Title: Phenological responses to climate change across taxa and local habitats in a high-Arctic arthropod community

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Open Research statement: Arthropod phenological data and climate data are already published and publicly available at https://data.g-e-m.dk/, with those publications properly cited in this submission.

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Abstract

Climate change has led to pronounced phenological responses that typically vary across taxa. The rate of warming is especially high in the Arctic, but comprehensive long-term data on phenological changes is rare in this region, especially for arthropods – a diverse taxonomic group that form important links to other trophic levels. Understanding the environmental drivers of arthropod phenological variation is necessary to predict future trends across taxa and habitats. Here, we analyze temporal trends and climate associations in arthropod phenology using 25 years of standardized monitoring data from five different habitats in high-Arctic Greenland. We observed earlier peak activity and extended activity periods in the arthropod community, but this directional trend was weak, and the magnitude of responses varied considerably among taxa and local habitats. Snowmelt timing was generally a strong driver of arthropod phenology, and a key cue for earlier activity of late-active taxa whereas temperature was an important driver of early-active taxa. Families of mixed feeders and parasitoids exhibited especially rapid phenological responses to snowmelt and temperature, but with pronounced heterogeneity in responses among habitats. Our findings highlight the complexity in arthropod community phenological responses to global climate change. However, by estimating phenological metrics across entire activity seasons in a functional and life-history trait perspective, general trends and consistent patterns can be identified amidst this complexity.

Introduction

The Earth is subject to rapid climatic changes with implications for ecosystems worldwide (Parmesan & Yohe, 2003; Walther et al., 2002). Numerous ecological changes have been associated with global warming (Halsch et al., 2021; Parmesan, 2006), with one of the most widely reported effects being shifts in phenological events (Visser & Both, 2005; Walther, 2010). Long-term studies report earlier phenological firsts and peak phenology in response to warming (CaraDonna et al., 2014; Cleland et al., 2007; Inouye, 2008; Menzel et al., 2020; Parmesan & Yohe, 2003), but studies predominantly focus on plants (Clark & May, 2002; Ramula et al., 2015). Being ectothermic, the developmental rate of arthropods is closely coupled to temperature, which facilitates strong responses of arthropods to climate change (Cohen et al., 2018; Halsch et al., 2021; Roslin et al., 2021; Thackeray et al., 2016). Despite their ecological importance, huge diversity, and sensitivity to climate variations (Boggs, 2016; Gillespie et al., 2020; Hodkinson & Jackson, 2005), there is a knowledge gap concerning arthropod community phenological responses to changing growing conditions.

High-Arctic ecosystems are experiencing rapid climate warming, with average annual temperatures rising at twice the global average rate (AMAP, 2017; Rantanen et al., 2022). While temperature trends are relatively clear, the timing of snowmelt varies substantially from year to year as snowmelt depends on both spring temperature and winter snowfall as well as its distribution, which is influenced by factors such as wind and topography (Bjorkman et al., 2015; Callaghan et al., 2011). Hence, earlier snowmelt in spring varies temporally and spatially (Dauginis & Brown, 2021; Hernández-Henríquez et al., 2015; Pedersen et al., 2016). The environmental condition in Arctic regions presents organisms with a very short window of activity, making species especially vulnerable to the rapid and major changes occurring (Bale & Hayward, 2010; Danks, 2004).

Warming has been linked to changes in arthropod community composition (Koltz, Schmidt, et al., 2018), increased growth and reproduction (Culler et al., 2015; Høye et al., 2020), range shifts (Chen et al., 2011; Ittonen et al., 2022) and modified phenology (Bolduc et al., 2013; Roslin et al., 2021). At the same time, snowmelt timing, another key driver of Arctic arthropod phenology (Høye & Forchhammer, 2008b; Rixen et al., 2022), determines the start of activity seasons. Earlier snowmelt advances spring or summer phenology, while delayed snowmelt is likely to delay phenology and shorten the period of optimal growth conditions. The interactions between temperature and snowmelt timing makes the analysis and prediction of future phenological patterns of Arctic arthropods complex and requires long time series data.

Arthropod functional groups and species can exhibit different phenological responses to climate variation depending 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 typically respond to warming by advancing and shortening their phenology whereas multivoltine species tend to delay their late-season phenology (Glazaczow et al., 2016). Species may also exhibit different temperature sensitivities (Buckley, 2022; Thackeray et al., 2016). For example, early-active species strongly advance their spring emergence (Roy & Sparks, 2000) while late-active species often delay their fall activity in response to warming (Bartomeus et al., 2011; Gallinat et al., 2015). Furthermore, different phenological responses can be associated with various sensitivities to environmental cues unaffected by climate change, such as photoperiod (Bale et al., 2002;

Danks, 2007). Arctic arthropod phenological shifts may also vary between populations of the same species, due to genetic differences between populations (Diez et al., 2012; Primack et al., 2009) or to site-specific differences in the magnitude of warming (Nufio & Buckley, 2019). Taken together, variation in phenological responses across populations, taxa and phenological events, contribute to changes in community-level phenology, highlighting the complexity in understanding and predicting responses to climate change.

The diverse life-history strategies among species and functional groups could give rise to various phenological responses to warming and changing snowmelt regimes. Changes in the relative timing of activity of individual arthropod taxa compared to other taxa in the community, termed the phenological niche breadth (Post, 2019; Prevey et al., 2019), may increase the temporal overlap and coexistence of species. However, this could also lead to a shorter duration of the entire arthropod community and thereby strongly influence competitive and trophic interactions (Rudolf, 2019; Sanz-Aguilar et al., 2015). On the other hand, differential shifts in the phenological niche might result in temporal mismatches between trophic levels, such as plant-pollinator or predator-prey interactions (Pyke et al., 2016; Reneerkens et al., 2016; Visser & Both, 2005). Assessing the effect and relative importance of abiotic cues on arthropod phenology and duration of activity can improve predictions of how climate change may shape the activity of individual taxa and the arthropod community as well as ecological interactions in a food web.

Reliable predictions about the impact of climate change on phenology require comprehensive, long-term monitoring schemes (Coulson et al., 2014; Gillespie et al., 2020; Hodkinson & Jackson, 2005; Inouye, 2022). Unfortunately, Arctic regions lack long-term data with sufficient spatial and temporal resolution, resulting in inadequate documentation of seasonal changes in arthropod activity across entire communities. Furthermore, studies investigating how multiple climate predictors influence the variation in arthropod phenology across diverse taxa and phenology metrics, representing the entire active season, are scarce (But see Prather et al., 2023; Roslin et al., 2021). The BioBasis program at Zackenberg in Northeast Greenland has been conducting arthropod monitoring since 1996 (Schmidt et al., 2019), representing the longest-running terrestrial arthropod monitoring program in the Arctic (Summary of monitoring programmes in Gillespie et al., 2020). The program offers a unique opportunity to address knowledge gaps regarding seasonal activity patterns of arthropod taxa in a remote and challenging research area, which can help predict the ecological impacts of climate change. Using this 25-year time series dataset, we explored variations in phenological responses throughout the entire active season of terrestrial and semiaquatic arthropods in different local habitats in relation to snowmelt timing and temperature.

We use this standardized dataset to test (i) whether arthropod phenology across all available family-habitat combinations have temporally changed over the study period; (ii) whether snowmelt timing or temperature are most closely associated to changes in arthropod phenology (specifically, peak activity and duration of activity); (iii) how snowmelt timing and temperature affect arthropod phenology and whether these relationships vary by habitat type or taxa as well as functional groups and general life-history traits.

In accordance with findings from prior studies on phenological responses of Arctic arthropods (Høye et al., 2007; Pearce-Higgins et al., 2005; Tulp & Schekkerman, 2008), we hypothesize that earlier snowmelt and warming lead to advances in peak phenology across taxa and habitats. Responses in the duration of activity are expected to be more variable among arthropods, as some taxa will shorten (Culler et al., 2015), not change (Høye et al., 2014) or extend (Høye et al., 2020; Karlsson, 2014) their activity seasons. We anticipate that snowmelt timing will be the primary driver of arthropod phenological variation, rather than temperature (Bowden et al., 2018; Høye et al., 2014; Høye & Forchhammer, 2008b). Advanced phenological shifts are expected with earlier snow melt and warmer temperatures (Høye et al., 2007). The magnitude of phenological responses will likely vary among taxa, making precise predictions challenging. As observed in many previous studies (Bartomeus et al., 2011; Brooks et al., 2014; Pau et al., 2011; Valtonen et al., 2011), we predict that early-active taxa will be more responsive to temperature than late-active. Conversely, late-active taxa will be more responsive to the timing of snowmelt (Høye & Forchhammer, 2008b).

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 by BioBasis Zackenberg within the Greenland Ecosystem Monitoring Program and included seven different plots (Schmidt et al., 2019). Plot 2 - 7 consisted of eight yellow pitfall traps (1997 to 2006) later reduced to four pitfall traps (also four traps in 1996 but otherwise from 2007 to 2020). Each pitfall sampling plot contained two rows of sections (first row: A – D and second row: E – H) with one trap in each section. After 2006, pitfalls in row E – H were closed. Plot 1 included two window traps (flight-interception traps), constructed as a window screen held in place by two angular aluminium bars between two chambers filled with water, detergent and salt, where specifically limnic insect emergence and flight activity was monitored. Individual traps were opened as they became snow-free (usually late May to early June), but for early snow melting habitats (plot 2 and plots 5 & 7), snowmelt often occurred prior to sampling initiation. Traps 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. Further details regarding sampling procedures are given in Schmidt et al. (2019). After collection, specimens were stored in 75% ethanol, and transported to Denmark where the arthropods were sorted by technicians at the Department of Ecoscience at Aarhus University. Spiders and most insects were sorted to family level, Aphidoidea, Chalcidoidea and Coccoidea were sorted to super family level, and other arthropods were sorted to subclass level, and all specimens were subsequently counted. The data is publicly available at http://data.g-e-m.dk. As the field season slightly varied from year-to-year depending on several factors such as timing of spring snowmelt as well as logistical challenges involved with initiating and ending the field season, we focused on arthropod data from only June, July and August which enabled comparison of arthropod capture numbers among years. 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) 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, three families of 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 normal distribution curves could be fit on abundance 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 & Forchhammer (2008b).

We divided the arthropod taxa in the following broad functional groups; decomposers (Acari and Collembola), predators (Linyphiidae, Lycosidae and Thomisidae), herbivores (Aphidoidea and Coccoidea), parasitoids (Hymenoptera families; Ichneumonidae and Chalcidoidea) and mixed feeders (Diptera families and Lepidoptera). Diptera (flies and mosquitoes) and Lepidoptera (butterflies and moths) were recognized as mixed feeders because of their role as predators and herbivores as larvae and as pollinators and predators in the adult life stage. These groupings were in accordance with previous studies of this high-Arctic arthropod community (Høye et al., 2021, Koltz et al., 2018). Further, we characterized the arthropods as being either surface-dwelling (decomposers, predators and herbivores) or flying insects (parasitoids and mixed feeders). See Supplementary Information S1 for more information.

Climate variables

We selected temperature and timing of snowmelt as climate variables to determine the effect of climate on emergence phenology as these variables were previously found to influence the timing of arthropod emergence (Høye & Forchhammer, 2008b; Kankaanpää et al., 2018). A meteorological station located in a mesic heath habitat 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 (Downloaded: 13th January 2022). Air temperature, rather than soil temperature, was chosen to explain temperature variations in the activity levels of arthropods in this study (see Supporting Information S2 for a detailed justification of the choice of air temperature) by compiling temperature predictors for each phenological event separately. While a growing degree day model might offer a more precise representation of arthropod responses (Cayton et al., 2015), this approach was not feasible due to limited knowledge regarding the lower developmental threshold temperatures for many arthropod taxa in our study and the use of coarse taxonomic resolution. Instead, we focused on the temperature in the period before activity, which has been considered closely related to arthropod development (Gillooly et al., 2002) and may therefore be a good predictor of adult arthropod phenological events. To this end, we determined the temperature predictor as an average over the 30 days leading up to a mean phenological date of an event minus the minimum standard deviation for each taxon-by-plot combination, so as not to use temperature values largely occurring after the phenological event to predict the response (Figure S2.4).

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 et al., 2020). Years 2009, 2013 and 2019 had limited snow accumulation resulting in the estimation of very early snow melting dates. 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). For those four years, 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.

Quantifying phenology

Annual onset, peak and end of activity of each arthropod taxa were calculated using generalized additive modelling (GAM) on the abundance per trap per day for each plot in each season. We predicted a non-linear phenological development across each season and used the partial smoothing method in GAMs to model the seasonal development in capture rates (Guisan et al., 2002). 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 constrain a symmetric activity curve as well as 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 calculated as the sum of individuals across all traps in a plot within a year. Also, the three phenological events should be possible to calculate (the taxa must be present in at least two weeks). Based on these criteria, the GAM curves provided a fit with a normal distribution for most arthropod taxa and an approximately symmetric distribution in activity due to the univoltine nature of most arthropods in the Arctic. Any indication of asymmetric phenological curves or multimodal distributions led us to exclude the taxa in a specific year from the analysis. When filtering for all these criteria, we excluded 768 years of taxa-by-plot combinations of 1,875 years in total. 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 S1.1). The duration of the activity period was estimated as the number of days between onset and end of the activity season.

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 among taxa, functional group and habitat, we used linear mixed models with each individual phenological event as the response variable and year, taxa or functional group as predictor. When functional groups were compared, we added random intercepts for taxa to account for nonindependence of observations among taxa within functional groups (Table S5.1). In addition, a year-plot interaction was included to allow for the year effect to vary among sites.

Correlation between climate variables

The climate variables included in this study (timing of snowmelt and air temperature) may be highly correlated. Yet, a proper 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 5 such that predictors with values above a VIF > 5 were considered contributing greatly to multicollinearity (Chatterjee & Hadi, 2013).

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 used taxa and plot specific estimates of the temperature predictor, we separated the within-subject effects from between-subject effects that we could not account for in the mixed models by implementing within-subject centering in the model (van de Pol & Wright, 2009). This was 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 expressed the within and between arthropod taxa and plot temperature variation component and was included as a fixed effect in the LMM. 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 (Table S5.1). 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 (Table 1). Plot was included as a categorical variable and to make the desired comparisons of slopes between plots, customized contrasts were used. For all flying insects, the random nested effect of trap type within plot and the random effect of trap type was included to account for the different methods of trapping in plot 1 (window traps) and plots 2 – 7 (pitfall traps). If trap type accounted for much of the variance in the model, trap type was included as a random effect in the final model (Supplementary Information S5.2). 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 model was selected based on lowest AIC scores. The chosen model is clearly indicated for each analysis in tables with results in the supplementary information.

Table 1 – Multiple regression models to determine the effect of climate predictors; timing of snowmelt (Snowmelt, the day of year where snow depth < 10 cm) and temperature (Temp, average temperature 30 days prior to a mean phenological event minus one standard deviation) on the response variable; peak activity or duration of activity (Phenological event). Plot is included as a covariate to determine differences in phenological responses of arthropod taxa among plots. Best model was selected based on lowest AIC score.

Model	Description
Model 1, simple linear regression snowmelt	*Snowmelt + Plot*
Model 2, simple linear regression temperature	*Temp + Plot*
Model 3, all covariates linear regression	*Snowmelt + Temp + Plot*
Model 4, interaction snowmelt and plot	*Snowmelt x Plot*
Model 5, interaction temperature and plot	*Temp x Plot*
Model 6, all interactions	*Snowmelt x Plot + Temp x Plot*
Model 7, three-way interaction	*Snowmelt*Temp*Plot*

Results

Environmental change

Snowmelt timing occurred earlier over the 25-year study period at Zackenberg (Snowmelt: -1.6 ± 3.2 days earlier per decade), but this trend was not significant and a substantial amount of among-year variation was found (Figure 1a, R^2 = 0.01, P = 0.62). Summer air temperature significantly increased by 0.6 ± 0.3 ºC per decade during the study period (Figure 1b, R^2 = 0.16, P = 0.045), whereas spring air temperature did not change significantly (Average spring air temperature: 0.04 ± 0.5 ºC per decade). A low level of multicollinearity between timing of snowmelt and air temperature was found (see Supplementary Information S4).

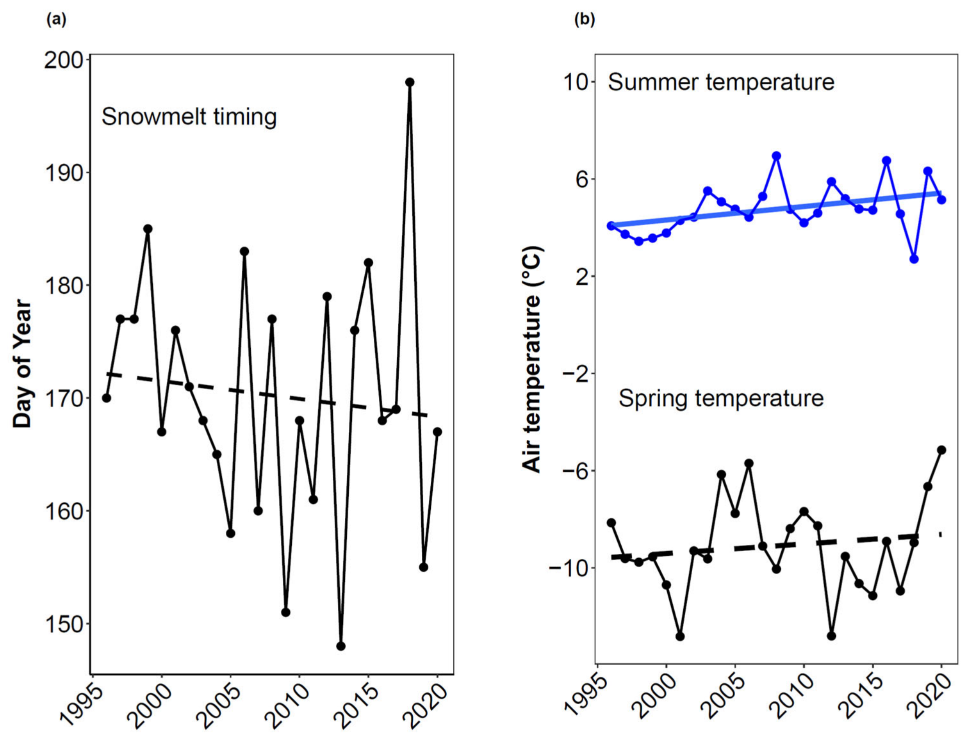

Figure 1 – Interannual variation and trends of (a) timing of snowmelt and (b) average seasonal air temperature for spring (April, May) and summer (June, July, August) at Zackenberg, Greenland during the study period of 1996 - 2020. Only summer air temperature changed significantly during the study period (indicated by solid regression line).

The phenological niche of arthropods

The timing of activity varied widely among arthropod taxa and habitats (Figure 2). Families of mixed feeders are active throughout most of the summer season. As an example, Chironomidae are present early in the season compared to Phoridae. The parasitoids and herbivores are active late in the season with considerable variation among habitats. Ichneumonidae 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.

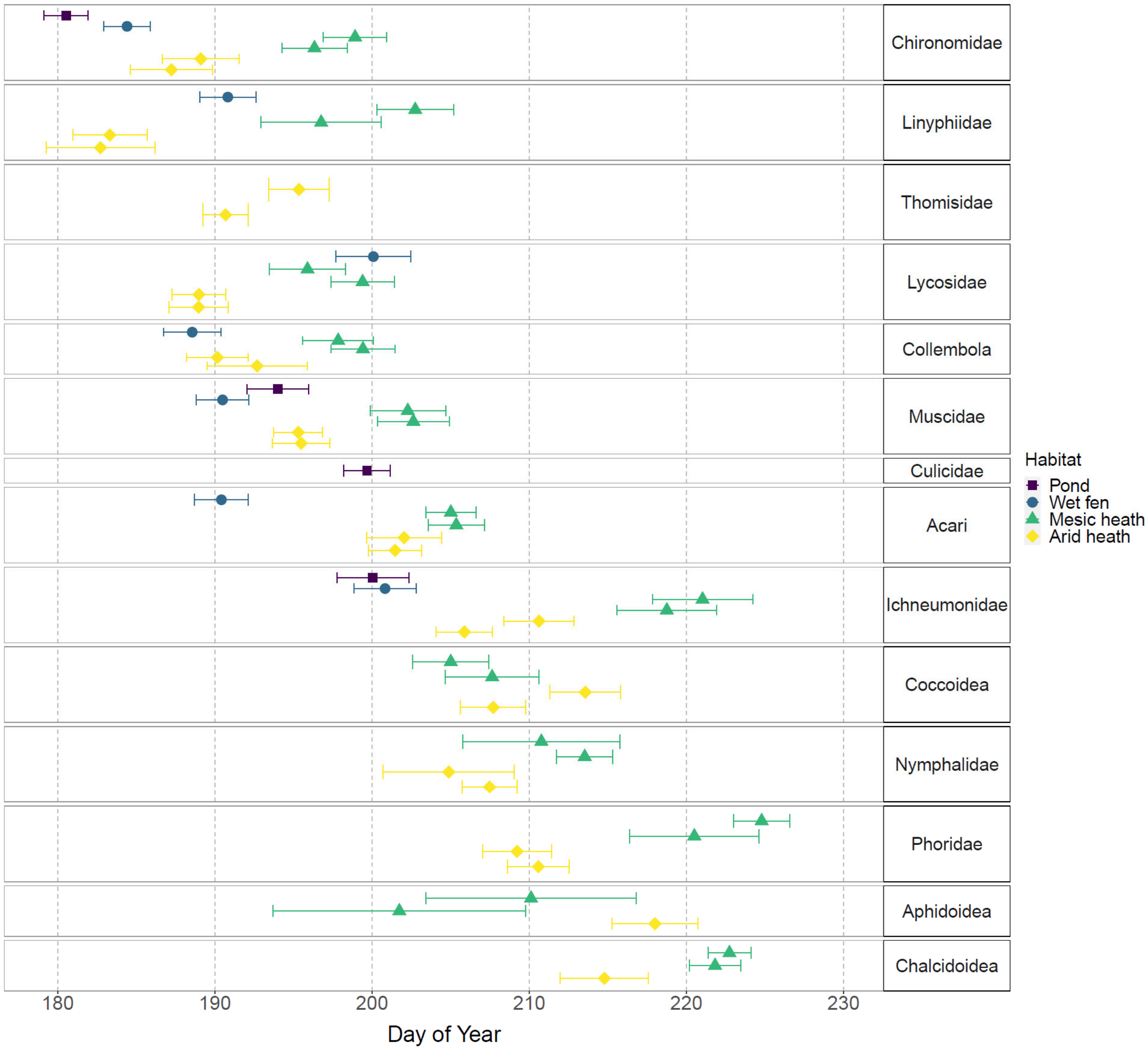

Figure 2 – The average peak phenological event (when 50% of the season capture was reached) of all taxa across multiple years represented by at least 50 individuals per season for each plot (day of year 140 – 240). The arthropods are listed in order of activity such that the top families are active earlier than the below families. The associated error bars indicate the standard error of the mean.

Temporal phenological responses

We observed earlier peak activity in the arthropod community over the study period (Figure S3.1), but only 21% of family-by-plot combinations across onset, peak and end of activity showed a significant shift over time. The community peak phenology occurred 3.07 ± 0.4 days earlier per decade ($R^2_{conditional}$= 0.56, P = <0.001) and the community duration of activity extended by 0.79 ± 0.4 days per decade, although marginally nonsignificant (R^2_c= 0.63, P =

0.06). While trends indicate that arthropod activity becomes earlier, we observed strong variation in responses among arthropod taxa and habitats in all phenological events (Figure S3.1). Sciaridae (5.1 ± 1.5 days earlier per decade), Nymphalidae (8.3 ± 2.2 days earlier per decade), Lycosidae (4.2 ± 1.3 days earlier per decade) and Collembola (5.9 ± 1.3 days earlier per decade) showed the strongest responses across the study period. While most arthropods showed trends of prolonged or no change in activity periods across the study period, herbivores exhibited trends of shortened activity (7.8 ± 3.8 days per decade).

Community phenological responses to snowmelt timing and temperature

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 average arthropod community peak activity was 0.26 ± 0.03 days earlier per day earlier snowmelt (R_c^2= 0.68, P = <0.001). Ten of 15 taxa showed a significant positive effect of snowmelt timing on peak phenology (Table S5.3), indicating that these taxa started their peak activity earlier in response to earlier timing of snowmelt. In response to temperature, the average community peak activity was 1.11 ± 0.46 days earlier per 1 ºC increase (R_c^2= 0.68, P = 0.02). Six of 15 taxa showed a negative effect of temperature on peak phenology, indicating that these taxa started their peak activity earlier in response to warming (Table S5.3).

Most taxa responded to earlier snowmelt and warming by extending the duration of activity, although the directional shift in responses to timing of snowmelt and temperature varied among taxa and habitats (Figure 3 & 4). Nevertheless, we found that the average duration of activity in the arthropod community in response to snowmelt timing extended at a rate of 0.10 ± 0.03 days per earlier snowmelt day ($R_c^2 = 0.63$, $P = <0.001$). In response to temperature, the community activity season did not change.

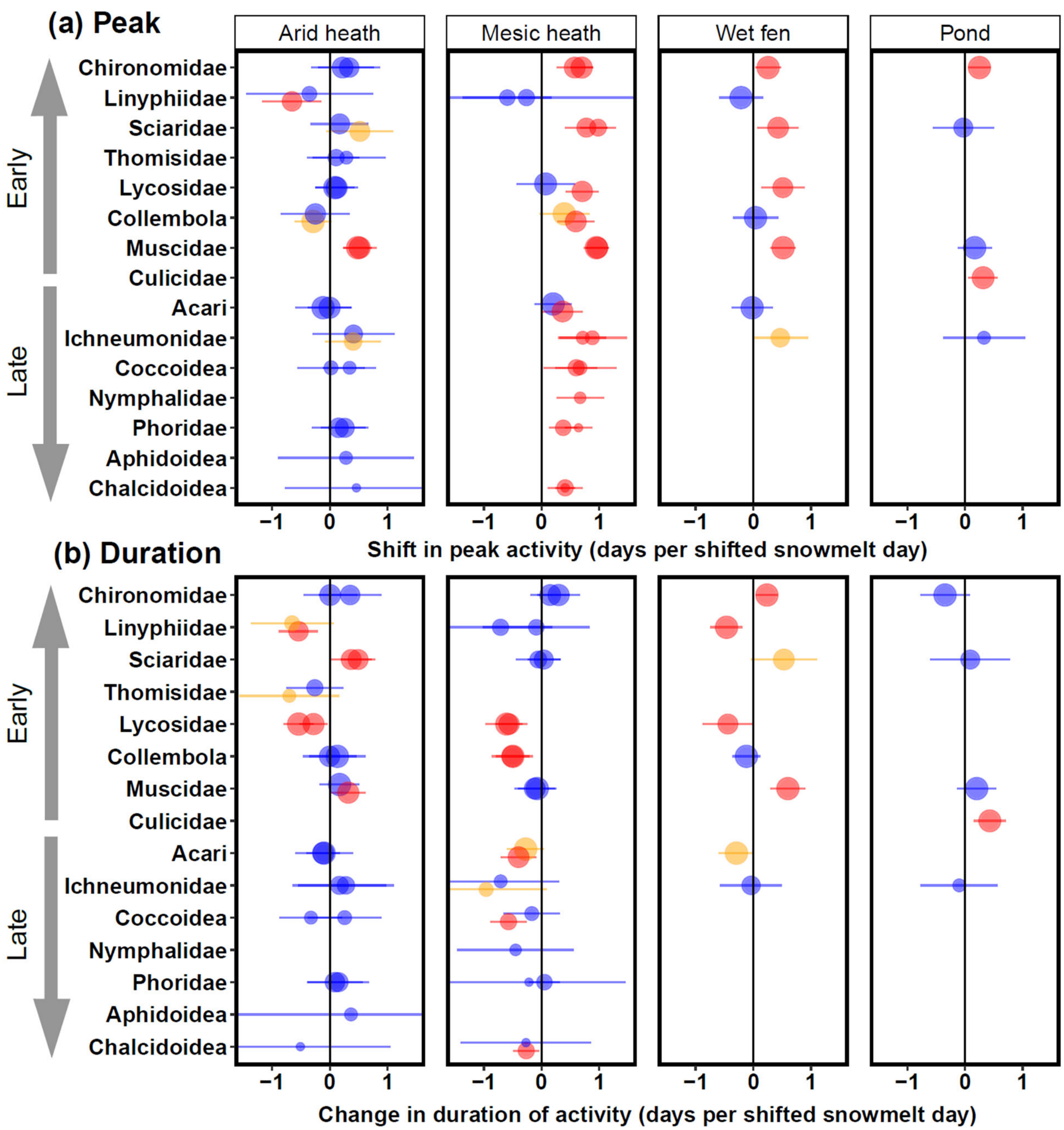

Figure 3 – The average phenological shift in days per change in snowmelt day in (a) peak and (b) duration of the activity season for taxa in each habitat. Taxa with peak phenological shifts that fall above zero advance their peak activity date with earlier snowmelt. Taxa with shifts in duration of activity that fall below zero extend the duration of activity with earlier snowmelt. Significant shifts are represented in red ($P \leq 0.05$), marginally significant shifts in orange ($0.05 < P \leq 0.10$) and nonsignificant shifts in blue ($P > 0.10$). The model is controlled for the effect of

temperature and year. 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. The associated error bars indicate the 95% confidence interval (CI). 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.

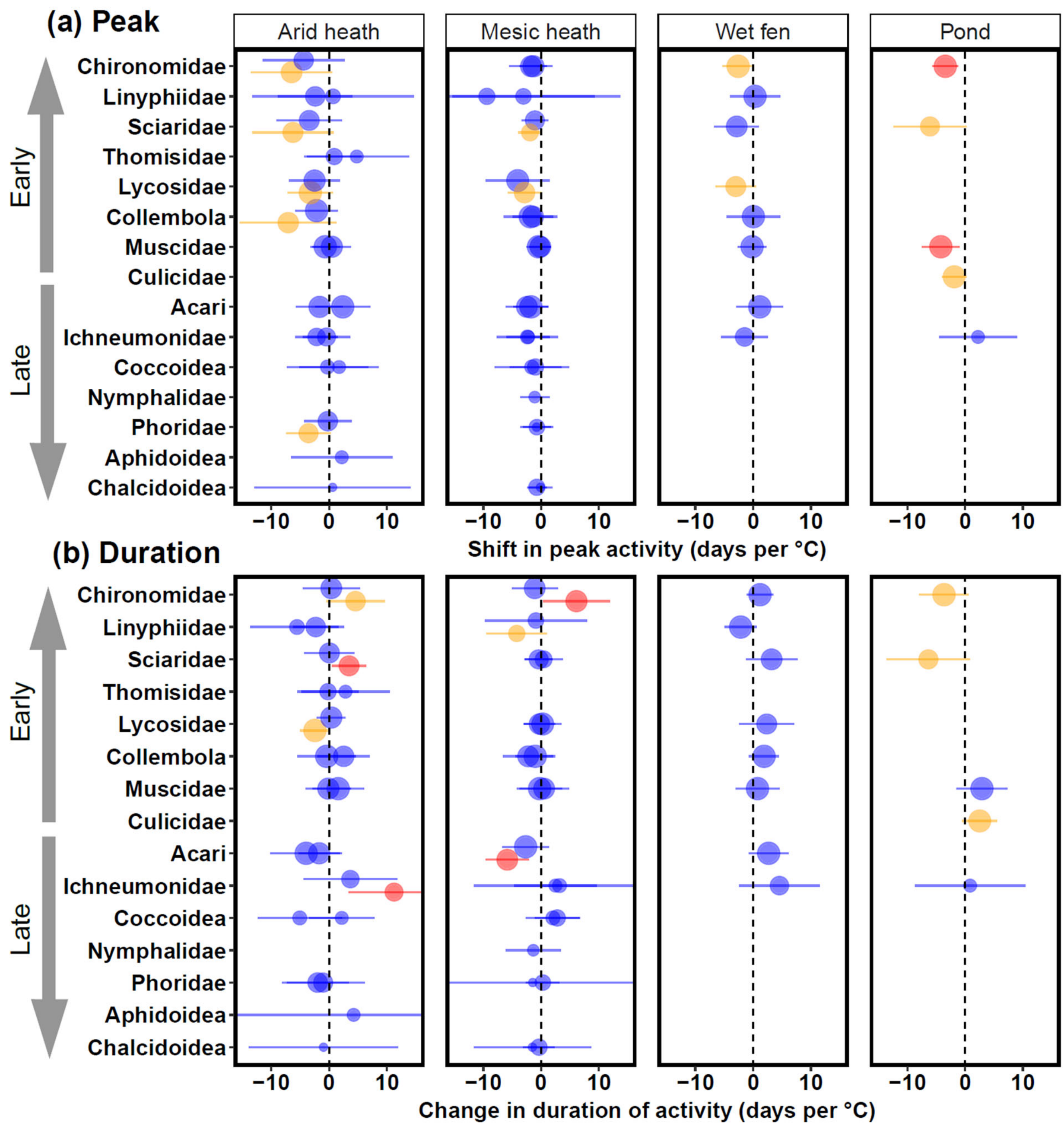

Figure 4 – The average phenological shift in days per 1 ºC in (a) peak and (b) duration of the activity season for taxa in each habitat. Taxa with peak phenological shifts that fall below zero advance their peak activity with warmer temperatures. Taxa with shifts in duration of activity that fall above zero extend their activity with warmer

temperatures. Significant shifts are represented in red ($P \leq 0.05$), marginally significant shifts in orange ($0.05 < P \leq 0.10$) and nonsignificant shifts in blue ($P > 0.05$). The model is controlled for the effect of snowmelt and year. 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. The associated error bars indicate the 95% confidence interval (CI). 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.

Environmental drivers of phenology

Model comparisons with timing of snowmelt and temperature as predictors showed that snowmelt explained more variation in peak phenology than temperature (Table S5.6). In most cases, however, the model including both predictors best explained arthropod phenology. The exception was Aphidoidea, Thomisidae, and Acari (except in the mesic heath) that did not respond strongly to snowmelt timing or temperature in their peak phenology. After detrending the time series by year, the significance of the linear phenology-temperature relationship diminished, while most linear phenology-snowmelt relationships persisted (Figure S6.3, S6.4). Lycosidae was the only taxa for which temperature explained more variation in peak phenology than snowmelt timing ($\Delta AIC > 2$).

For duration of activity, temperature was found to explain more variation than snowmelt timing (Table S5.6), particularly for flying insects. We found that the model including both predictors best explained arthropod duration of activity. Aphidoidea was the only taxon that did not respond to either snowmelt timing or temperature in duration of activity.

We also found strong taxon-by-plot differences in the importance of environmental drivers of phenology. Taxa in the pond habitat responded strongly to temperature compared to the other habitats (Table S5.3). Timing of snowmelt was a better predictor of peak phenology in the mesic heath habitat compared to the other habitats.

Phenological responses among taxa and habitats to snowmelt timing and temperature

While we found trends of earlier peak activity in the arthropod community in response to earlier snowmelt and increasing temperature, the response varied substantially among taxa and habitats (Figure 3 & 4). Earlier snowmelt caused earlier peak activity of all taxa responding to snowmelt timing, except for Linyphiidae showing delayed activity, but the rate at which arthropods responded with earlier peak activity to earlier snowmelt varied substantially among taxa. Taxa from the mesic heath showed stronger responses of earlier peak activity to earlier snowmelt dates than taxa from the arid heath and wet fen habitats (Figure 3 & Table S5.3). The peak phenological responses to temperature among arthropod taxa was less clear compared to snowmelt timing (Figure 4) and most taxon-by-plot phenological responses were not significant.

The effect of snowmelt timing and temperature on duration of activity also varied among taxa and habitats, both in the directional effects (whether taxon-by-plot combinations extended or shortened their activity periods) and in the rate of shortened or extended activity periods. For example, Chironomidae and Sciaridae experienced shortened activity periods in the pond habitat in response to warmer temperature, which was not found in other habitats (Figure 4 & Table S5.4). Muscidae and Sciaridae responded with shorter activity periods to earlier snowmelt in the wet fen and arid heath (Table S5.4). Some taxa experienced substantial changes in activity periods to warming. For example, Ichneumonidae extended their activity period with 5.29 ± 1.62 days per ºC on average across habitats, which was of a greater magnitude than other taxa (Table S5.4). A few taxa exhibited contrasting responses in duration of activity to climate variables.

Acari and Linyphiidae extended their activity with earlier snowmelt but shortened their activity in response to warmer temperatures.

Phenological responses among functional groups and groups with different traits

Mixed feeders and parasitoids shifted their activity to earlier in the season (Mixed feeders, slope: 0.45 ± 0.11; Parasitoids, slope: 0.44 ± 0.04) at a significantly greater rate in response to earlier snowmelt compared to the other functional groups (Figure 5). Herbivores also responded with earlier peak activity to earlier snowmelt, however, at lower rates (slope: 0.25 ± 0.12).

Parasitoids was the only group to significantly shorten their duration of activity in response to earlier snowmelt (slope: 0.16 ± 0.06). Predators extended the duration of their activity with earlier snowmelt (slope: -0.50 ± 0.07), but exhibited trends towards shorter activity periods with warming (Figure 5). No functional groups responded significantly in peak activity or duration of activity to temperature (Figure 5), except peak phenology of parasitoids, which became earlier with warming. Our results showed positive trends in the duration of activity of mixed feeders to increasing temperature, suggesting overall extended activity periods with warming. Herbivores showed trends of shorter duration of activity in response to warming, although this trend was not significant.

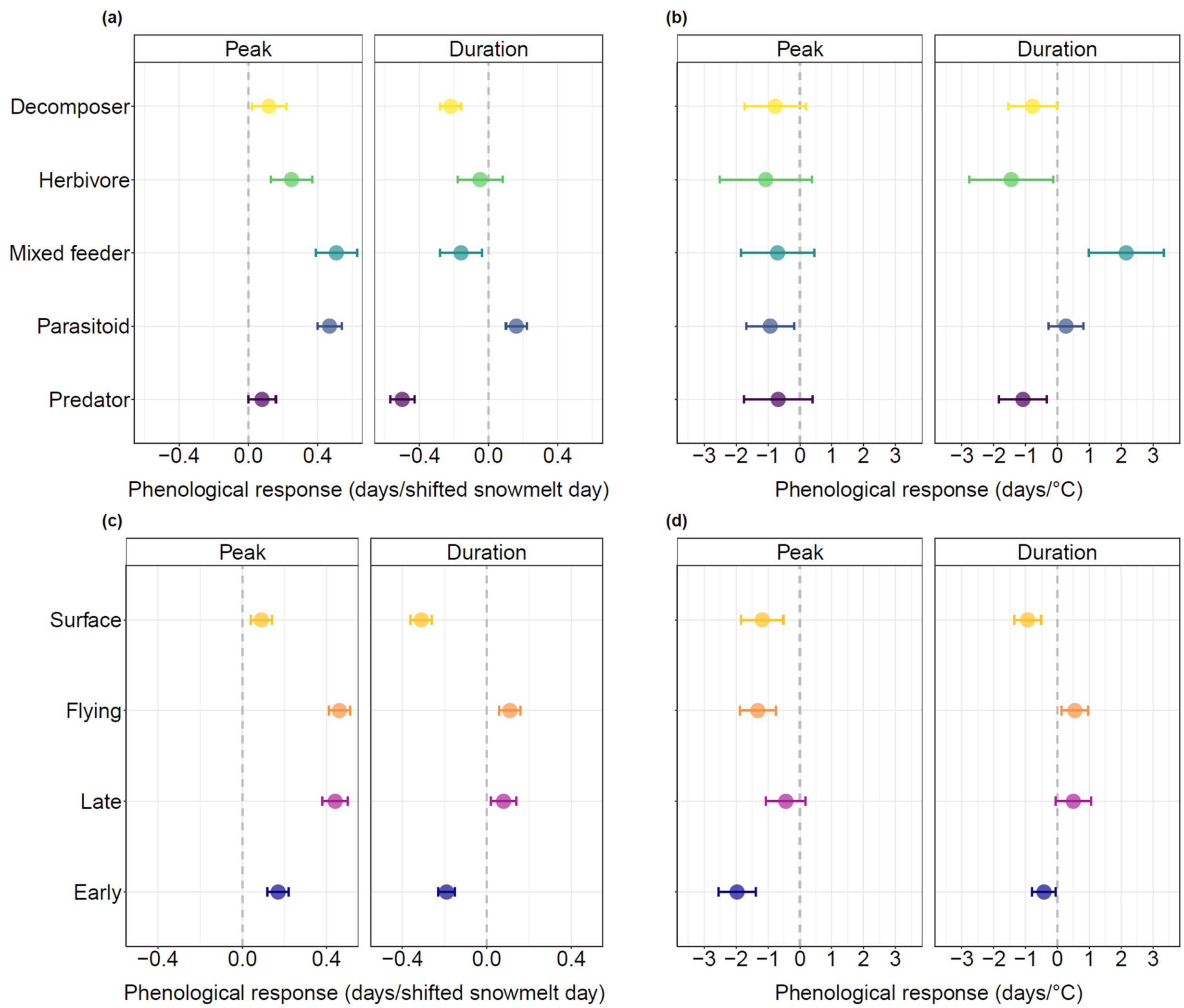

Figure 5 – The average phenological shift in (a, c) days per change in snowmelt day and (b, d) days per 1 ºC in duration and peak of the activity season for each functional group (a, b) and arthropods with different traits (c, d). Average peak phenological shifts that fall above zero in response to snowmelt advance their peak activity with earlier snow melting days. Average peak phenological shifts that fall below zero in response to temperature advance their peak activity with warmer temperatures. An average change in duration of activity that fall below zero in response to snowmelt increase the length of the activity period with earlier snow melting days. An average change in duration of activity that fall above zero in response to temperature increase the length of the activity period with warmer temperatures. The associated error bars indicate the standard error of the mean.

Comparisons of responses between early and late active taxa as well as flying and surface-dwelling taxa were modelled together to consider all interactions and effects. In response to temperature, the peak activity of early active taxa was 1.97 ± 0.58 days earlier per 1 ºC increase, while late active taxa were less responsive (Figure 5). Instead, late active taxa were more responsive to timing of snowmelt with peak phenology shifting 0.44 ± 0.06 days earlier per day earlier snowmelt. Similarly, flying insects responded with earlier peak activity by 0.46 ± 0.04 days per day earlier snowmelt while surface-dwelling arthropods' peak activity barely changed.

Taxa with different traits responded very differently to timing of snowmelt and temperature in the duration of phenology (Figure 5). Surface-dwelling and early active taxa extended the duration of their activity period in response to earlier snowmelt, while flying and late active taxa showed trends towards shortened activity in response to earlier snowmelt. At the same time, surface-dwelling and early active taxa exhibited trends towards shortened activity periods to warming, while flying and late active taxa showed trends of extended duration of activity periods in response to warming.

Discussion

Our study highlights three main findings in congruence with our hypotheses:

(i) Arthropods displayed weak directional trends towards earlier activity over the study period, with considerable variation in the rate of change among different arthropod taxa and habitats.

(ii) Timing of snowmelt was confirmed to be a key driver of arthropod phenology, but temperature explained much of the variation in the duration of activity among taxa compared to timing of snowmelt. Models including both climate variables received the strongest support when testing climate effects on arthropod phenology.

(iii) This high-Arctic arthropod community showed responses towards earlier activity with earlier timing of snowmelt and warmer temperatures. However, notable variation in climate-associated phenological shifts were observed among taxa and habitats, both in the direction and magnitude of phenological response. Some of this variation could be explained by the functional roles and general life history traits of arthropods. Late-active taxa responded strongly to snowmelt timing, whereas early-active taxa showed stronger responses to warming. Mixed feeders and parasitiods were especially sensitive to snowmelt timing, showing significantly earlier activity with earlier snowmelt. Predators showed contrasting phenological responses to snowmelt and temperature, indicating that altered snowmelt patterns could counter the effects of warming. This suggests that life-history traits of arthropod taxa may aid in determining sensitivity to climate change, as proposed in other studies (Diamond et al., 2011; Dorian et al., 2022; Pacifici et al., 2017; Zografou et al., 2021).

Snowmelt as a key driver of Arctic arthropod phenology

Our study highlights the importance of snowmelt timing as an environmental driver of arthropod phenology, indicating that local snowmelt conditions, even when controlling for the effect of temperature, play a pivotal role in shaping Arctic arthropod responses to global change (Hein et al., 2014; Kankaanpää et al., 2018; Rixen et al., 2022; Saalfeld et al., 2019). Temperature interacts with winter and spring precipitation in determining the duration of the snow-free season (Callaghan et al., 2011), leading to only partial correlation between snowmelt timing and temperature (Bjorkman et al., 2015; Wheeler et al., 2015). As the climate warms, temperature and snowmelt is expected to increasingly decouple in some regions (Callaghan et al., 2011; Raisanen, 2008), resulting in greater variability in snowmelt timing despite generally warmer seasonal temperatures. The strong relationship we identified between phenology and snowmelt is likely due to plastic responses to large temporal variations in snowmelt patterns (Høye et al., 2007; Pedersen et al., 2016). Consequently, the anticipated changes in snowmelt dynamics could enhance landscape-scale heterogeneity, leading to more localised variations in arthropod activity patterns (Gillespie et al., 2016; Leingartner et al., 2014). Taken together, snowmelt currently serves as an important determining factor of phenology and will likely remain essential in shaping Arctic arthropod phenological responses to global change, potentially having implications for arthropod population and community dynamics.

Heterogeneity in phenological responses to climate change

Our findings indicate heterogeneity in phenological sensitivity to environmental factors in this high-Arctic arthropod community. A key factor shaping changes in arthropod phenology to changing environmental conditions was their general life-history traits. The timing of snowmelt demonstrated greater explanatory power for late-active arthropod taxa and taxa in habitats (mesic heath) with later snowmelt compared to early-active taxa and taxa in habitats (arid heath and wet fen) with earlier snowmelt (Figure 3 & 5). Late-active taxa thus exhibited greater plasticity to snowmelt and snowmelt timing acts as an important environmental control on phenology. Conversely, we found early-active taxa and taxa from early snow melting habitats to be more responsive to temperature, indicating that temperature serves as a more reliable cue for activity in the beginning of the growing season (Brooks et al., 2014; Roy & Sparks, 2000). This may imply that early-active arthropods are approaching the limits of phenological plasticity to snowmelt (Iler et al., 2013; Jochner et al., 2016; Stemkovski et al., 2023), hindering the ability of arthropods to track the changing climate. Perhaps early-active taxa rely more on a stable abiotic driver such as photoperiod, when snowmelt is early (Bowden et al., 2018; Høye & Forchhammer, 2008a). By adjusting to photoperiod, arthropods can delay their activity until later in the season when temperature conditions are more stable, thereby avoiding exposure to freezing (Gehrmann et al., 2017; Regan & Sheldon, 2023; Rixen et al., 2022).

We also observed more pronounced advancements in peak phenology among flying and late-active taxa in response to earlier snowmelt. Surface-dwelling and early active taxa prolonged their activity period with earlier snowmelt, but shortened their activity period with warming. Most Arctic arthropods are univoltine (Høye et al., 2020), and because they grow faster with warming (Chaves et al., 2015; Culler et al., 2015), shortened activity periods could be common in the Arctic. However, warmer environments could facilitate the production of additional generations, a consequence of climate change that has been previously demonstrated (Altermatt, 2010; Braune et al., 2008; Kerr et al., 2020; Tobin et al., 2008), and has been observed in the wolf spider *Pardosa glacialis* at Zackenberg (Høye et al., 2020). The extended activity periods found in this study for a few functional groups and individual taxa may indicate that patterns of voltinism in Arctic arthropods are shifting with a changing climate. Future studies should therefore consider other types of distributions, such as bimodal distributions, when modelling seasonal activity patterns of species (Hodgson et al., 2011).

These observations suggest that predicting phenological responses of arthropod taxa to future climate change may depend on general trait characteristics such as early or late activity and surface-dwelling or flying arthropods.

Community and ecosystem consequences of climate and phenological changes

We found mixed feeders, parasitoids and herbivores to show strong trends of earlier peak phenology in years with earlier snowmelt. In years with early snowmelt and warmer temperatures, Diptera families (categorized as mixed feeders) exhibited shorter activity periods in certain habitats. Predators showed contradicting responses to climate variables as they prolonged their activity period in early snow melting years but shortened their activity period in response to warming. Herbivores and decomposers showed weaker correlations with climate variables compared to other functional groups. The temporal trends of shorter activity periods exhibited by herbivores could be linked to warming (Figure 5), but we found no significant responses to snowmelt timing or temperature in our study. The length of activity seasons of herbivores could instead be driven by strong interactions with their plant food source (Gillespie et al., 2007; Koltz et al., 2022; Strathdee et al., 1993).

The diversity in phenological responses associated with climate change in this high-Arctic arthropod community may entail major reorganization within the arthropod community under climate change, potentially impacting interaction networks (Schmidt et al., 2017; Walther, 2010). For instance, earlier pollinator activity could temporally decouple them from flowering host plants, resulting in reduced pollination services (Pyke et al., 2016; Schmidt et al., 2016). Plants at Zackenberg have been found to rapidly advance and shorten their flowering season (Høye et al., 2013; Iler et al., 2017), but it remains uncertain if pollinators shift their phenology sufficiently to track timing of flowering, particularly because plants seem to respond more rapidly to warming than pollinators (mixed feeders) found in this study (Plants: -3.19 ± 0.06 d/ºC (Iler et al., 2017); Mixed feeders: -0.79 ± 1.15 d/ºC). Extended or shortened predator activity could affect top-down control in the food web (Koltz et al., 2018). Given that arthropod peak activity has shifted to earlier in the season at Zackenberg in the past 25 years, there could be an increased risk of trophic mismatch between Arctic shorebirds' insectivorous chicks and the availability of arthropod prey (Both et al., 2009; Reneerkens et al., 2016). However, the host-parasitoid interaction may remain intact, as parasitoids appear to track their hosts (families of predators and mixed feeders) (Abrego et al., 2021). These findings indicate that climate change in the Arctic may affect trophic interactions and food web dynamics.

An important caveat when interpreting our results is the rather coarse taxonomic resolution used in our study, which may obscure important species-level variations. At the family-level taxonomic resolution, we cannot differentiate between the effects of changing species composition between years and the interannual variation in the phenology of individual species. Consequently, we may derive erroneous conclusions, such as estimating an advanced emergence date in early snow melting years when, in reality, early emerging species become more common. Conversely, among the more diverse arthropod taxa, there may be underlying variations in interspecific phenological responses to abiotic drivers that, when examined at a broader taxonomic resolution, might appear as if there is no response to climate change. However, our aim with the present study was to elucidate broader patterns in the phenological responses of various taxonomical groups using robust abundance estimates allowing us to analyse phenology and climate relationships with greater statistical power. In addition, it is essential to attain a better understanding of community-level responses to climate change on various taxonomic levels (Koltz, Schmidt, et al., 2018; Legagneux et al., 2014), because changes in the structure and seasonal dynamics of broader taxonomic groups affect how ecosystems function.

Conclusions

Our study highlights that phenological responses across taxa and populations within an arthropod community exposed to changing climatic conditions are complex and does not follow broad overall patterns. Therefore, to gain a comprehensive understanding and make credible predictions regarding future changes in arthropod seasonal activity, detailed investigations into the environmental drivers of change at high spatial and taxonomic resolution is critical. We were able to identify some general trends and consistent patterns in phenological responses to a changing climate in this high-Arctic arthropod community. We found that snowmelt timing is an important determinant of arthropod phenology, but the relative importance of snowmelt timing and temperature as predictors of arthropod phenology varies among taxa and local habitats. The magnitude of phenological responses to climate predictors also varied by taxa and habitat, indicating that general predictions of phenological change for all taxa and locations is not feasible. However, including information on functional groups and life-history traits will likely strengthen our ability to predict future phenological trends of arthropods in cold regions.

Supplementary material

All supplementary information has been provided in separate files.

Author contributions

H.S.G.: Conceived the study, conducted data analyses, statistics, and drafted the manuscript.
T.T.H.: Acquired funding, participated in the design of the study, and 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 and climate 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 are available: https://github.com/soerinegerlich/high_arctic_arthropod_phenology_manuscript

Competing Interest Statement

We have no conflict of interest to declare.

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