







## ARTICLE

# Increasing variability in resource supply over time disrupts plant–pollinator interactions

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## Abstract

Insect–plant interactions are key determinants of plant and insect fitness, providing important ecosystem services around the world—including the Arctic region. Recently, it has been suggested that climate warming causes rifts between flower and pollinator phenology. To what extent the progression of pollinators matches the availability of flowers in the Arctic season is poorly known. In this study, we aimed to characterize the community phenology of flowers and insects in a rapidly changing Arctic environment from a descriptive and functional perspective. To this end, we inferred changes in resource availability from both a plant and an insect point of view, by connecting resource and consumer species through a metaweb of all the plant–insect interactions ever observed at a site. Specifically, we: (1) characterized species-specific phenology among plants and insects at two High-Arctic sites—Cambridge Bay in Nunavut, Canada, and Zackenberg in Northeast Greenland; (2) quantified competition for flowers using sticky flower mimics; (3) used

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information on plant–pollinator interactions to quantify supply and demand for pollinator services versus flower resources during the summer; and (4) compared patterns observed within a focal summer at each site to patterns of long-term change at Zackenberg, using a 25-year time series of plant flowering and insect phenology. Within summers, we found evidence of a general mismatch between supply and demand. Over the 25-year time series, the number of weeks per summer when resource supply fell below a standardized threshold increased significantly over time. In addition, variation in resource availability increased significantly over years. We suggest that the number of resource-poor weeks per year is increasing and becoming less predictable in the High Arctic. This will have important implications for plant pollination, pollinator fitness, and the future of the Arctic ecosystem, as both plants and their pollinators are faced with widening resource gaps.

#### KEYWORDS

competition, Diptera, *Dryas*, flowering phenology, global change, insect phenology, pollination, resource mismatch

## INTRODUCTION

Increases in global air temperatures are having serious consequences for the Earth's ecosystems and their inhabitants (IPBES, 2019). Climate change has already been shown to disrupt biotic interactions across all trophic levels and ecosystems, as well as alter evolutionary adaptations of species such as resource use and dispersal (Parmesan, 2006). Interactions can be disrupted through range shifts of plants and/or animals, and through changing life history patterns and phenologies such as the timing of emergence or flowering of plants (Kharouba et al., 2018; Parmesan, 2006). This can have profound effects on ecological network structure, including both mutualistic and antagonistic interactions (Takemoto & Kajihara, 2016).

Mutualistic networks such as those of plant and pollinator interactions are driven by phenology, since species must overlap in time before they can interact. Shifts in the timing of life cycle events can therefore threaten the stability of interactions by decreasing temporal overlaps in species occurrence (Encinas-Viso et al., 2012). A plant blooming early or an insect emerging prematurely after early snowmelt can disrupt individual plant–pollinator interactions (Kharouba et al., 2018; Visser & Both, 2005). At worst, this can result in temporal mismatches, which have already been observed in many systems (Renner & Zohner, 2018), including mutualistic networks (Memmott et al., 2007). A functional collapse in interactions can then disrupt key ecosystem services such as pollination and biological pest control (Tylianakis et al., 2010).

The Arctic has warmed approximately four times faster than the global average (Rantanen et al., 2022), which has already impacted plants and pollinators

significantly (Høye et al., 2013; Kerr et al., 2015; Schmidt et al., 2017). Seasonal growth, species reproduction, dispersal, and activity patterns have changed in response to both warmer temperatures and earlier snowmelt (Kankaanpää et al., 2018, 2020; Tiusanen et al., 2016, 2019; Wielgolaski & Inouye, 2013). Consequently, insect diversity is decreasing and ranges are shifting (Hoegh-Guldberg & Bruno, 2010; Laws, 2017; Naito & Cairns, 2011). While Arctic ecosystems contain fewer species compared with lower latitudes, Arctic pollination networks do not differ significantly from their warmer counterparts with regard to the number of interactions or complexity (Dupont et al., 2009; Olesen et al., 2008). As such, changes observed in the Arctic can serve as early warnings for other ecosystems.

In High-Arctic Zackenberg, Greenland, in-depth long-term monitoring has revealed earlier snowmelt and other abiotic indicators of spring coupled with earlier flowering of plants (Høye et al., 2007; Schmidt et al., 2016). This advanced phenological window has resulted in insects being out of synch with their food sources (Schmidt et al., 2017). A recent reanalysis of Høye et al. (2007), adding 15 years of additional data, suggests that the advance of flowering time has slowed and/or changed patterns over time, whereas inter-annual variability in phenology has increased for plants and insects (Schmidt et al., 2023). The functional consequences of these changes are less clear, as alternative pollinator species may provide stable pollen transport (Cirtwill et al., 2023). Thus, the question remains as to how interaction structure reflects resource availability from the perspective of individual plant and pollinator taxa, and whether within-season dynamics observed at

Zackenberg can be generalized to other Arctic sites. As a key knowledge gap, we need to understand how individual insect taxa in the Arctic region are affected by the ongoing changes. Specifically, we need to address whether pollinator species are keeping up with longer term changes or going hungry and—from a plant perspective—whether individual plants are receiving the pollinator visits that they need or lacking the visitors required for successful pollination.

To resolve patterns in contemporary resource availability, we characterized patterns within and among seasons, both from an insect and a plant perspective. We did so by (1) exploring how the phenology of insects and flowers progressed across the summer at two High-Arctic sites: Zackenberg in Greenland and Cambridge Bay in Nunavut, Canada; (2) determining whether the shifts in flower availability were reflected in competition for flowers; (3) characterizing who visits whom in the networks of Arctic plants and pollinators; (4) probing for a mismatch between supply and demand within years; and (5) establishing whether a potential mismatch has changed over time in the sole long-term time series available from the High Arctic, that is, the 25-year time series of Zackenberg (Schmidt et al., 2023). To advance from general patterns in flowering and insect activity (Schmidt et al., 2017) to actual taxon-specific patterns of demand and supply, we drew upon an explicit mapping of consumers on resources, that is, who has been found to visit whom at Zackenberg and Cambridge Bay, respectively. To characterize this structure of interactions, we drew on the metaweb of interactions available from each site, that is, the time-integrated record of pairwise interactions among plant and insect species in the respective system.

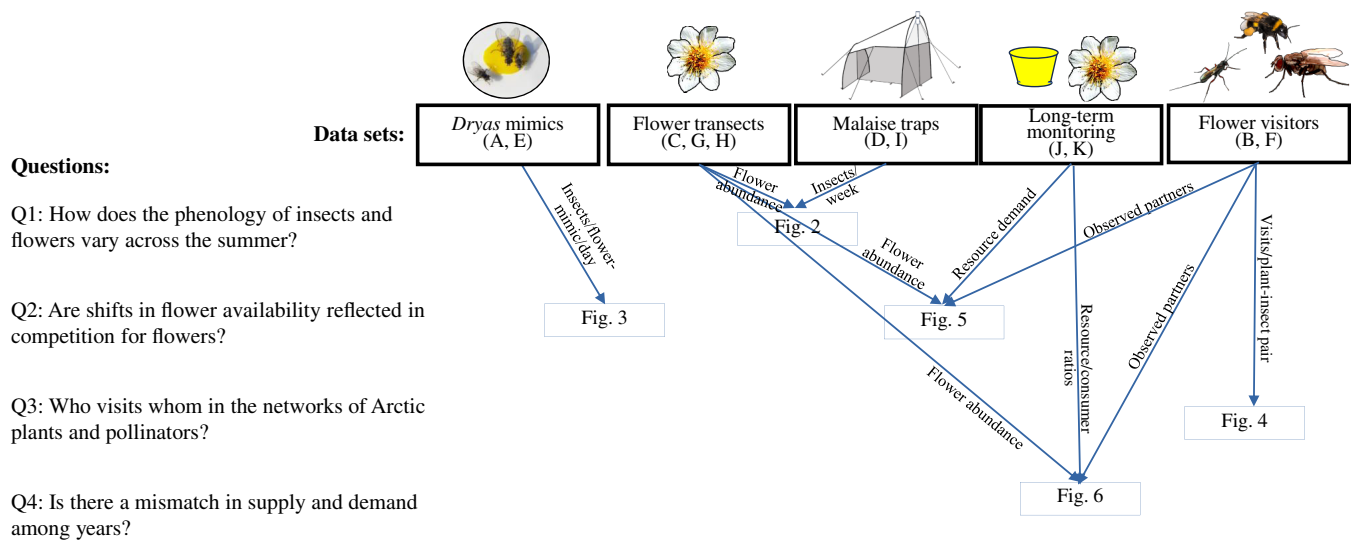
## MATERIALS AND METHODS

To characterize the overall phenology of insects at each site, the links between resources and consumers, and patterns of variation within and across years, we drew on a versatile material of 11 different data sets (Figure 1). The size and design of each data set, their internal relations, and their use are summarized in Table 1, with full details given below.

### Study sites

Our study sites were located near Cambridge Bay, Nunavut, Canada (69°7' N, 105°2.6' W), situated in Victoria Island and the Zackenberg Valley (74°28' N, 20°35' W), located within Northeast Greenland National Park (Figure 2). Both our study sites are located in the Arctic zone (Figure 2), and thus share general similarities in faunistic and floristic composition and climate.

The mean annual temperature of Cambridge Bay is around −13.3°C and precipitation is low (100–200 mm). This temperature has increased by 1.6°C between 1961 and 2020, with the most significant warming during the winter months (December–March). The highest and most significant warming rate has been recorded during 1981–2000 (Canadian Centre for Climate Services, 2023). The area is surrounded by dwarf shrub tundra, with approximately 150 plant species and hundreds of insect and spider species. Permafrost is also continuous, and at upland sites, it can have active layers of up to 1.5 m in depth.

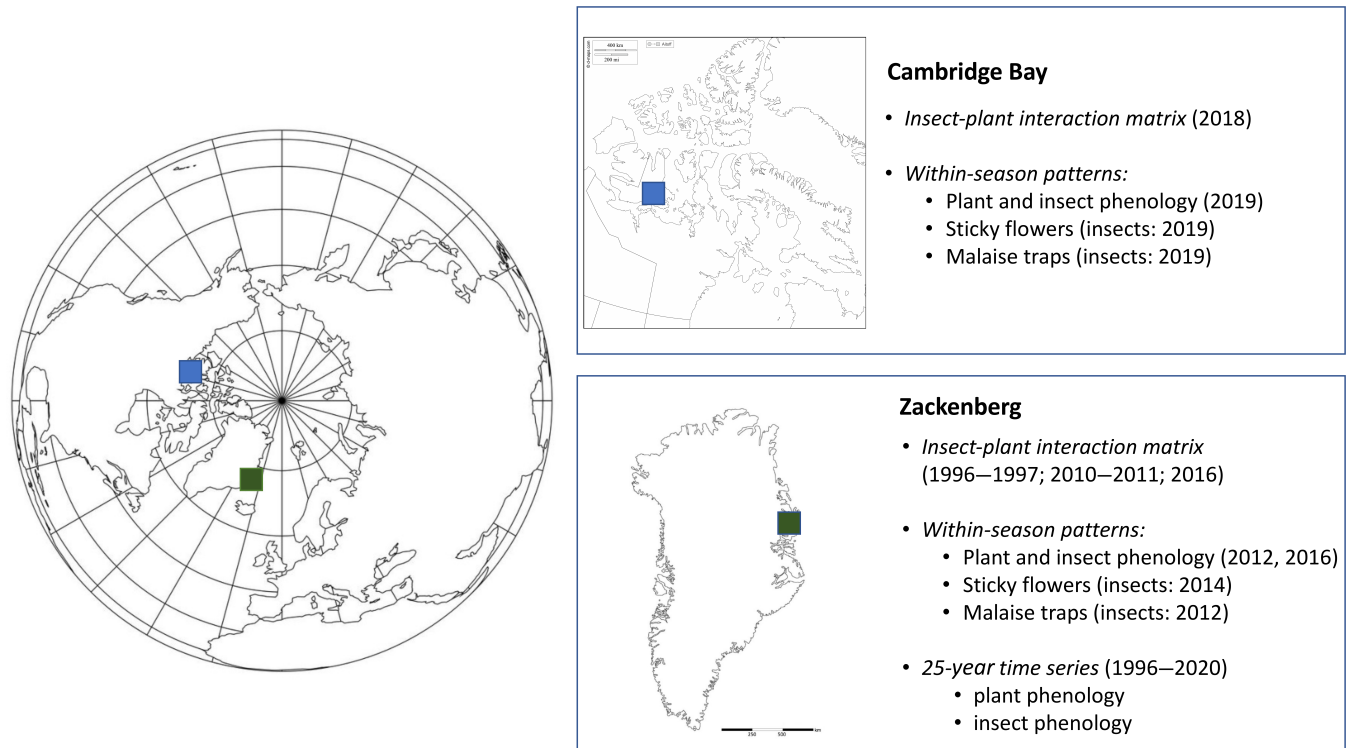


**FIGURE 1** A conceptual overview of how the 11 data sets used in this study were combined in analyses, results, tables, and figures. Images by Tomas Roslin.

**TABLE 1** An overview of the 11 data sets used in this study, and their use in analyses, results, tables, and figures.

Site and ID	Data set	Year	Sample size	Sampling frequency	Sampling extent	Use	Figures	Tables	Source
Cambridge Bay									
A	<i>Dryas</i> flower mimics	2019	1600 flower mimics (100 per site per flowering period)	4 flowering phases (early, peak, late, and past flowering of <i>Dryas</i> )	72 h exposure per flower	Measure competition for flowers, match between <i>Dryas</i> and insect phenology	3		The authors
B	Flower visitors	2018	12 mesic and xeric sites	Approximately weekly (June–August)	18 flowering plant species	Establish family-level interactions between plants and pollinating insects	4, 5		Culjak Mathieu (2021)
C	Flowering phenology	2019	Total 44 (Fen: 9, Mesic: 9, Snowbed: 13, Upland: 13)	Approximately weekly (June–August; varies by site)	One 2-m-wide transect per site (no. open recorded)	Measure flower abundance over time	2, 5		The authors
D	Malaise traps	2019	72 (18 per each of 4 sites)	Approximately every 5 days (June–September)	1 trap per site	Measure insect abundance over time	2, 5		The authors
Zackenbergl									
E	<i>Dryas</i> flower mimics	2014	2100 flower mimics (1500 across 15 early-flowering sites; 600 across 6 late-flowering sites)	2 flowering phases (early, late flowering of local <i>Dryas</i> )	72 h exposure per flower	Measure competition for flowers, match between <i>Dryas</i> and insect phenology	3		Tiusanen et al. (2016)
F	Flower visitors	2016	2 plots	Approximately every 4 days during flowering	51 days	Establish interactions between plants and insects, pooled to family level	4, 5, 6	2, 3	Cirtwill et al. (2023)
G	Flowering phenology	2012	48 plots	Approximately weekly (May–September)	6 focal plant genera (% open, recorded based on >50 plants per plot)	Measure flower abundance over time	2	2, 3	G-E-M Database
H	Flowering phenology	2016	22 transects across 2 plots	Every 4 days	50 m × 2 m transects, all flowering plants (30 species)	Measure flower abundance over time, convert long-term proportions to estimated abundances	2, 5, 6	2,3	The authors
I	Malaise traps	2012	20 (10 per trap)	Approximately weekly (June–August)	2 traps, 1 site	Measure insect abundance over time	2		Wirta et al. (2016)
J	Pitfall traps	1996–2020	379 weekly samples (9–20 per year)	Approximately weekly (June–August)	4 traps, 4–7 sites per year	Measure insect abundance over time	5, 6	2, 3	Schmidt et al. (2023)
K	Flowering phenology	1996–2020	344 weekly samples (10–20 per year)	Approximately weekly (June–August)	48 plots, 6 plant species	Measure flowering stage over time	5, 6	2, 3	Schmidt et al. (2023)

*Note:* We identify the site at which each data set was collected, the year(s) in which it was generated, the total sample size, the sampling frequency, the sampling extent, the use of the data in analyses, the figure(s) and table(s) in which the data appear, and the source of the data.



**FIGURE 2** Location of the two study sites and types of data collected at each site. Source of map of Cambridge Bay: [https://d-maps.com/carte.php?Num\\_car=23677&lang=en](https://d-maps.com/carte.php?Num_car=23677&lang=en).

Zackenberg is a particularly well-studied area, with a mean annual temperature of about  $-9.5^{\circ}\text{C}$  and an annual precipitation of 150–200 mm (Elberling et al., 2008). The mean summer temperature increased significantly between 1996 and 2005, whereas later time periods show no consistent increase in mean summer temperatures (Schmidt et al., 2023). Widespread surveys have documented 160 vascular plants and 403 terrestrial animal species (Wirta et al., 2016). Permafrost is continuous in the area, where active layer thickness at upland sites can be more than 2 m (and has increased significantly by 0.8–1.5 cm per year between 1996 and 2012) (Elberling et al., 2013).

At both sites, *Dryas* in the family Rosales is a particularly common flower resource (Tiusanen et al., 2019). At Cambridge Bay, all *Dryas* individuals belong to the North American species *Dryas integrifolia*, whereas at Zackenberg, most individuals are hybrids with the European species, *Dryas octopetala*  $\times$  *integrifolia* (Elkington, 1965; Philipp & Siegismund, 2003).

### Cambridge Bay

To cover relevant variation in local plant communities and phenologies in Cambridge Bay, we selected a set of four plots representing a range of conditions: fen, mesic

tundra, upland, and snowbed, located within an 18-km radius of the Canadian High Arctic Research Station (Cambridge Bay; Figure 2; for a more detailed description of the sites, see Appendix S1: Figure S1). Plant–pollinator and plant phenology data were collected from the beginning of June to late September 2019.

Flower phenology counts were conducted in the four plots along a transect selected at the beginning of the season. Inflorescences of all plant species were counted within 1 m on both sides of a 50-m transect. The number of flowers was recorded per plant species and counts were conducted weekly throughout the summer period to quantify absolute abundances per unit area (e.g., number of inflorescences per square meter).

To determine how resident arthropods overlapped with flower availability, insect abundances were sampled approximately every 5 days using Malaise traps. One trap was set out in each of the four sites from late June to late September (18 sampling occasions). Thus, we obtained a total of 72 separate Malaise trap samples. As Malaise traps are passive flight intercept traps, they will sample a large and representative part of the local insect community, while exhibiting some selectivity against strongly flying, visually guided insects and beetles (Srivathsan et al., 2023).

To record plant-to-insect ratios on a key flowering plant (arthropod visits per inflorescence), we set out sticky mimics of the focal plant *Dryas integrifolia*. These

flower mimics consisted of flower-sized round circles cut out of white sticky trapping sheets, then attached to a wire stalk (Tiusanen et al., 2016). Twenty such sticky mimics of *Dryas* flowers were placed by *Dryas* flowers at five subplots, within each plot during each of the four phases of subplot-specific *Dryas* phenology corresponding to early, peak, and late flowering, and for two weeks after flowering times. Individual subplots were 1 × 1 m in size and placed at least 1–2 m apart; five subplots of similar-density *Dryas* flower patches were selected with flower mimics placed in the highest density *Dryas* areas. The sticky flowers were exposed for 72 h of potential foraging activity during appropriate weather conditions (no strong wind, rain, or snow) before being collected and dried.

Information on plant–insect links (i.e., who visits whom) was extracted from a previous study conducted to categorize the full plant–pollinator network at Cambridge Bay. Here, Culjak Mathieu (2021) measured plant–insect interactions and abundances of 18 flowering plant species at 12 sites from mesic and xeric microclimates in 2018. These surveys were conducted weekly during the summer season until the end of flowering in August. Network data from this study were manually extracted by measuring links between plants and pollinators in Fig. 11 of Culjak Mathieu (2021). Taxonomic identifications in Culjak Mathieu (2021) were resolved only to a rough family level for insects (for a full list of taxonomic categories used, see Appendix S1: Section S1). To arrive at comparable data across locations (i.e., Zackenberg vs. Cambridge Bay), we applied the same taxonomic classification (i.e., genera for plants and families for insects) to all data throughout the analyses.

## Zackenberg

To place the patterns observed at Cambridge Bay into a longer term and wider scale context, we used data from long-term biotic and abiotic monitoring at the Zackenberg Research Station (established 1996; Schmidt et al., 2019). Assessments of the plant–pollinator community have centered around the most common (45/94 total flowering species) flowering species found in mesic heath areas (Wirta et al., 2017). As well as flowering phenology and insect abundances, data from this site included a highly resolved and well-studied plant–pollinator network for mesic heath species (Bascompte et al., 2003; Cirtwill et al., 2023; Dupont et al., 2009; Olesen et al., 2008; Rasmussen et al., 2013).

For within-season patterns of flowering and insect phenology at Zackenberg, we focused on two years for which particularly extensive flower and insect data were

available: 2012 and 2016. For 2012, we had access to detailed data on insect phenology from Malaise traps (see below). For flower counts, we used data on relative flowering phenology as tracked at 48 plots in the Biobasis monitoring program (Schmidt et al., 2019). To arrive at rough counts, we combined data on the proportion of flowers for each genus open on each sampling day (as available in G-E-M data <https://g-e-m.dk/gem-localities/zackenberg/data>), with the total counts observed in 2016. The proportion of open flowers per day was averaged across plots. These proportions were then multiplied by the total number of flowers for the genus observed in 2016 to obtain an estimate of the absolute number of open flowers available on each day.

In 2016, flower counts were taken in multiple 50-m-long and 2-m-wide transects within two 500 × 500 m plots close to each other, both located close to the areas used for long-term monitoring of flowering phenology (for maps, see Cirtwill et al., 2023; Schmidt et al., 2019). Every four days, all open flowers in transects were identified and counted. Transects were first conducted in an early-phenology plot where insect phenologies were also recorded. Once flowering had finished in these first selected transects, we chose a new plot of slightly later phenology. This way, we were able to estimate landscape-level flower availability throughout the entire season. Overall, the two plots covered the full spectrum of flowering habitats at Zackenberg and represented variation in flowering phenology across low hillsides and valleys with different levels of snow accumulation (Kankaanpää et al., 2018).

Detailed data on within-season phenology were derived for years 2012 and 2016. In 2012, Wirta et al. (2016) operated two Malaise traps for the main part of the season (from June 16 to August 21) to sample insect phenology. Traps were cleared weekly and samples were processed according to the Global Malaise Trap Program protocol (see Appendix S4 in the Supporting Information of Wirta et al., 2016). In 2016, insects were collected while visiting flowers and then identified using DNA barcoding (Wirta et al., 2014), as outlined in Cirtwill et al. (2023). In brief, pollinators were observed on flowers for 51 days in 500 × 500 mesic heath plots near the Zackenberg Research Station (Olesen et al., 2008; Rasmussen et al., 2013). During each field day (from 0900 to 1700), two individuals of each species of entomophilous flowering plant were observed for 20 min each (i.e., 40 min of observation for each plant species per day), and all insect visitors to flowers were recorded as potential pollinators (Olesen et al., 2008; Rasmussen et al., 2013). For further details about interaction sampling methods, see Olesen et al. (2008) and Rasmussen

et al. (2013). All insects visiting these plants were captured and identified via DNA barcoding (see Appendix S1: Section S2 in Cirtwill et al., 2023). If the DNA barcoding identification failed or insects were not caught, then individuals were identified morphologically to the lowest taxonomic level possible. Taxon names were harmonized over the data sets to account for taxonomic and/or methodologic differences over time (see Appendix S1: Section S3 in Cirtwill et al., 2023).

As per the Cambridge Bay sites, sticky flower mimics were used to derive measures of insect visits per inflorescence, as previously reported in Tiusanen et al. (2016). Within each of the 15 sites, 5 × 20 flower mimics were placed in *Dryas* patches between June 20 and July 5, 2014, on days when weather was suitable for insects. These sampling times corresponded to the “early” and “late” phases of flowering sampled at Cambridge Bay. Traps were set out weekly and collected 72 h of fair weather after the deployment (pollinators were inactive during rainy or windy days). Flowering peak at each site was defined as the date when half of all flowers were open. To determine whether insect abundances also peaked later in the season, additional locations near six of the 15 study sites were resampled again during July 10–21, 2014, to establish insect abundances occurring later in the season. The timing of this second sampling was determined by a person on site throughout the season, who was constantly recording insect densities.

To reconstruct an overall metaweb of plant–pollinator interactions (i.e., observations on any pairwise interaction between a plant and an insect taxon) at Zackenberg, we used data sampled at Zackenberg over four summers: in 1996 and 1997 by Olesen et al. (2008), and in 2010 and 2011 by Rasmussen et al. (2013). In addition, we used the data for 2016 described above. Links were based on insects visiting focal flowers in all years, and in 2016, they were supplemented by links detected based on identification of the pollen on insects’ bodies (see Cirtwill et al., 2023). Each study period lasted from the last snowmelt in spring to the first frost and snowfall in autumn. In 1996 and 1997, this covered 43 and 69 days, respectively, of which 25 in each year had sufficiently fine weather to permit observation (Olesen et al., 2008). In 2010 and 2011, the study period covered 70 and 69 days, respectively, of which 54 and 52 days were spent observing in the field (Rasmussen et al., 2013). Observations were only conducted on days of weather suitable for foraging insects (i.e., no rain, snow, or strong winds), following the methods described above. We pooled data into the same taxonomic categories as used for Cambridge Bay sites (Appendix S1: Section S1).

## Long-term data

Long-term data on the phenology of insect activity and plant flowering were extracted from the open data source of Greenland Ecosystem Monitoring (<http://data.g-e-m.dk>). For plants, inflorescences of six focal plant species in 48 long-term plots were counted from late May to early June until late August to early September at weekly intervals, weather permitting (if not, the next suitable day was sampled instead; Schmidt et al., 2019). This long-term sampling is focused on six flowering species: *Cassiope tetragona*, *Dryas integrifolia* × *octopetala*, *Papaver radicum*, *Salix arctica*, *Saxifraga oppositifolia*, and *Silene acaulis*. Together, these six plant species account for the main part of all floral resources at Zackenberg; in a survey of all plant species in 2016, these six species made up 82.3% of open flowers across the whole season (Tiusanen et al., 2020). We note that the long-term data concern phenology alone, whereas absolute abundances of plants have been shown not to change over time (see Becker-Scarpitta et al., 2023, who also offer graphs on variation).

For insects, seven trapping stations were established in different vegetation types. Each plot measures 5 × 20 m<sup>2</sup> and is made up of four 5 × 5 m<sup>2</sup> squares. Four yellow pitfall traps were randomly placed in each square and emptied near-weekly. The position, vegetation description, and coordinates of plots can be found in tab. 2.1.4 of Schmidt et al. (2019). Weekly insect catches from each trap were kept separate and stored in 96% ethanol. Expert entomologists at the Department of Ecoscience, University of Aarhus, sorted the arthropods according to different taxonomic levels, mainly family (see Appendix S1: Section S1).

## Molecular analyses

All insects collected were identified by DNA metabarcoding, except for the long-term data from Zackenberg (see *Long-term data*, above). Summary statistics on Malaise trap catches from Zackenberg in 2012 have been previously published in Wirta et al. (2016). In brief, each individual insect was separately DNA barcoded following the standard protocol of the Global Malaise Trap Program (<https://biodiversitygenomics.net/projects/gmp/>; for full details and data, see Appendix S4 of Wirta et al., 2016). Malaise trap samples collected at Cambridge Bay in 2019 were processed by the same workflow and are shared as BOLD projects: MCHAA, MCHAB, MCHAC, and MCHAE.

Data on insects collected by sticky flower mimics at Zackenberg in 2016 have been previously published in Tiusanen et al. (2016). In brief, DNA was extracted from a small piece of tissue from every insect specimen that

was sampled, and then sequenced for the standard CO1 barcode region (Hebert et al., 2003) following the protocols applied to “Arthropod samples” in Wirta et al. (2016). Taxonomic assignment was achieved using the Identification Engine of BOLD (Ratnasingham & Hebert, 2007).

Insects collected as part of network reconstruction in 2016 were individually barcoded following procedures described in Cirtwill et al. (2023; see Appendix S1 of that paper, Section S2.1 *DNA barcoding*).

Insects collected at Cambridge Bay by sticky flower mimics in 2019 were individually identified by DNA barcoding. A leg of each insect was individually removed and placed into a well of a 96-well plate with clean forceps, following the protocols of the Canadian Center for DNA Barcoding (CCDB). The material was analyzed using the alkaline lysis protocol of CCDB (Ivanova et al., 2006) and was completed using single primer cock-tails for Malaise trap samples sequenced once on a v3 SMRTcell on Sequel I. The sequence analysis was completed using the standard mBrave (Ratnasingham, 2019) pipeline and validated through the CCDB verification and submission to BOLD procedure. In cases where multiple sequences were produced from a single specimen, we focused our analyses on the most abundant variant (except for obvious contaminants such as bacterial sequences). All data are available as a public project POLCO on BOLD.

## STATISTICAL ANALYSES

### How does the phenology of insects and flowers vary across the summer at two High-Arctic sites?

#### Cambridge Bay

To characterize weekly changes in the abundance of plants and insects, we utilized Malaise trap and flower counts from each plot. Data were pooled across plots and used to examine insect abundance versus flower phenology. Flower counts for each sampling day were grouped across all plots (yielding one total count of floral resources per plant taxon in the whole sampling area). Sampling days were then grouped into seven-day intervals to obtain weekly totals. Plots were generally sampled weekly; however, due to weather and time constraints, all sites were not always sampled on the same date. Insect counts for each sampling day were grouped to family across all sites (for a full list of taxonomic categories used, see Appendix S1: Section S1), and then converted to weekly sums as above, to account for cases where not all sites were sampled on the same day. Insects

were generally grouped at the family level and plants were analyzed at the level of species.

#### Zackenberg

To characterize weekly abundance changes in plants and insects, we used weekly data compiled for the resolution of plant–pollinator networks. For 2012, we used the catches from weekly Malaise trapping to derive highly resolved data on the locally sampled insect community. Insects were pooled to family and counts per sampling day were converted to weekly sums as at Cambridge Bay. Flower counts were unavailable for 2012 at Zackenberg; instead, phenology was recorded as the proportion of flowers (for each genus) that were open on each sampling day, out of at least 50 (100 for *Salix*) inflorescences inspected (Schmidt et al., 2019). To estimate the counts of open flowers in 2012, we multiplied these proportions by the total number of open flowers observed in 2016. In 2012, flower phenology for six species was tracked at three to six (depending on taxon) plots and then averaged across plots. In 2016, flower phenology was tracked for 30 species at a single plot.

### Are shifts in flower availability reflected in competition for flowers?

#### Cambridge Bay

To determine consumer-to-resource ratios across the summer, we measured insect abundances per sticky flower during the season. Counts of individuals within each insect species for a given date and plot were used to plot insect abundance per sticky trap against flower counts per flower-day. Conversion to insects per flower-day was performed via pooled family counts, which were then divided by the number of flower-days sampled per subplot (approximately 80; 20 flowers for 4 days each, with slight variations by subplot). Dates were grouped into samples taken during the early, peak, late, and post-flowering periods of *Dryas*, according to the flowering phenology scored along the line transect. Counts of each insect family per flower-day were summed within each time period in each plot; the mean and SE across the four plots and five subplots/plot (20 in total) were then calculated for each time period.

#### Zackenberg

Counts of individuals within each insect taxon for a given subplot (5 per site, 15 + 6 sites) at Zackenberg sites were



used for a comparative plot of insect abundances on sticky flowers versus flower counts. Conversion to insects per flower-day was performed via counts pooled per family (Appendix S1: Section S2) and then divided by 20 to reflect 20 sticky flowers per subplot placed for one day. Following the distinction made by Tiusanen et al. (2016), individual plots were grouped into those flowering during the early (site labels 1–15 in Tiusanen et al., 2016) versus late (site labels 16–21 in Tiusanen et al., 2016) part of the landscape-level *Dryas* flowering period. Means and SEs of insect counts per subplot were calculated for each time period ( $n = 75$  and  $30$ , respectively).

### Who visits whom among Arctic plants and pollinators?

Insect and flower counts were used to compile a quantitative plant–pollinator network. For flower–visitor networks, both binary and weighted versions of connectance and nestedness were calculated. These networks were calculated using R (R Core Team, 2023) function “networklevel” from the *bipartite* package version 2.19 (Dormann et al., 2008).

### Is there a mismatch between supply and demand within years?

To resolve mismatches between insect versus flowering phenology within years, we compared the temporal distributions of flowering versus insect phenology within the years for which data were available (see section [How does the phenology of insects and flowers vary across the summer at two High-Arctic sites?](#)).

### Does the mismatch between supply and demand change over time?

To examine the longer term temporal dynamics of plant–insect interactions, we tested for trends over time in the incidence of periods of lean resources and the variance of this incidence. Resource threshold can be described as low quantiles of the overall distribution of floral resource availability, thus corresponding to periods of particularly low resources. Thus, testing for a linear trend in the number of such periods per year allows us to determine whether the resource–consumer mismatch is significant and rising. To test whether the mean number of weeks below resource threshold increased over time, we fit a general linear model for each case, relating the number of weeks below threshold to year, taxon ID

(order for plants, family for insects), and their interaction, assuming a Poisson error distribution and a log link function. To fit the models, we used base function “glm” in R version 2.19 (R Core Team, 2023).

To arrive at the final model, we used a likelihood ratio test of each model against the next smallest model (i.e., the model including year, order, and their interaction compared with a model including year and order, the model including year compared with an intercept-only model). We compared the model including year and order with both a model including year only and a model including order only. All likelihood ratio tests were fit using the R function “lrtest” from the package *lmtest* (Zeileis & Hothorn, 2002).

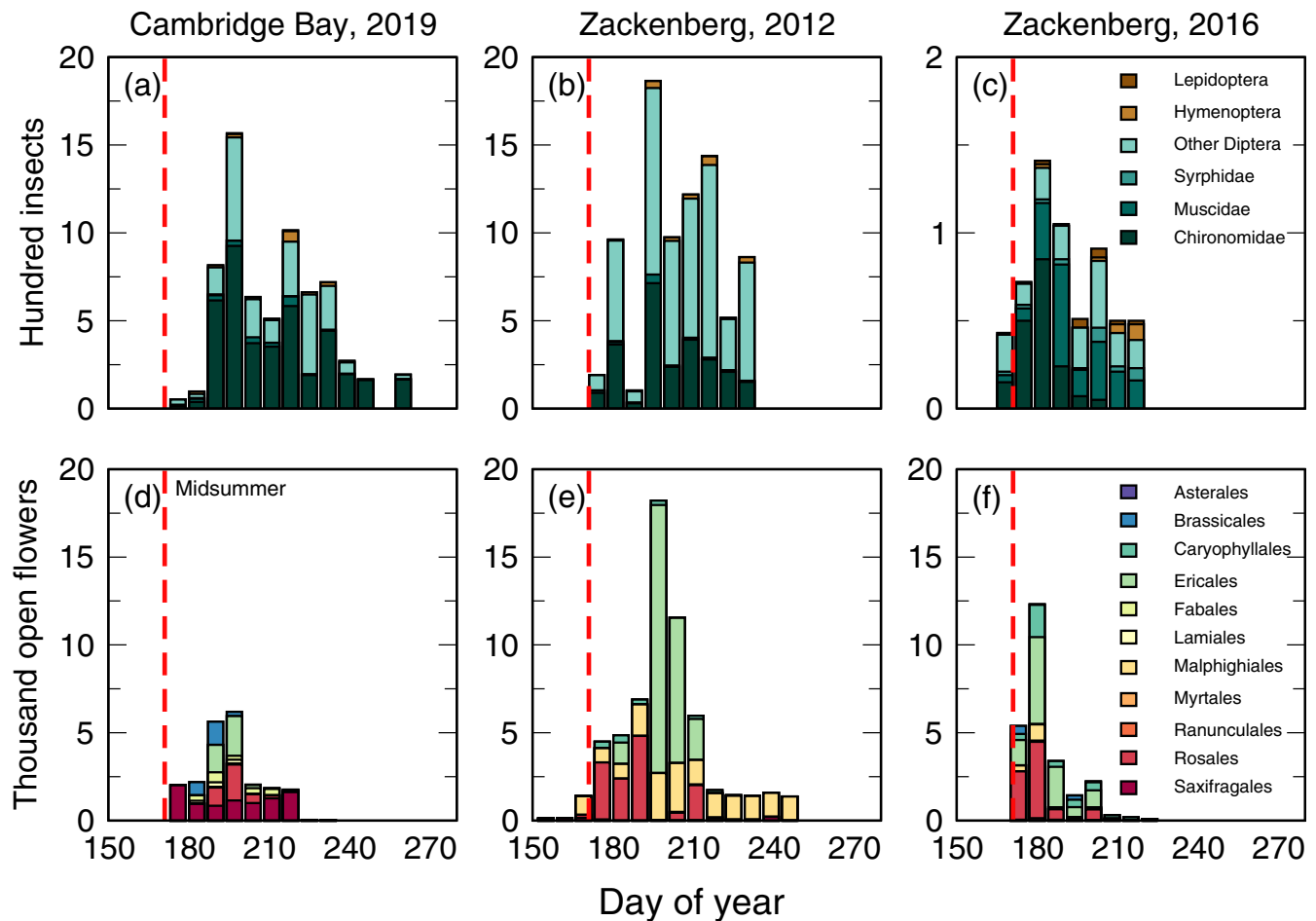
As increasing variation and unpredictability in plant–pollinator networks have been observed over years (Cirtwill et al., 2023), we were also interested in the variance of lean periods, as a measure of stability. To apply Levene’s (1960) test of equality of variance, we thus calculated the residuals from the model described above, fitting a second linear model relating the absolute value of residuals to year. This second model assumed a normal error distribution and an identity link function. To fit the models, we used base function “glm” in R version 2.19 (R Core Team, 2023).

## RESULTS

In total, we sampled 9120 individual insects by Malaise traps and 13,631 insects (excluding nonpollinators and unidentifiable insects, see Appendix S1: Section S1) by sticky flower mimics. The exact number of taxa included in each analysis is identified in the legends of the respective figure.

### How does the phenology of insects and flowers vary across the summer at two High-Arctic sites?

At both Cambridge Bay and Zackenberg, peak insect abundances in Malaise trap catches more or less coincided with the peak in flowering time, but insects remained abundant over a longer period, while plants showed a stronger peak (Figure 3). Across both sites, a residual tail of insects can be seen well after peak flowering time has passed, extending beyond late summer (Figure 3). Flower counts decreased after Day 200 for Cambridge Bay 2019 and Zackenberg 2012, and even earlier (after Day 180) for Zackenberg 2016 (Figure 3). *Dryas* counts also decline earlier in the season before peak insect times (Figure 3). A general downward



**FIGURE 3** The abundance of insects versus the flowering phenology of plants. Plots on the top row show insect numbers from each summer sampled in Cambridge Bay (2019) and Zackenberg (2012, 2016). Insect data for Cambridge Bay 2019 and Zackenberg 2012 were derived from Malaise traps, whereas insect counts from Zackenberg 2016 were directly observed on flowers—absolute numbers on the y-axis differ accordingly. Plots on the bottom row show the abundance of flowering plants. Red dashed line indicates midsummer (Day 171). The range and scale of the x-axis match across panels, thus allowing a direct comparison of insect-to-flower abundances. Both sets of plots in Figure 2 revealed that after peak abundance, floral counts decrease earlier and more rapidly than insects across all sites. For Zackenberg, field sampling ended before the end of insect activity was observed. Overall, we observed 11 plant genera and 35 insect families at Cambridge Bay, versus 6 plant genera and 21 insect families observed at Zackenberg in 2012, and 30 plant genera and 22 insect families in 2016.

slope can be seen for both plants and pollinators, with pollinators decreasing more slowly and later than the floral counts—the latter of which already declined before midsummer (see red dashed line on Day 171, Figure 3).

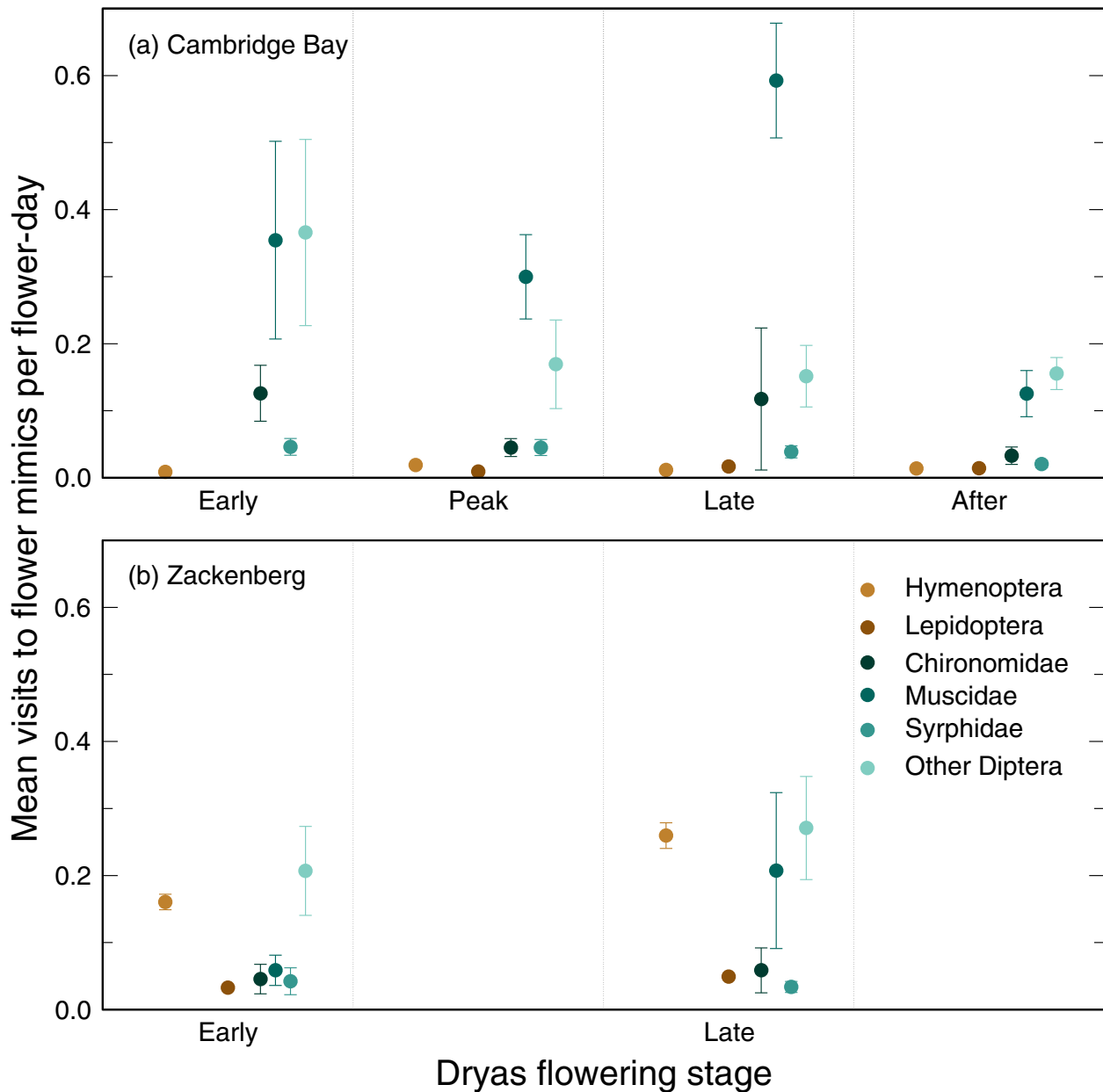
### Are shifts in flower availability reflected in competition for flowers?

A general mismatch in the timing of insect versus flower abundances (Figure 3) was also revealed by the sticky flower traps. These flowers attracted the greatest number of insects visiting flowers during the late flowering stages. At Cambridge Bay, flies in the family Muscidae were especially abundant during this time, making 63.1% of the mean visits per flowering day late

in the summer season (Figure 4a). Zackenberg showed a similar pattern, with higher insect landings on sticky flower traps in the late *Dryas* flowering stage (Figure 4b). At Zackenberg, Muscidae were less dominant (although still the most active single insect family) and made only 25.4% of mean visit per flowering day in late summer, with other Diptera and Hymenoptera making similar proportions of visits (33.1% and 23.1%, respectively).

### Who visits whom among Arctic plants and pollinators?

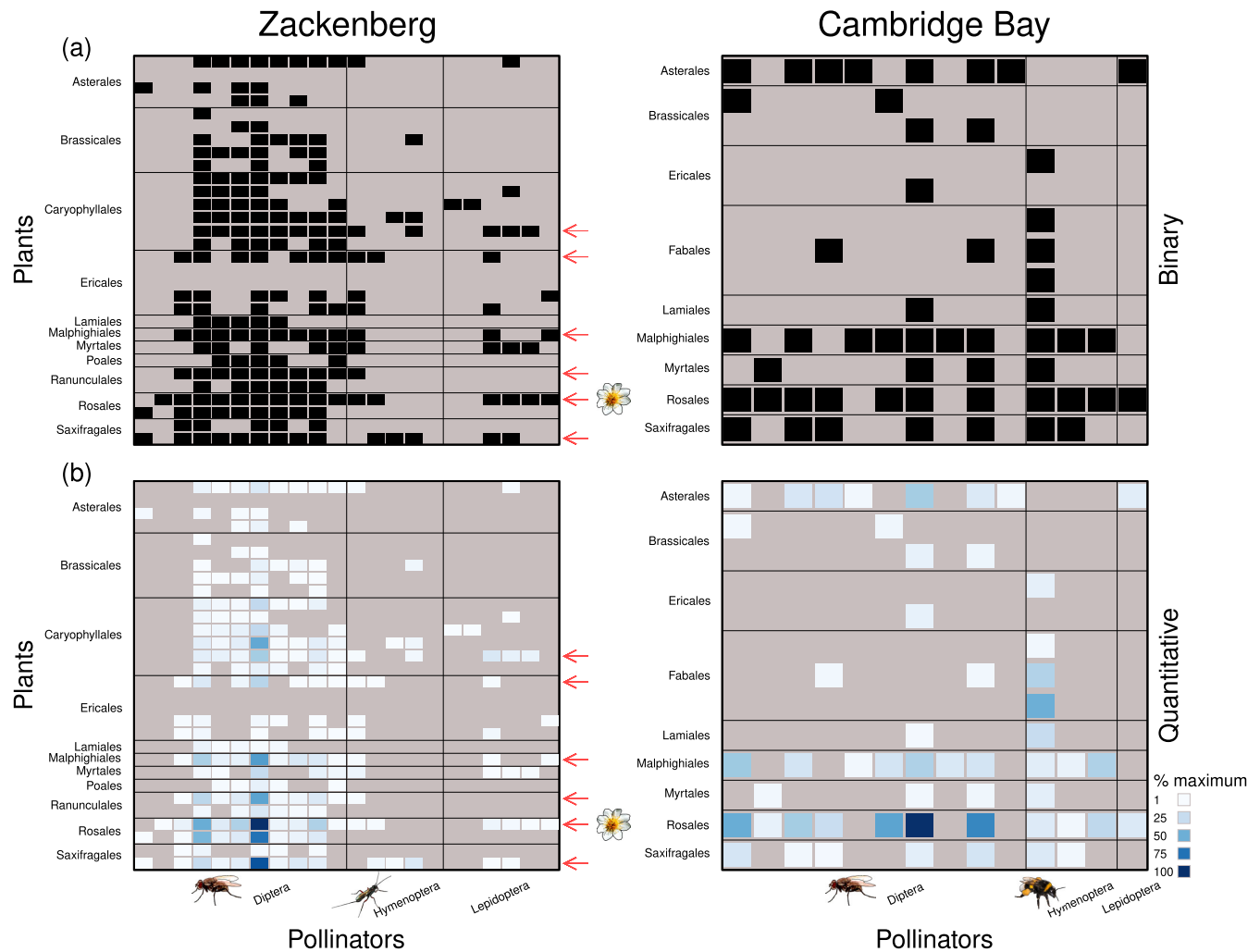
At Cambridge Bay and Zackenberg, the metaweb of insect–plant interactions was sparsely connected—even



**FIGURE 4** Mean insect visits per phase of the *Dryas* flowering period, scored by sticky *Dryas* flower traps at (a) Cambridge Bay and (b) Zackenberg. At both sites, the late phases of flowering, including the post-flowering period at Cambridge Bay, are associated with high insect densities. Error bars show 95% CIs. Overall, we observed 34 insect families at Cambridge Bay and 22 insect families at Zackenberg.

when insects were pooled to families and plants to genera (Figure 5a). Only 40.9% of possible links at Zackenberg and 29.7% of possible links at Cambridge Bay were actually observed; at the species level, interactions between taxa would necessarily be rarer. At Zackenberg, *Dryas* was visited by the most insect families (18 of 22) and Muscidae visited the most plant genera (27 of 30). At Cambridge Bay, *Dryas* was likewise visited by the most insect families (11 of 14) and Apidae visited the most plant genera (9 of 13).

Moving beyond binary interactions, the strongest link at both sites occurred between *Dryas* and Muscidae (Figure 5b). For Cambridge Bay, the next three strongest links also involved *Dryas* (visited by Syrphidae, Empididae, and Anthomyiidae). At Zackenberg, the next three strongest links also involved Muscidae (visiting *Saxifraga*, *Potentilla*, and *Cerastium*). Despite Hymenoptera (Apidae) visiting the most plants at Cambridge Bay, pollination in both systems is strongly fly-dependent in a quantitative sense.



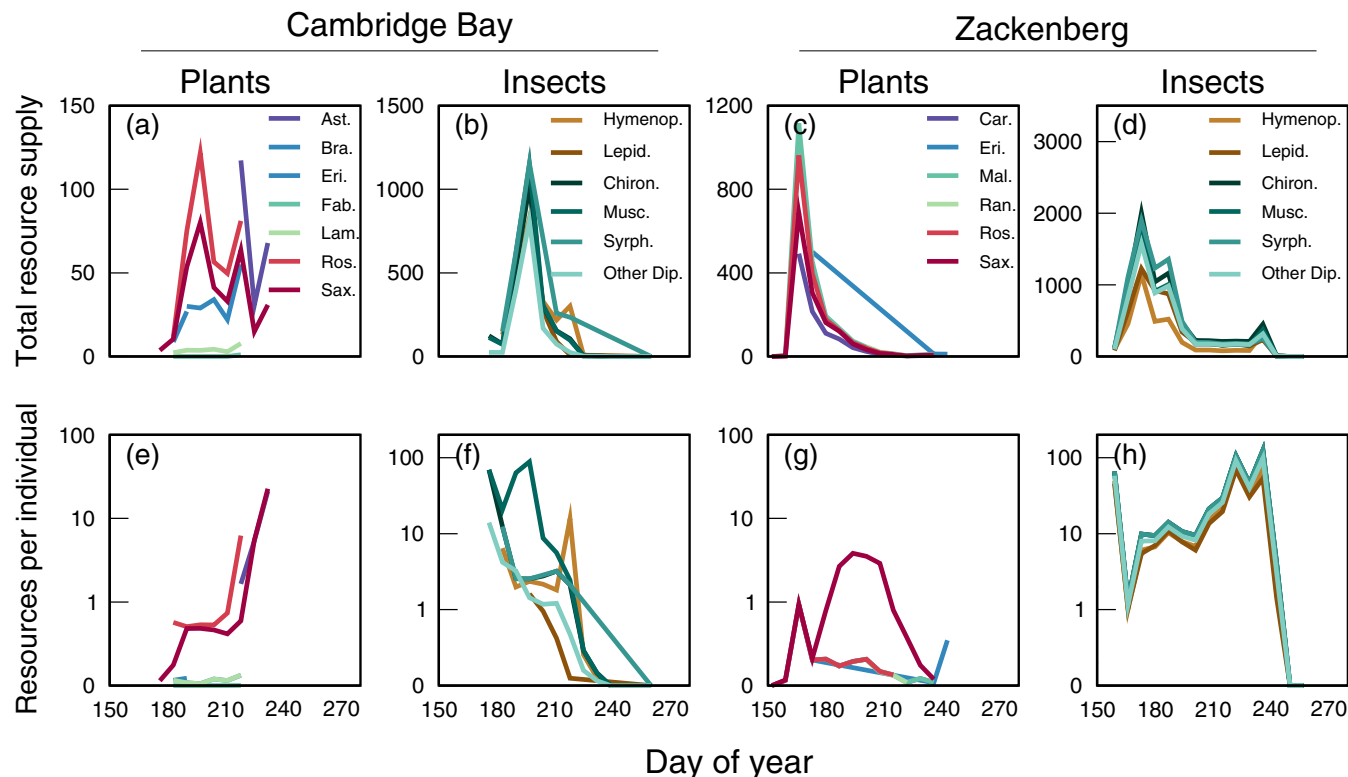
**FIGURE 5** (a) Binary and (b) weighted metawebs for Zackenberg and Cambridge Bay, consisting of all possible plant and pollinator interactions. Families (for insects) and genera (for plants) are shown in a row or column within their order. Black squares indicate an interaction has been observed, while most interactions were never realized and thus shown in gray. Darker colors on weighted webs (b) indicate more frequently observed interactions, whereas lighter colors are rare interactions. Interaction frequencies are scaled relative to the maximum observed frequency at each site. Overall, we observed 14 plant genera and 14 insect families at Cambridge Bay, versus 30 plant genera and 22 insect families at Zackenberg. The *Dryas* flower icon pinpoints the abundance of interactions involving *Dryas* (Rosaceae: Rosales), whereas the parasitoid wasp versus the bumblebee indicates a general difference in the composition of Hymenoptera at Zackenberg and Cambridge Bay, as also reflected in the number of interactions in which these insects are involved. Red arrows highlight the plant genera at Zackenberg where phenology was tracked in long-term monitoring.

### Is there a mismatch between supply and demand within years?

Within summers, resource availability drastically changed with the season. At Cambridge Bay, the overall resource supply (i.e., the total number of insects available per plant taxon) peaked during the mid-part of the summer (Figure 6a). At Zackenberg, plants had access to ample insect resources early in the season—after which total resource supply quickly decreased (Figure 6c). For insects, we found more consistent patterns between the two sites, with high availability of plant resources

during the early summer, but a decrease toward the late part of the summer (Figure 6b,d). This decline was more pronounced at Cambridge Bay than at Zackenberg, where for most insect taxa, availability of plant resources declined until the end of the season (Figure 6d).

At the level of resource supply per individual, the availability of insects per flower rapidly increased with the day of year at Cambridge Bay (Figure 6e). The opposite was true for insects, and the supply of flowers per insect rapidly decreased over the summer (Figure 6f). At Zackenberg, we found an almost opposite pattern, with



**FIGURE 6** Plant resource and pollinator availability per week (with plants assigned to genera and insects to families) for Cambridge Bay and Zackenberg in 2019. In the top row (panels a–d), we show overall resource supply (i.e., total numbers) of insects available to plants (a, c) and plants available to insects (b, d) for Cambridge Bay (a, b) and Zackenberg (c, d). In the bottom row (panels e–h), we show the resource supply per insect–plant individual (e, g) and insect individual (f, h) for Cambridge Bay (e, f) and Zackenberg (g, h). Note the logarithmic scale of and variation in the absolute scales of the y-axes among panels. To establish taxon-specific resource availability, we used the metawebs shown in Figure 4. Overall, these analyses were based on 6 plant genera and 30 insect families for Cambridge Bay, versus 6 plant genera and 21 insect families for Zackenberg. Plant families are abbreviated as follows: Ast. = Asterales; Bra. = Brassicales; Car. = Caryophyllales; Eri. = Ericales; Fab. = Fabales; Lam. = Lamiales; Mal. = Maphighiales; Ran. = Ranunculales; Ros. = Rosales; Sax. = Saxifragales. Note that only Rosales and Saxifragales were represented at both sites. Insect families are abbreviated as follows: Chiron. = Chironomidae (Diptera); Hymenop. = Hymenoptera; Lepid. = Lepidoptera; Musc. = Muscidae (Diptera); Other Dip. = Other Diptera; Syrph. = Syrphidae (Diptera). All insect orders/families were present at both sites. For plants, the lines show means across species within families; for insects, the lines show means across families within orders or key Diptera families.

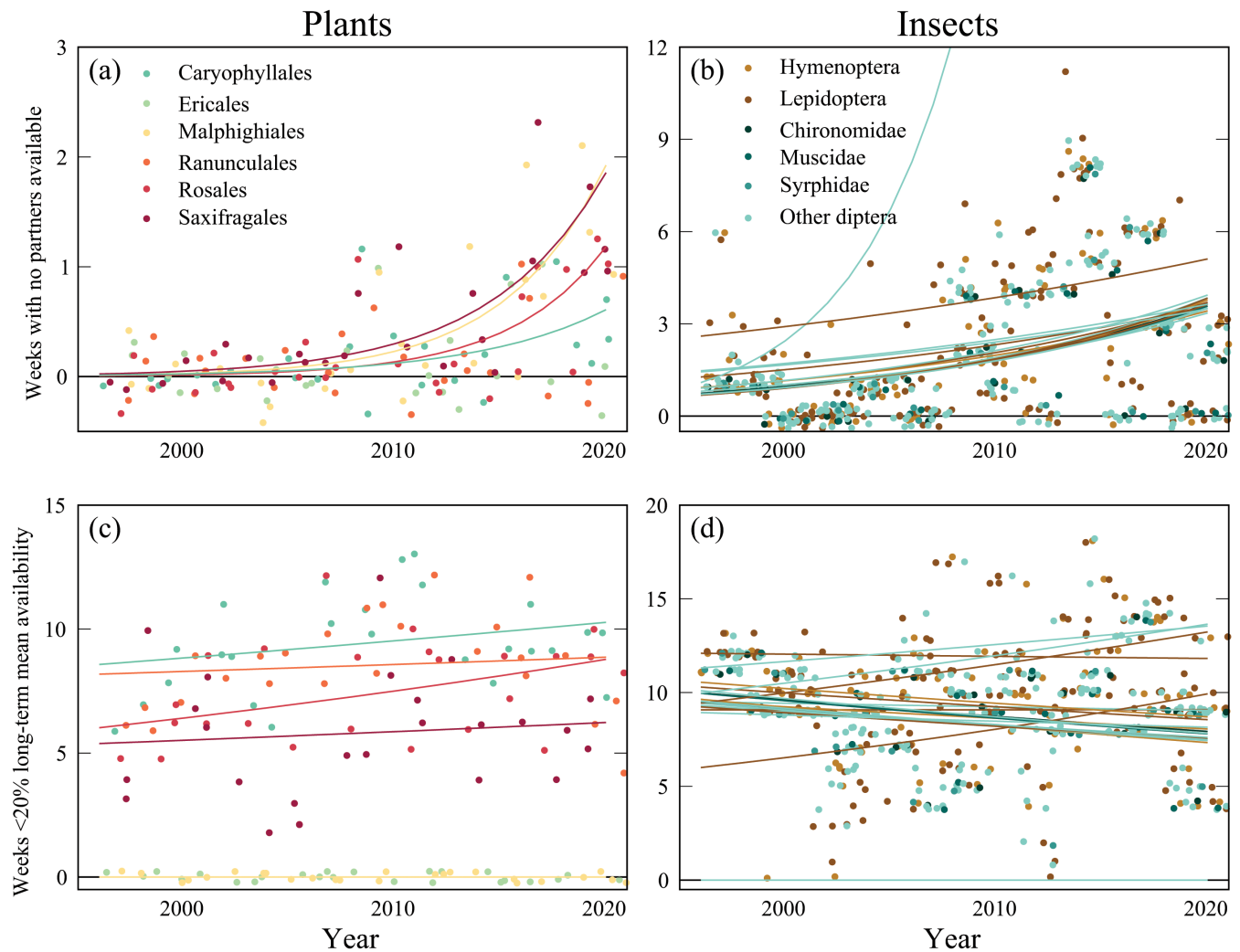
the highest resource supply in the early summer—except for the order Saxifragales (Figure 6g). Moreover, at Zackenberg, we found an early-summer peak, and a second, late-summer peak in the availability of flowers to insect individuals—before resource availability eventually crashed at the end of the summer. In 2019, this pattern was remarkably consistent across insect families (Figure 6h).

Importantly, the patterns observed in resources per individual insect seemed fundamentally different at Cambridge Bay versus Zackenberg (Figure 6f, h). At Cambridge Bay, we only had access to data for a single summer. However, the long-term data available for Zackenberg allowed us to reconstruct patterns for each of the 25 years. None of these years had a pattern resembling that observed at Cambridge Bay in 2019—neither from a plant nor from an insect perspective (see Appendix S1: Section S2; compare red and blue lines in Appendix S1: Figure S2).

### Does the mismatch between supply and demand change over time?

From a plant perspective, the number of weeks without any interaction partners increased over time, with significant differences in the rate of increase among taxa (Figure 7a; Table 2). The number of weeks with less than one-fifth of the long-term resource supply per individual showed a similar, but nonsignificant, pattern (Figure 7c; Table 2).

The same was true from an insect perspective, where the number of weeks without any interaction partners also showed an increase over time, with significant variation among taxa (Figure 7b; Table 2). In terms of weeks with less than one fifth of the long-term resource supply per individual, we again found a significant, taxon-specific increase (Figure 7d; Table 2).



**FIGURE 7** Temporal trends in mean resource availability over the 25-year data period for Zackenberg. For plants on the left and insects on the right, we show the number of weeks for which a taxon did not have access to any interaction partner (a, b), and the number of weeks for which resource availability per individual dropped below a threshold of 20% of the long-term mean of availability (c, d). Fitted lines represent model fits from a Poisson regression outlined in Table 2. These analyses were based on 6 plant genera and 22 insect families.

Beyond changes in the mean incidence of resource-poor weeks (above), the number of resource-poor weeks for plants and pollinators at Zackenberg is also becoming increasingly unpredictable over time. For plants, variability in the number of weeks of no available interaction partners significantly increased over years (see residuals around the fitted lines in Figure 7; Table 3). In terms of the average resource supply per individual, changes were negligible over time, with a very slight decrease observed across the 25-year time series (Figure 7; Table 3).

For insects, variability in the number of weeks of no available interaction partners very slightly decreased over time (see residuals around the fitted lines in Figure 7; Table 3). In terms of the average resource supply per individual, there was a pronounced and significant increase (Table 3).

## DISCUSSION

This study of two Arctic regions reveals a general phenological mismatch between resource supply and demand for plants and pollinators. These patterns were revealed by the novel approach of using the metaweb of plant–insect interactions to match consumers with resources from both a plant and an insect perspective. Over the course of the summer, we find rapid turnover in both insect and plant resources, and this turnover is not synchronized between interaction partners at Zackenberg or Cambridge Bay. In particular, insect abundances remained high well after the peak flowering times of the plants they visited. As the summer progressed at Cambridge Bay, flower availability per insect decreased, whereas insect availability per flower increased. At Zackenberg, where long-term data were

**TABLE 2** Poisson regression models of the number of weeks without available partners (columns Partners) or resource availability per individual (columns Availability) as a function of year, taxonomic group (order for plants, family for insects), and their interaction.

Model	Partners		Availability	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Plants				
Year	<b>46.5</b>	<b>&lt;0.001</b>	2.60	0.107
Order	7.58	0.181	<b>653</b>	<b>&lt;0.001</b>
Year + order (vs. year)	7.58	0.182	<b>653</b>	<b>&lt;0.001</b>
Year + order (vs. order)	<b>46.5</b>	<b>&lt;0.001</b>	2.60	0.107
Year × order	0.441	0.994	0.831	0.975
Insects				
Year	<b>158</b>	<b>&lt;0.001</b>	2.25	0.134
Family	<b>41.2</b>	<b>0.005</b>	<b>112</b>	<b>&lt;0.001</b>
Year + family (vs. year)	<b>42.5</b>	<b>0.004</b>	<b>112</b>	<b>&lt;0.001</b>
Year + family (vs. family)	<b>159</b>	<b>&lt;0.001</b>	2.63	0.105
Year × family	10.4	0.973	19.4	0.562

Note: The table gives the results of likelihood ratio tests of each model against the next smallest model (i.e., the model including year, order, and their interaction compared with a model including year and order, the model including year compared with an intercept-only model). We compared the model including year and order with both a model including year only and a model including order only. Significant values (*p* < 0.05) are highlighted in bold. If none of the interactions between taxonomy and year were significant, the interaction term was removed and the model was refit. If none of the taxonomy main effects was significant, the model was refit including only year.

**TABLE 3** Linear regression models of variance in resource availability over time.

Model	Partners		Availability	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Plants				
Year	0.109	0.741	0.264	0.607
Insects				
Year	<b>7.72</b>	<b>0.005</b>	<b>6.65</b>	<b>0.010</b>

Note: Here, we model the absolute residuals from models outlined in Table 2 as a function of year. We do not include any effects of taxonomic group as these are incorporated in the models above. The table gives the results of likelihood ratio tests of each model against the intercept-only model. Significant values (*p* < 0.05) are highlighted in bold.

available, there was less of a mismatch between insects and available flower resources. However, there was evidence for longer periods of resource scarcity and increasing variability in resource availability over time for plants, but not for insects. Below, we consider each of these aspects in turn.

## Who visits whom in Arctic plant–pollinator networks?

The networks we constructed from Cambridge Bay and Zackenberg were more densely connected than other published plant–pollinator networks (Bascompte & Jordano, 2007; Bastolla et al., 2009; Dupont et al., 2009; Olesen et al., 2007). However, pooling insect taxa to families may create the impression of a more generalized network than if the same network had been resolved to the species level (Roslin & Majaneva, 2016). For example, Cirtwill et al. (2023) used Zackenberg network data with species-level designations, and showed much lower connectance than the present study. As family-level networks over-represent the number of interactions occurring between pairs of species, our metrics will constitute a conservative approach to estimate phenological mismatch, as it is often suggested that insects may visit alternative plants if their preferred floral resources are unavailable (Mayhew, 1997; Revilla & Křivan, 2016). In this case, we effectively assume that insects can freely switch between plants visited by any member of their family. Any mismatch that we observe is therefore what remains after allowing for a large amount of potential rewiring.

In both networks, *Dryas* emerged as a keystone flowering species, while Muscid flies dominated as pollinators (Cirtwill et al., 2023; Culjak Mathieu, 2021; Tiusanen et al., 2016). *Salix* was the second most visited plant genus, which is likely due to its early appearance in combination with long flowering times (Cirtwill et al., 2023). Interestingly, Hymenoptera were among the most dominant pollinators at Cambridge Bay, making more visits to keystone flowers than any Muscid (Figure 5). By comparison, Hymenoptera formed a very minor part of the Zackenberg pollinator fauna. This difference in importance is likely due to the specific Hymenoptera taxa present at each site. At Cambridge Bay, Hymenoptera were dominated by bees (Apidae), while no honeybees are present at these High-Arctic sites. At Zackenberg, Hymenoptera were mainly small parasitoid wasps, whereas the two species of Apidae: *Bombus* were both rare and no other bees were present. Bees are characterized by long flight times and will visit multiple flowers to collect sufficient resources for themselves and for nesting larvae (Michener, 2000). By contrast, parasitic wasps visit fewer flowers and only use flowers for their own sustenance, whereas their larvae parasitize other living organisms (Doutt, 1959). This highlights potentially important differences between the two sites in the net amount of pollination services provided by Hymenoptera versus Diptera.

## How does the phenology of insects and flowers vary across the summer—and is there a mismatch in resource supply and demand?

At both Cambridge Bay and Zackenberg, the short Arctic summer is associated with rapid phenological shifts. Each plant species typically flowers for only a few weeks (Høye et al., 2013), resulting in rapid turnover of specific insect–plant associations over time (Cirtwill et al., 2023). In our study, we examined the consequences of such turnover for patterns of overall resource abundance over time. Overall, we observed clear seasonal dynamics, with a maximum number of flowers available per individual insect in early summer, although there was considerable variation in supply and demand for both plants and insects (Figure 6).

At Cambridge Bay, early flying insects had many options for flowers to visit, although plants had few individual pollinators available. As the season progressed, this scenario was reversed, and the many insects seeking flower resources had a limited choice. However, late-flowering plants had many pollinators available (Figure 6a). Thus, the total resource supply for insects and plants showed opposite trends over the summer due to temporally mismatched peak abundances.

At Zackenberg, we found an early-summer peak and a second, late-summer peak in the availability of flowers to insect individuals, before resource availability eventually crashed at the end of the summer. In 2019, this pattern was remarkably consistent across insect families, similar to patterns previously reported from montane Colorado (Aldridge et al., 2011). Nonetheless, there was much variation between the years, and no year resembled the pattern observed at Cambridge Bay (Appendix S1: Section S2). The contrast between sites is likely due to differences in plant community composition and inter-annual variation in plant flowering between the two sites.

Shifts in the insect-to-flower ratios were clearly reflected in our sampling of insects by sticky flower mimics at both Cambridge Bay and Zackenberg. This sampling was focused on a key flower resource in both systems (*Dryas*), and shifts in insect-to-flower ratios for this genus will reflect two key processes: competition for flowers (Tiusanen et al., 2020) and pollen transfer among conspecific plants (Kortsch et al., 2023). Early in the season, when flowers generally were most abundant, there were fewer pollinators landing on the sticky flowers at Cambridge Bay and Zackenberg. This suggests low competition for flowers and, likely, low pollen transfer. This is consistent with previous work

suggesting a peak in pollen deposition on *Dryas* in the middle of the summer (Cirtwill et al., 2023). The highest insect densities per flower were observed during the late part of the season, when flowers were least abundant (Figure 4).

For insects, the patterns observed suggest greater competition and greater resource mismatches later in the season. Individuals did not always experience low resources (and likely stronger competition) at the end of summer, although some such periods were observed in each year (Figure 7). Over time, this could lead to fewer pollinators, as shorter flowering times and accentuated mismatches have been linked to declining pollinator population densities the following year (Høye et al., 2013).

Insect-pollinated plants likewise need a sufficient supply of visitors, to obtain successful pollen transfer among individuals (Di Pasquale & Jacobi, 1998). *Dryas* is a particularly strong competitor for insect visitors and can reduce the reproductive success of other species (Tiusanen et al., 2020). Thus, low numbers of visitors per flower early in the season imply strong competition among early-flowering *Dryas* for pollen transport, while late in the season, *Dryas* may outcompete other plant species. Similar to insects, the timing of high competition for flower visitors varied between years, but some such periods occurred each year (Figure 7). In terms of pollen transfer among conspecific plants, more conspecifics means increasing pollen loads (Kortsch et al., 2023). This can act in two ways: too much pollen may clog stigma, whereas too little will result in poor pollination (Aizen & Harder, 2007).

The observed peak in flower abundances in the early summer may at least partially be a consequence of recent climate change. As plants respond to a warmer climate by shortening the duration of the flowering period (Høye et al., 2013), the phenological window for intense plant–pollinator interactions may have shrunk toward an earlier time window (Schmidt et al., 2016), leaving insects with limited available resources toward the end of the summer. Insects in the Arctic have longer generational times than insects in warmer parts of the world and may thus be less responsive to climatic cues, because their development will be affected by temperatures acting over multiple years (Høye & Sikes, 2013). What is more, insect responses to temperature tend to be weaker than those of plants (Ellwood et al., 2012). These factors—and our current findings—suggest that insects may not be keeping up with the current and rapid rates of shifting plant phenology. However, patterns observed within a single year will provide only circumstantial evidence for longer term change. Thus, we next turn to the long-term data from Zackenberg for more direct evidence of temporal trends.



## The predictability of resources is declining over time

To predict the future of Arctic plants and insect pollinators, we turn to the only time series available: the 25-year data set from the Greenland Ecosystem Monitoring project in Zackenberg. Here, the number of weeks without interaction partners increased over time for both plants and insects, and number of weeks with low visitors per flower increased over time for plants. At the same time, variability in the number of weeks where insects had no available flowers to visit increased across the years.

To identify potential environmental drivers of phenological mismatches, we examined the impact of annual variation in snow conditions (Appendix S1: Section S3; cf. Kankaanpää et al., 2018). For insects, periods of low resources (i.e., times of no interaction partners or low availability of partners per individual) decreased with increasing spring snow cover. As snowmelt signals the onset of spring for most species, this suggests that insects experience fewer resource limitations in “early” years. For plants, snow cover was not related to limited resources. Variability in weeks without partners increased with increasing snow cover for both plants and insects, while variability in low resource availability for insects increased with increasing snow cover; however, there was no significant trend for plants (Appendix S1: Table S4). This suggests that while years with heavy snow cover tend to have shorter periods of low resources, the effects of snow cover are not simple enough to constitute a proxy for the onset of spring. Snowmelt allows light to reach the soil, warms it, and permits photosynthesis as well as the release of liquid water. This meltwater likely interacts with varying amounts of rain to influence flowering and insect emergence times independently from temperature effects (Høye et al., 2013).

The consequences of the observed resource mismatches are poorly studied. However, consumer–resource mismatches will likely increase with climate change due to declining resource availability and species range shifts (Twining et al., 2022). Thus far, the strongest evidence for the deleterious effects of resource mismatches has been for trophic interactions in the Arctic, with limited evidence for any effect on mutualistic interactions (Renner & Zohner, 2018). In insects, phenological mismatches have been observed from predator–prey to host–parasitoid interactions, with negative effects on the trophic web, ecosystem services, and biological pest control (Damien & Tougeron, 2019). At Zackenberg, pollination of *Dryas* does not appear to have declined thus far, although it is quite variable between years. However, as *Dryas* is a strong competitor, it is likely that other plants will experience

declines in pollination before *Dryas* does (Cirtwill et al., 2023).

## Conclusions

Working across two regions of the Arctic, we found a general mismatch of plant–pollinator resource supply and demand over the summer. This mismatch is increasing over the years for plants, and so is variation among years for both plants and insects. At the end of the season, plants still have many options for resources, but insects do not and are unable to keep up with the rapid phenological shifts exhibited by plants. Early-flowering plants, on the other hand, may not overlap with enough pollinators to ensure adequate pollination. Further, the number of resource-poor weeks over a recent 25-year period at Zackenberg is becoming more unpredictable, potentially limiting the ability of insects to adapt to the change. We suggest that Arctic ecosystems may experience considerable disruption over the short term, where a strong resource mismatch leaves plant reproduction compromised and insects hungry, with little capacity for adaptation in an erratic and rapidly warming climate.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.


## DATA AVAILABILITY STATEMENT

Data for Malaise trap catches from Zackenberg in 2012 (Wirta et al., 2016) are available in Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert, 2007) at <https://doi.org/10.5883/DS-ZACKGM>. Data for sticky trap catches from Zackenberg in 2014 (Tiusanen et al., 2016) are available in BOLD at <https://doi.org/10.5883/DS-POLARC>. Data for Malaise trap and sticky trap catches from Cambridge Bay in 2019 (this study) are available in BOLD: <https://doi.org/10.5883/DS-CAMBRINS>. Data for individually collected insects from Zackenberg in 2016 (Cirtwill et al., 2023) are available in National Center for Biotechnology Information Sequence Read Archive under accession no. PRJNA748227 at [www.ncbi.nlm.nih.gov/bioproject/PRJNA748227](http://www.ncbi.nlm.nih.gov/bioproject/PRJNA748227). Long-term phenology data are available from Greenland Ecosystem Monitoring as follows: Cassiope phenology (Greenland Ecosystem Monitoring, 2024a), <https://doi.org/10.17897/X0MY-K003>; Dryas phenology (Greenland Ecosystem Monitoring, 2024b), <https://doi.org/10.17897/JSQ7-6355>; Papaver phenology (Greenland Ecosystem Monitoring, 2024c), <https://doi.org/10.17897/NK32-H804>; Salix phenology (Greenland Ecosystem Monitoring, 2024d), <https://doi.org/10.17897/NS7W-JT18>; Saxifraga phenology (Greenland Ecosystem Monitoring, 2024e), <https://doi.org/10.17897/YXH1-ZB25>; Silene phenology (Greenland Ecosystem Monitoring, 2024f), <https://doi.org/10.17897/6GVG-QH42>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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