribute to insect population declines (Høye et al. 2013; Schmidt et al. 2016). These changes, in turn, may have cascading effects on population trends and community dynamics (Klady et al. 2011; Settele et al. 2016).

The first step in untangling the complex consequences of phenological changes on plant-pollinator interactions is understanding baseline trends at a regional level. While the High Arctic has received significant attention in these respects, many areas of the Low Arctic including the North Slope of Alaska have not been well studied. This deficit is especially important to address given clear compositional differences in insect fauna in the Low and High Arctic, especially the increased presence of bumblebees in the Low Arctic (Eidesen et al. 2017). To address these gaps, we investigated the temporal dynamics of network structure, floral resources, insect visitation, and insect pollen transfer over a single growing season in the Low Arctic of Alaska.

A primary goal of this research was to construct preliminary plant-pollinator visitation networks for both the entire growing season (static networks), and for time-slices within the growing season (dynamic networks). These are the first plant-insect visitor networks created on the North Slope of Alaska, which serve as a solid baseline for understanding interactions in this area. We tested four specific research questions at two sites: (Q1) how does this Alaskan plant-insect visitor network compare to other Arctic networks in species richness, structure, and temporal patterns? (Q2) How do floral resources and insect visitation vary spatially and temporally throughout the growing season? (Q3) How do visitation rates made by different insect orders differ throughout the growing season? And (Q4) how does conspecific and total pollen load differ between insect orders and families throughout the growing season?

Methods

Study site and experimental design

Field observations were conducted over the summer of 2022 near Toolik Field Station, on the Alaskan North Slope just north of the Brooks Range, Alaska, USA. Data were collected at two study sites: Imnavait Creek (68°625 N, 149°325 W, elevation 930m) and Toolik Lake (68°380 N, 149°360 W, elevation 730 m). While there is inter-annual variation, snowmelt generally occurs at Toolik between the middle and end of May, and Imnavait experiences snowmelt about one week later (Walker et al. 1994; Betway et al. 2022). Sampling was conducted using 64 1m^2 control plots established and monitored by the International Tundra Experiment (ITEX, see Walker et al. 1994, Walker et al. 1999; and Khorsand et al. *in review* for detailed descriptions of the study sites). While ITEX also monitors experimental plots warmed by Open-Top Chambers (OTCs) at these sites (see Webber and Walker 1991), this study only used unmanipulated control plots. In each site, we worked in two community types: dry heath tundra (Dry) and moist acidic tundra (Moist). Each community type at each site contained 16 control plots, resulting in 64 control plots total. Additionally, outplots were established and monitored throughout the summer in order to survey plant species not present within control plots. These outplots are functionally treated as controls, as they have undergone no experimental warming manipulation.

Plant flowering phenology

Between June 1, 2022 and August 4, 2022, we conducted biweekly phenological surveys of all control plots in each site. Surveys were conducted multiple times a week between 2 and 4 days apart in order to increase the accuracy of detecting phenological changes, following Miller-Rushing et al. (2008) and Khorsand et al. (*in review*). During these surveys, we noted all plant species that were in anthesis in each plot, including flower sex when applicable in dioecious species. We considered species in anthesis when petals and reproductive structures (stamens, pistils) were intact and not withered, and pollen was readily dispersed from the anthers. Additionally, we quantified floral density in a 30.5 by 30.5 cm frame in the center of each plot by counting all open flowers. For most species, every flower was counted individually, however we considered an inflorescence as the unit of measurement in a subset of species (*Bistorta officinalis,* all species of Asteraceae including *Arnica lessingii, Arnica griscomii, Antennaria monocephala*, and *Petasites frigidus,* all catkin-bearing species like *Salix spp.* and *Betula nana*).

Floral Visitor Observations

Between June 3, 2022 and August 4, 2022, we performed a total of 185 ten-minute observations (1850 minutes, about 31 hours) on both control plots and outplots in both study sites. Observations were carried out on days with favorable weather conditions, as rain, wind, freezing temperatures, or snow diminish insect visitor activity. This resulted in visitor observations being conducted on 37 days over the growing season (16 days in Imnavait, 31 days in Toolik). While no strict quota was established for visitor watches, we attempted to perform observations twice a week at each site and observe all flowering plant species in bloom at least once per day. However, various factors led to an uneven sampling effort both between study sites and plant species. These factors included nonrandom plot selection, differing weather conditions between study sites, rare plant species not present within control plots, and late-season patches of high floral density not present within control plots.

Before each floral visitor observation, the general weather conditions, time, plot number, and all plant species in bloom within the plot were recorded. During each observation, we sat four to six feet from the plot to minimize any possible obstruction to floral visitor activity. Then, for ten minutes, all insect visitation to flowers was recorded. We considered an insect visit to be when an insect landed on or contacted floral reproductive structures (anthers or stigma) for any period of time. Landings on petals or the outside of a flower were not considered visits. For each visitation event, we noted the plant species being visited, the Order of the visitor (Coleoptera, Diptera, Hymenoptera, Lepidoptera, Thysanoptera, Trichoptera, or other), the broad functional group based off discernable morphological features (ex. bumblebee, solitary bee, vespid wasp, ichneumon wasp, syrphid fly, large fly, small fly, mosquito, micro-moth, butterfly, beetle), the number of individuals of visitor, the number of distinct visits made to different flowers, and notable visitor behavior including foraging activity and the time spent on each flower. We only conducted floral visitor observations on plots that had flowers. Additional outplots were monitored in order to observe plant species not present within established plots or areas of high insect activity, following Robinson et al. (2018) and Gillespie and Cooper (2021).

Insect collection

Between June 1, 2022 and August 4, 2022, we collected a subsample of insect floral visitors (N= 255) in order to (1) identify visitors to higher taxonomic resolution, and (2) quantify insect pollen transport. Insects were netted while actively visiting flowers and transferred to their own clean glass vials. Insects were not collected during floral visitor observations. Vials were then placed upside-down in a killing jar charged with ethyl acetate to euthanize the insects inside (Kearns and Inouye 1993). This methodology prevented cross contamination of pollen, as insects remained separated in their respective vials throughout the euthanization process. Following collection, all insects were frozen in their vials for 12 hours, then thawed and pinned.

Insects were collected during structured collecting watches and opportunistically throughout field days. During collecting watches, one field researcher would walk randomly around one habitat in a study site (e.g. Toolik Dry), collecting any insect visitors they observed during that time. Structured watches varied in time from 10 minutes to over and hour. These watches also differed from opportunistic collection because the collector made an effort to collect insects off of every plant species they could find in the site. No quota for collecting watches was set, however we tried to collect multiple times per week in each site. Over the entire season, we conducted 50 structured collecting watches totaling 1050 minutes (17.5 hours), plus additional opportunistic collection. Following collection, insects were identified to order and family. Some taxa, mainly Syrphid flies, Vespid wasps, and bumblebees, were further identified to genus and species.

Pollen Analysis

To quantify insect pollen load, we removed, visualized, and counted pollen grains off of the collected insects' bodies using a standardized fuchsin dye protocol detailed in Kearns and Inouye (1993). We removed pollen off of the insect's bodies by swabbing them for 20-30 seconds with a small cube of fuchsin jelly. During this time, we swabbed available surfaces on the head, thorax, abdomen, and wings of each insect. However, we did not swab the hind legs or bee corbiculae, as the pollen in these specialized structures are not available for plants (Alarcón 2010; Schmidt et al. 2016). We then placed the fuchsin on a ruled microscope slide (containing 64 2-mm squares), heated for 20-30 seconds until the jelly liquified, and covered with a cover slip. Prepared slides were then observed under 40x and 100x magnification using a compound light microscope. Using the gridded slide to prevent double-counting, we then counted every pollen grain on the slide. Pollen grains were identified into three groups following Alarcón (2010): (1) conspecific pollen defined as pollen belonging to the plant species that the insect was caught on, (2) heterospecific pollen defined as pollen belonging to other plant species, and (3) damaged pollen included grains that could not be identified to either group with confidence. Pollen grains were identified to species through comparison to pollen reference slides and images from our project's pollen reference library (see Khorsand et al. *in review* for details).

Data Analysis

Statistical analyses were performed using R (R Core Team 2022). The *bipartite* package (Dormann et al. 2008) was used to construct plant-pollinator interaction networks and the package *mgcv* (Wood 2017) was used to perform Generalized Additive Mixed Models (GAMM).

Bipartite network analysis

Bipartite network analysis was used to quantify plant-insect interactions over the entire growing season across both sites combined (cumulative), as well as in each individual study site (Toolik and Imnavait), and in each community type (Dry and Moist). To construct the networks, we used collected insect specimens to identify binary relationships (e.g. did plant species X interact with insect family Y). Due to the resolution of our data and the limitations of identifying all insects to species, we constructed networks at a resolution of plant species and insect family following (Gillespie and Cooper, 2021). While this limits comparison to species-level networks and inhibits conclusions about species-specialization, it still provides a valuable tool to understand which taxa interacted in the network. Data were aggregated into data-matrices based on location and week, then plotted as networks using the function *visweb* in *bipartite* (Dormann et al. 2008). The network metrics connectance and nestedness were calculated using the function *networklevel* for each network, then qualitatively compared to understand network structure. Connectance represents the proportion of possible interactions in a network that were observed (Dormann et al. 2008). Nestedness, ranging from 0 to 100, is a pattern in networks where generalist species interact with specialists, and vice versa (Bascompte et al. 2003). Highly nested networks have lower nestedness values, while high nestedness values indicate that the network is organized randomly (Dormann et al. 2008). Nestedness relates to network generalization, as nested communities have a core group of highly generalized species (Bascompte 2003).

Along with the static networks for the entire season, we also created plant-insect visitor networks for weekly time slices throughout the growing season (dynamic networks) for both the cumulative network and the subset networks by site and community. Week one started on June 1st, 2022 (Julian day 152) and week ten ended on August 10th, 2022 (Julian Day 222). To investigate patterns in network complexity, network parameters (number of plant species active in network, number of insect families active in network, and number of interactions active in network) were graphed for each weekly network over the growing season.

Temporal Dynamics with GAMM Models

To investigate if temporal patterns in floral density and insect visitation differed between (1) study sites (Toolik and Imnavait), (2) community type (Dry and Moist), and (3) plants visited by different groups of insects (primarily bumblebee and primarily fly), we fit GAMM models with both quasipoisson and negative-binomial families to account for differing data distributions. Specifically, we wanted to account for over-dispersion and hard right-skew in plot floral density and insect visitation rates, as many plots and watches recorded zero data points. We modelled the temporal trends in our response variables using a penalized thin plate regression spline smoother using Julian Day as the primary predictor. For both questions, we investigated temporal trends in two response variables: (1) plot-level floral density, and (2) insect visitation rate per ten-minute watch. For the first two questions addressing differences between sites and community types over time, site and community type were entered as fixed effects and plot number was considered a random effect (random intercept and random slope). Outplots were each assigned unique plot numbers to enable this analysis. The resulting smoothed splines were graphed to visually represent differences between sites and community types. As this analysis only highlighted if there were differences over the entire time-frame, we made qualitative observations of spline trends to understand at what times temporal trends differed.

For plant visitation groups, we first needed to group plant species by dominant visitor taxa. The goal of this analysis was to understand how the most important floral resources for different insect groups varied over time. Thus, we compiled a cumulative visitation log for each plant species based off of (1) recorded visits during visitor observations, and (2) collected insects. Collected insects were assumed to have visited only once, as we did not record the number of observed visits for collected insects. Each insect visitor was then assigned to a broad insect functional group, which we uniquely defined based on (1) insect order, (2) insect foraging behavior, (3) insect size, and (4) easily discernable taxonomic differences for some Hymenopterans and Dipterans. The insect functional groups used in this study are as follows: beetle, large non-syrphid fly, small non-syrphid fly, syrphid fly, mosquito, bumblebee, solitary bee, Vespid wasp, Ichneumon wasp, micromoth, butterfly, other. While these functional groups lack taxonomic specificity, we argue that they represent a valuable resolution to understand patterns in floral visitation given the limitations of our sampling protocol (Valverde et al. 2015).

Following the assignment of functional groups, we quantified the percentage of total insect visits to each plant species from each functional group. From these data, it became clear that some plant species were primarily visited by bumblebees (*Bombus spp.*), and received few visits from other insect taxa. The remaining species often were primarily visited by Dipterans; however, few species exhibited a clear dominance for one group of Dipterans. Consequently, we decided upon grouping plant species into two groups: those that were primarily visited by bumblebees (hereafter *Bombus* plants), and those that were primarily visited by flies (hereafter Dipteran plants). We set a cutoff at 60% of visitations to determine visitor dominance. We only considered species with at least 10 recorded visits for this analysis, as small sample sizes could skew groupings. One plant species (*Saxifraga bronchialis*) fulfilled sample size requirements but lacked a clear visitor dominance of 60%, however it was not found in phenology plots so it was excluded from analysis. To understand how the floral density and insect visitation of *Bombus* plants and Dipteran plants varied over time, Julian day was assigned as the primary predictor in the GAMM model. The visitor group was assigned as a fixed effect, and the plot number was assigned as a random effect (random intercept and random slope). Finally, to investigate differences in visitation rate by insect order, order was assigned as a fixed effect and plot number was assigned as a random effect.

Pollen load comparison

Total pollen load, conspecific pollen load, and the ratio of conspecific pollen to total pollen were compared between insect orders and families using non-parametric Kruskal Wallis and follow-up pairwise Mann Whitney U tests. Only Orders Diptera and Hymenoptera fulfilled sample size requirements, and the other collected orders were excluded from analysis. To understand temporal dynamics in pollen-carrying, we ran GAMM models with negative binomial families and penalized thin-plate regression spline smoothers, as detailed above. Total and conspecific pollen loads were assigned as response variables, while Julian day was the primary predictor variable. Insect order was assigned as a fixed effect, and plot as a random effect. We did not test for differences in pollen load between sites or community types.

Results

Plant Phenology and Insect Visitation

Between June 1st 2023 and August 4th 2023, we observed the flowering phenology of 33 plant species at both Toolik and Imnavait. Flowering duration for each species, measured by both the absolute and mean first and last days of flowering, ranged from one to four weeks and differed between plant species (Figure 1). Of the plant species that received visitation from insects, *Kalmia procumbens, Rhododendron tomentosum,* and *Vaccinium vitis-idaea* all flowered for over three weeks (Figure 1). In contrast, *Pedicularis lanata, Petasites frigidus,* and *Dryas octopetala* were in flower for under two weeks (Figure 1). These short species phenophases resulted in clear turnover between early, middle, and late flowering species (Figure 1). We also conducted 185 visitor watches (totaling 30.8 hours of observation time) spread out over 37 days. We observed 248 insect visitors make 1029 visits to flowers. The majority of these visitors were flies (Order Diptera, n=179, 72% of individuals), and the remaining were bees and wasps (Order Hymenoptera, n=67, 27% of individuals), a single butterfly (Order Lepidoptera, n=1, 0.5% of individuals) and one thrip (Order Thysanoptera, n=1, 0.5% of individuals). In contrast, the majority of observed visits were made by Order Hymenoptera (n=712, 69% of visits), followed by Order Diptera (n=315, 31% of visits), and negligible visitation from the other insect orders. The majority of individuals and visits by Order Hymenoptera were made by bumblebees (*Bombus spp.*), with the remainder being social wasps (Vespidae, *Dolichovespula spp.*) and Ichneumonid wasps (Ichneumonidae).

The majority of insect visits were made to a subset of plant species (Figure 2). Not accounting for sampling effort, *Kalmia procumbens, Chamerion angustifolium,* and *Chamerion latifolium* received the most visits, primarily from bumblebees (*Bombus spp.*). *Bistorta officinalis, Rhododendron tomentosum,* and *Kalmia procumbens* received the most visits from flies (Order Diptera). Of all plant species observed, only 15 received at least 10 visits *Arctous alpina, Androsace chamaejasme, Bistorta officinalis, Chamerion angustifolium, Chamerion latifolium, Dasiphora fruticosa, Dryas octopetala, Kalmia procumbens, Petasites frigidus, Pedicularis lanata, Rhododendron tomentosum, Rubus chamaemorus, Salix pulchra, Saxifraga bronchialis,* and *Vaccinium vitis-idaea.* All but one of these species (*Saxifraga bronchialis*) showed a clear visitor dominance from either bumblebees (*Bombus spp.,* Hymenoptera) or flies (Diptera). Six species, hereafter referred to as *Bombus* plants, received more than 60% of their visits from bumblebees (*Arctous alpina, Chamerion angustifolium, Chamerion latifolium, Kalmia procumbens, Pedicularis lanata,* and *Vaccinium vitis-idaea*). Eight species (hereafter

Dipteran plants) received more than 60% of their visits from flies (*Androsace chamaejasme, Bistorta officinalis, Dasiphora fruticosa, Dryas octopetala, Petasites frigidus, Rhododendron tomentosum, Rubus chamaemorus,* and *Salix pulchra*).

Network Analysis

Network inputs

Over the entire season, we collected 255 insect specimens belonging to 5 orders and 28 families (Supplementary Table S1). The majority of collected insects belonged to Order Diptera (n=182, 71% of specimens), and the remainder belonged to Order Hymenoptera (n=62, 24% of specimens), Order Lepidoptera (n=9, 3% of specimens), Order Coleoptera (n=1, 0.5% of specimens), and Order Trichoptera (n=1, 0.5% of specimens). The most abundantly collected insect families were flower flies (Syrphidae), house flies (Muscidae) and bumblebees (Apidae). While we used family as the standard taxonomic level for input in the network analysis, we identified some specimens, primarily bumblebees and Vespid wasp, to species. The two most common species of bumblebee at our sites were *Bombus lapponicus sylvicola* and *B. jonellus.* However, we also collected specimens of *B. polaris, B. kirbiellius, B. neoboreus, B. cryptarum, B. natvigi,* and *B. johanseni.* Our Vespid wasp specimens were all in the genus *Dolichovespula,* mostly *Dolichovespula albida.*

Static Networks

The cumulative network for the entire growing season included 41 plant species and 28 insect families, as well as 128 unique interactions between them (Figure 3). The cumulative network exhibited low connectance (C=0.11) and was highly nested (N= 4.78). *Bistorta officinalis, Rhododendron tomentosum,* and *Salix pulchra* were visited by the greatest number of insect families. Likewise, the families Syrphidae, Muscidae, and Apidae interacted with the most plant species (Figure 3).

The subset networks for each study site (Toolik and Imnavait) and each community type (Dry and Moist) were smaller than the cumulative network, but showed similar structure (Supplementary Figures S1-4). The Toolik network had more plant species, insect families, and interactions than the Imnavait network (Table 1). Likewise, the combined Dry network had more species, families, and interactions than the Moist network (Table 1). Network structure was similar between subset networks: connectance was low and nestedness was high (Table 1).

Dynamic Networks and Temporal Dynamics

To understand the temporal build-up of network structure over time, we visualized network parameters for each weekly time-slice network. The number of plant species and plant-insect interactions active in the network gradually increased until the first week of July (DOY 180-186), then began decreasing (Figure 4). The number of insect families in the network showed an initial peak in early June (DOY 159-165) followed by another increase to the true peak during the second week in July (DOY 187-193). Following this week, all network parameters declined sharply in week 7 (DOY 194-200), then continually declined towards the end of the season (Figure 4). Temporal trends differed slightly between study site and community subset networks. The Toolik network had higher network complexity during the first few weeks (DOY 159-179) and last few weeks of the season (DOY 187-222), while the Imnavait network showed a brief abrupt peak in the number of interactions during week five (DOY 180-186) (Supplementary Figure S5). The Dry community subset network also maintained a high number of interactions for multiple weeks (DOY 166-193), while the Moist community showed a more rapid increase and decline in the number of interactions in week five (DOY 180-186).

Temporal trends

Study Site

The GAMM models found significant differences in the temporal trends of floral density between the Toolik and Imnavait study sites including all plant species ($F_{5.50} = 42.88$, $p<0.001$; Figure 5), and flowering species that received at least 10 visits (hereafter floral resources) ($F_{2.62} = 8.48$, $p<0.05$; Supplemental Figure S7). In both cases, mean floral density was higher throughout the growing season in Toolik plots than in Imnavait plots (all species: $Z=2.73$, $p<0.01$; floral resources: $Z=3.143$, $p<0.01$; Figure 5 and Supplementary Figure S7). Accounting for all plant species, floral density at Imnavait showed two peaks: week two (DOY 159-165) and week five (DOY 187-193). Floral density at Toolik peaked later in the season, during week four (DOY 173-179) and week five (DOY 180-186) (Figure 5). The splines for only insect floral resources were less complex (Supplemental Figure S7). Imnavait floral resources remained relatively consistent throughout the summer, while Toolik floral resources exhibited a distinct peak in week four (DOY 173-179). Insect visitation did not significantly differ in either magnitude ($Z=0.60$, $p=0.55$) or temporal trends ($F_{1.00} = 1.83$, $p=0.18$) between the two study sites (Supplemental Figure S8).

Community Type

The GAMM models found significant differences in the temporal trends of floral density between dry and moist community types for all plant species ($F_{2.02}= 36.41$, $p<0.001$, Figure 6). Specifically, floral density peaked earlier in Dry than in Moist. Floral density in Dry peaked at the beginning of week two (DOY 159-165), then slowly declined for three weeks before dropping to zero in week seven (DOY 194-200) (Figure 6). In contrast, floral density in moist communities gradually increased to a peak at the end of week five (DOY 180-186) and the beginning of week six (DOY 187-193), then rapidly decreased (Figure 6). The mean magnitude of floral density did not significantly differ between community types (Z=0.09, p=0.93). Accounting for only insect floral resources, the GAMM model did not find a significant difference in temporal trend of floral density between the two community types ($F_{2.46}$= 6.438, p>0.05; Supplemental Figure S9). Dry floral density peaked in week four (DOY 173-179), while moist floral density peaked in week five (DOY 180-186) (Supplemental Figure S9). The mean floral density of insect floral resources in dry plots was significantly higher than the mean floral density in moist plots (Z=3.68, p<0.001; Supplemental Figure S9).

The temporal trends of insect visitation showed no significant differences between dry and moist communities ($F_{2.36}$= 9.28, p<0.1; Supplemental Figure S10). However, the mean visitation rate per observation was significantly higher for dry plots than moist plots over the entire growing season (Z=4.02, p<0.001). Both communities exhibited an early season peak in insect visitation in week two (DOY 159-165) (Supplemental Figure S10). In the dry communities, early season activity (weeks 1-3) was primarily on *Kalmia procumbens* (81% of all visits), while activity in the moist communities during this time was primarily on *Salix pulchra* inflorescences (71% of all visits). The moist communities did not show another clear peak, while the dry community experienced another peak in insect activity at the end of week 7 (DOY 194-199) (Supplemental Figure S10). Along with that peak, insect visitation rates in the dry communities were higher throughout the last few weeks of the season (Supplemental Figure S10). Late season (weeks 7-10) visitation in the dry communities was primarily on the two fireweed species: *Chamerion latifolium* (35% of visits) and *Chamerion angustifolium* (45% of visits). These species flowered in large conspicuous patches, and were not present within control plots. Consequently, they are not represented in the plant phenology data.

Plant Visitation Group

The floral density of plants visited primarily by bumblebees (*Bombus* plants) and of plants visited primarily by Dipterans (Dipteran plants) differed significantly temporally over the growing season ($F_{3.08}$ =12.72, p<0.05, Figure 8). *Bombus* plants showed a peak in floral density during week four (DOY 173-179), while Dipteran plants peaked in week five (DOY 180-186). Additionally, the mean floral density of *Bombus* plants was significantly higher than the mean floral density of Dipteran plants (Z=4.70, p<0.001) (Figure 8). In contrast, temporal trends in the visitation rates to plants in these two groups were not significantly different ($F_{2.69}$ =6.88, p<0.1, Supplemental Figure S11), and did not differ in mean visitation rate (Z=0.76, p=0.45). Both plant groups received increased visitation rates during the end of week two (DOY 159-165) and the beginning of week three (DOY 166-172) (Supplemental Figure S11). These peaks corresponded to the flowering of *Arctous alpina, Kalmia procumbens* and *Salix pulchra.* Visitation to Dipteran plants stayed higher than visitation to *Bombus* plants over weeks four through seven (DOY 173-200) during the peak flowering of *Rhododendron tomentosum* and *Bistorta officinalis.* In the late season, *Bombus* plant received higher visitation rates in weeks eight and nine (DOY 201-215) during the flowering of *Chamerion latifolium* and *Chamerion angustifolium.*

Insect Order

The vast majority of observed visits (>99%) were made by members of the Orders Diptera and Hymenoptera. Consequently, we only tested for differences between these two orders. The GAMM model found no significant differences in the temporal trends of insect visitation rates over the growing season between Dipterans and Hymenopterans ($F_{5.78}$ =2.36, p<0.1; Figure 7). However, the mean rate of floral visitation was significantly higher for Hymenopterans than Dipterans (Z=3.01, p<0.01) (Figure 7). Dipteran visitation rates did not show a strong temporal pattern over the growing season, maintaining at a constant low level. In contrast, Hymenopteran visitation showed three pulses in activity throughout the season. Hymenopteran visitation rates were high during weeks one and two (DOY 152 -165), during week seven (DOY 194-200), and again during week ten (DOY 215-222) (Figure 7). Based on observational data as well as collected specimens, early season Hymenopteran activity was entirely emerging queen bumblebees, while the later pulses were workers, males, and new queens. While we did not quantify the numbers of queens, workers, and males, we clearly observed distinctions between these bumblebee castes based on body size, pollen-carrying corbiculae, and the number of antennal segments. Queens were visibly larger than workers, and males lacked corbiculae and had more antennal segments.

Pollen Load

Insect Orders

Pollen was collected and counted off of all 255 insect specimens. As 95% of collected insect specimens belonged to the Orders Diptera and Hymenoptera, we only tested for differences between these groups. The median number of pollen grains of all plant species found on Hymenopterans (median = 30.5, mean = 325.7, SD = 1528.5, range = 0-12,006) was significantly higher than on Dipterans (median = 3, mean = 27.3, SD = 84.1, range = 0-820) (Mann Whitney U = 2628, $p<0.001$; Figure 9 and Supplementary Table S2). Considering only conspecific pollen, Hymenopterans (median = 8, mean = 101.7, SD =233.1, range = 0-1,189) also carried significantly more pollen than Dipterans (median=0.5, mean = 16.3, SD = 77.1, range = 0-820) (Mann Whitney U = 3314, $p<0.001$; Figure 10 and Supplementary Table S2). Hymenopterans and Dipterans did not significantly differ in the ratio of conspecific pollen to total pollen found on their bodies (Mann Whitney U = 3429.5, p=0.16; Supplemental Figure S12).

When examining how total pollen load changed over the growing season, GAMM models found a significant temporal difference in pollen load between Hymenopterans and Dipterans ($F_{2.47}$= 20.43, p<0.001; Figure 10). Dipteran pollen load remained fairly stable over the growing season, while Hymenopteran pollen load showed a distinct peak in the second week of June (DOY 159-165) and a gradual decline from that point. Examining only conspecific pollen, Hymenopteran and Dipteran pollen load did not differ significantly in temporal trend over the growing season ($F_{2.13}$ = 5.15, p=0.11; Supplemental Figure S13). There was also no significantly different temporal trend between orders in the ratio of conspecific and total pollen ($F_{1.0}$= 0.61, p<0.435).

Insect Family

Only five insect families had more than 10 collected specimens: Apidae and Vespidae in Order Hymenoptera and Empididae, Fanniidae, Muscidae, and Syrphidae in Order Diptera. Kruskal-Wallis tests found significant differences in the total pollen load found on insects of different families (H_5 = 60.35, p<0.001). Follow-up pairwise Mann Whitney tests showed numerous significant pairwise differences (Figure 11). Summary statistics for each insect family can be viewed in Supplementary Table S2. Apid bees had a significantly higher median total pollen load than the fly families Empididae (p<0.001), Fanniidae (p<0.001), and Syrphidae (p<0.001). Vespid wasps also had a significantly higher median total pollen load than Empidids (p<0.001) and Fanniids (p<0.01). Within the fly families, Muscidae carried the highest median number of pollen grains. Muscids had significantly more pollen grains than Empidids (p<0.001) and Fanniids ($p<0.01$). Finally, Syrphids had significantly more pollen than Empidids ($p<0.001$) (Figure 11).

While less significant than for total pollen load, the insect families also differed significantly in conspecific pollen load (Kruskal Wallis, $H_5 = 33.32$, $p<0.001$). Pairwise comparisons are visualized in Figure 12 and summary statistics for each family are found in Supplementary Table 2b. Apid bees carried significantly more conspecific pollen than Empidids ($p<0.001$) and Fanniids ($p<0.01$). Vespid wasps had significantly more pollen than Empidids ($p<0.001$) and Fanniids ($p<0.05$). Between flies, both Muscids and Syrphids carried significantly more pollen than Empidids ($p<0.05$). Finally, a Kruskal Wallis test found no significant differences in the ratio of conspecific to total pollen carried by different insect families ($H_5=10.03$, $p=0.07$).

Discussion

Q1: Plant-insect visitation networks

The cumulative static network produced from our sites had a higher number of plant species than comparable High Arctic networks. We observed insect visitation to 41 plant species, exceeding all other published Arctic networks: Zackenberg, Greenland: 31 species (Olesen et al. 2008), Abisko, Sweden: 23 species (Elberling and Olesen 1999), Svalbard, Norway: 19 species (Gillespie and Cooper 2021), Uummannaq, Greenland: 17 species (Lundgren and Olesen 2005), and Ellesmere Island, Canada: 8 species (Robinson et al. 2018), Additionally, we observed 28 flower-visiting insect families, exceeding most High Arctic networks (Ellesmere Island, Canada: 23 families (Robinson et al. 2018), Uummannaq, Greenland: 19 families (Lundgren and Olesen 2005), and Svalbard, Norway: 11 families (Gillespie and Cooper 2021). The better studied High Arctic site in Zackenburg, Greenland, which had 28 insect families, shared the same number of families as our site (Olesen et al. 2008). These species diversity trends underscore broad biogeographical theories regarding decreased species richness at high latitudes (Callaghan et al. 2004).

In terms of structure, the cumulative network was nested with a core group of generalized plants and insects and two tails of asymmetrically specialized plants and insects (Bascompte and Jordano 2007). High generalization and nestedness have been reported in network studies across the Arctic (Elberling and Olesen 1999; Lundgren and Olesen 2005; Olesen et al. 2008; Robinson et al. 2018; Gillespie and Cooper 2021), as is expected at high latitudes (Olesen and Jordano 2002). Hoiss et al. (2015) assert that insects and plants living in arctic and alpine environments must widen their niches to cope with limiting abiotic conditions and unpredictable/sparse resources. In this way, generalization relates directly with community stability and resiliency in stressful environments like Arctic tundra (Bascompte and Jordano 2007; Hoiss et al. 2015). The generalized and nested structure of our observed plant-visitor network is especially important in the context of phenological shifts, as generalization may buffer communities from the impacts of trophic mismatch (Gillespie and Cooper 2021).

We observed lower connectance in our static network than in other published Arctic networks. Connectance in our network was around 0.11 at the family level for the cumulative network, and only slightly higher in the subset networks. In contrast, family level connectance ranged from 0.20 to 0.52 in the High Arctic (Lundren and Olesen 2005; Olesen et al. 2008). One possible explanation for this difference is network size, as connectance has been shown to decrease exponentially as the number of species in a network increases (Olesen and Jordano 2002). However, this should not entirely account for the deficit we observed.

Another possibility is that our sampling effort was insufficient to detect some rare interactions that occurred in the network. Other studies have found that the most abundant, long-active, plants and insects in arctic networks shared the most interactions with other taxa (Olesen et al. 2008; Gillespie and Cooper 2021). These findings corroborate the neutrality hypothesis of species interactions, which posits that abundance predicts interaction frequencies in generalized communities (Vázquez et al. 2007; Krishna et al. 2008; Vázquez et al. 2009). Under this hypothesis, rare species in a network would interact with fewer partners than common species. In utilizing a plot-based sampling method without clear species-observation quotas we likely over-sampled abundant species and under-sampled rare species not found in plots. In this way, undersampling may have created the illusion of specialization, and decreased community connectance. Consequently, our observed network connectance should be taken with caution given the limitations of our sampling protocol.

We encountered numerous other barriers to directly comparing the network structure observed at our site to other Arctic networks. To begin, most arctic pollination network studies have taken place in the High Arctic (Lundgren and Olesen 2005; Olesen et al. 2008; Robinson et al. 2018; Gilllespie and Cooper 2021), and many have used insect species, rather than families, for analysis. Only one study (Elberling and Olesen 1999) was conducted at a similar latitude, but it took place in the subarctic life zone of Sweden. Additionally, we used a plot-based protocol to sample interactions, which differs from other methodologies that sample plant species evenly (Olesen et al. 2008). In doing so, our plot-sampling inherently biased observations towards abundant species and may have missed interactions between rare species (Jordano 2016). Despite our sampling limitations, our findings still represent a valuable description of plant-insect interactions in Low Arctic Alaska.

The temporal dynamics in our network were similar to other Arctic networks. Individual flowering plant species generally had short phenophases lasting one to four weeks, resulting in clear turnover between early, middle, and late flowering plant species over the 10 weeks of observation. Olesen et al. (2008) found that species in the Zackenberg network had short phenophases, and that species phenophase length predicted generalization. Species that were flowering or foraging for longer periods of time generally interacted with more partners than those that were active for a short period (Olesen et al. 2008). While we did not empirically test for this relationship, the duration of flowering for individual species, as well as turnover between short-flowering species, likely contributed to the temporal progression of our network (Olesen et al. 2008; Cirtwill et al. 2018). The plant species present at a given time in each community are also likely a driver of network structure, as floral diversity and composition has been shown to structure networks in other Arctic sites (Robinson et al. 2018).

We observed a gradual increase in the number of species and interactions present in the network through the first half of the growing season as plant species and insect families entered the network, corroborating other Arctic studies (Pradal et al. 2009; Robinson et al. 2018; & Gillespie and Cooper 2021). This growth culminated in a peak in the number of interactions during the first week of July, corresponding with the peak in plant species richness at our sites. The relationship between plant richness and network complexity supports the importance of floral diversity for network complexity (Robinson et al. 2018). In contrast, our observations of network decline do not corroborate the findings at other Arctic sites. In Zackenberg, Greenland, Pradal et al. (2009) observed a complete collapse of their network shortly after it peaked, likely due to a sudden onset of low temperatures or snowfall. However, at an even higher latitude in Svalbard, Norway, Gillespie and Cooper (2021) observed a more gradual decline in network complexity due to plant and insect senescence. Interestingly, our Low Arctic cumulative network showed a gradual temporal decline similar to Gillespie and Cooper (2021).

Viewing our results at a smaller spatial scale, we found different temporal patterns of network decline in Toolik and Imnavait. The Toolik network mirrored the trend of our cumulative network and of Gillespie and Cooper (2021). In contrast, the Imnavait network exhibited a complete collapse after a destructive hailstorm on July 9th, 2022 (DOY 190). The storm completely removed all flowers from plants, just a few days after peak floral density was reached at the site. While at a regional level, our cumulative network showed a gradual build-up and decline, smaller spatial scales showed varying trends including a complete collapse. This heterogeneity underscores how the temporal dynamics of network decline can vary across small spatial scales due to the unpredictable weather conditions in the Arctic. Extreme weather events may play an increasing role in impacting plant-insect interactions, as Arctic extreme weather events are forecasted to increase in frequency in a warming future (Saha et al. 2006). Along with impacting network structure and plant-insect interactions at a community level, these extreme events will likely also impact the reproductive success of individual plant species as observed in the High Arctic of Canada (Panchen et al. 2022).

Q2: Temporal trends in floral resources and visitation rates

While our findings support the conclusion that floral resources vary temporally between sites and community types, we did not find significant temporal variation in insect visitation. Floral density showed significantly different temporal trends between Toolik and Imnavait and between dry and moist communities. These differences in floral density can likely be attributed to heterogenous species distributions and heterogeneity in snowmelt timing. However, temporal trends in insect visitation rates did not reflect these changes in floral density, and were not significantly different between sites.

At a community-level, floral density trends are a result of unique plant communities in dry heath and moist acidic tundra. While many common species like *Bistorta officinalis, Rhododendron tomentosum, Salix pulchra,* and *Vaccinium vitis-idaea* were found across community types, other species resided in only one. *Arctous alpina,* both *Chamerion* species, *Dryas octopetala,* and *Kalmia procumbens* were strictly found in dry heath, while *Rubus chamaemorus* only grew in moist acidic tundra. Even when species grew in both community types, they were often more abundant in one, or flowered in condensed patches. As each plant species flowered for a short period of the whole season, the mosaic of flowering plants present at a given time in a community was quite heterogenous.

Examining the summation of these mosaics of flowers, floral density in dry communities showed a significant temporal difference from moist communities, with dry heath floral density peaking early in the season at the beginning of June. These peaks in dry heath were associated with the early-season blooms of *Arctous alpina* and *Kalmia procumbens.* Moist acidic tundra floral density peaked significantly later in early July, coinciding with the flowering of *Bistorta officinalis, Rhododendron tomentosum, Andromeda polifolia, Vaccinium uliginosum,* and *Vaccinium vitis-idaea.* Scaling up to the site level, Toolik and Imnavait also showed different temporal patterns in flowering. Plant species were present in different abundances in Toolik and Imnavait. For example, *Kalmia procumbens* flowered profusely at Toolik, but was largely absent from Imnavait. Similarly, *Bistorta officinalis* was much more abundant at Imnavait. These compositional differences may have contributed to the divergent trends in floral density between study sites.

Heterogeneity in the timing of floral density peaks could also be attributed to snowmelt, as moist acidic tundra often maintains snow later in the season than the more exposed dry heath. Tundra vegetative community composition interplays with microtopography, as depressions with higher snow retention facilitate increased soil moisture and more mesic plant communities (Peterson and Billings 1980; Bhattarai et al. 2020). Although we did not quantify snowmelt dates in the present study, we observed that dry heath plots at both Toolik and Imnavait were free of snow before moist acidic plots. Gillespie and Cooper (2021) observed that hillside slopes and depressions, dominated by mesic plant communities, retained snow for a one to two weeks longer than adjacent ridgetops. Snowmelt has been shown to be tightly linked to phenology and floral production in Arctic plants (Wipf and Rixen 2010; Oberbauer et al. 2013; Bjorkman et al. 2015, Semenchuk et al. 2016) and may also influence plant flowering through soil moisture, as early snowmelt decreases soil moisture in Arctic tundra (Scharn et al. 2021). Considering the findings of Høye et al. (2013) that landscape-level floral duration is decreasing in the High Arctic, further inquiry into the role of topographic heterogeneity on plant flowering patterns is warranted.

Regardless of the cause, temporal differences in floral density peaks between closely adjacent communities may result in more consistent floral resource availability for mobile pollinators than if habitats flowered in synchrony. Heterogenous temporal trends in plant flowering also have the potential to either increase or decrease the total duration of floral availability across the landscape in a warmer future. Gillespie and Cooper (2021) hypothesized that differences in snowmelt timing between ridges and depressions in High Arctic tundra contributes to a lengthening of landscape-level flowering duration, which benefits some plants and insects. In a temperate grassland ecosystem in California, Olliff-Yang and Ackerly (2020) found that spatial heterogeneity in plant flowering increased the total time that flowers were available to pollinators across the landscape. However, the benefits of this spatial heterogeneity for insects relies on insect foraging range, as insects must be able to travel between adjacent habitats. While we do not have data to support fly or bumblebee foraging areas, we observed bumblebees flying hundreds of meters between adjacent habitats and nesting in areas with no surrounding flowers. In a study in the UK, Osborne et al. (2008) found that *Bombus terrestris* workers foraged up to 1.5 km away from their colonies, highlighting the large potential foraging area of bumblebees. While data on foraging distances is less abundant for Dipterans, Inouye et al. (2015) referenced multiple cases of flies travelling kilometers between foraging resources. This movement may enable early or late emerging insects to locate floral resources, even if their nearby community is not in bloom. In this way, spatio-temporal heterogeneity in floral resources for insects may buffer insects and plants from disturbance caused by phenological shifts (Gillespie and Cooper 2021).

Q3: Differences in visitation between insect orders

While bee and wasp (Order Hymenoptera) and fly (Order Diptera) visitation rates did not differ significantly in temporal trend over the growing season, Hymenopterans visited at a significantly higher rate and made up the majority of observed visits. Specifically, we observed high visitation rates from numerous bumblebee (*Bombus*) species, as well as vespid wasps (*Dolichovespula spp.*). The disproportionately high visitation rates by bumblebees contrasts both the findings of insect-plant interaction studies in the High Arctic (Kevan 1972; Robinson et al. 2018; Elberling and Olesen 1999; Lundgren and Olesen 2005; Olesen et al. 2008; Gillespie et al. 2016; Gillespie and Cooper 2021), as well as preliminary data collected by our team at Toolik Field Station in 2019 (Khorsand et al. *in review*). However, the importance of Alaskan bumblebees as pollinators has been documented in the past. Williams and Batzli (1982) found that bumblebees, specifically queens, were essential for seed production in multiple species of *Pedicularis* in the Alaskan Arctic. Additionally, Williams and Batzli (1982) noted that bumblebee populations were variable year-to-year at their site, which could potentially explain the higher proportion of bumblebee visits at our sites in the 2022 season compared to 2019 and 2020 (Khorsand et al. *in review*).

While Dipterans made up a minority of observed visits, they were more abundant than Hymenopterans. Flies have been shown to be the most common floral visitors at sites across the Arctic (Kevan 1972; Robinson et al. 2018; Elberling and Olesen 1999; Lundgren and Olesen 2005; Olesen et al. 2008; Gillespie et al. 2016; Gillespie and Cooper 2021). These findings are contextualized by global patterns in pollinator diversity, as other common anthophilous insects like bees decline in abundance and species richness at high altitudes and latitudes (Orr et al. 2020). Flies, on the other hand, maintain abundance and diversity in high latitude and altitude sites due to physiological and ecological tolerances of cold temperatures and unpredictable resources (Danks 2004; Elberling and Olesen 2005; Inouye et al. 2015). As pollinators, flies may make up for lower visitation rates with increased abundance (Larson et al. 2001)

At a higher taxonomic level, the Dipteran families we observed most often (Syrphidae, Muscidae, Fanniidae, and Empididae) have been highlighted as crucial flower-visitors in the Arctic. Tiusanen et al. (2016) assert that Muscid flies are one of the most important insect pollinators in Zackenburg, Greenland, due to their role in facilitating seed set in *Dryas spp.* (Tiusanen et al. 2016). While we did not identify muscid flies to genus, Pont (1993), Elberling and Olesen (1999), and Olesen et al. (2008) all highlight Arctic muscid genera like *Thricops* and *Spilogona* as important floral visitors due to their foraging behavior and elongated proboscis.

Additionally, Skevington and Dang (2002) highlight the fact that muscids have high hair density and bristles that trap pollen. Along with muscid flies, syrphid flies are common and important pollinators in arctic and alpine areas (Larson et al. 2001; Iler et al. 2013; Inouye et al. 2015). Muscid and syrphid pollination have also been observed in other common plant species in our sites that we observed flies visiting, including *Rhododendron tomentosum* (Dlusskiĭ et al. 2005) and *Bistorta spp.* (Momose and Inoue 1993).

While we did not find significant differences in temporal patterns of visitation, we did observe clear biologically relevant patterns in visitation rates by Dipterans and Hymenopterans. Dipteran visitation rates were stable at a relatively low, but constant level throughout the growing season. In contrast, Hymenopteran visitation exhibited distinct peaks corresponding to the emergence of different colony castes. At the beginning of the season in early June, we observed emerging queen bumblebees foraging at constant, high rates on *Arctous alpina, Kalmia procumbens, Pedicularis lanata,* and *Salix pulchra.* Following this activity, bumblebees were rare across all sites and habitats during the end of June and beginning of July. Bumblebee activity increased again in mid-July with the emergence of bumblebee workers, males, and new queens. During this time, we observed visitation to *Bistorta officinalis, Pedicularis lapponica, Vaccinium vitis-idaea, Chamerion angustifolium,* and *C. latifolium.*

The distinct pulses we observed in bumblebee visitation compared to the steady, reliable, visitation rates of flies have important implications for the entire plant-pollinator community. Temporal shifts in these short peaks could result in reduced pollination rates in plants that rely on bumblebees. At our sites, we identified a group of species that primarily received visitation from bumblebees. These species exhibited a suite of floral features including urn-shaped flowers (*Arctous alpina* and *Vaccinium vitis*-idaea), zygomorphic flowers (*Pedicularis lanata* and *P.*

lapponica), and large pink/purple flowers (*Chamerion angustifolium* and *C. latifolium*). These observations support a degree of morphological trait matching and color preference between bumblebees and the plants in our site, as bumblebees have been shown to preferentially forage on tubular floral shapes (Suzuki 1992; Dohzono et al. 2011) and purple flowers (Chitka & Menzel 1992; Eidesen et al. 2017). While the flowering of the previously mentioned species coincided with the peaks in bumblebee activity in 2022, other species with similar floral morphologies received few visits when flowering during the bumblebee inactive period (weeks 4-6). *Vaccinium uliginosum* flowered during the inactive period, had urn-shaped flowers that closely resemble those of *Vaccinium vitis-idaea,* and has been shown to be bumblebee pollinated in temperate regions (Mayer et al. 2012). During this inactive period, *V. uliginosum* received low visitation from all insects, including bumblebees. *Pedicularis capitata,* which relied fully on bumblebees for fruit set in another Alaskan study (Williams and Bratzli 1982), also flowered during the inactive period and received no bumblebee visitation. Temporal shifts in bumblebee activity could impact floral visitation and resulting seed set in these species.

Another potential consequence of shifts in the timing of bumblebee activity relates to early flowering species. In temperate regions, shifts in the emergence of queen bumblebees have been shown to impact seed set in spring ephemerals (Kudo and Cooper 2019). In this study, bumblebee emergence was related to increases in soil temperature following snowmelt, but was less sensitive to early snowmelt and warm temperatures than plant flowering (Kudo and Cooper 2019). While bumblebee overwintering ecology is poorly studied in the Arctic, similar differences in phenological drivers between plants and bumblebees could result in phenological asynchrony (Kudo and Cooper 2019). Consequently, early flowering species that receive visitation primarily from queen bumblebees like *Arctous alpina, Kalmia procumbens,* and

Pedicularis lanata might be more susceptible to trophic mismatch if the timing of flowering or insect emergence were to shift. The interplay between the phenology of Arctic bumblebee life history and the pollination of bumblebee-reliant plants warrants further investigation given the deficit of research on these relationships in the Arctic and the clear temporal variation observed in this study.

Q4: Differences in pollen load between insect orders over time

Visitation alone does not fully indicate if an insect might be an effective pollinator (Ne'eman et al. 2010). Insects must also be able to transfer pollen on their bodies from anthers to stigmata (Larson et al. 2001). Hymenopterans carried significantly more total and conspecific pollen than Dipterans. The high pollen loads on Hymenopterans, specifically bumblebees, support the findings of Alarcón et al. (2010) in California, Rader et al. (2011) in New Zealand, and Moissan-Deserres et al. (2014) in Canada. Differences in pollen transfer between insect taxa likely relates to body size, active pollen foraging behavior, hair density, and the presence of specialized pollen-carrying structures (Phillips et al. 2018).

At a family level, bumblebees (Apidae) and wasps (Vespidae) did not differ from each other in pollen load, nor did they differ significantly from muscid flies. This finding emphasizes the potential these families have for effectively pollinating plants, as all of them are able to transport pollen between flowers. The fact that muscid flies did not significantly differ from bumblebees further asserts their position as a crucial fly pollinator (Tiusanen et al. 2016, Loboda et al. 2018), and makes sense considering they are larger than other flies and have a high density of hairs to trap pollen (Skevington and Dang 2002). Unlike the Muscidae, Empididae and Fanniidae carried significantly fewer total and conspecific pollen grains than the other families. Consequently, these families may serve less of a role in pollination to the plants they visit. In contrast to our findings, Empididae were found to carry high pollen loads in the Alps (Lefebvre et al. 2014), and in the High Arctic in Zackenburg, Greenland (Cirtwill et al. 2023).

Not only did insect orders differ in mean pollen transfer, Hymenopterans also showed a significantly different temporal trend in pollen transfer compared to Dipterans. Dipteran pollen load remained steady throughout the season, while Hymenopteran pollen load exhibited a clear peak at the beginning of the season. During this time, both bumblebees and vespid wasps carried high quantities of pollen from *Salix* species (likely *Salix pulchra*) and *Pedicularis lanata.* Early-blooming willows likely serve as a crucial pollen resource for emerging bumblebees and other insects, as *Salix* pollen is abundant and easily accessible (Ostaff et al. 2015). While many willows are considered to be wind pollinated, some species have been found to depend on insects for pollination services (Ostaff et al. 2015). In our sites, it is unclear whether insects carrying *Salix* pollen contributed to the plant's reproduction, or simply robbed pollen. The high quantities of *Pedicularis* pollen of bumblebees at the beginning of the season supports the findings of Williams and Bratzli (1982) that queen bumblebees are essential for *Pedicularis lanata* fruit set. These findings further highlight the need for future research into bumblebee emergence and early-season flowering in the Alaskan Arctic.

Conclusions

In this study, we described the first plant-insect visitor network for the Toolik Field Station area, and for the Alaskan North Slope. Our described network exceeded the number of species of other High Arctic plant-visitor networks, but showed a similarly generalized and nested structure. We observed clear temporal dynamics in network structure over the growing season, with network size increasing until early July then declining. Network scale impacted the observed pattern in network decline, with the Toolik site declining gradually and the Imnavait site showing a distinct collapse due to an extreme weather event. Floral density varied heterogeneously between sites and communities. While Dipterans were the most abundant visitors, Hymenopterans showed significantly higher visitation rates over the summer, as well as distinct peaks in activity corresponding to bumblebee life history. Hymenopterans also carried more pollen than Dipterans, but the Muscidae showed similar pollen loads to Hymenopteran families. Finally, Hymenopterans carried more pollen earlier in the season, underscoring the potential importance of queen bumblebees for early emerging plant species. While further study in necessary to understand how these observed patterns change between years and in a warming future, these findings have crucial implications on our understanding of the vulnerability of different taxa to phenological shifts. At a community level, high generalization and spatial heterogeneity may buffer phenological shifts. However, specific plant species visited primarily by bumblebees may be more vulnerable than plants visited by flies, given the strong temporal pulses of bumblebee activity over the season. These findings provide a baseline understanding of the temporal dynamics of plant-insect interactions in the Low Arctic of Alaska, and will help guide further inquiry into how these patterns change in the future.

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Figures

Figure 1. Plant species flowering phenology. Open lines indicate the absolute first and last day of species flowering in control plots. Brackets indicate the mean first and last day of flowering. Species are ordered by mean first day of flowering, and are grouped by dominant visitor group.

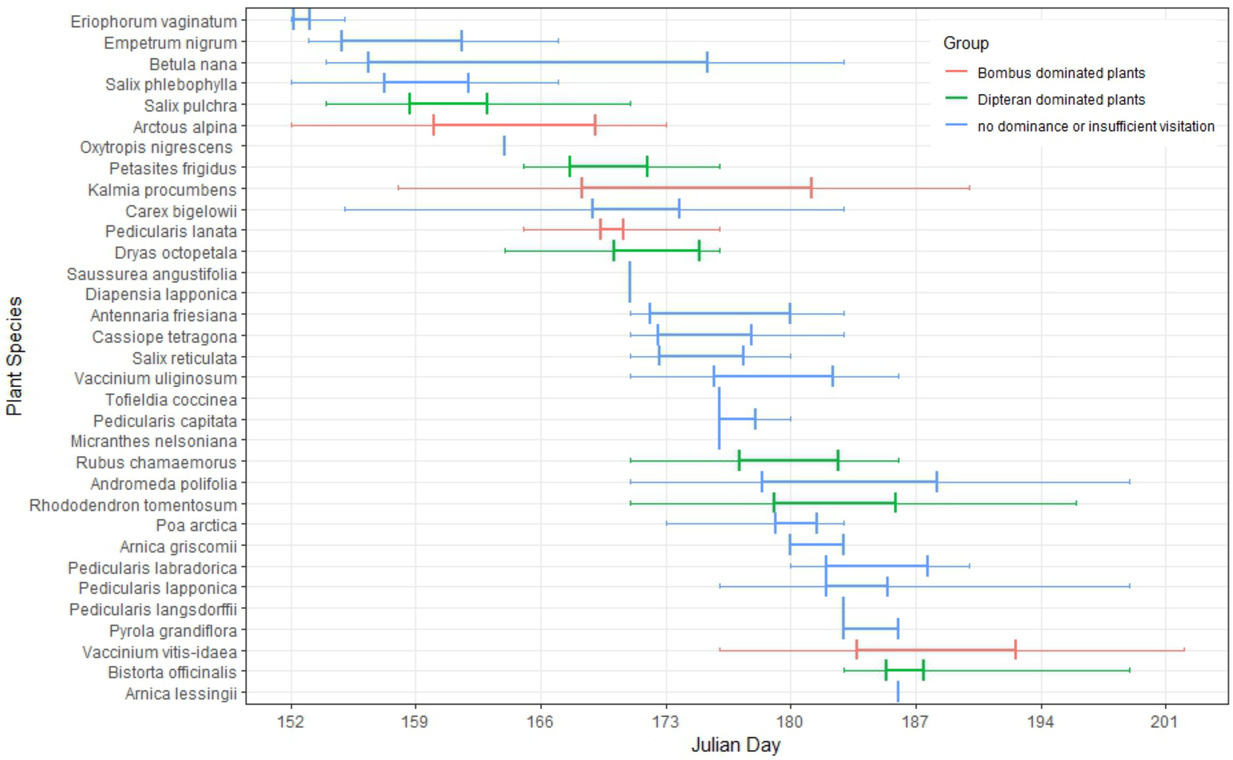


Figure 2. Total insect visitation to plant species grouped by visitor order. Plant species with zero visits were observed in visitor watches but did not receive any visits.

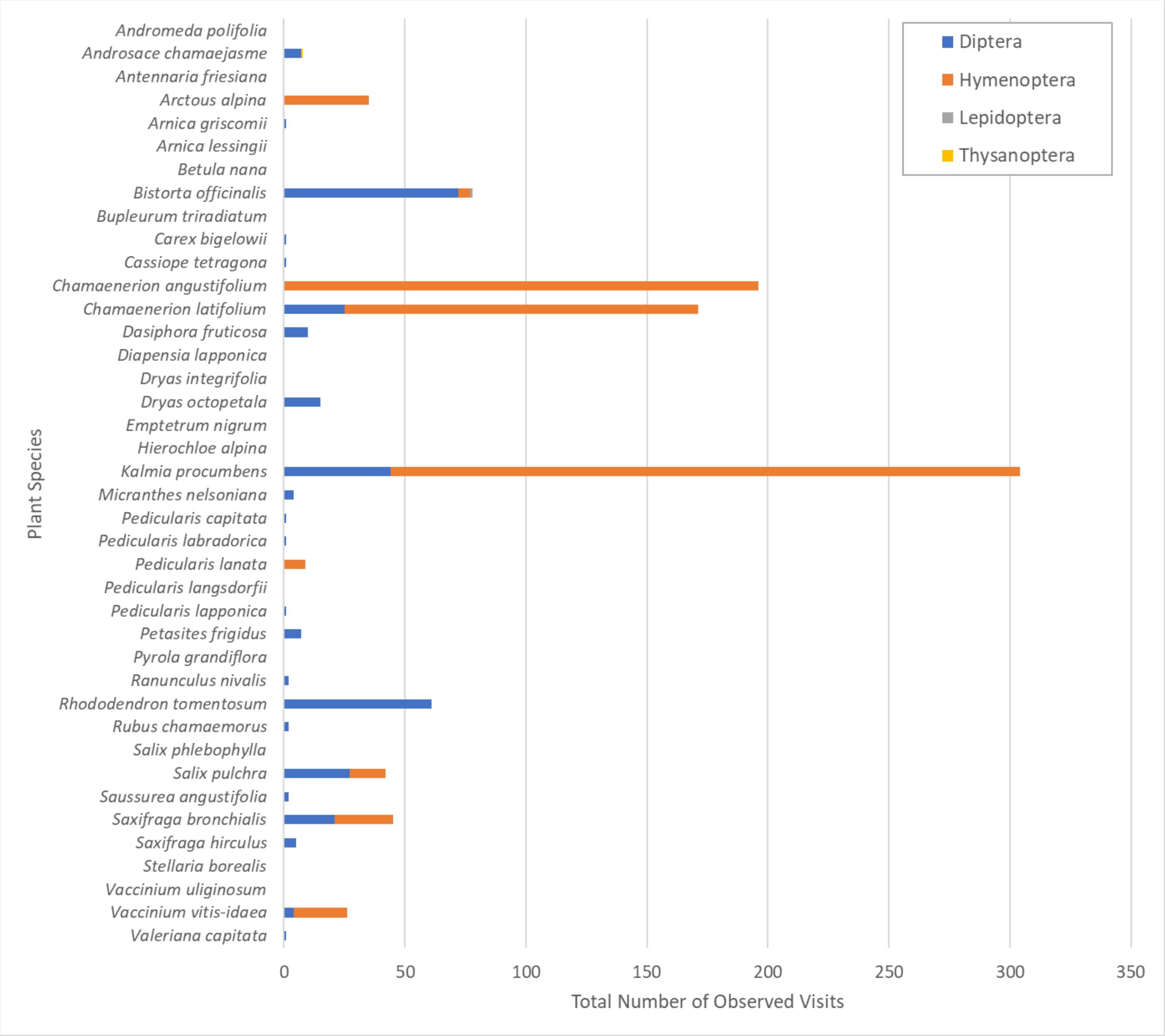


Figure 3. Static plant-insect visitor network for the entire growing season and both study sites (Toolik and Imnavait). Filled-in squares indicate that an interaction was observed between that plant species and insect family. Axes are ordered by number of interactions, with plant species on the top and insect families on the left being the most generalized.

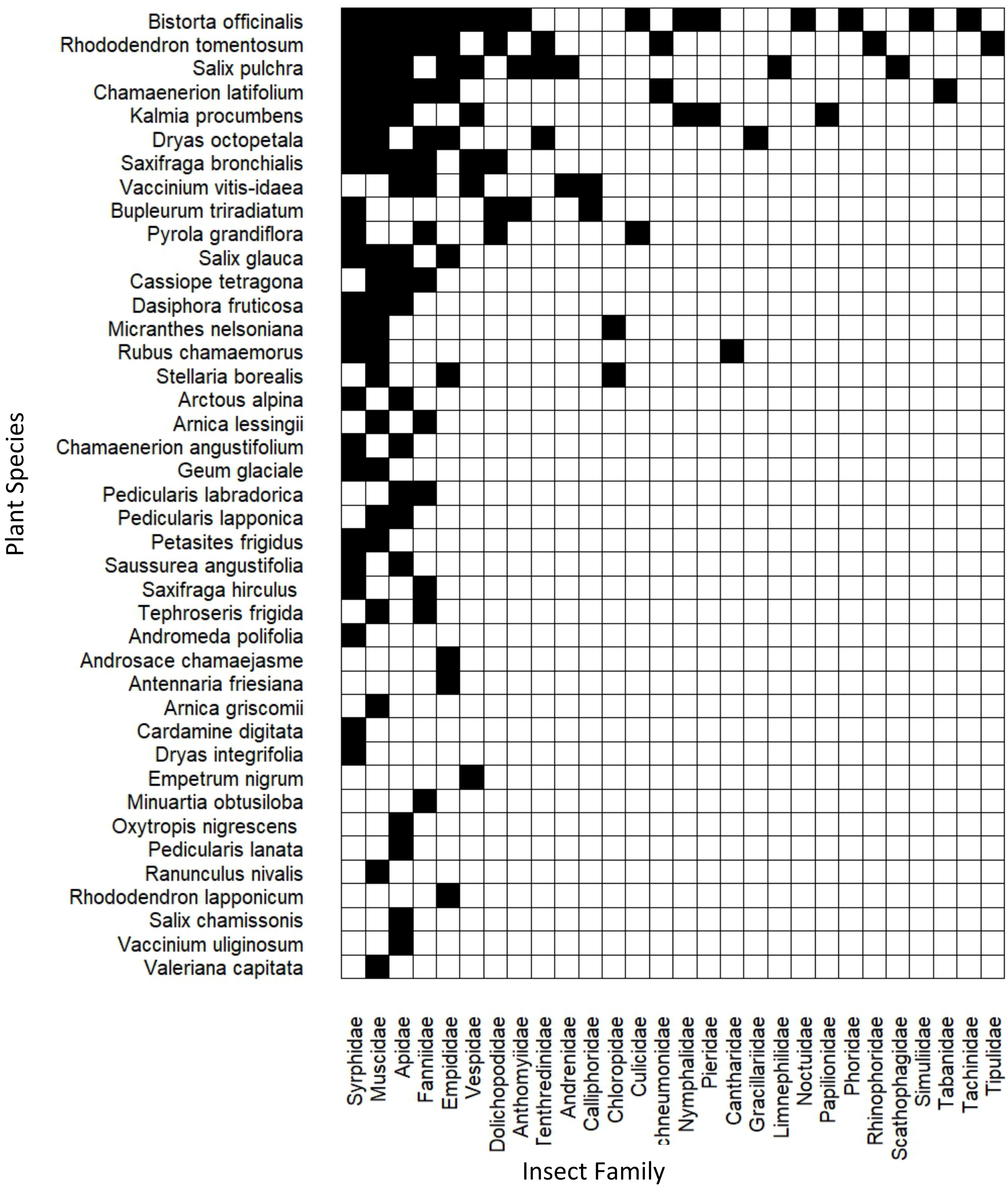


Figure 4. Temporal dynamics of the cumulative plant-visitor network. (a) Network parameters (number of plant species, number of insect families, number of interactions) graphed over time, compiled in weekly time slices. (b) time-slice networks. The vertical axis represents plant species and the horizontal axis represents insect families. Both axes are organized in alphabetical order. Vertical axis: *Andromeda polifolia, Androsace chamaejasme, Antennaria friesiana, Arctous alpina, Arnica griscomii, Arnica lessingii, Bistorta officinalis, Bupleurum triradiatum, Cardamine digitata, Cassiope tetragona, Chamaenerion angustifolium, Chamaenerion latifolium, Dasiphora fruticose, Dryas integrifolia, Dryas octopetala, Empetrum nigrum, Geum glaciale, Kalmia procumbens, Micranthes nelsoniana. Minuartia obtusiloba, Oxytropis nigrescens , Pedicularis labradorica, Pedicularis lanata, Pedicularis lapponica, Petasites frigidus, Pyrola grandiflora, Ranunculus nivalis, Rhododendron lapponicum, Rhododendron tomentosum, Rubus chamaemorus, Salix chamissonis, Salix glauca, Salix pulchra, Saussurea angustifolia, Saxifraga bronchialis, Saxifraga hirculus , Stellaria borealis, Tephroseris frigida, Vaccinium uliginosum, Vaccinium vitis-idaea, Valeriana capitata.* Horizontal axis: Andrenidae, Anthomyiidae, Apidae, Calliphoridae, Cantharidae, Chloropidae, Culicidae, Dolichopodidae, Empididae, Fanniidae, Gracillariidae, Ichneumonidae, Limnephilidae, Muscidae, Noctuidae, Nymphalidae, Papilionidae, Phoridae, Pieridae, Rhinophoridae, Scathophagidae, Simuliidae, Syrphidae, Tabanidae, Tachinidae, Tenthredinidae, Tipulidae, Vespidae

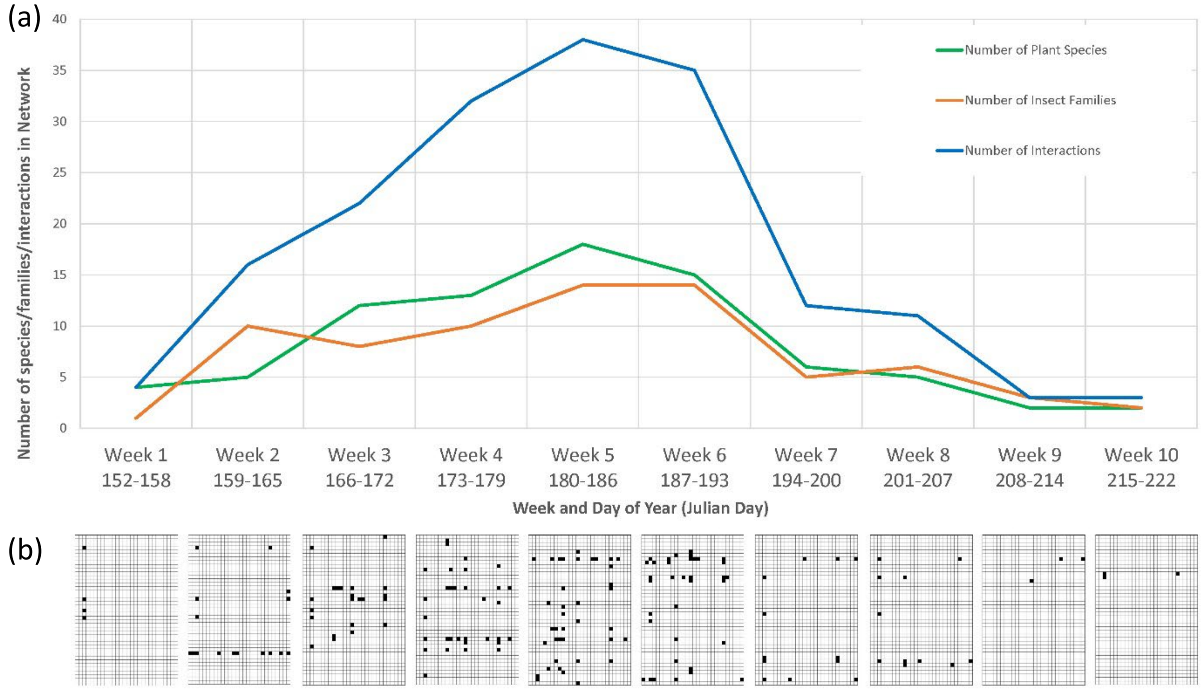


Figure 5. Floral density trends over time in each study site (Toolik and Imnavait) including all flowering plant species.

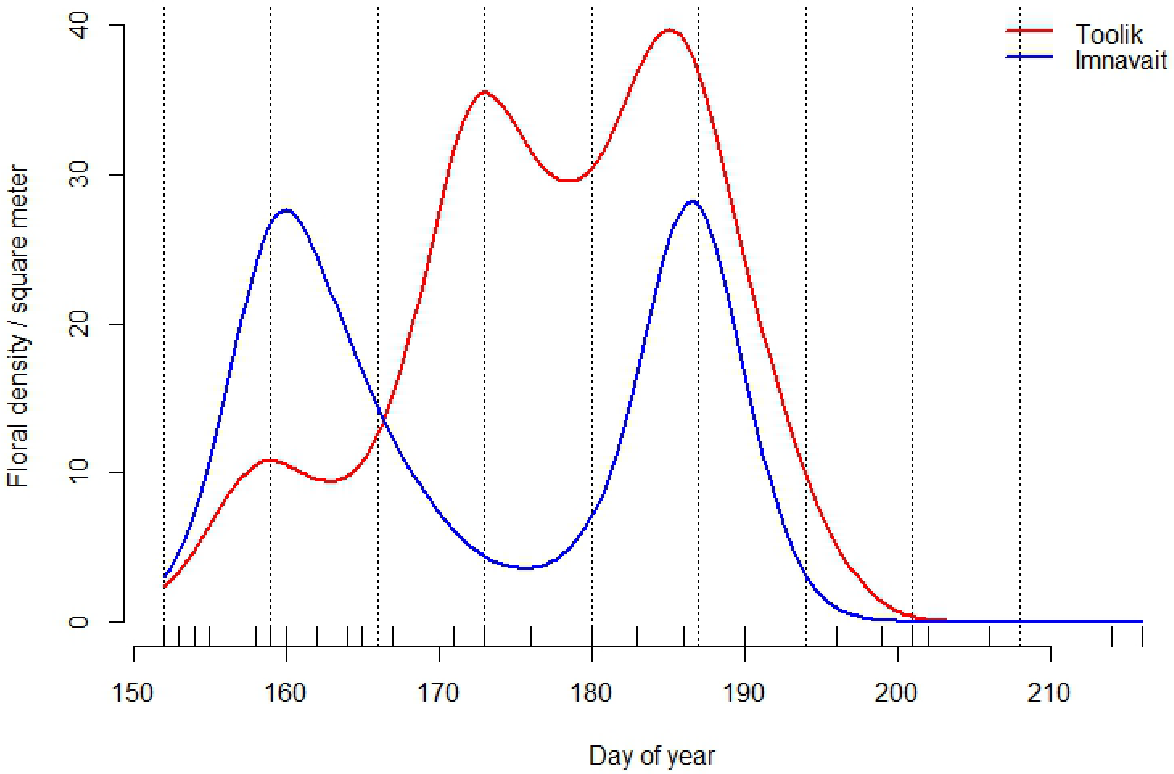


Figure 6. Floral density trends over time in each community type (Dry and Moist) including all flowering plant species.

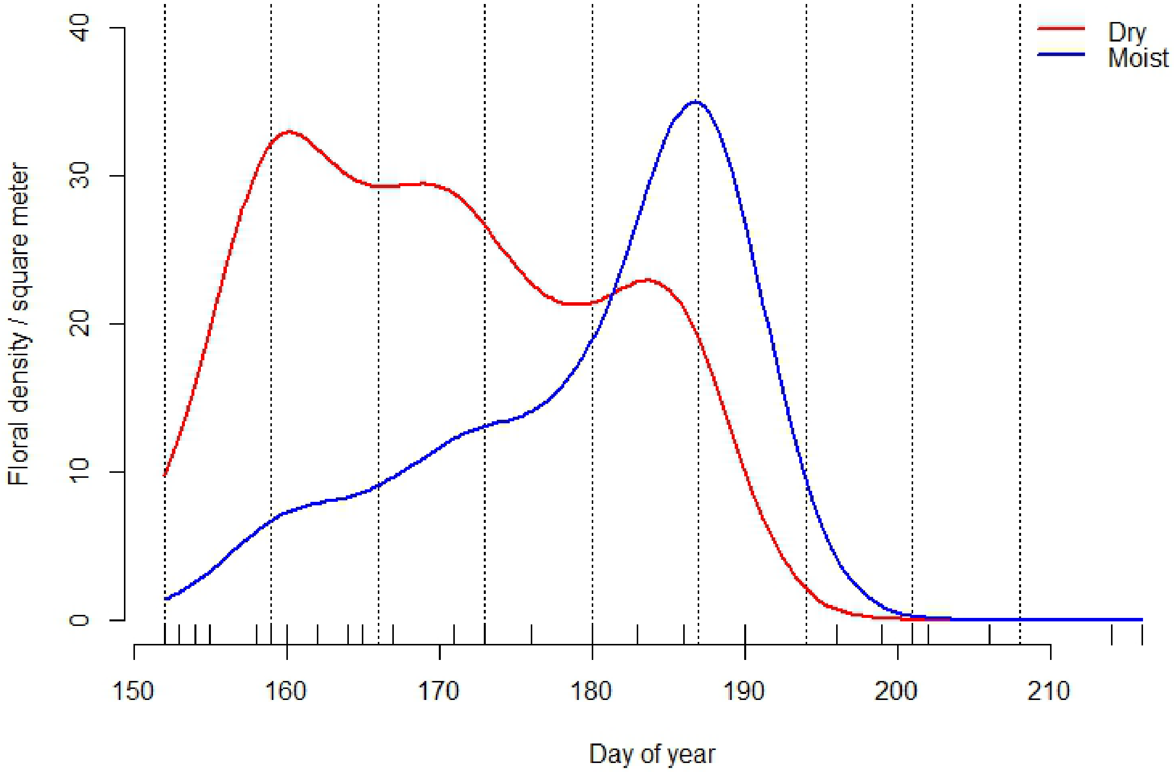


Figure 7. Insect visitation rate over time by flies (Order Diptera) and bees and wasps (Order Hymenoptera.

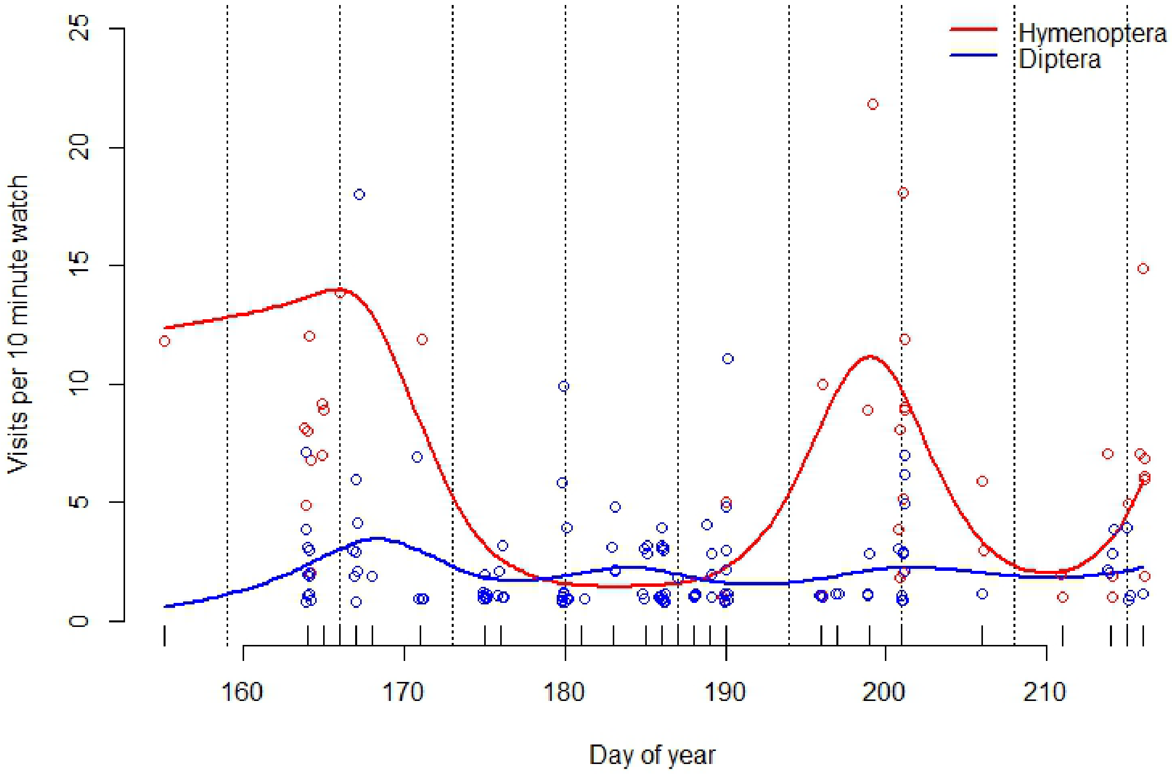


Figure 8. Floral density of flowers visited primarily by bumblebees (*Bombus* plants) and flowers visited primarily by Dipterans (Dipteran plants)

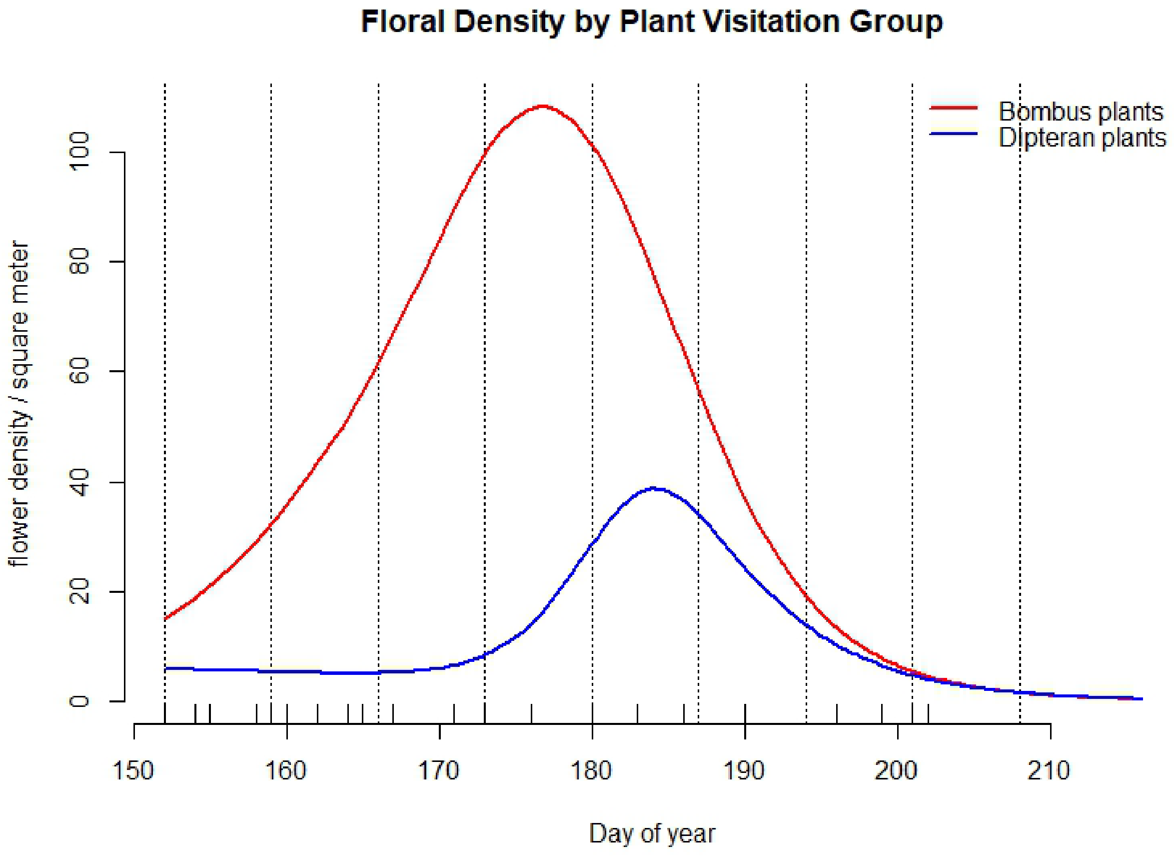


Figure 9. Median number of pollen grains per insect found on flies (Order Diptera, n=182 specimens) and bees and wasps (Order Hymenoptera, n=62 specimens). *** indicates p<0.001. Outliers not shown.

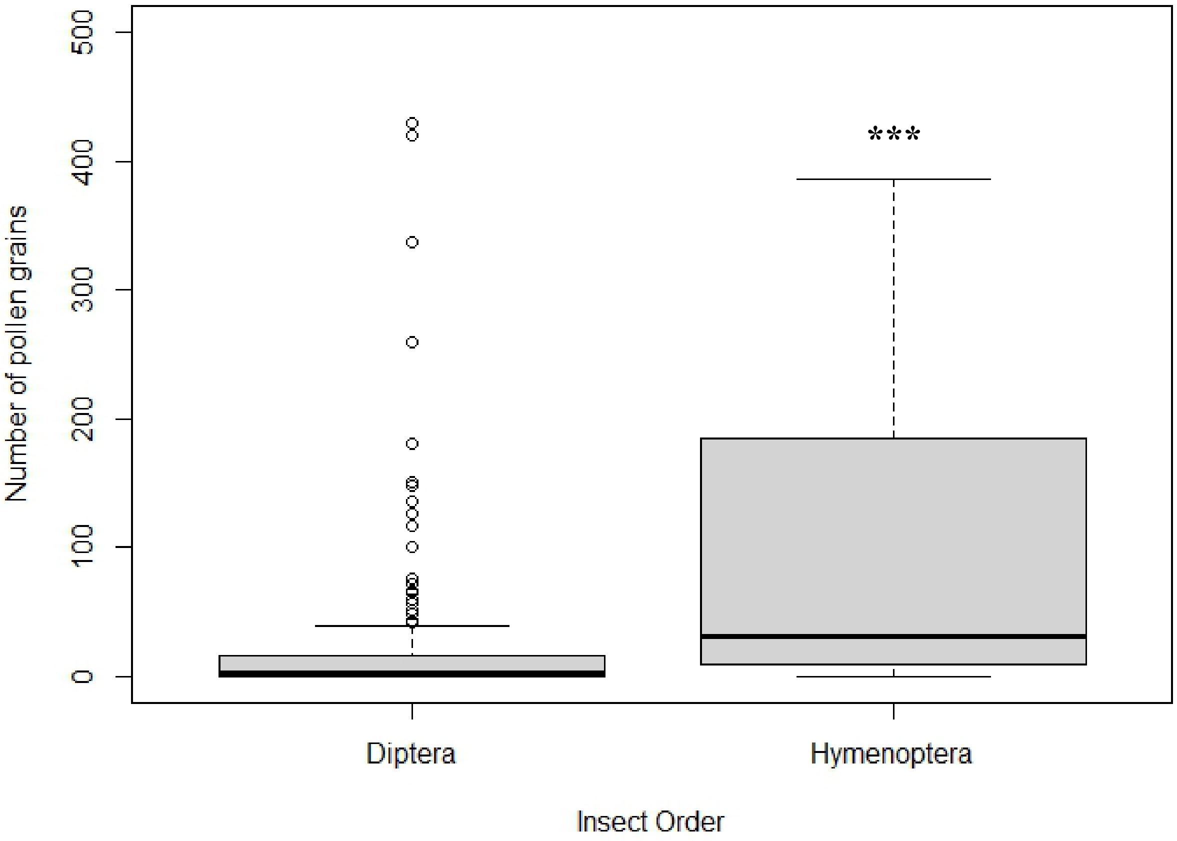


Figure 10. Median number of conspecific pollen grains per insect found on flies Order Diptera, n=182 specimens) and bees and wasps (Order Hymenoptera, n=62 specimens).
*** indicates p<0.001. Outliers not shown.

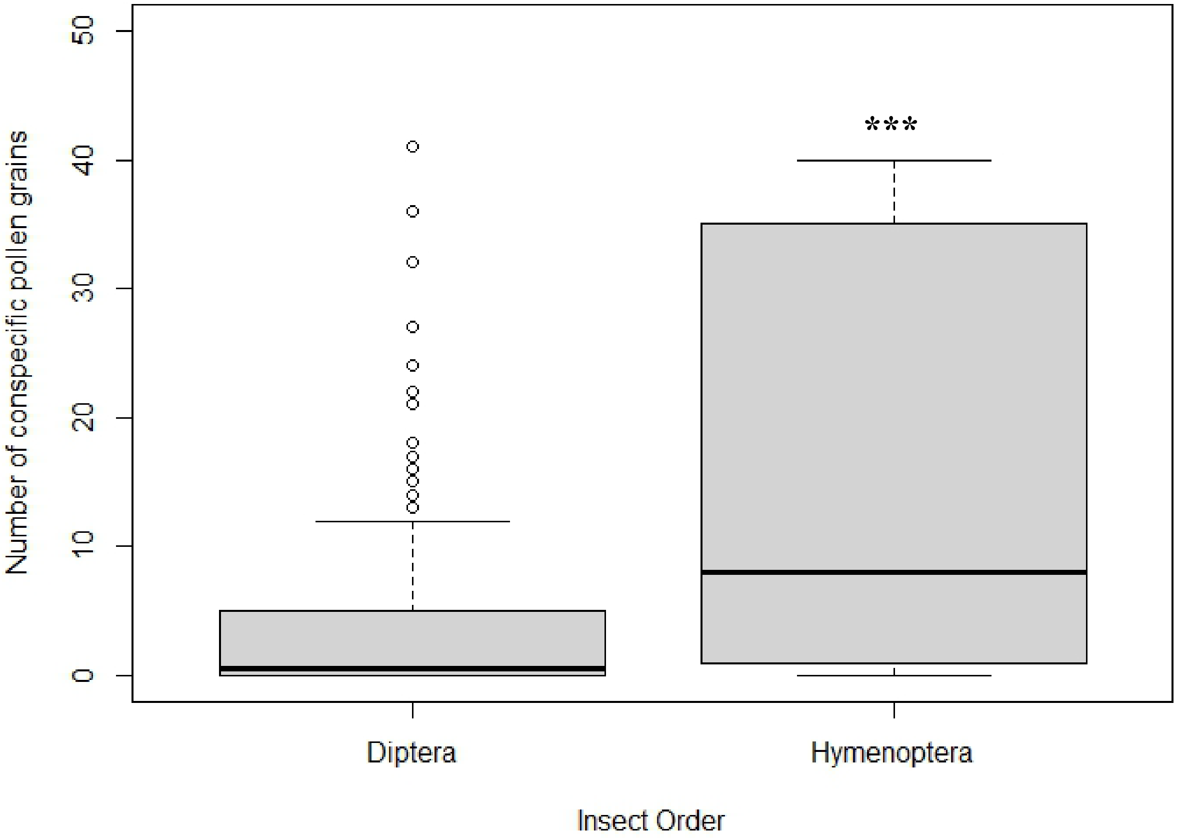


Figure 11. Temporal trend of total number of pollen grains per insect over the growing season between flies (Order Diptera) and bees and wasps (Order Hymenoptera)

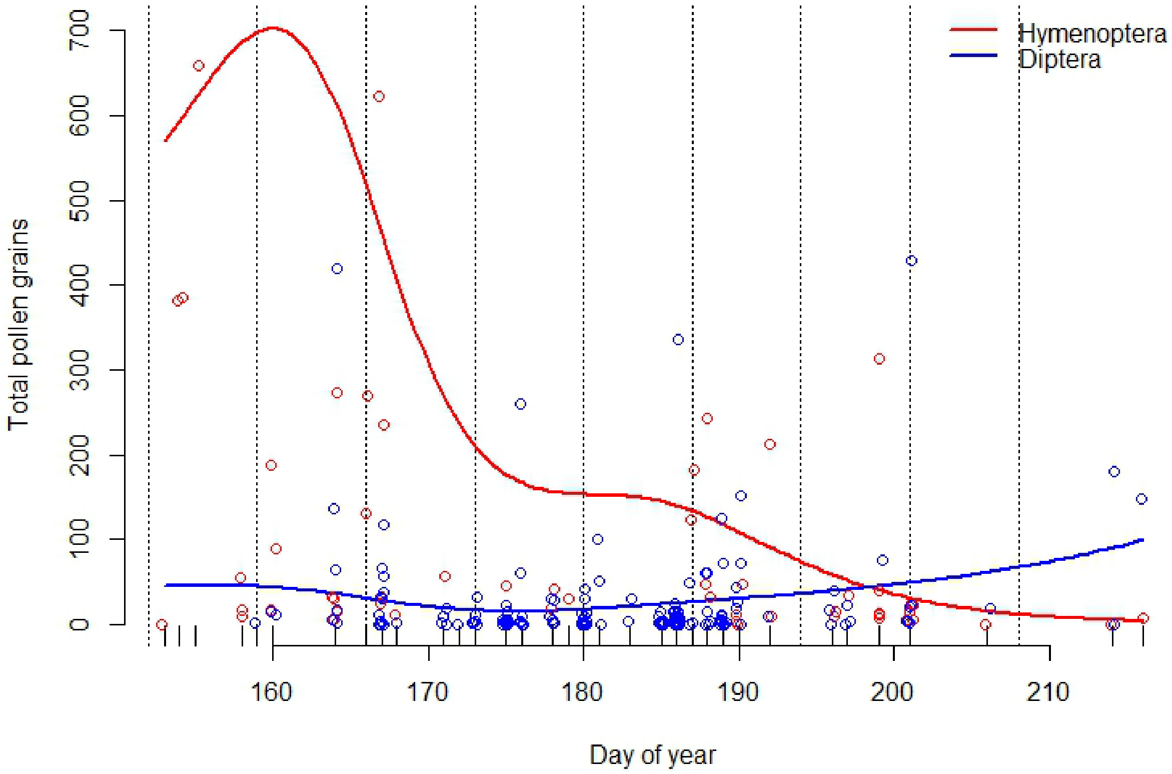


Figure 11. Total number of pollen grains by insect family. Unique letters indicate significant differences between families at p<0.01. Outliers not shown.

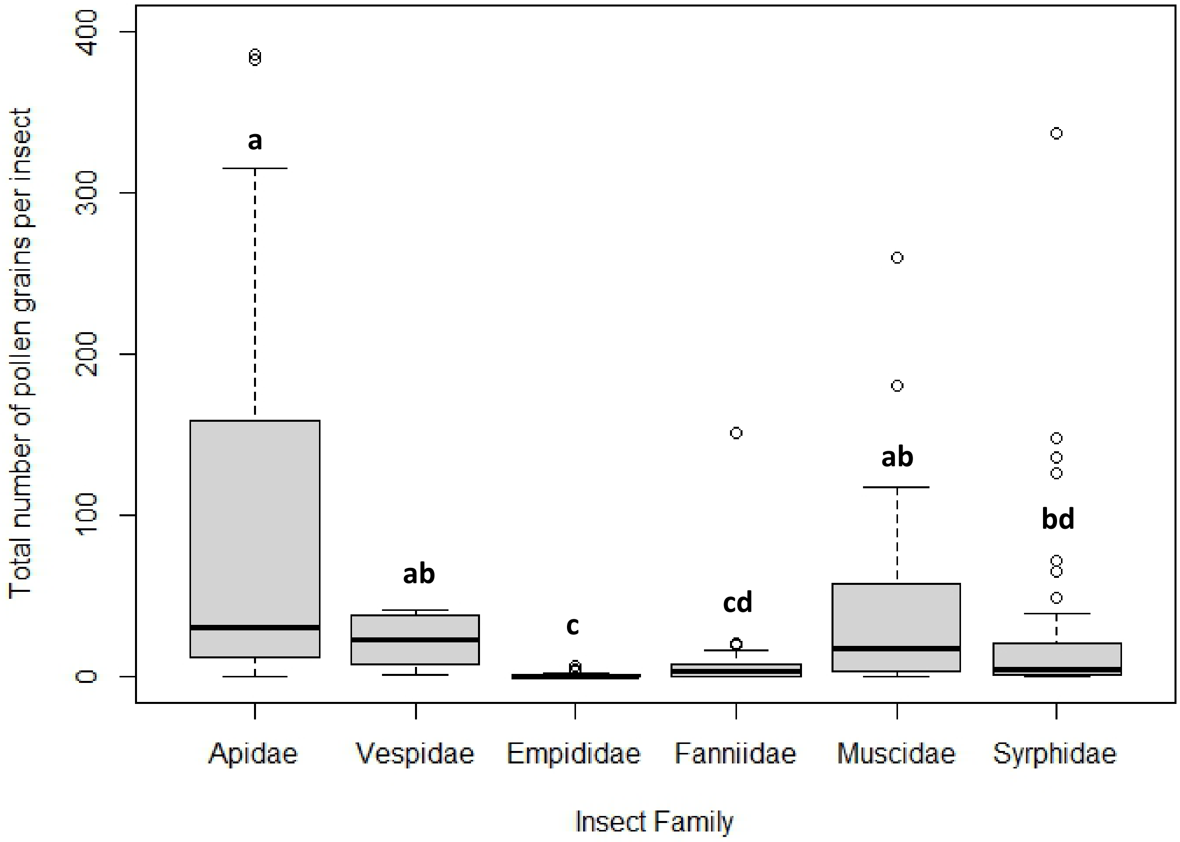


Figure 12. Number of conspecific pollen grains per insect by insect family. Unique letters indicate significant differences between families at $p<0.05$. Outliers not shown.

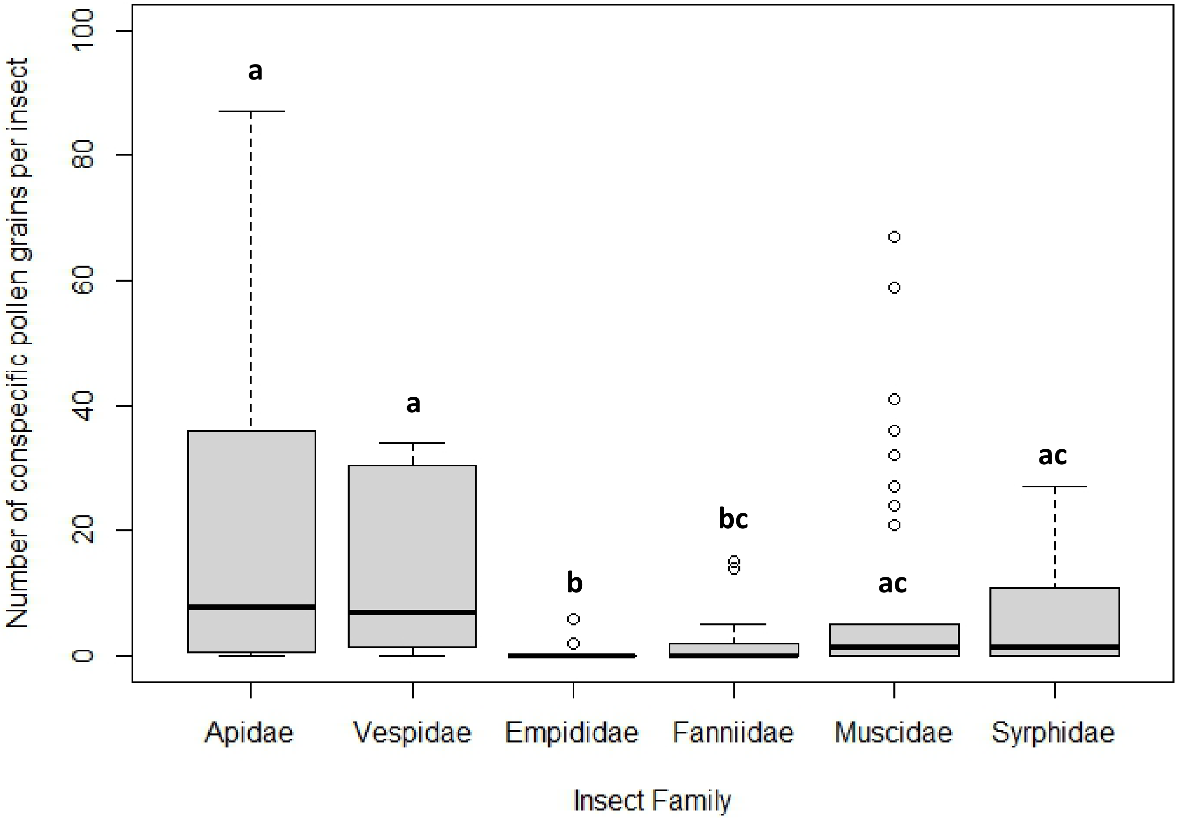


Table 1. Network parameters (number of plant species, insect families, interactions, Connectance, Nestedness) for each static network. Toolik and Imnavait are sites, Dry and Moist are plant community types within each site.

Network	**Number of Plant Species**	**Number of Insect Families**	**Number Interactions**	**Connectance**	**Nestedness**
Combined	41	28	128	0.11	4.78
Toolik	30	24	95	0.13	5.48
Imnavait	28	16	61	0.14	9.78
Dry	29	22	82	0.13	7.38
Moist	26	21	65	0.12	5.42

Supplementary Figures

Supplementary Table S1. Number of collected insects by order and family.

Insect Order and Family	Number of Specimens
Coleoptera	**1**
Cantharidae	1
Diptera	**182**
Anthomyiidae	4
Calliphoridae	2
Chloropidae	2
Culicidae	4
Dolichopodidae	6
Empididae	25
Fanniidae	27
Muscidae	50
Phoridae	1
Rhinophoridae	1
Scathophagidae	1
Simuliidae	1
Syrphidae	52
Tabanidae	1
Tachinidae	3
Tipulidae	2
Hymenoptera	**62**
Andrenidae	2
Apidae	43
Ichneumonidae	2
Tenthredinidae	3
Vespidae	12
Lepidoptera	**9**
Gracillariidae	3
Noctuidae	1
Nymphalidae	2
Papilionidae	1
Pieridae	2
Trichoptera	**1**
Limnephilidae	1
Grand Total	**255**

Supplementary Table S2. Summary statistics of (a) total and (b) conspecific pollen load on each insect order and family.

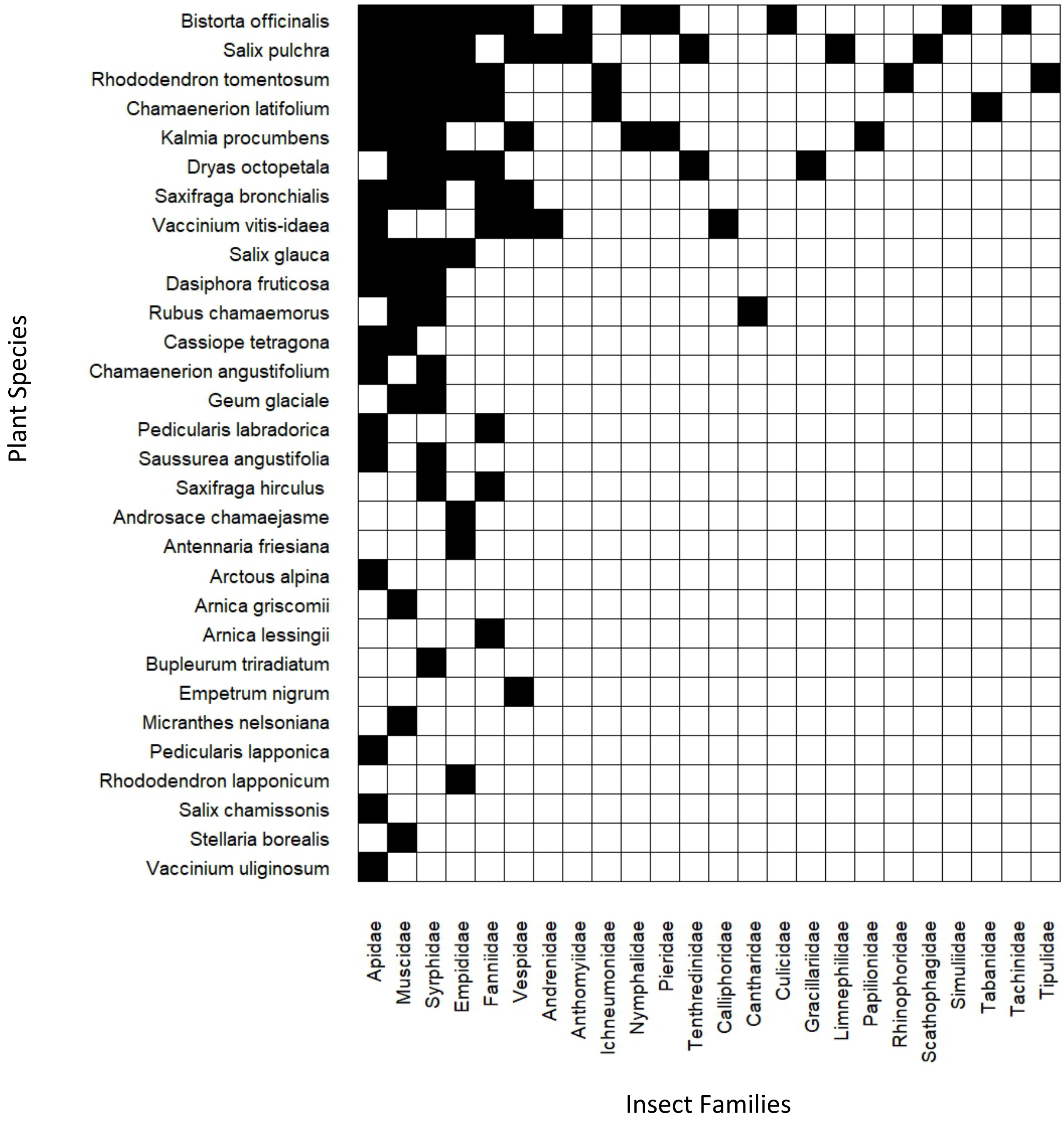
(a) Total Pollen

Insect Order	Insect Family	N	Median	Mean	SD	Range
Diptera		182	3	27.3	84.1	0 - 820
	Empididae	25	0	33.7	163.8	0 - 820
	Fanniidae	27	3	10.1	28.8	0 - 151
	Muscidae	50	17	48.8	91.3	0 - 429
	Syrphidae	52	4.5	25.1	55.4	0 - 337
Hymenoptera		68	30.5	324.7	1527.5	0 - 12006
	Apidae	43	30	130.8	230.4	0 - 1193
	Vespidae	12	23	1080	3447.6	0 - 12006

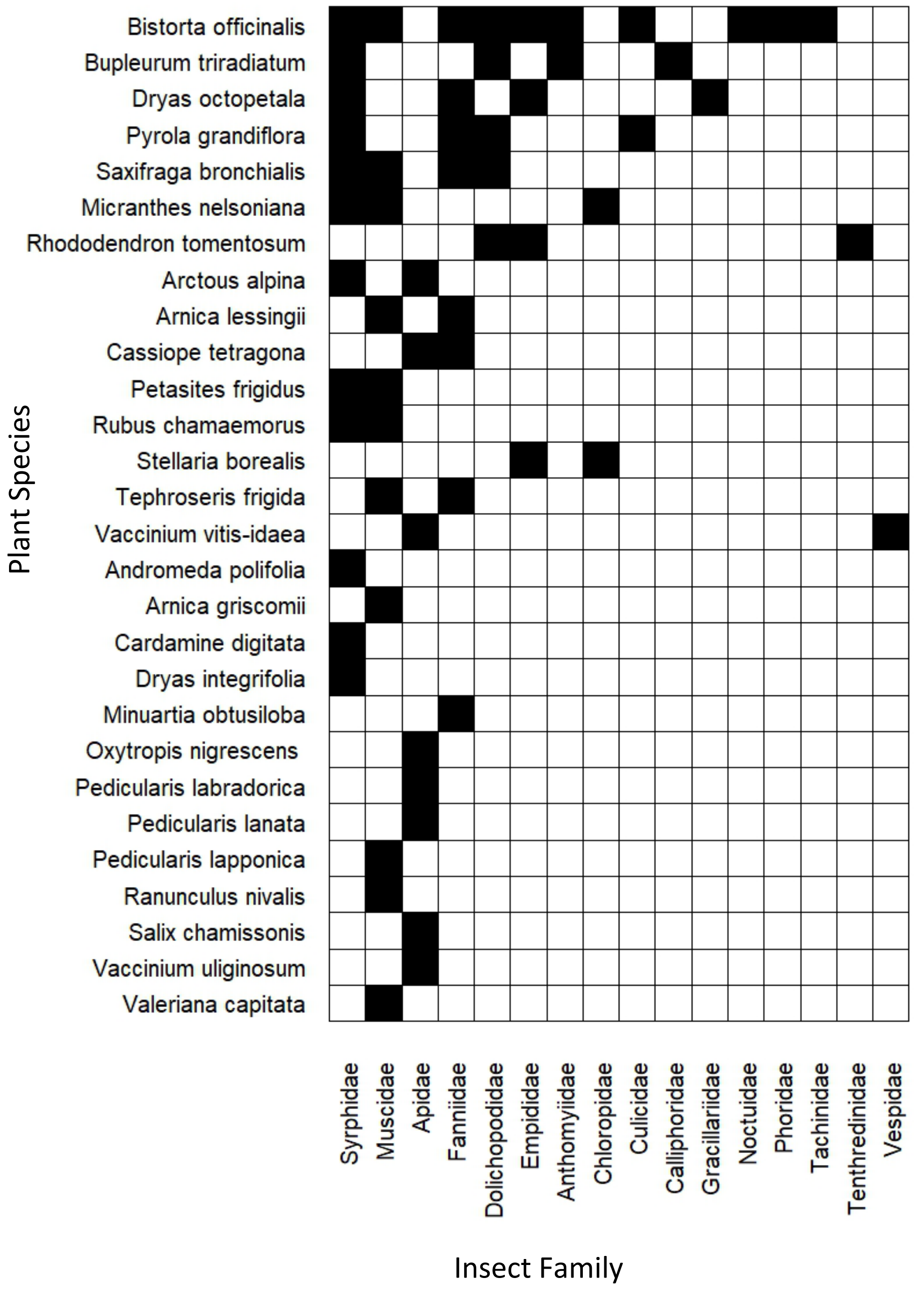
(b) Conspecific Pollen

Insect Order	Insect Family	N	Median	Mean	SD	Range
Diptera		182	0.5	16.3	77.1	0 - 820
	Empididae	25	0	33.2	163.9	0 - 820
	Fanniidae	27	0	2	2.9	0 - 15
	Muscidae	50	1.5	23.9	76.4	0 - 418
	Syrphidae	52	1.5	15.4	49.3	0 - 322
Hymenoptera		68	8	101.7	233.1	0 - 1189
	Apidae	43	8	90.8	211.9	0 - 1189
	Vespidae	12	7	72.6	212.1	0 - 745

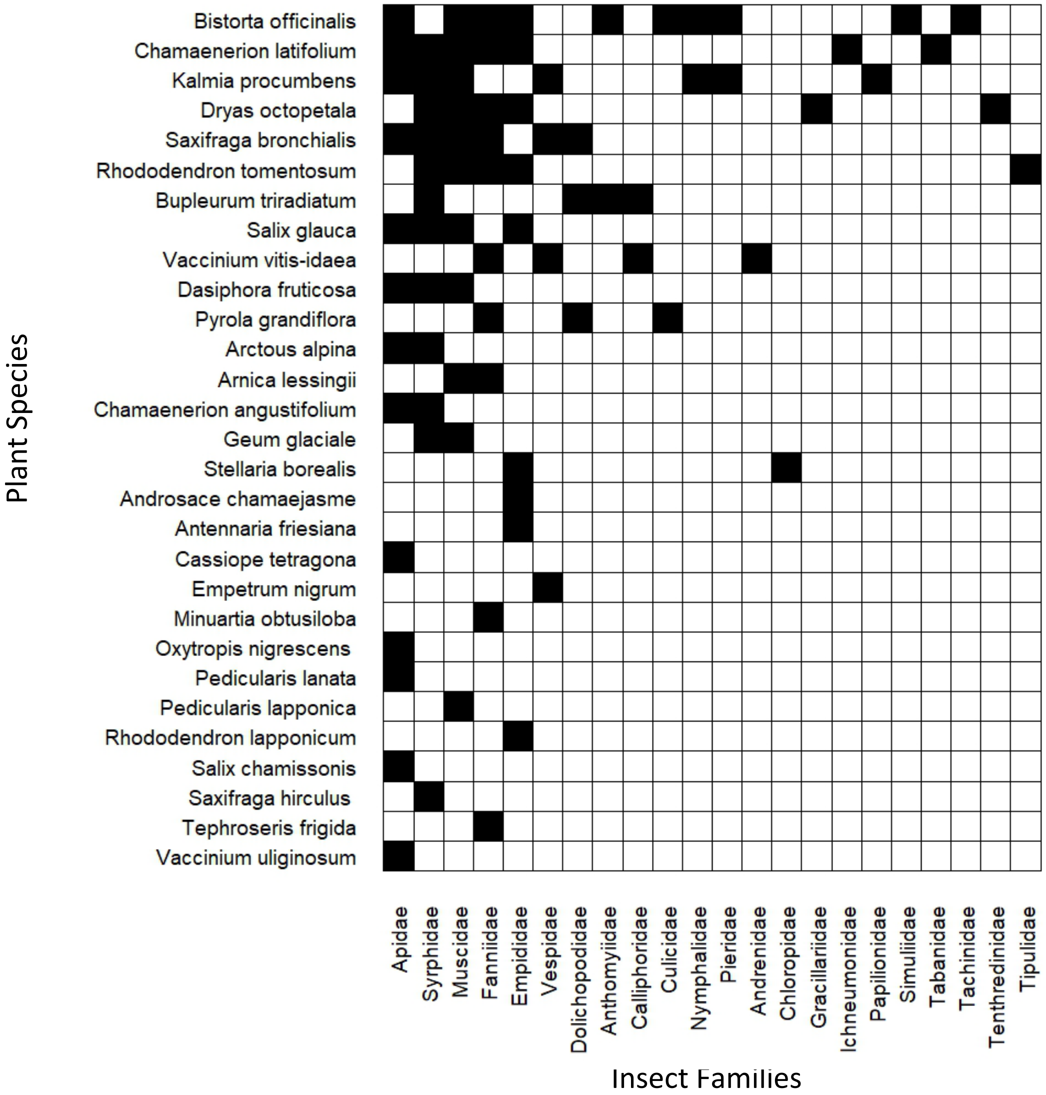
Supplementary Figure S1. Static plant-insect visitor network for the entire growing season for Toolik. Plant species are on the vertical axis and insect families are on the horizontal axis. Filled in squares indicate that an interaction was observed between that plant species and insect family. Axes are ordered by number of interactions, with plant species on the top and insect families on the left being the most generalized.



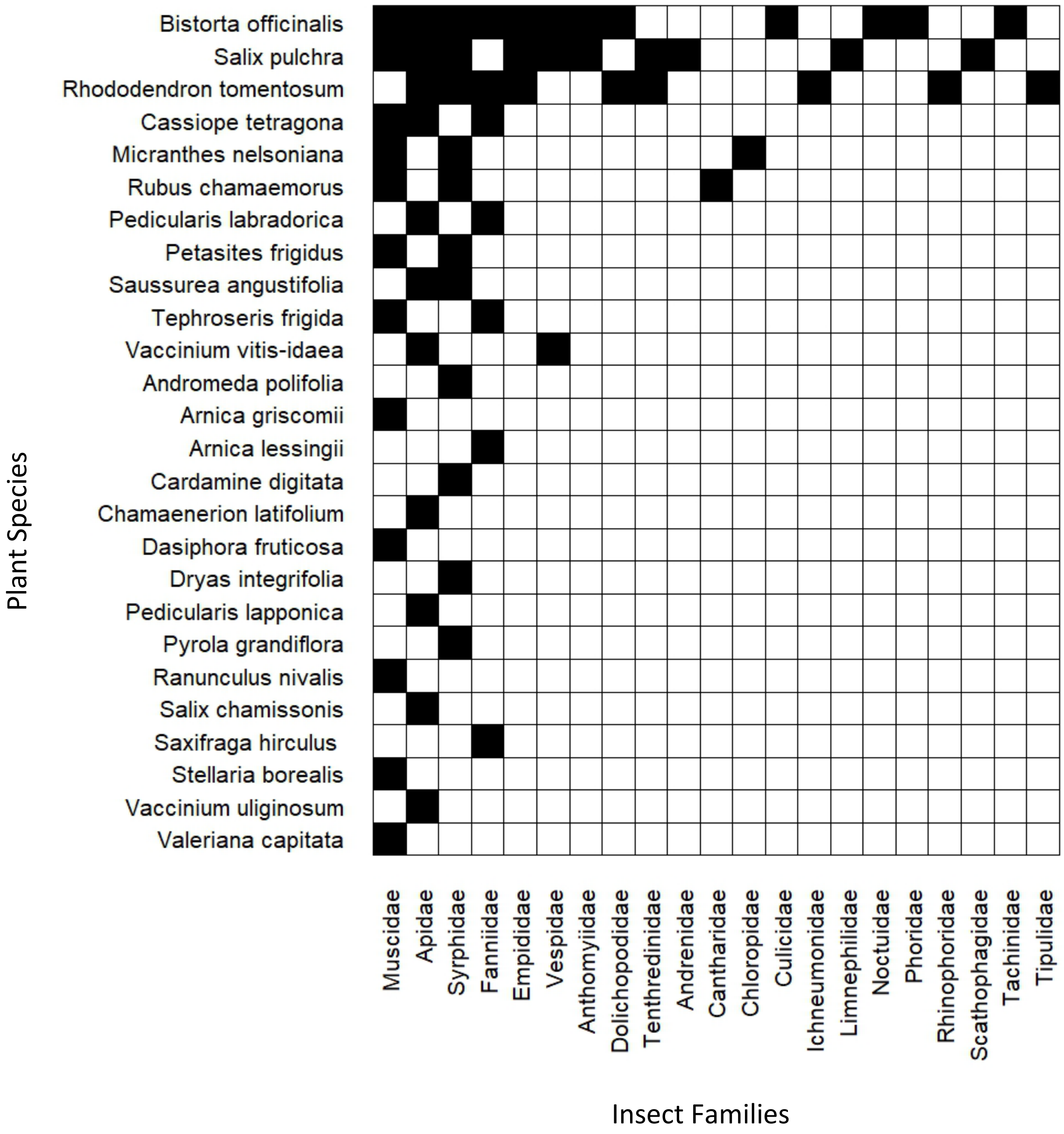
Supplementary Figure S2. Static plant-insect visitor network for the entire growing season for Toolik. Plant species are on the vertical axis and insect families are on the horizontal axis. Filled in squares indicate that an interaction was observed between that plant species and insect family. Axes are ordered by number of interactions, with plant species on the top and insect families on the left being the most generalized.



Supplementary Figure S3. Static plant-insect visitor network for the entire growing season for the dry communities at both sites. Plant species are on the vertical axis and insect families are on the horizontal axis. Filled in squares indicate that an interaction was observed between that plant species and insect family. Axes are ordered by number of interactions, with plant species on the top and insect families on the left being the most generalized.

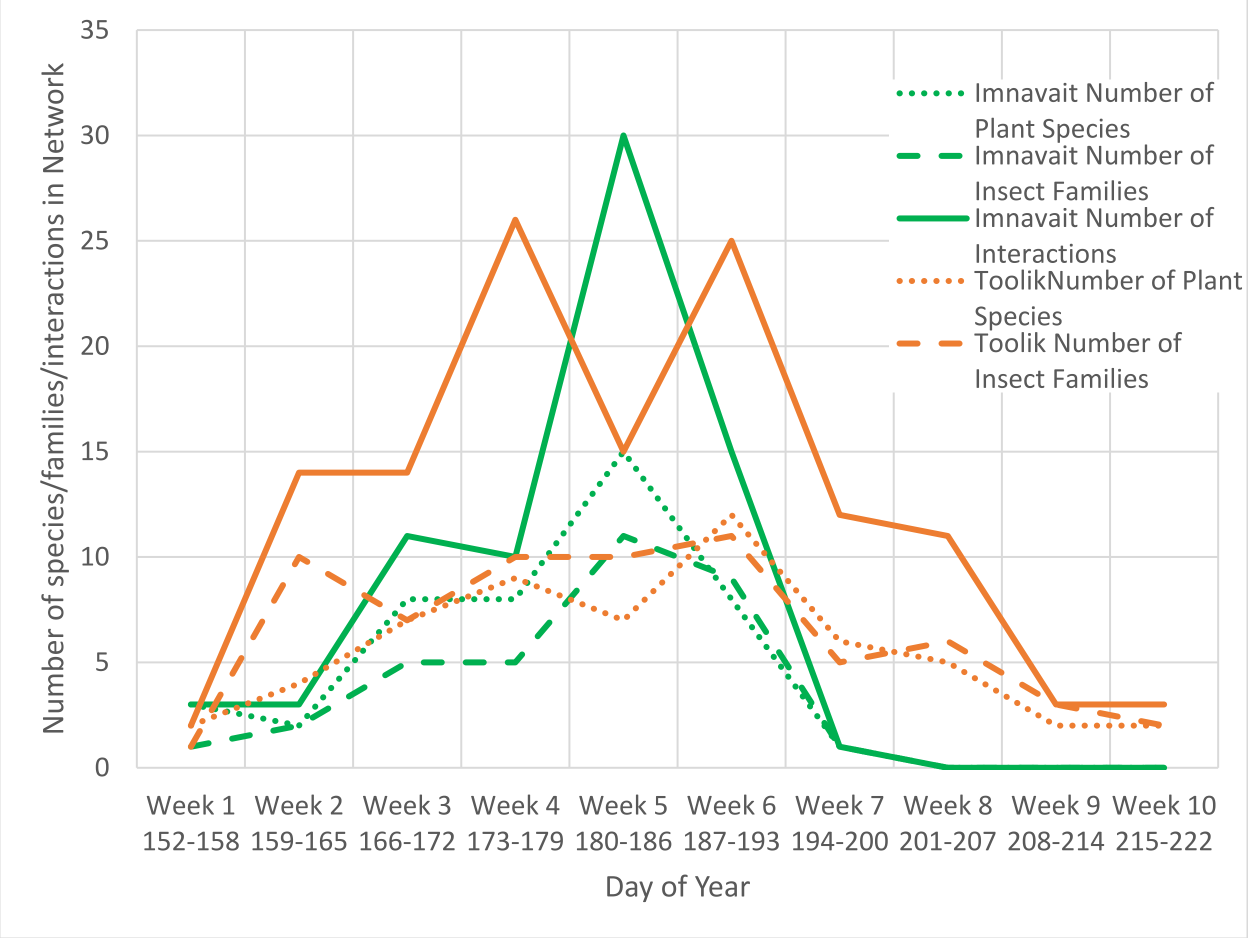


Supplementary Figure S4. Static plant-insect visitor network for the entire growing season for the moist communities at both sites. Plant species are on the vertical axis and insect families are on the horizontal axis. Filled in squares indicate that an interaction was observed between that plant species and insect family. Axes are ordered by number of interactions, with plant species on the top and insect families on the left being the most generalized.

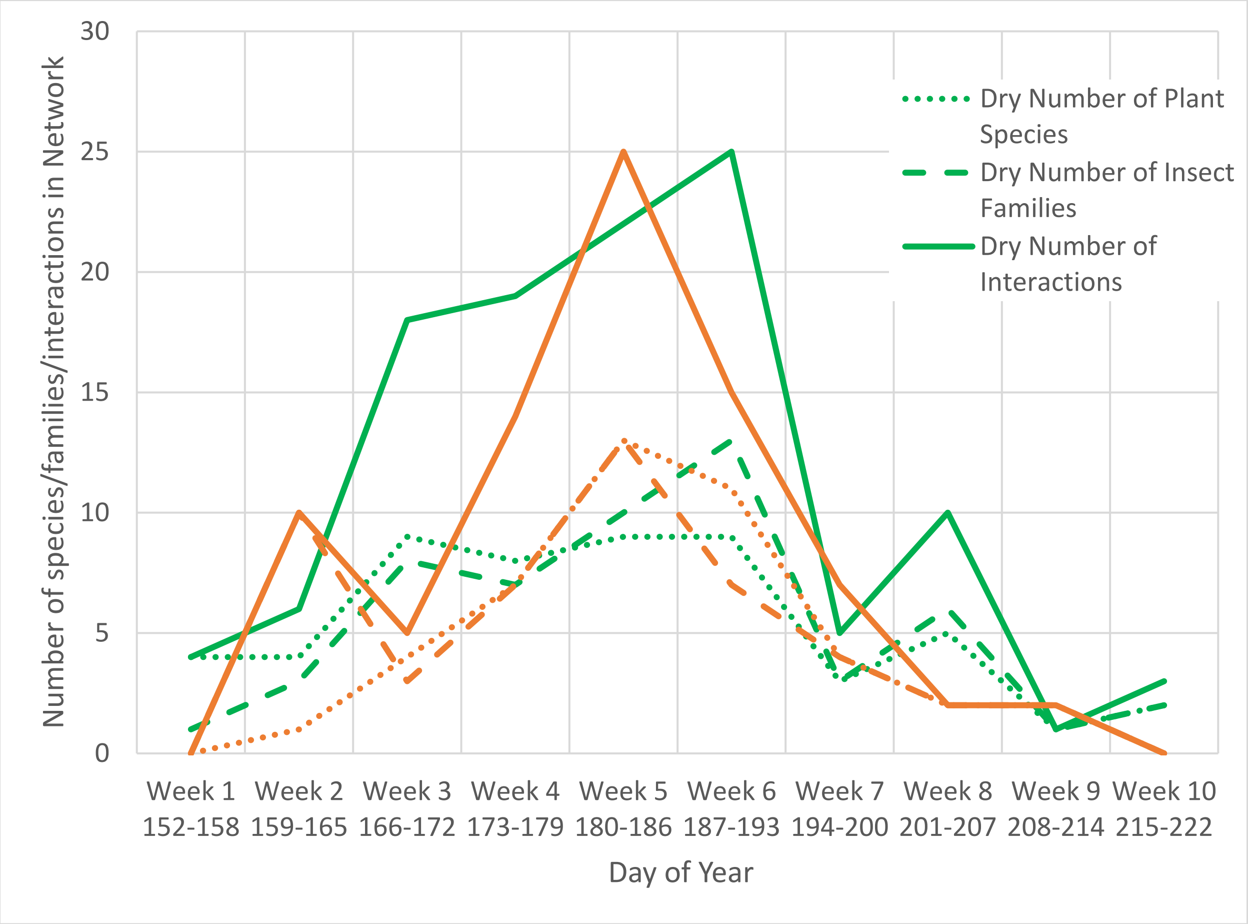


	Muscidae	Apidae	Syrphidae	Fanniidae	Empididae	Vespidae	Anthomyiidae	Dolichopodidae	Tenthredinidae	Andrenidae	Cantharidae	Chloropidae	Culicidae	Ichneumonidae	Limnephilidae	Noctuidae	Phoridae	Rhinophoridae	Scathophagidae	Tachinidae	Tipulidae
Bistorta officinalis	■	■	■	■	■	■	■	■					■			■	■			■	
Salix pulchra	■	■	■		■	■	■		■	■					■				■		
Rhododendron tomentosum		■	■	■	■			■	■					■				■			■
Cassiope tetragona	■	■		■																	
Micranthes nelsoniana	■		■									■									
Rubus chamaemorus	■		■								■										
Pedicularis labradorica		■		■																	
Petasites frigidus	■		■																		
Saussurea angustifolia		■	■																		
Tephroseris frigida	■			■																	
Vaccinium vitis-idaea		■				■															
Andromeda polifolia			■																		
Arnica griscomii	■																				
Arnica lessingii				■																	
Cardamine digitata			■																		
Chamaenerion latifolium		■																			
Dasiphora fruticosa	■																				
Dryas integrifolia			■																		
Pedicularis lapponica		■																			
Pyrola grandiflora			■																		
Ranunculus nivalis	■																				
Salix chamissonis		■																			
Saxifraga hirculus				■																	
Stellaria borealis	■																				
Vaccinium uliginosum		■																			
Valeriana capitata	■																				

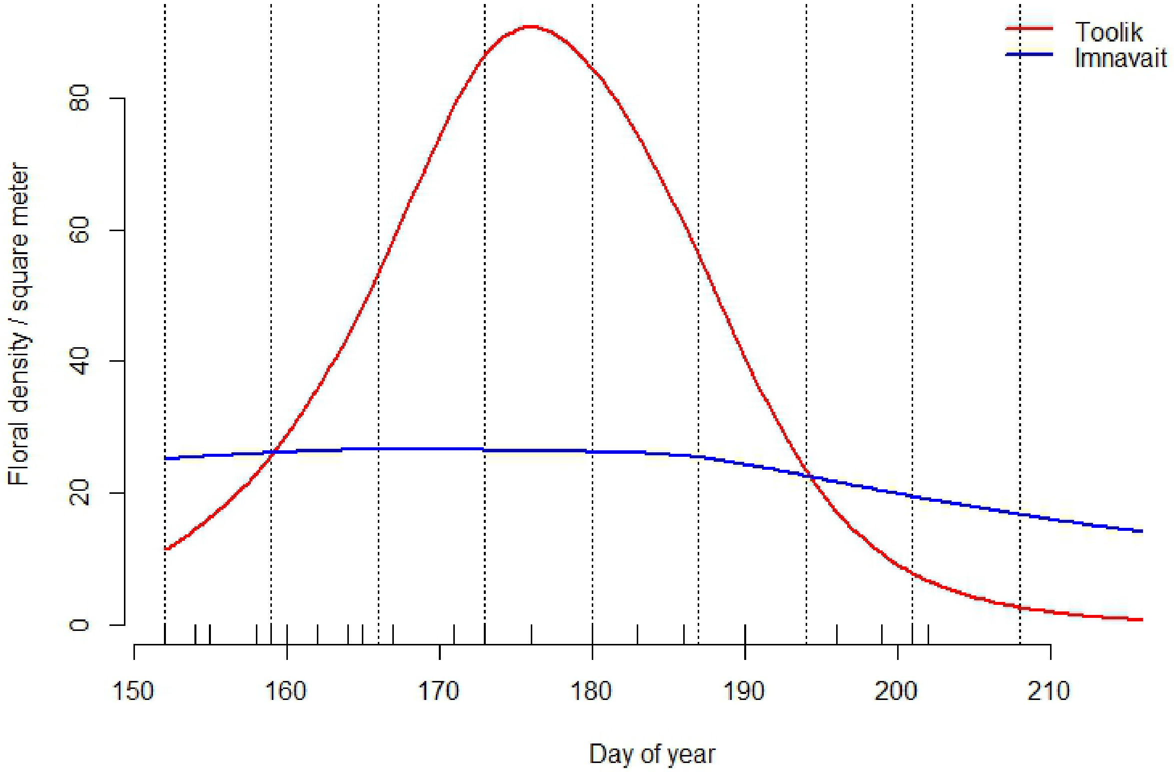
Supplementary Figure S5. Change in site-level network parameters (number of plant species, number of insect families, number of interactions) over the growing season between Toolik and Imnavait.



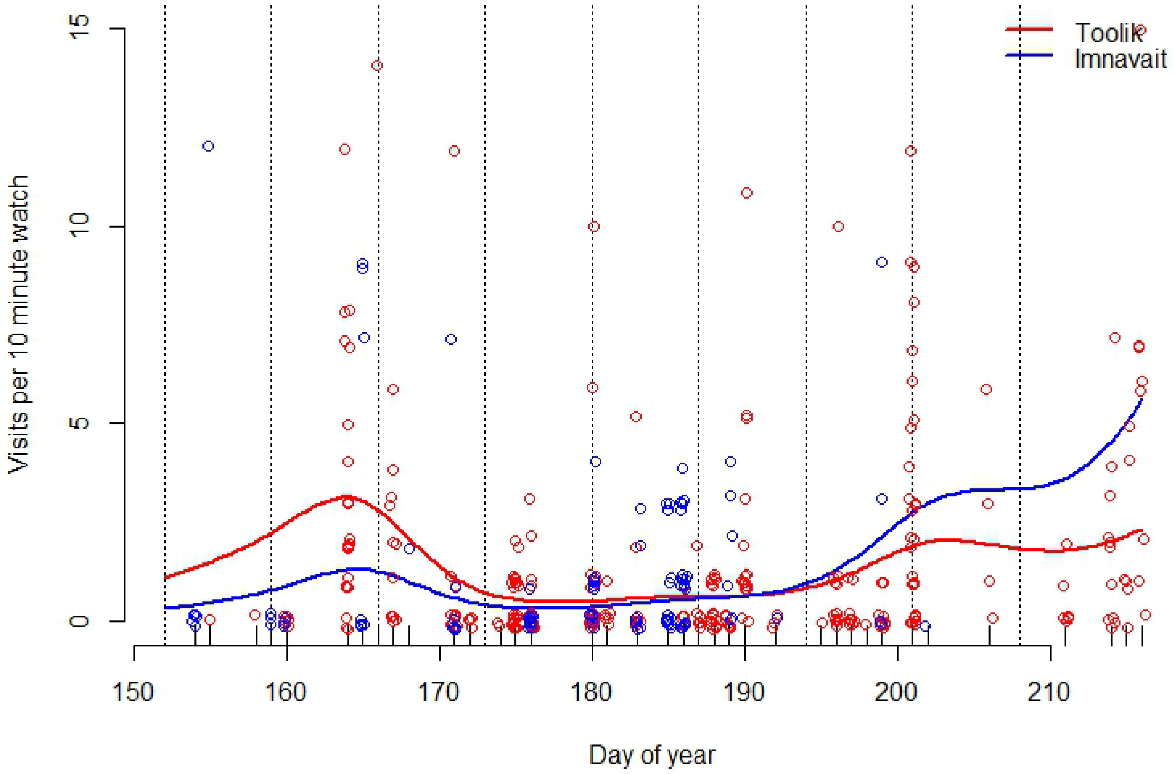
Supplementary Figure S6. Change in community-level network parameters (number of plant species, number of insect families, number of interactions) over the growing season between dry and moist community-types.



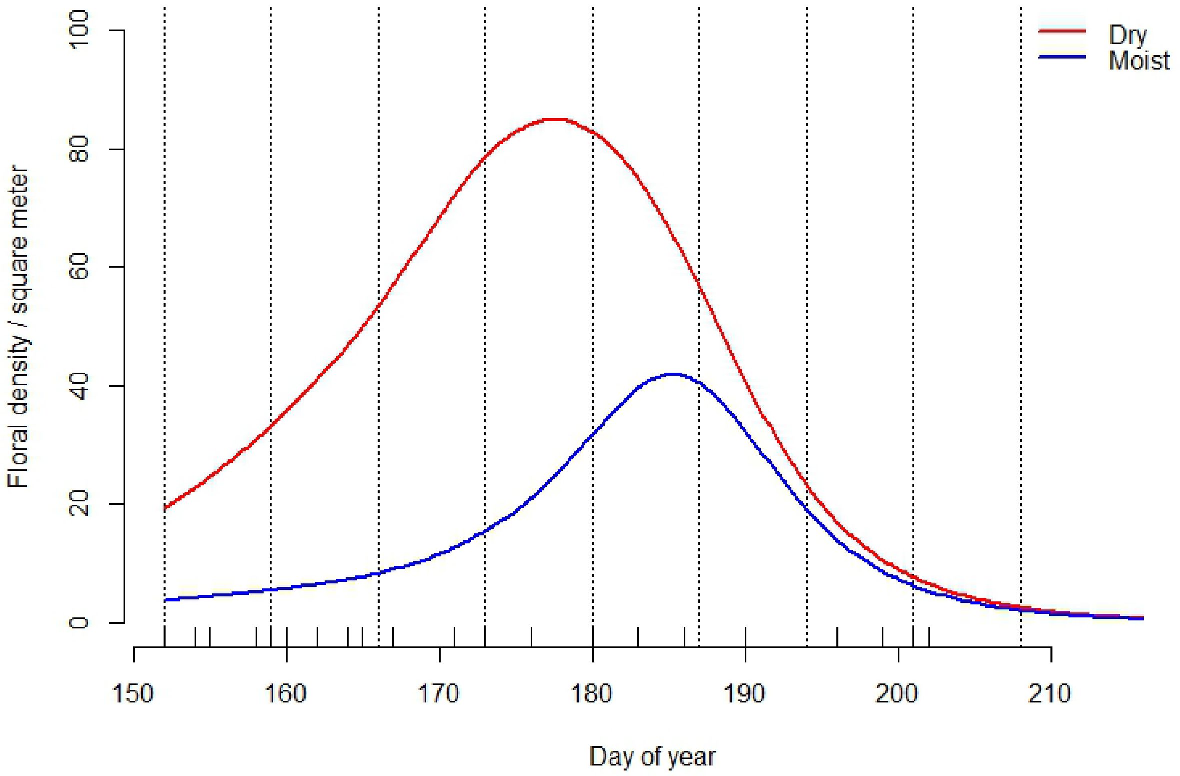
Supplemental Figure S7. Floral density trends over time in each study site (Toolik and Imnavait) including only flowering plant species that received at least 10 visits from insects.



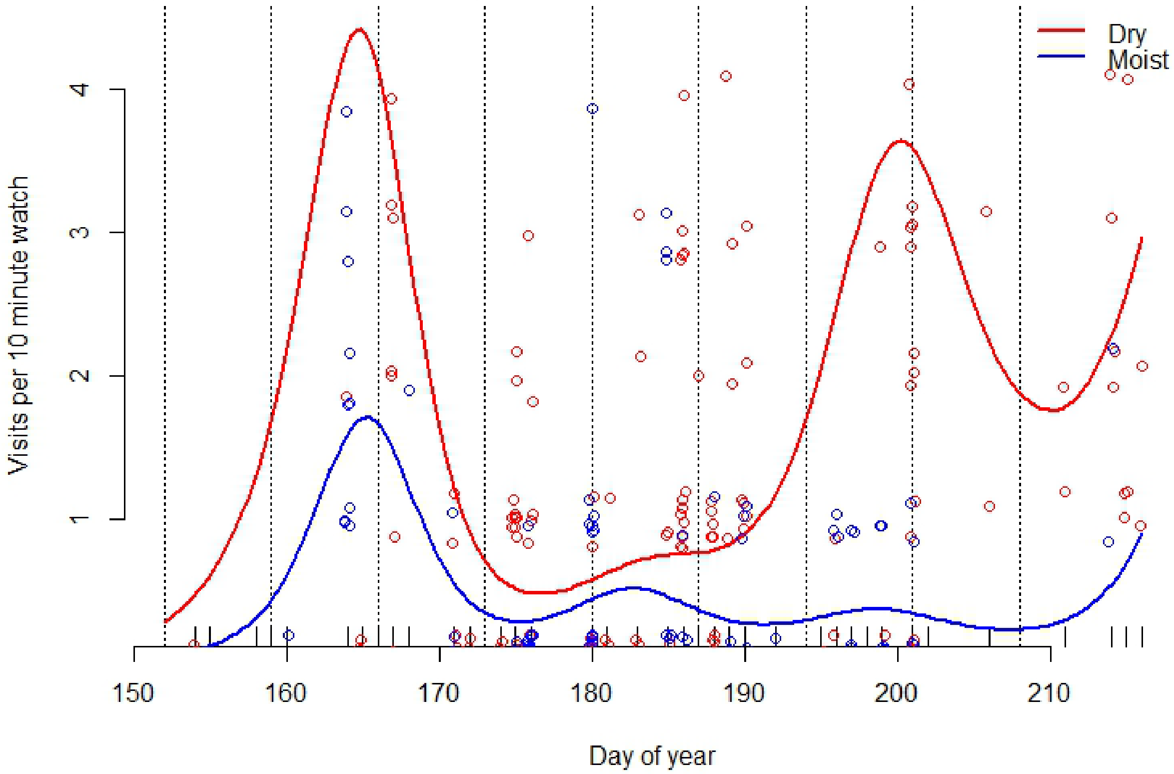
Supplemental Figure S8. Insect visitation rate trends over time in each study site (Toolik and Imnavait).



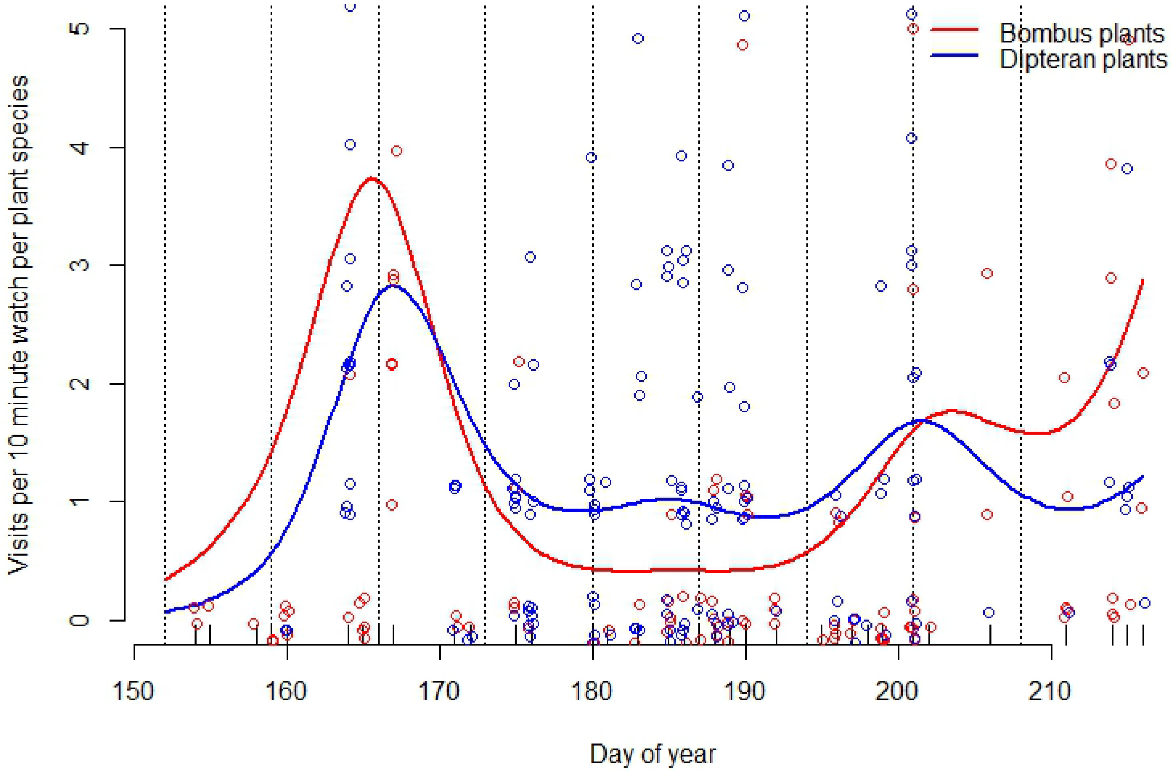
Supplemental Figure S9. Floral density trends over time in each community type (dry and moist) including only flowering plant species that received at least 10 visits from insects.



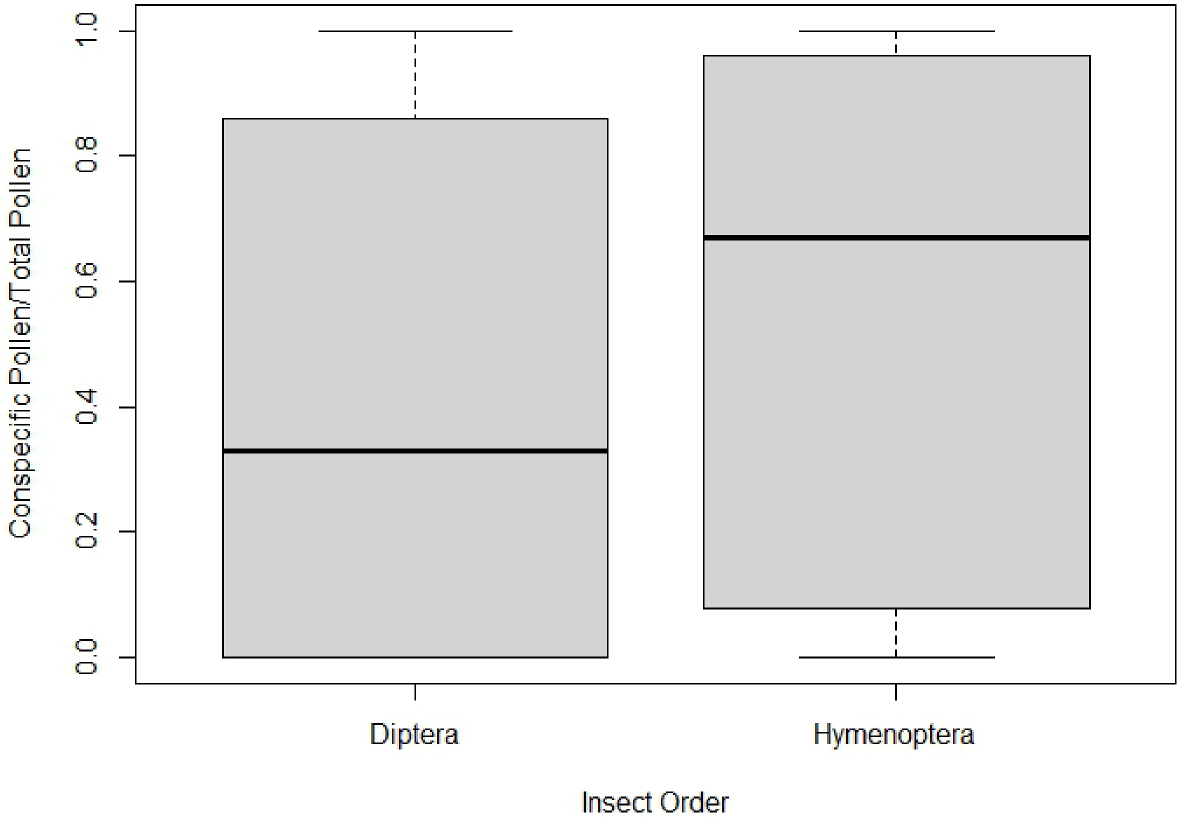
Supplemental Figure S10. Insect visitation rate trends over time in each community type (dry and moist).



Supplemental Figure S11. Insect visitation rates to flowers visited primarily by bumblebees (*Bombus* plants) and flowers visited primarily by Dipterans (Dipteran plants).



Supplemental Figure S12. Proportion of conspecific to total pollen found on each insect on flies (Order Diptera) and bees and wasps (Order Hymenoptera).



Supplemental Figure S13. Temporal trend of number of conspecific pollen grains per insect over the growing season between flies (Order Diptera) and bees and wasps (Order Hymenoptera).