Phenological sensitivity to climate across taxa and local habitats in a high-Arctic arthropod community

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Author contributions

H.S.G.: Conducted data analysis, statistics and drafted the manuscript. T.T.H.: Acquired funding, conducted data analysis and participated in drafting the manuscript. M.H.: Acquired funding and participated in drafting the manuscript. N.M.S.: Oversaw collection of the field data.

All authors participated with intellectual contributions and revised the manuscript.

Data accessibility

Arthropod monitoring data is available through the open-source GEM-database: https://data.g-e-m.dk/. The R-scripts necessary to replicate the findings of this manuscript will be made available at the time of publication in an open-access repository.

Competing Interest Statement

We have no conflict of interest to declare.

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Abstract

Arthropods respond to climate change by shifting their phenology in the spring and summer seasons. These phenological shifts are rarely uniform, and taxa show distinct variation in the direction and magnitude of phenological responses to climate drivers. To gain insights into the most climate-sensitive taxa and forecast the implications of climate change on community-wide activity and biotic interactions, it is important to understand how the climate affects the timing of activity of different taxa in local sites within a community. Here, we examined the temporal trends of arthropod phenology, and associations between arthropod phenological responses and climate predictors using arthropod monitoring data from five different habitats in high-Arctic Greenland covering a 25-year period. We found that, for most taxa, advanced arthropod phenology was associated with earlier snowmelt, and, to a lesser extent, warmer temperatures. However, the magnitude of advanced activity varied considerably between arthropod taxa and local habitats. Our study also revealed that pollinators were the most climate-sensitive group, with advanced and, in some habitats, shortened seasonal activities. Late active taxa and late snow melting habitats advanced phenology at greater magnitudes than early active taxa and early snow melting habitats. The magnitude of phenological shifts of arthropod taxa was dependent on habitat, highlighting the substantial spatial variation in phenological responses. Overall, our results demonstrate that high-Arctic arthropods are capable of tracking local climate drivers of phenology well, but the phenological responses of arthropod taxa to global climate change are complex, and community-wide trends may mask the variation in direction and magnitude of phenological shifts in different taxa and locally adapted populations.

Keywords: arthropods, climate change, phenology, high-Arctic, snowmelt, temperature, long-term monitoring, phenological mismatch

Introduction

Phenology in a global change context

The globe is undergoing unprecedented climatic changes, which have implications for ecosystems across the world. Numerous ecological changes have been associated with global warming (Halsch et al., 2021; Parmesan, 2006; Walther et al., 2002), but the most reported effects are shifts in phenological events (Thackeray et al., 2016; Visser & Both, 2005). Long-term studies report advancements of arthropod phenological events in response to warming (Menzel et al., 2006; Parmesan & Yohe, 2003; Post et al., 2018; Root et al., 2003; Vitasse et al., 2021). For example, terrestrial insects in European alpine (Vitasse et al., 2021) and north-temperate areas (Cohen et al., 2018) have shown advanced emergence of 6.0 and 4.15 days per decade, respectively. While most studies on phenological change are from temperate regions of Europe and North America (Cohen et al., 2018), arthropods in the Arctic are experiencing even greater warming (AMAP, 2017; IPCC, 2021; Rantanen et al., 2022). Due to the short arctic growing seasons, arthropods begin their active season as soon as temperatures become favourable in the spring (Danks, 2004). Consequently, small changes in temperatures during the growing season can have a significant impact on the phenology of arctic arthropods, making them particularly sensitive to climate change (Bolduc et al., 2013; Høye, Post, Meltofte, Schmidt, et al., 2007; Post et al., 2018; Tulp & Schekkerman, 2008). This is especially interesting because arthropods dominate in animal species richness and abundance in the Arctic and play important roles in ecosystem functioning (Barrio et al., 2017; Hodkinson, 2013; Hodkinson & Coulson, 2004).

Variation in the direction and magnitude of phenological change

Arthropod taxa can exhibit greatly varying phenological sensitivities to environmental changes, which may depend on specific life history traits such as voltinism and body size (Diamond et al., 2011; Gillespie et al., 2017; Pacifici et al., 2017). Univoltine species tend to advance and shorten their phenology compared to multivoltine species that often delay their late season phenology (Glazaczow et al., 2016). Temperature sensitivity among species can also explain differential phenological responses (Buckley, 2022; Thackeray et al., 2016), where early active species advance their spring emergence and late active species delay their fall activity (Bartomeus et al., 2011; Brooks et al., 2017; Gallinat et al., 2015; Kharouba et al., 2014). Furthermore, differences in phenological responses can be associated with greater sensitivity to environmental cues that are not affected by climate change, such as photoperiod (Bale et al., 2002; Danks, 2007). The extent of phenological shifts is also highly site-specific (Chmura et al., 2019; Kharouba et al., 2014; Primack et al., 2009), especially in Arctic snow-dominated environments characterized by topographic heterogeneity creating pronounced spatial variation in timing of arthropod emergence (Kankaanpää et al., 2018). Temperature and particularly timing of snowmelt are important environmental drivers of interannual variation in Arctic arthropod spring emergence (Høye & Forchhammer, 2008). However, predicting arthropod population- and community-level responses to climate change remains a challenge, especially when multiple environmental drivers act in concert to determine arthropod phenology.

Heterogeneous phenological shifts can reshape a community

Arthropod populations in habitats with early snowmelt emerge earlier than those in late snow melting habitats. This local scale emergence affects the duration of activity for the entire arthropod community (Phillimore et al., 2010; Roy et al., 2015) and defines the community phenological niche, which is the overall temporal occupancy of individual taxa and population phenology in a season (Post, 2019). If species and populations differ in their sensitivity to climate drivers (Brooks et al., 2017; Prevey et al., 2017; Stalhandske et al., 2014; Tyukmaeva et al., 2020; Valtonen et al., 2014), warmer seasons could lead to rapid advanced emergence in sites with early snowmelt compared to sites with late snowmelt or vice versa. As a result, overlap in duration of activity could increase or shorten, which ultimately affects the temporal synchronization of arthropod community activity and thus the community phenological niche breadth (Post, 2019). For instance, dominant plant species at Zackenberg have shown reduced community flowering because late flowering populations advanced their flowering time faster than early flowering populations (Høye et al., 2013). It remains unclear how the phenological niche breath of arthropod taxa is affected by a changing environment (But see Altermatt, 2012; Gutierrez & Wilson, 2021; Phillimore et al., 2010; Roy et al., 2015), and if the total duration of arthropod community activity season has changed. Changes in arthropod community activity can lead to a temporal mismatch between trophic levels, such as plant-pollinator or predator-prey interactions (Pyke et al., 2016; Reneerkens et al., 2016; Visser & Both, 2005), which could have serious consequences for ecosystem functioning (Samplonius et al., 2021). Therefore, understanding how rates of phenological change vary among taxa in the face of increasing climatic variability is crucial.

Comprehensive long-term capture data is essential to gain insights into the impact of climate change on the phenology of arthropods at the community level (Coulson et al., 2014; Gillespie et al., 2020; Hodkinson, 2013; Inouye, 2022). The arthropod monitoring program at Zackenberg, Northeast Greenland has provided long-term standardized collection data since 1996 (Schmidt et al., 2019), offering a unique opportunity to investigate the ecological impacts of climate change. Here, we used this data to investigate the variation in phenological responses of terrestrial and semiaquatic arthropods from different local habitats to the timing of snowmelt and temperature using abundance data from weekly trappings. Our objective was threefold. First, we aimed to provide an assessment of the temporal dynamics on arthropod phenology for all available family-habitat combinations. In accordance with previous short-term studies on phenological responses of arthropods (Høye, Post, Meltofte, & Schmidt, 2007), we expected temporal advancements in phenological responses and prolonged activity periods of most arthropod taxa. Second, we aimed to evaluate the relative contribution of snowmelt timing and temperature on the phenological responses (peak activity and duration of activity). We expected the variation in phenology of arthropods to be driven by timing of snowmelt rather than temperature, but early active taxa and taxa in early snow melting habitats were expected to respond more strongly to temperature than late active taxa. Third, we aimed to assess whether phenological responses to climate variation differed among taxa and habitats to derive knowledge on the variation in phenological sensitivity to climate variables within the community. We expected the climate sensitivity of early season taxa and populations to be greater than the sensitivity of late season taxa and populations, resulting in longer overall activity seasons at the community level.

Materials and methods

Study site and arthropod sampling

Arthropods were collected at the Zackenberg Research Station, located in high-Arctic Northeast Greenland (74°28’ N; 20°34’ W). The collection of arthropods was conducted from 1996 to 2020 through the Greenland Ecosystem Monitoring Program and included seven different plots. Plot 2 - 7 consisted of eight yellow pitfall traps (1997 to 2006) later reduced to four pitfall traps (1996 and 2007 to 2020) and plot 1 included four window traps where specifically limnitic insect emergence and aerial activity was monitored. The traps opened at snowmelt in late May to early June, operated during the growing season and ended by 1st September, which often coincided with freeze up. The traps were emptied weekly at fixed dates, unless the weather prohibited handling the samples in which case the traps were emptied the following day. After collection, specimens were stored in 75% ethanol, later changed to 96% ethanol, and transported to Denmark where the arthropods were sorted by the technicians at the Department of Ecoscience at Aarhus University to the family level for spiders and most insects, superfamily level for Aphidoidea, Chalcidoidea and Coccoidea, and subclass for other arthropods, and subsequently counted. The data is publicly available at data.g-e-m.dk. To enable comparison of arthropod capture numbers between years, we focused on arthropod data from only June, July and August. Further, weekly abundance counts for each arthropod group were standardized by calculating individuals per trap per day for each plot.

The plots represented pond (Plot 1), wet fen (Plot 2), mesic heath (Plots 3 and 4), snow bed (Plot 6) and arid heath (Plots 5 and 7) habitats where each habitat differed in plant community composition, soil moisture and the timing of snowmelt. The wet fen habitat was primarily dominated by mosses and grasses and has high soil moisture and early snowmelt. The mesic heath habitat was dominated by lichens, *Cassiope tetragona*, *Dryas* sp. and *Salix arctica* and typically had snowmelt two weeks later than the fen and arid heath area. The arid heath habitat was composed primarily of lichens, *Dryas* sp. and grasses, had relatively low soil moisture and experienced early snowmelt. A small islet in a shallow pond represented the pond habitat (Schmidt et al., 2019).

Our analysis focused on the most abundant arthropod taxa within the community, which we defined as taxa for which at least 50 individuals were caught per plot in a season. The arthropod taxa that were sufficiently represented based on this criterion were soil mites (Acari), collembolans, spiders and the insect orders; Diptera, Hymenoptera, Hemiptera and Lepidoptera (see Supporting Information S1). Some traps showed major spikes in the number of mites caught, which was linked to the capture of mite-infested bumblebees in a trap thus resulting in the capture of several hundred mites. These spike numbers were changed to the average of the other traps in a plot from identical capture periods (see Supporting Information S1). An identical problem with large spikes in abundance estimates was found for the spider family Lycosidae caused by the capture of many juveniles along with female individuals. This was managed by changing spike numbers to the average of the other traps in a plot from the same capture period. Another spider family; Linyphiidae exhibited deviations in annual adult activity patterns causing problems when generating the phenological curves as bimodal distributions were found for some years. The different species of spiders within Linyphiidae may overwinter in different life stages causing bimodal distributions in abundance estimates across a season. A distinction between juveniles and adults was not made in the data for all years and so, abundance estimates for Linyphiidae could not be corrected. However, it was carefully considered if satisfying phenological curves could be generated across a season for each year and thus, it was regarded as appropriate to keep this family in the study (see Supporting Information S1). This approach was identical to the approach taken in Høye et al. (2007).

Climate variables

We selected temperature and snowmelt timing as climate variables to determine the effect of climate on emergence phenology as these variables previously was found to influence the timing of arthropod emergence (Høye & Forchhammer, 2008; Kankaanpää et al., 2018). A meteorological station located centrally and within 600 m from all plots operated through the entire study period and measured soil (0-, 5-, and 10-cm depth) and air (2 m above the ground) temperature on an hourly basis. Air temperature, rather than soil temperature, was chosen to explain temperature variations in the activity levels of arthropods in this study (please see Supporting Information S2 for a detailed justification of the choice of air temperature). Timing of snowmelt was estimated as the date by which less than 10 cm of snow was measured by an automatic ultrasonic snow depth sensor installed at the meteorological station (Skov, 2020). Years 2009, 2013 and 2019 had limited snow accumulation resulting in the estimation of very early snow melting dates. As these years became obvious outliers, we used soil temperature data (averaged from 0, 5 and 10 cm depth) to estimate more reliable snow melting dates for the years 2009, 2013 and 2019 as well as 1996 where no snow depth data was available, following the method in Rixen et al. (2022). We identified the time period towards the end of the winter when ground temperatures were stable near 0 ºC and subsequently started fluctuating when the snow cover disappeared (defined as the zero-curtain window). From this, we defined the date of snowmelt as when the mean daily soil temperature rose above +1 ºC after a period with diurnal fluctuations of less than 2 K and mean daily temperatures between -1 ºC and 1 ºC (Rixen et al., 2022).

This also enabled us to estimate a snow melt day for the year 1996 where no snow depth data was available. The correlation between day of snowmelt estimated from the snow depth sensor and soil temperature data can be seen in Figure S2.1.

We used hourly data on air temperature measured at 2 m height at the Zackenberg climate station (Downloaded: 13th January 2022). We then compiled temperature predictors for each phenological event separately. Temperature in the period before emergence is closely related to arthropod development (Gillooly et al., 2002) and may thus be a good predictor of adult arthropod emergence. Therefore, we first calculated the temperature predictor as temperatures through the 30 days prior to a phenological event, so as not to use temperature values largely occurring after the phenological event to predict the response. This was done by calculating the mean date of the phenological event across years for each family and habitat combination and then extracting the mean temperature during the 30 days prior to this date for each year.

Quantifying phenology

Annual onset, peak and end of emergence of arthropod taxa across each habitat and each year were calculated using generalized additive modelling (GAM). We predicted a non-linear phenological development across each season, however, as the shape was unknown, it was ideal to take advantage of the partial smoothing method in GAMs to model the seasonal development in capture rates (Guisan et al., 2002). In addition, GAMs provide fairly accurate estimations of species phenology despite gaps in the distribution due to varying sample size (Moussus et al., 2010). Curves of arthropod abundance were fit across a season using GAM, assuming a poisson distribution with k = 4 (basis dimensions) to ensure appropriate smoothing and a log link function. We used the package '*mgcv'* version 1.8-40 to fit the GAMs (Wood, 2017). Some taxa had low capture numbers in some plots in some years, and consequently, we restricted our analyses to years and plots where at least 50 individuals of a given taxa were caught. Also, the three phenological events should be possible to calculate (the taxa must be present in at least two weeks) and a sensible seasonal curve must be generated. Annual onset, peak and end of the activity season were then calculated as the day at which 10%, 50% and 90% of the accumulated abundance (area under the curve) was reached, respectively (Figure 1). The duration of the activity period was estimated as the number of days between onset and end of the activity season.

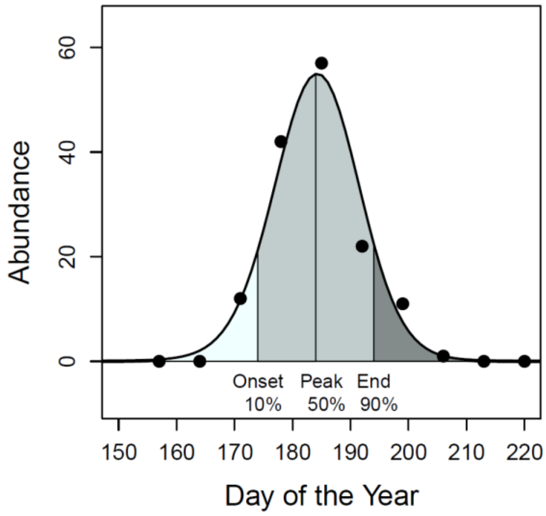

Figure 1– Example of fitting phenological curves using GAM (Poisson family) for abundance data of arthropod taxa to estimate onset, peak and end of emergence. Data from Culicidae in plot 1 in year 2019.

Statistical analyses

Temporal trends in climate and arthropod phenology

Temporal trends in air temperature and timing of snowmelt were calculated as the slope of the regression against year as a continuous predictor using simple linear regression. Additionally, linear regression was used to calculate the temporal trends in the onset, peak and end of arthropod activity as the slope of the regression against year. This was done for each taxon for which it was possible to estimate phenology of the activity period for at least five years across the time series data. Data for analysis of temporal trends was sufficient for 15 taxa (full list available in Supplementary Information S1). To test if temporal trends of arthropod phenology differed between taxa, functional group and habitat, we used multiple regression with each individual phenological event as the response variable and year, plot and taxa or functional group as predictor variables. When functional groups were compared, we added random intercepts for taxa to account for nonindependence of observations among taxa within functional groups. In addition, a year-plot interaction was included to allow for the year effect to vary among sites. The functional groups were defined as; pollinators (Diptera families and Nymphalidae), predators (Aranae families), herbivores (Hemiptera families), parasitoids (Hymenoptera families) and decomposers (Acari and Collembola) (Table S1.1).

Correlation between climate variables

The climate variables included in this study (timing of snowmelt and air temperature) may be highly correlated. An appropriate correlation analysis between climate variables was not feasible because specific air temperature predictor values were calculated for the individual average emergence date for each arthropod taxa in each plot. To appropriately examine a potential issue of multicollinearity, variance inflation factors (VIFs) were derived using the R package '*car*' version 3.1-1 for timing of snowmelt and temperature in all family and plot combinations for each phenological event (Zuur et al., 2010). VIF values were also derived for timing of snowmelt and soil temperature measured at the same climate station at a depth of 0

– 10 cm to compare the correlation of the two temperature variables with timing of snowmelt. We used a threshold criterion of 10 such that predictors with values above a VIF > 10 were considered contributing greatly to multicollinearity.

Effect of environmental predictors on phenological events

To determine the effect of snowmelt and temperature on arthropod phenology, we used timing of snowmelt and temperature as explanatory variables of each phenological response variable while accounting for the random slope and intercept parameters of arthropod taxa and plot in linear mixed models (LMM) using the '*lme4'* R package version 1.1-31 (Bates et al., 2015). As we use taxa and plot specific estimates of the temperature predictor, we separated the within-subject effects from between-subject effects that we cannot account for in the mixed models by implementing within-subject centering in the model (van de Pol & Wright, 2009). This is done by subtracting an average temperature value for each arthropod taxa and plot combination from the specific temperature value for each arthropod taxa and plot combination. This new temperature predictor derived is then included as a fixed effect in the LMM that expresses the within and between arthropod taxa and plot temperature variation component. We also detrended the climate variables by adding year as a covariate in the model. Interactions between climate variables and plot, taxon and functional group was included in the model. A significant interaction term indicated that the slope of the linear relationship between phenological response and climate differed between taxa, functional group or plot.

To determine the differences in phenology of individual taxa among plots, multiple linear regression analysis with timing of snowmelt and temperature as predictors and plot as a fixed effect was performed. Plot was included as a categorical variable and to make the desired comparisons of slopes between plots, customized contrasts were used. We also tested all possible interactions between plots and climate variables. We did not include a random intercept for year, as there was no within-year replication of the site-specific environmental variables. A significant interaction term indicated that the slope of the linear relationship between a phenological response and climate variable differed among habitats. The best models were selected based on ANOVA comparison between nested models. The chosen model is clearly indicated for each analysis in tables with results in the supplementary information.

Results

Warmer summers but high interannual variation in climate variables

Snowmelt timing and spring air temperature has not changed significantly during the 25-year study period at Zackenberg (Snowmelt: $R^2 = 0.01$, $F_{1,23} = 0.25$, $P = 0.62$, -1.6 days earlier per decade; Average spring air temperature: $R^2 = 0.02$, $F_{1,23} = 0.52$, $P = 0.48$, 0.04 ºC per decade), but show increasing variation since the mid-2000s (Figure 2). However, summer air temperature has significantly increased by 0.6 ± 0.3 ºC per decade during the study period (average summer air temperature: $R^2 = 0.16$, $F_{1,23} = 4.49$, $P = 0.045$). A low level of multicollinearity between timing of snowmelt and air temperature was found (see Supplementary Information S4).

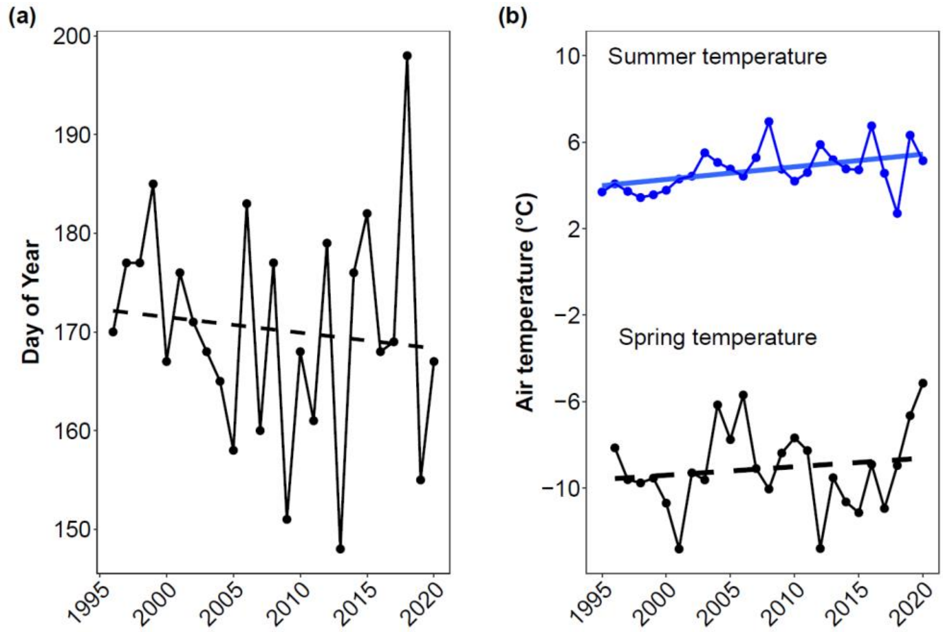

Figure 2 – Interannual variation and trends of (a) timing of snowmelt and (b) average seasonal air temperature for spring (April, May) and summer (June, July, August) at Zackenberg, Greenland during the study period of 1996 - 2020. Only summer air temperature changed significantly during the study period.

The phenological niche of arthropods differ among taxa and habitats

The timing of activity varied widely among arthropod taxa and habitats (Figure 3). Families of pollinators are active early and late in the season. As an example, Chironomidae is present early in the season compared to the late emerging Phoridae. The parasitoids and herbivores are active late in the season with considerable variation between habitats. Within Ichneumonidae, the peak activity occurs on average on day 201 in the wet fen with early snowmelt as opposed to day 220 in the mesic heath with late snowmelt. A longer duration of the activity season is predominant for decomposers and predators.

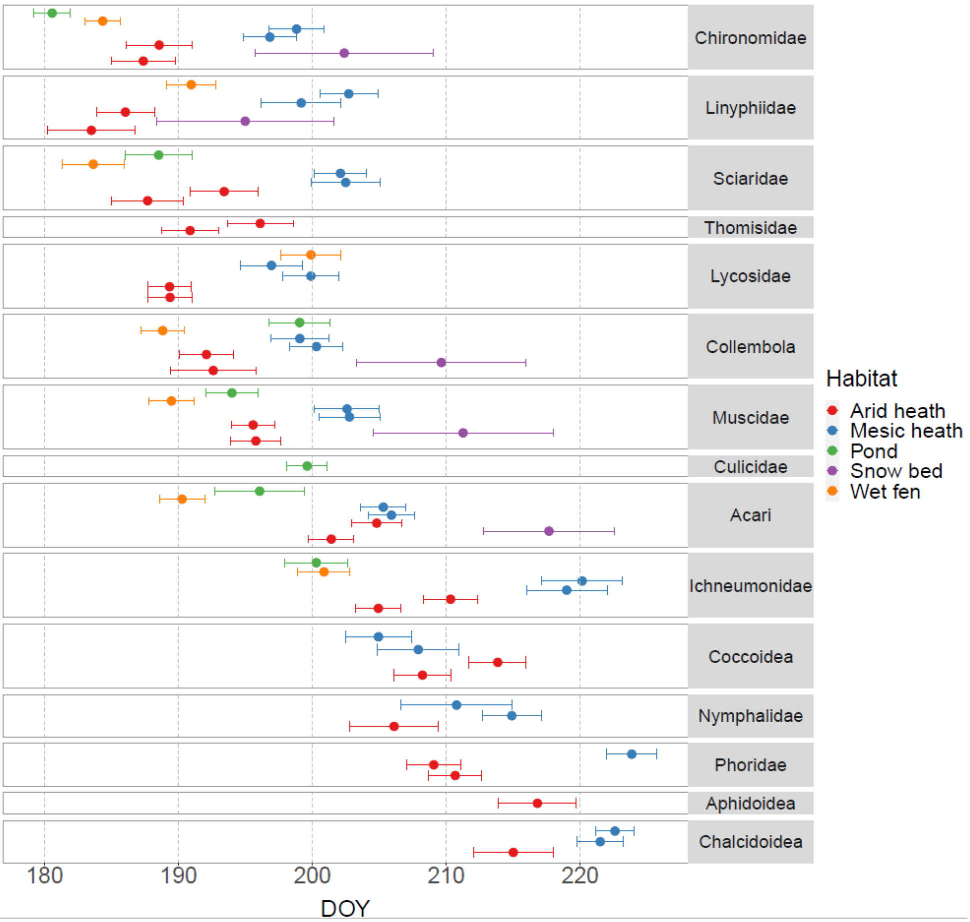

Figure 3 – The average peak phenological event (when 50% of the season capture was reached) of all taxa across multiple years represented by at least 50 individuals per season for each plot and habitat (day of year 140 – 240). Associated error bars are given. The arthropods are listed in order of activity such that the top families are active earlier than the below families. The associated error bars indicate the standard error of the mean. Estimations of all phenological events are available in Supporting Information.

Temporal advancements in community phenology but weak overall directional shift

Consistent with the lack of temporal trends in climate variables, there were limited phenological shifts across time (only 18% of all cases showed a significant shift across time) and significant phenological shifts were almost entirely advancements (Figure S3.1). Of all the family and plot combinations exhibiting a significant phenological shift, 51% (20/39) showed a significant change in the onset of emergence. Only 23% (9/39) and 26% (10/39) of the family and plot combinations showed a significant shift in the peak and end of activity, respectively. The average community peak phenology advanced by 2.6 ± 0.4 days per decade. There was no significant change in the community duration of activity. Multiple regression analysis revealed a significant difference in the rate of temporal advancements among arthropod taxa (peak and duration of activity) and habitats (only for duration of activity) (Table S3.2). When merging taxa in functional groups, there was a significant difference among groups in the temporal trends of the peak activity and duration of activity (see Supporting Information S3). Predators had significantly extended the duration of their activity by 3.9 ± 1.9 days per decade. The pollinators shifted their phenology considerably in the wet fen habitat with peak phenology advancing 6.8 ± 1.3 days per decade on average and Sciaridae advancing the most (advancing 10.2 ± 2.7 days per decade).

Advanced arthropod phenology with earlier snowmelt and increasing temperatures

We only present results of the effect of climate on the peak and duration (difference between onset and end of activity) of activity to facilitate a better understanding of the results.

The timing of snowmelt was a better predictor of arthropod phenology than air temperature, as temperature explained less variation in phenological events (see Supporting Information S4). After detrending the time series by year, the significance of the linear temperature-phenology relationship diminished, while most linear phenology-snowmelt relationships persisted. Most taxa exhibited a significant response of peak phenology to timing of snowmelt, temperature or both, except Aphidoidea and Thomisidae (Table S5.1). The most common trend was advanced phenology in response to earlier snowmelt and increasing temperature (Figure 4, 5 & Table S5.1). The average community phenology advanced by 0.35 ± 0.06 days per earlier snowmelt day. In response to temperature, average community phenology advanced by 1.11 ± 0.51 days per 1 °C increase (Table S5.3). Most taxa responded to snowmelt and temperature by either extending or shortening the duration of activity (Figure 4, 5 & Table S5.2). Shifts in duration of activity was only significant in response to snowmelt with a slight increase of -0.12 ± 0.05 days per advanced snowmelt day, but substantial variation in duration of activity in response to climate among taxa and habitat was found (Table S5.3). 12 out of 15 taxa showed a significant positive effect of snowmelt timing on peak phenology (Table S5.1), meaning that these taxa advanced their phenology in response to timing of snowmelt. Seven taxa showed a significant negative effect of air temperature (results not shown), thereby advancing their peak phenology in warmer years. However, after detrending the time series data, the significance of the linear relationships between arthropod phenology and temperature decreased such that five taxa showed a significant effect of air temperature (Table S5.1).

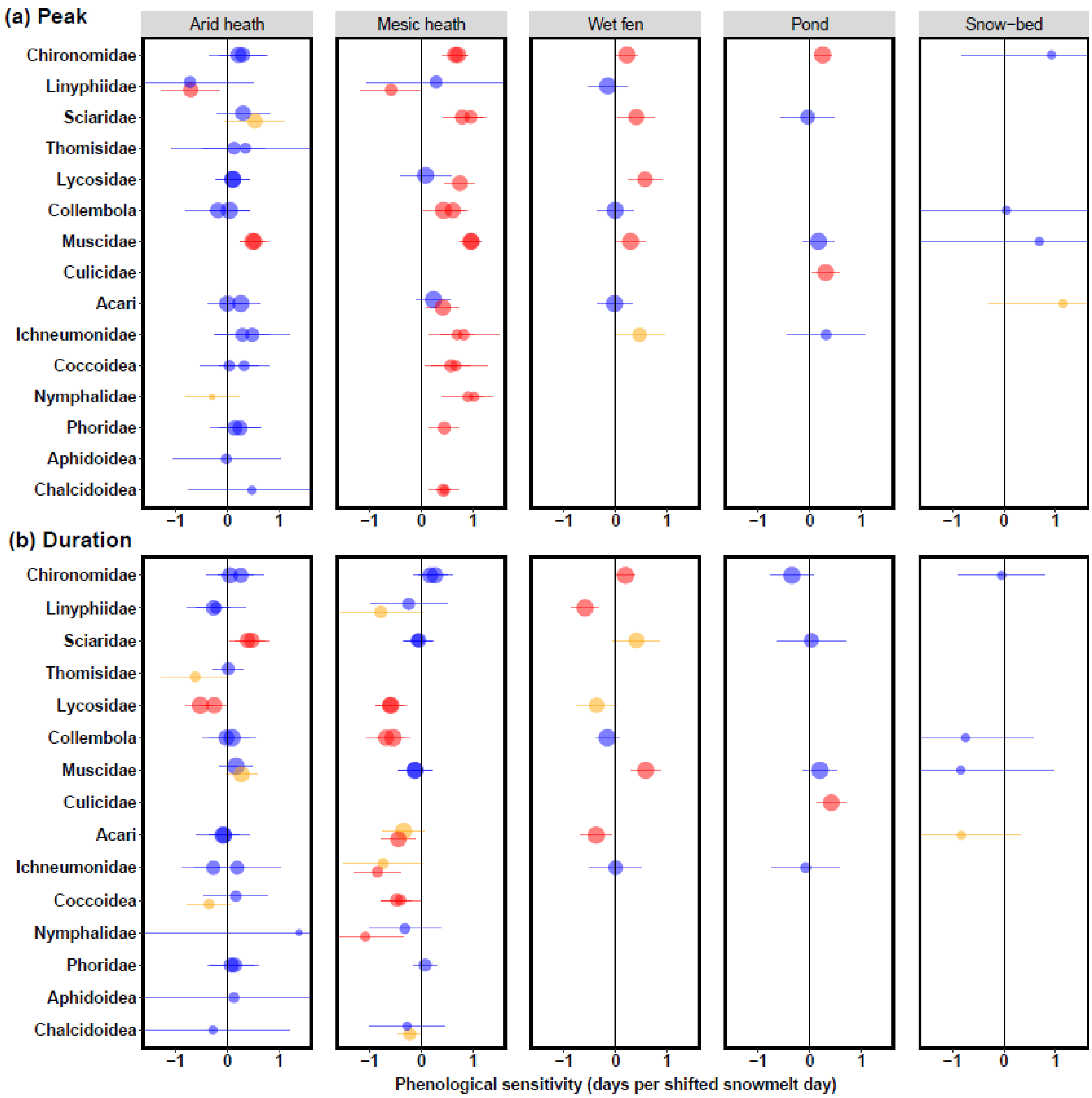

Figure 4 – The phenological sensitivity (days per shifted snowmelt day) in (A) peak and (B) duration of the activity season for taxa in each plot within habitats with each panel representing the different habitats where arthropods were collected. The model is controlled for the effect of temperature. The arthropods are listed in order of activity such that the top families are active earlier than the below families. The size of each point represents the number of observations in each family and plot combination. Significant shifts are represented in red (P ≤ 0.05), marginally significant shifts in orange (0.05 < P ≤ 0.10) and nonsignificant shifts in blue (P > 0.05). We refer to trends as significant when the 95% confidence interval (CI) for a parameter of the fitted models did not overlap zero. The associated error bars indicate the 95% CI's. To ease comparison, all panels are equally scaled causing a cut-off of CI's. In the mesic heath and arid heath panels, two points are shown indicating the two plots in these habitats. If points have different significance levels, the points are slightly separated to ease visibility.

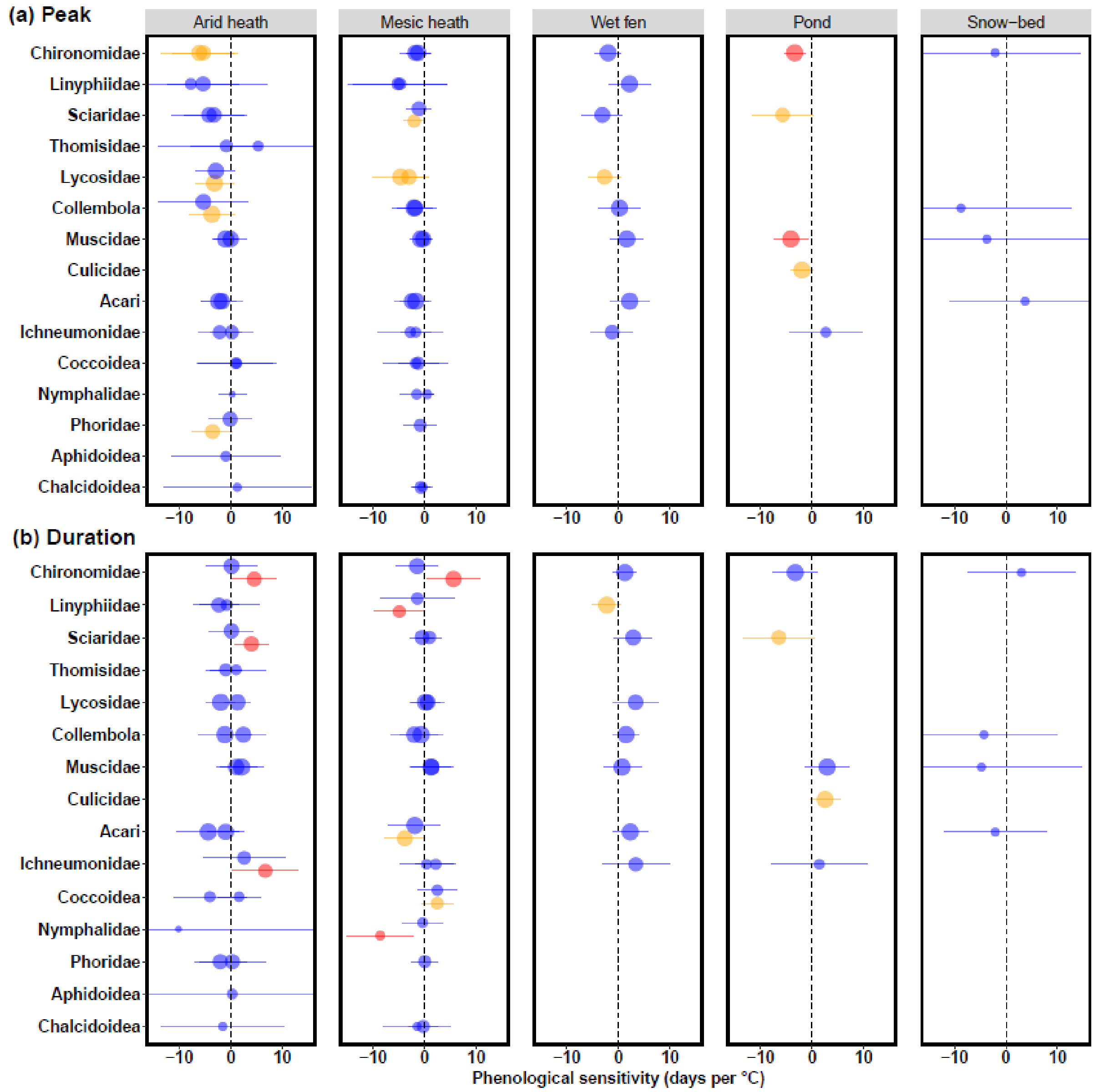

Figure 5 – The phenological sensitivity (days per ºC) in (A) peak and (B) duration of the activity season for taxa in each plot with each panel representing the different habitats where arthropods were collected. The model is controlled for the effect of snowmelt. The arthropods are listed in order of activity such that the top families are active earlier than the below families. The size of each point represents the number of observations in each family and plot combination. Significant shifts are represented in red (P ≤ 0.05), marginally significant shifts in orange (0.05 < P ≤ 0.10) and nonsignificant shifts in blue (P > 0.05). We refer to trends as significant when the 95% confidence interval (CI) for a parameter of the fitted models did not overlap zero. The associated error bars indicate the 95% CI's. To ease comparison, all panels are equally scaled causing a cut-off of CI's. In the mesic heath and arid heath panels, two points are shown indicating the two plots in these habitats. If points have different significance levels, the points are slightly separated to ease visibility.

Differential phenological responses among functional groups and early vs late active taxa

Taxa within functional groups responded with the same directional change in phenology to climate variables, even though the rate of change varied for some taxa (see Supporting Information S7 for details). When comparing slopes between functional groups, pollinators and parasitoids was found to advance their phenology (Pollinators, slope: 0.52 ± 0.07; Parasitoids, slope: 0.55 ± 0.13) to a greater extent in response to earlier snowmelt compared to predators and decomposers (Predators, slope: 0.11 ± 0.08; Decomposers, slope: 0.25 ± 0.08) (Table S6.1). Predators and decomposers extended the duration of their activity strongly in response to earlier snowmelt (Predators, slope: -0.48 ± 0.07; Decomposers, slope: -0.30 ± 0.06) compared to all other functional groups. Pollinators did not show significant changes in duration of activity in response to snowmelt (Table S6.2), but considerable variation among families and habitats was found in this group (Figure 4, Table S5.2 & S6.2). As temperatures increased, the peak activity of pollinators became substantially earlier (Pollinators, slope: -1.57 ± 0.52). There was no significant change in the duration of activity of functional groups in response to temperature (Table S6.2).

In response to earlier snowmelt, late active taxa advanced their peak phenology by 0.47 ± 0.07 days per day earlier snowmelt whereas early active taxa advanced their peak phenology by only 0.26 ± 0.07 days per day earlier snowmelt (Table S6.3, Figure S6.1). In response to temperature, early active taxa advanced their peak phenology by -1.71 ± 0.62 days per 1 ^{o}C increase, while late active taxa did not advance their phenology, however, the slopes were not significantly different (Table S6.3). Early active taxa extended their activity period with 0.21 ± 0.03 days per day earlier snowmelt, while late active taxa did not change the period of activity (Slope: 0.01 ± 0.04).

The random effect of the interaction between plot and arthropod taxa explained up to 73% of the total variation in phenological responses to climate variables (not shown but see Supporting Information S7). Thus, a detailed investigation of the spatial variation in phenological responses to climate within each taxon separately was highly relevant.

Spatial variation in phenological responses to climate

We found strong support for spatial variation in arthropod phenology indicated by a significant effect of habitat as explanatory variable for taxa found at different sites (Figure 4 & 5, Table S7.6 & S7.7). Populations from late snow melting mesic heath and snow bed habitats showed more rapid peak phenological shifts in response to earlier snowmelt than populations from early snow melting arid heath and wet fen habitats (Figure 4). Whether taxa shortened or extended their activity period in response to snowmelt and temperature was dependent on habitat for families of pollinators (Figure 4 & 5, Table S5.2).

Spatial variation in phenological responses to snowmelt in particular, but also temperature, were pronounced for families of pollinators. For Chironomidae, Muscidae, Phoridae and Sciaridae, there were stronger phenological responses in late compared to early snow melting habitats (Table S5.1). Muscidae, Chironomidae and Phoridae advanced peak phenology at a greater rate in response to earlier snowmelt in late snow melting mesic heath habitats than in the early snow melting arid heath and wet fen habitats. In addition, Muscidae shortened the duration of activity in the wet fen habitat (Table S5.2). Families in the pond habitat advanced their phenology at fast rates in response to temperature, e.g., Muscidae peak phenology was 4.63 ± 1.47 days earlier per 1 °C, which was significantly greater than in other habitats (Table S5.1). In addition, Sciaridae experienced shortened activity periods in the pond habitat in response to warmer summers (Table S5.2). Culicidae was also active for shorter periods in the pond habitat in response to earlier snowmelt (Table S5.2, Figure 4). Duration shortened in warmer years and years with earlier snowmelt because the end of activity advanced at faster rates than onset to increasing temperatures and advancing snowmelt (Figure S7.1, S7.2).

For Herbivores, Parasitoids and Decomposers, most families extended their activity periods in response to earlier snowmelt in the late snow melting mesic heath habitat, which was not found in the early snow melting arid heath habitat (Table S5.2). Additionally, the significance of slopes in response to climate variables was greater in the mesic heath habitat (Figure 4, 5), but the statistical analysis did not find any significant differences in rates of advanced peak phenology between habitats (except for Coccoidea advancing peak phenology more in mesic heath habitats) (Table S5.1). The two dominant predator families; Lycosidae and Linyphiidae, extended their activity periods in all habitats in response to warmer summers and earlier snowmelt, but Linyphiidae delayed peak phenology in response to earlier snowmelt whereas Lycosidae advanced peak phenology (Figure 4).

Discussion

The Zackenberg area of Northeast Greenland has experienced warmer summers but also large interannual variation in timing of snowmelt and temperature in the past 25 years. Consistent with a lack of directional change in climate conditions, the arthropod community phenology showed only weak advancements through the study period, and variation amongst taxa and habitats in the rate of temporal phenological advancements were large. Timing of snowmelt was a key driver of arthropod phenology, which was particularly evident following detrending of the phenological time series where the temperature-phenology relationship was markedly reduced but the snowmelt-phenology relationship persisted. We found that while most arthropod taxa in this high-Arctic community were able to track climate change well, the climate-associated phenological shifts varied among taxa and populations in different habitat types. Specifically, pollinators demonstrated rapid phenological advancements and, in some habitats, shortened seasonal activity in response to earlier snowmelt and warmer summers, while predators responded by extending their seasonal activity. We were able to show that late active taxa and populations in late snow melting habitats advanced their phenology more in response to earlier snowmelt than early active taxa and populations in early snow melting habitats. Our results indicate that the community-wide trends may mask the variation in direction and magnitude of phenological shifts in different taxa and locally adapted populations, thus emphasizing the idiosyncratic nature of individual taxa and population responses to climate change. These findings further highlight the substantial heterogeneity in phenological responses to climate change in arthropods and could facilitate a mismatch in the seasonal timing of interacting organisms.

Our study highlights the importance of timing of snowmelt as an environmental predictor of arthropod phenology, which could be a response to the large interannual variation in snowmelt patterns (Høye, Post, Meltofte, & Schmidt, 2007; Pedersen et al., 2016). Importantly, the reduced temperature-phenology relationship and the persisting snowmelt-phenology relationship found after detrending by year shows that multiple drivers of phenology may exist and accentuates that the importance of climate variables can vary depending on region. Thus, for predicting Arctic arthropod phenological responses to climate change, incorporating information on timing of snowmelt, other than temperature, is important, which is also suggested from other cold region arthropod phenology studies (Kankaanpää et al., 2018; Leingartner et al., 2014; Mortensen et al., 2016; Ovaskainen et al., 2013).

We found a greater phenological sensitivity of arthropod taxa to timing of snowmelt in late compared to early snow melting habitats demonstrating local spatial variation in the strength of arthropod phenological responses to timing of snowmelt. Tundra environments can create substantial spatial variation in arthropod emergence and abundance across small spatial scales because of local differences in timing of snowmelt (Høye & Forchhammer, 2008; Kankaanpää et al., 2018; Koltz, Schmidt, et al., 2018) and temperature at the soil surface due to variation in vegetation and snow cover (For example, Bjorkman et al., 2020; Elmendorf et al., 2012). In an environment with inherently high spatial variability (Kankaanpää et al., 2018) combined with large interannual variation in climate variables, the environmental controls of phenology as well as the rate of phenological responses of arthropod taxa to climate may vary substantially. Thus, populations of taxa from late snow melting habitats may be more plastic allowing them to track timing of snowmelt. Conversely, it can be a disadvantage for taxa in early snow melting habitats to track timing of snowmelt as the interannual variation in snowmelt increases the possibility of taxa being exposed to unfavourable environmental conditions (Regan & Sheldon, 2023; Rixen et al., 2022), such as exposure to freezing. This could explain the strong responses of populations of taxa in late snow melting habitats to timing of snowmelt compared to populations in early snow melting habitats. These results highlight the implications of failing to capture the spatial variation in phenological responses to climate change as it may encompass under- or overestimating the vulnerability of arthropod communities to climate warming because the sensitivity of taxa to climate change is highly habitat dependent.

We find extended activity periods for most arthropod taxa in the late snow melting mesic heath habitat, which could indicate that arthropod taxa attain a wider phenological niche in early snow melting years. Conversely, some taxa from early snow melting habitats experienced shorter activity periods and thus a reduction in their phenological niche. We cannot reject that the coarse taxonomic resolution in this study masks information on species composition between plots. Different arthropod species and populations vary in their phenology within a community. Hence, the site-specific phenologies could be attributed different species compositions in early and late snow melting sites (Bowden & Buddle, 2010; Hansen et al., 2016). Previous studies from Zackenberg have demonstrated different species assemblages of muscid flies and spiders between habitats (Bowden et al., 2018; Loboda et al., 2018). Thus, the spatial variation in phenological shifts could be due to interspecific variation in climatic sensitivity such that late active species respond more rapidly to warmer seasons. The likelihood of an underlying taxonomic variability in phenological sensitivity of taxa to climate change in our study may entail a conservative estimate of the magnitude of phenological shifts in response to a changing climate and we could be underestimating the true ecological effects of a changing climate.

Our findings document varying rates of phenological responses among functional groups to environmental cues. Pollinator and parasitoid peak phenology were earlier in years with earlier snowmelt than peak phenology of predators. Some families of pollinators had shorter activity periods in years with early snowmelt, though this trend was highly habitat dependent. The phenology of herbivores and decomposers were not as strongly related to climate variables compared to other functional groups suggesting that other abiotic or biotic cues may drive the phenology of these taxa. These results confirm that most arthropod taxa in this high-Arctic community are able to track environmental changes, but also highlights the variation in climate-associated phenological responses among functional groups. This strongly increases the complexity of phenological impacts in a community context. Ultimately, this may entail major reorganization in the arthropod community, which could have considerable impacts on the way organisms interact within ecological networks (Walther, 2010). For example, earlier and shorter pollinator activity periods could temporally decouple them from flowering host plants leading to a reduction in pollination services (Pyke et al., 2016, Schmidt et al., 2016), and extended activity of predators could influence top-down control in a food web (Koltz, Classen, et al., 2018). Further, as the community-level activity of arthropods at Zackenberg has advanced in the past 25 years, the risk of trophic mismatch between breeding Arctic shorebirds' insectivorous chicks and the availability of arthropod prey increases (Both et al., 2009; Reneerkens et al., 2016). Meanwhile, the host-parasitoid interaction could be kept intact as parasitoids seem to be following their hosts (families of predators and pollinators). We do suspect that the different responses of arthropod taxa to climate in this study could reflect their life history strategies (Buckley, 2022; Gallinat et al., 2015). As temperatures rise, the growth rate of insects increase (Chaves et al., 2015), and univoltine insects, that dominate in the Arctic (Høye et al., 2020), are therefore expected to advance their fall senescence. On the other hand, invertebrate species may extend their activity seasons by producing additional generations in response to longer growing seasons (Altermatt, 2010; Braune et al., 2008; Kerr et al., 2020; Roy & Sparks, 2000), hence the shorter activity seasons we find for some taxa in warmer years. We also found that the predators are rapidly extending the duration of their activity in response to a warmer climate. This trend could be attributed climate warming facilitating the production of additional generations of spider species, which has been documented for the wolf spider *Pardosa glacialis* at Zackenberg (Høye et al., 2020). Thus, the extended duration of activity of the spider families found in our study across the past 25 years could reflect an adaptation in reproductive strategies.

Our results point towards pollinators being particularly climate sensitive. At one of our local sites, pollinators became active 6.8 days earlier per decade, which is greater than what has been observed for temperate pollinators. For example, wild bees in North America have advanced their phenology in the range of 0.8 and 1.62 days per decade in the past 40 – 50 years (Bartomeus et al., 2011; Dorian et al., 2022). In addition, species of temperate butterflies and bees show patterns of increased flight duration (Altermatt, 2010; Dorian et al., 2022; Michielini et al., 2021), and while pollinators have not changed the duration of activity across years in our study, the important pollinator families Chironomidae and Muscidae shortened the length of their activity seasons in early snow melting years in the wet fen. From the perspective of pollination services in the community, shifts in the timing of activity and changes in flight duration of pollinators is concerning because it may influence the phenological overlap with plant species that depend on pollination for reproductive success, such as *Dryas sp.* At Zackenberg (Tiusanen et al., 2016). Relevant to this, the dominant plant species at Zackenberg have been found to rapidly advance their phenology (Høye, Post, Meltofte, Schmidt, et al., 2007; Høye et al., 2013; Iler et al., 2013) with average peak flowering occurring 8.8 days earlier per decade (Iler et al., 2013). In comparison, the average peak activity of pollinators in this study was 3.1 days earlier per decade. While the pollination services at

Zackenberg seem to be stable till now (Cirtwill et al., 2022), there is a concern that the temporal overlap between flowering plants and pollinators may be further reduced (Schmidt et al., 2016).

The heterogenous phenological responses among arthropod taxa and habitats entail that community- and family-level changes in phenology does not necessarily correspond. A few dominant taxonomic groups may drive the community response or compensate with dynamics that moderate the community shift, for example if climate change is causing changes in species composition with varying seasonal activities (Walther, 2010). Our study would certainly benefit by linking species-level changes in phenology to our findings on family-, population- and community-level phenology (Walters et al., 2013). However, our results have important implications in terms of incorporating both spatial and temporal components of phenological variation among arthropod taxa to climate variables, which is generally lacking in studies investigating arthropod population and community phenology (Ellwood et al., 2012; Samplonius et al., 2021). At the same time, we demonstrate that arthropod taxa respond strongly to a changing climate, and on a community-level, arthropods seem to be tracking the changing climate quite well, however, arthropod taxa track climate variables at different rates and this diversity in phenological shifts can lead to substantial reshaping of communities with potential implications for species interactions.

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