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ORIGINAL PAPER

Analysis of trophic interactions reveals highly plastic response to climate change in a tri-trophic High-Arctic ecosystem

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Abstract As a response to current climate changes, individual species have changed various biological traits, illustrating an inherent phenotypic plasticity. However, as species are embedded in an ecological network characterised by multiple consumer–resource interactions, ecological mismatches are likely to arise when interacting species do not respond homogeneously. The approach of biological networks analysis calls for the use of structural equation modelling (SEM), a multidimensional analytical setup that has proven particularly useful for analysing multiple interactions across trophic levels. Here we apply SEM to a long-term dataset from a High-Arctic ecosystem to analyse how phenological responses across three trophic levels are coupled to snowmelt patterns and how changes may cascade through consumer–resource interactions. Specifically, the model included the effect of snowmelt on a High-Arctic tri-trophic system of flowers, insects and waders (Charadriiformes), with latent factors representing phenology (timing of life history events) and performance (abundance or reproduction success) for each trophic level. The effects derived from the model demonstrated that the time of snowmelt directly affected plant and arthropod phenology as well as the performance of all included trophic levels. Additionally, timing of snowmelt appeared to indirectly influence wader phenology as well as plant, arthropod and wader performance through effects on adjacent trophic levels and lagged effects. The results from the tri-trophic community presented here emphasise that effects of climate on species in consumer–resource systems may propagate through trophic levels.

Keywords Arctic ecosystem · Trophic interactions · Greenland · Phenology · Performance · Trophic mismatch · Plants · Arthropods · Waders · Structural equation modelling

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Introduction

The global climate is warming, and as a response, species are shifting phenology to match the new environmental state of their respective habitats (Post et al. 2009; Berg et al. 2010; Montoya and Raffaelli 2010; Van der Putten et al. 2010; Walther 2010; Høye et al. 2013). Multiple studies have demonstrated individual species responses to climate changes (Root et al. 2003; Walther 2004; Dullinger et al. 2012; Grabowski et al. 2013; Amano et al. 2014), illustrating an inherent plasticity in the species ecology. For instance, an average 2-week advancement in spring phenology per decade was reported in a High-Arctic ecosystem, across multiple plant and animal species (Høye et al. 2007). However, since every species is embedded in a

network characterised by multiple consumer–resource interactions, ecological mismatches are likely to arise if interacting species do not respond homogeneously. Cascading effects due to trophic mismatch have already been demonstrated in a range of communities (Pace et al. 1999; Zarnetske et al. 2012) with substantial effects across adjacent trophic levels. For example, McKinnon et al. (2012) found that chicks of waders (Charadriiformes) hatching in synchrony with peak emergence of their food resource had higher growth rates than chicks hatched outside food resource peaks. Thus, the integration of the network of consumer–resource interactions, together with the direct climate effects on population dynamics, is pivotal for the assessment and prediction of the overall impact of climate changes at an ecosystem level.

High-Arctic ecosystems are characterised by a long winter of dormancy, following a short period of warmth and activity (Callaghan et al. 2004). However, during the last decade, climate warming has induced drastic changes in the physical environment in the Arctic region (Kattsov and Källén 2005; McBean 2005), with an increase in average annual temperature occurring at twice the rate of global averages (Kattsov and Källén 2005) and snowmelt dates advanced by up to 14 days/decade (Mortensen et al. 2014). Additionally, Arctic tundra ecosystems display relatively low biodiversity with a potentially low functional group redundancy, and species adapted to the extreme seasonal environments (Callaghan et al. 2004; Post et al. 2009). Thus, the characteristics of the High-Arctic ecosystems suggest that effects of external disturbances, such as climate change, are likely to cascade across trophic levels in the ecosystem (Pace et al. 1999; Schmitz et al. 2000; Terborgh and Estes 2010), through changes in the biotic interaction patterns, due to a differential response of species to changes in their environment (Forchhammer and Post 2004; Forchhammer et al. 2008; Post et al. 2008; Høye et al. 2013). However, Mortensen et al. (2014) demonstrated that very few species and abiotic characteristics (less than 36 %) across a High-Arctic ecosystem displayed any significant temporal trends across 14 years, despite the observed increase in both temperature and advance of snow melt dates. Hence, it is not clear why climate effects are apparently not propagating into the ecosystem.

To disentangle the direct and indirect effects of climate in the High-Arctic, we used fine-grained spatio-temporal ecosystem data collected annually over a period of 17 years from the same High-Arctic ecosystem. Data were analysed for phenological responses across three trophic levels and coupled to snowmelt patterns. Additionally, analyses were extended to include how changes have cascaded through two consumer–resource systems, including (1) plant–pollinator interactions and (2) arthropod–wader interactions. Focusing on several sets of potential consumer–resource interactions, we apply structural equation modelling (SEM) to evaluate the weighted influence of direct and indirect (Forchhammer and Post 2004; Forchhammer et al. 2008) responses to a changing snow regime on species phenology and performance. We expected that direct responses to a changing snow regime are likely to be found in phenology within the trophic levels, while indirect effects are visible in the abundances.

Methods

Study site, species and field data

The study site was the Zackenberg Valley, located in Northeast Greenland (74°28′N, 20°34′W) (Fig. 1). Data were collected from a study area covering approximately 15 km^2 comprised of the central low-lying valley floor surrounded by mountains, ranging from 1000 to 1400 m above sea level (Meltofte and Rasch 2008). The vegetation composition of the valley ranges from heaths to fens, dominated by white Arctic bell-heather (*Cassiope tetragona*) heaths mixed with Arctic willow (*Salix arctica*) snowbeds, and shifts into open dry heaths of mountain avens (*Dryas* sp.) with increasing altitude (Elberling et al. 2008). The ground dwelling arthropod fauna is mainly dominated by mites, spiders and collembolans, while Muscidae and Chironomidae are the most numerous flower visitors in the area (Høye and Forchhammer 2008). Additionally, six wader species breed in the Zackenberg Valley, predominantly sanderling (*Calidris alba*), dunlin (*Calidris alpina*) and ruddy turnstone (*Arenaria interpres*) (Meltofte et al. 2008b).

Data were collected annually from 1996 until 2012, as a part of the Zackenberg Basic monitoring program, by permanent staff and assistants. Thus, the dataset comprised of 17 annual observations per variable and embraced both phenological and performance variables. Some variable had multiple annual replicas, but overall data were sampled through time rather than space. Overview of variables and sampling is shown in Table 1. For a detailed sampling procedure, see Schmidt et al. (2012).

Structural equation model: measurement component

A structural equation model (SEM) framework was used to evaluate hypotheses about direct and indirect interaction patterns of the selected consumer–resource system and to use latent variables (Pugesek 2003). Applying latent variables enables the merging of identical variable types from different species into trophic levels through a coherent assemblage of indicators (Grace 2006). The analysis

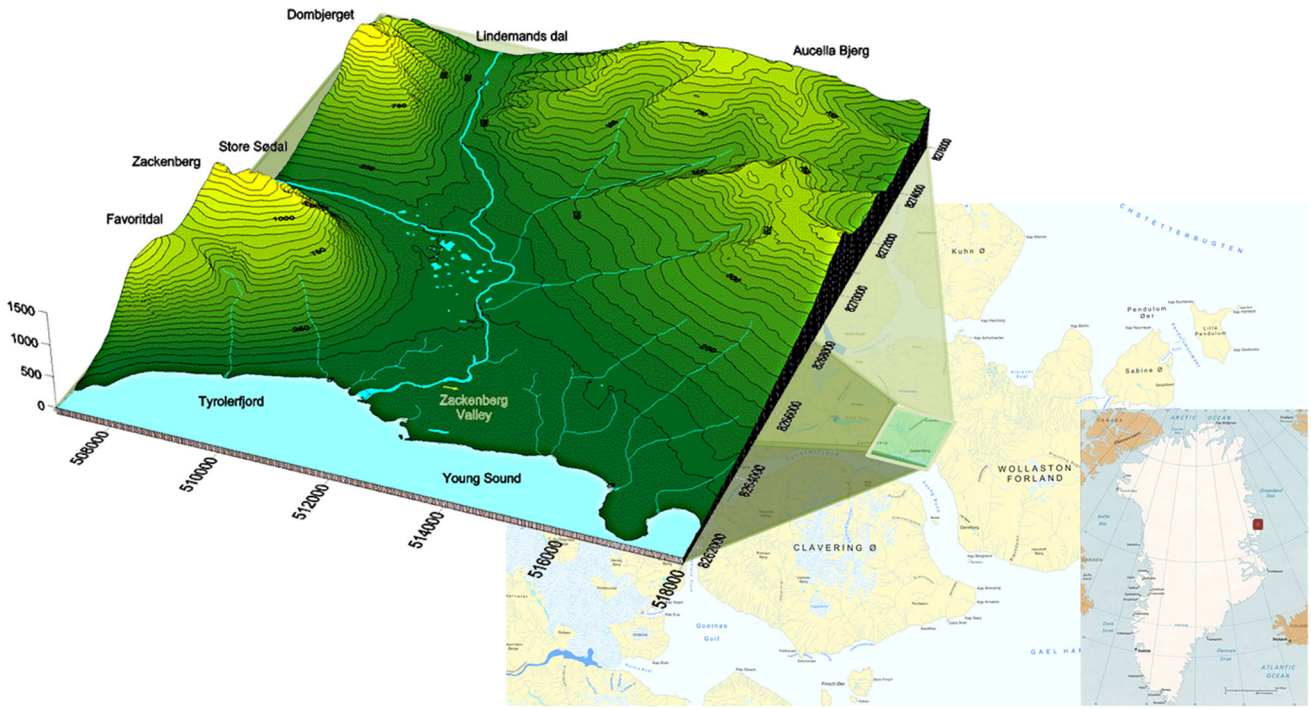

Fig. 1 Map of Zackenberg Valley (74°30′N, 20°30′W) adapted from Mortensen et al. (2014)

included two measures of snowmelt, two measures for two species of plants (i.e. indicators for phenology, performance in year t and performance in year $t + 1$), two measures for two families of arthropods (i.e. indicators for phenology, performance in year t and performance in year $t + 1$) and two measures for three species of waders (i.e. indicators for phenology and performance) (Table 1), respectively, which were used as indicators for the nine latent factors included in the tri-trophic system. Latent variables were only used in the biotic components of the model and were used to group individual trophic levels into phenological and performance latent variables. Latent variables for phenological measures were assumed to be unspecified underlying shared mechanisms causing the initiation of the measured life cycle trait in the individual trophic level. The performance latent variables were assumed to be measures of how well each trophic level is performing and are expressed in both reproductive and abundance measures. However, the common term "performance" was used across all trophic levels to offer a comparable terminology.

The two snow phenology variables were expressed as the timing of snowmelt (Table 1), described by the day of year with 50 % (DOY50 %) snow cover in plant plots and arthropod plots, respectively. DOY50 % was calculated from weekly snow observations in plant and arthropod plots, by linearly interpolated the day with 50 % from days with above and below 50 % snow cover (Høye et al. 2007).

The plant community was represented by three latent factors (Table 1), covering plant phenology and plant performance in current (year t) and the following year (year $t + 1$). Each latent factor used three indicators species: Arctic bell-heather (*C. tetragona*), mountain avens (*Dryas* sp.) and Arctic willow (*S. arctica*), which are the three most abundant plant species in the valley aside from grasses (Elberling et al. 2008) and therefore also potentially the primary resources for flower-visiting arthropods (Olesen et al. 2008). As an estimate of plant phenology, the day of year with 50 % open flowers was estimated by linear interpolation from the weekly counts of buds and open flowers. The average number of flowers produced per m^2 across monitoring plots was used as a plant performance measure. This number was calculated by summarising the total number of buds, flowers and senescent flowers counted at peak flowering, divided by the plot area (m^2) and averaging across plots of each species (Table 1).

The latent factors for the arthropod community's phenology and performance were represented by two Diptera families: nonbiting midges (Chironomidae) and house flies (Muscidae), which are the two most abundant families of insects in the valley and also represent the main food items of Arctic breeding waders (Warnock and Gill 1996; Nettleship 2000; Macwhiter et al. 2002) (Fig. 2). Arthropods were sampled weekly from late May to end of August from five stations, each containing eight pitfall traps (1996–2006) or four pitfall traps (2007–2012), distributed

Table 1 Overview of latent variables used in the model and the indicators used to describe them, along with indicator measures (Schmidt et al. 2012)

Latent variable	Indicator	*N*	Area	Measures	Calculation
Snowmelt	Snowmelt in plant plots	22 plots		Day of year when 50 % snow cover has melted from monitoring plant plots	Average DOY50 across all plant plots
	Snowmelt in arthropod plots	6 stations		Day of year when 50 % snow cover has melted from monitoring arthropod plots	Average DOY50 across all arthropod plots
Plant flowering phenology	Arctic bell-heather (*Cassiope tetragona*)	4 plots	10 m^2	Day of year when 50 % flowers have emerged in monitoring plant plots	Plots visited on weekly intervals and day with 50 % emerged flowers are extrapolated across visits
	Mountain avens (*Dryas sp.*)	6 plots	169 m^2		
	Arctic willow (*Salix arctica*)	7 plots	756 m^2		
Arthropod emergence phenology	Chironomidae sp. emergence Muscidae sp.	2 window traps and 20 pitfall traps distributed on 6 stations	Day of year when 50 % of the total number of arthropods has been caught	Traps were emptied on a weekly basis, and 50 % caught individuals were extrapolated across weeks	
Wader phenology (Egg laying phenology)	Ruddy turnstone (*Arenaria interpres*) Sanderling (*Calidris alba*) Dunlin (*Calidris alpina*)	15.8 km^2 survey area sampled in mid-June. All snow-free patches are inspected	Average day of year for first egg laying estimated from 2–4 nest visits		
Plant performance in year t and $t + 1$ (flower density N/m2)	Arctic bell-heather (*Cassiope tetragona*)	4 plots	10 m^2	Total number of flowers produced per m2, estimated from number of buds, flowers and senescent flowers	All flowers, mature flower buds and senescent flowers in each plot are counted peak flowering and averaged across plots
	Mountain avens (*Dryas* sp.)	6 plots	169 m^2		
	Arctic willow (*Salix arctica*)	7 plots	756 m^2		
Arthropod performance (numbers caught per trap day)	Chironomidae sp. emergence Muscidae sp.	2 window traps and 20 pitfall traps distributed on 6 stations	Total abundance of arthropods caught in pitfall traps divided by the number of trap days		
Bird performance (nest success)	Ruddy turnstone (*Arenaria interpres*) Sanderling (*Calidris alba*) Dunlin (*Calidris alpina*)	15.8 km^2 survey area sampled in mid-June	Estimated nest success (%)		

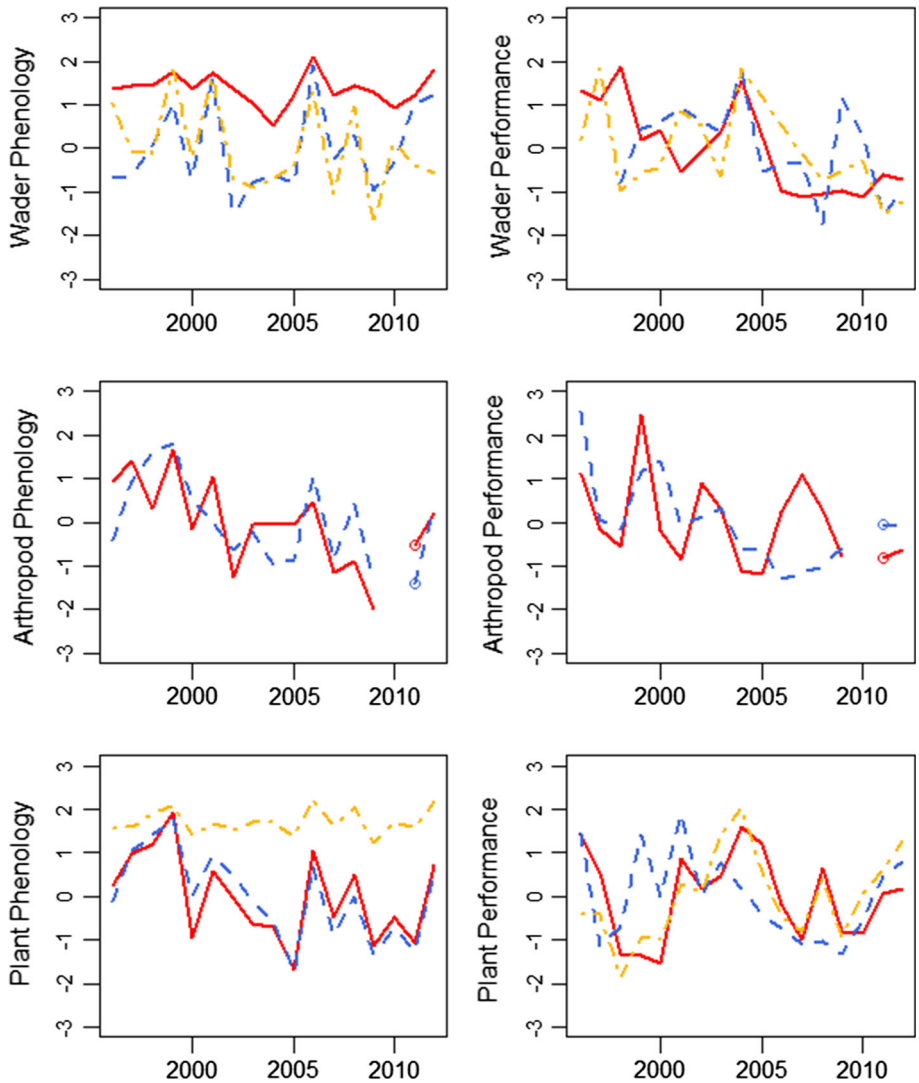

Fig. 2 Temporal trends of indicators used in the structural equation model. Plants include Arctic bell-heather (*C. tetragona*, red solid), mountain avens (*Dryas octopetala*, *blue dashed*) and Arctic willow (*S. arctica*, *yellow dot dashed*). Arthropods embrace Chironomidae (*red solid*) and Muscidae (*blue dashed*). Waders embrace sanderling (*C. alba*, *red solid*), dunlin (*C. alpina*, *blue dashed*) and ruddy turnstone (*Arenaria interpres*, *yellow dot dashed*). The *y*-axis of all phenology variables shows square-root-transformed day of year measurements, and all performance variables were standardised by $V_n = {}^{V-\bar{x}}/_{SD}$, where V_n is the normalised value, V the original value, $\bar{x}$ the time series average across years, and SD the standard deviation of the time series. Note that gap in arthropod data is due to missing data in 2010

in the valley. The day of year when 50 % of the total number of arthropods of each family has been caught (DOY50 %) was used as measure for arthropod emergence phenology. DOY50 % was interpolated by accumulating weekly samples, until the day of year with more than 50 % caught arthropods, and the median DOY before and after 50 % caught arthropods was calculated. Arthropod performance was expressed as the total number of arthropods of each family caught in all pitfall traps during each season divided by the number of trap days (Schmidt et al. 2012). No arthropod data were available for 2010 (see data analysis and model challenges).

The latent factors for the wader community's indicators were represented by sanderling, dunlin and ruddy turnstone, which are the most common wader species in the valley (Meltofte et al. 2008b) (Fig. 2). Nests searches were carried out within a designated census area covering 15 km^2 (Schmidt et al. 2012), and day of year for average nest initiation was estimated by egg flotation (Hansen et al. 2011), constituting the measure for wader phenology (Schmidt et al. 2012). The wader performance measure was the nest success (i.e. eggs surviving until hatched) in percentages of each wader species.

All day of year measurements were square-root-transformed, and all performance variables were normalised by $V_n = {}^{V-\bar{x}}/_{SD}$, where V_n is the normalised value, V the original value, $\bar{x}$ the time series average across years, and SD the standard deviation of the time series (Fig. 2.). All data were normally distributed (Lilliefors test, $p > 0.05$) after standardisation and transformation.

Structural equation model: structural component

The analysis encompassed a tri-trophic system (Fig. 3), where the annual timing of snowmelt was used as climatic driver, while the reproductive/emergence phenology (timing) and performance (abundance and nest success) of

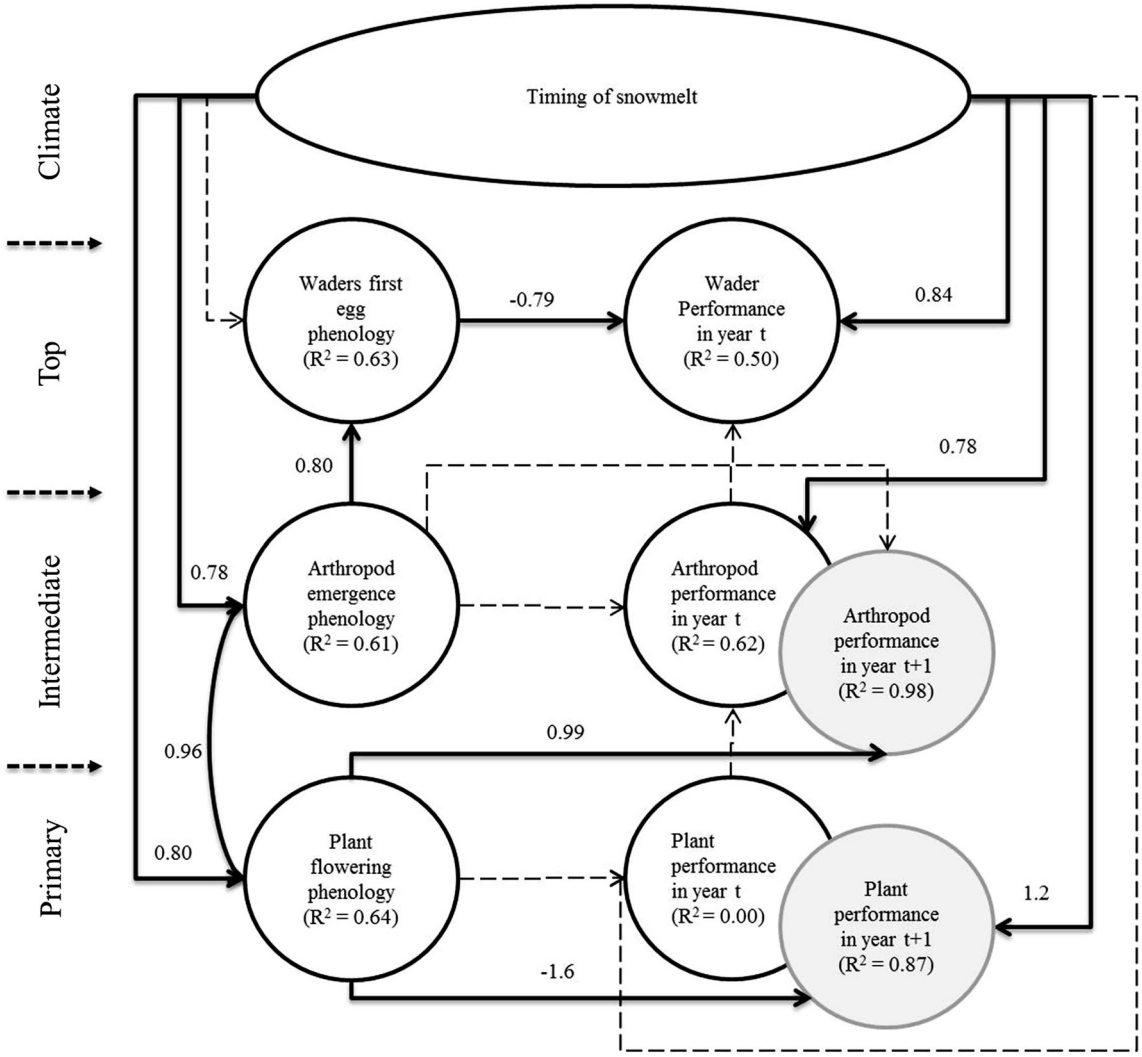

Fig. 3 Structural equation model of a tri-trophic system in Zackenberg, Greenland. Measurement model is congeneric, with key species and taxa as indicators for each latent factor. *Black circles* are temporally in year *t*, while *grey circles* are in year $t + 1$. The structural model hypothesised an effect of snow cover on all latent factors, while the phenology of arthropods is also hypothesised to affect wader phenology. In turn, the phenology of each trophic level is hypothesised to affect the performance of the same trophic level, while changes in one trophic level are likely to cascade onto the next level. Arthropod performance and plant phenology were also hypothesised to affect the plant performance in the following year. Removed links and latent variables through model reduction are dashed, whereas the resulting significant ($p < 0.05$) links are indicated by *thick black lines* with standardised values. R^2 values represent the proportion of variation explained in the individual latent variable. Sign of numbers indicates an increase or decrease. Values indicate magnitude of change

plants, arthropods and waders were used as the tri-trophic system response. Timing of snowmelt was hypothesised to affect each trophic level in the full SEM (Fig. 3), as defined in Hair et al. (2010). The timing of snowmelt was selected as the sole climate variable, as the duration of snow cover is one of the most important governing factors controlling Arctic ecosystems (Meltofte et al. 2008a). Previously, the duration of snow cover has been shown to have significant effects on plant growth and phenology (Jonas et al. 2008; Cooper et al. 2011), arthropod emergence phenology (Høye and Forchhammer 2008) and birds' nest initiation phenology (Meltofte et al. 2008b). Therefore, effects of snow cover were hypothesised to have a significant effect on the phenology and performance of all included species. Additionally, because Arctic flowers produce flower buds the year prior to flowering, current year's snowmelt was also hypothesised to affect flower performance in the following years (Sørensen 1941). Although other climatic variables have been demonstrated to have an impact on Arctic systems (e.g. Bolduc et al. 2013), these were not selected in order to keep as simplistic a model as possible.

Synchrony between arthropods and plants has previously been observed (Iler et al. 2013b), likely due to identical climate drivers, and a covariation between plant and arthropod phenology was therefore expected. Additionally, because timing of food availability is a major determinant of nest initiation for waders of the High-Arctic (Meltofte et al. 2008b; McKinnon et al. 2012), we expected an interaction between arthropod and wader phenologies.

An effect of phenology on performance within all trophic levels was integrated in the full SEM, as previous studies have demonstrated changes in performance as a result of a changing phenology (Miller-Rushing et al. 2010; Cooper et al. 2011). For example, time of flowering can affect current year's number of flowers, if early flowering induces frost damage on flower buds (Inouye 2008; Semenchuk et al. 2013). Likewise, time of emergence of the arthropods could affect the arthropod abundance by affecting the hatching success, where early emergence could expose arthropods to adverse conditions, as with the flowers (Strathdee and Bale 1998).

The effect of plant phenology on plant performance in the following year was also included in the model, as Arctic vascular plants produce flower buds the year before flowering and current year's effects could therefore proliferate onto next year (Bell and Bliss 1980). The effect of arthropod phenology on arthropod performance in the subsequent year was also included in the model, as it has been demonstrated that the timing of arthropod emergence in relationship with the flowering season affects the population size in the following year (Høye et al. 2013). We did not expect wader phenology to affect performance in the subsequent year, because waders are migratory and effects on the subsequent year are likely to be outside the current study area.

A cascading effect from plan–arthropod–wader performance was also hypothesised, as changes in a lower trophic level could affect higher trophic levels as food resource changes, in this externally forced system. Additionally, Høye et al. (2013) proposed an effect of overlap between the plants' flowering season and flower visitor flight season on arthropod abundance in the subsequent year. We therefore included an effect of the plant phenology on the arthropod performance in the full SEM. Effects of current year performance on the subsequent year performance were not included in the latent variable of each trophic level, as no autoregressive structure has been reported within the included species.

Data analysis and model challenges

Tests and modelling were performed in R (version 2.15.1) using the package "`lavaan`" for the structural equation modelling (Rosseel 2012). Missing data were estimated by maximum likelihood, using the "`missing=''ml''`" function in "`lavaan`," and maximum likelihood function was used as estimator in the SEM. Final model selection was accomplished using a model generation approach (Kline 2011), which means that the initial SEM defined in previous paragraph was reduced through a stepwise removal of the relationships with the highest p value until only significant regression remained.

A series of solutions with negative error variances or standardised factor loadings above one arose during the initial modelling phase, probably due to the low sample size-to-the number of indicators ratio (16 samples to 21 indicators) (Sharma et al. 2005) and too many free parameters (Kline 2012). While the dataset covered 17 annual observations, there was no spatial replication. To reduce the number of free parameters, factor loadings of all performance indicators were constrained to 1, thus assuming tau-equivalence between the indicators of each latent factor (Hair et al. 2010). Additionally, the variance of the latent variables was set to 1 during model reduction, until sufficient parameters had been constrained by model reduction. For comparison, a model with averages of indicators instead of latent variables was also reduced from the initial SEM, which had a sufficient amount of free parameters for model estimation.

Direct effects were estimated as beta-coefficients (standardised estimates), indirect effects as the product of beta-coefficients involved and total effects as the sum of direct and indirect effects.

Results

The initial full model contained 8 latent factors, 21 indicators, 16 regressions and 1 covariation (Fig. 3). Stepwise pruning of paths resulted in a reduced model (SEM_{lat}) including 9 regressions and 1 covariance (Fig. 3). However, the resulting model with latent variables (SEM_{lat}) did not show any significant goodness-of-fit indices ($\chi^2 = 1626$, $p < 0.0001$, RMSEA $= 0.69$, $p < 0.0001$), probably due to a low sample size-to-indicator ratio (Iacobucci 2010). Thus, a path analysis approach was used in order to validate the model structure, as path analysis is a simplified SEM without latent variables (Grace 2006). The standardised indicators of each latent variable were averaged, resulting in one measurement variable per latent variable, reducing the number of variables in the model from 21 to 8. The path analysis model (SEM_{avg}) was reduced as with the SEM_{lat}, by stepwise pruning of paths. Results from the path analysis (SEM_{avg}) yielded almost the same results as the latent variable SEM (Table 2) in addition to significant goodness-of-fit indices ($\chi^2 = 32$, $p = 0.17$, RMSEA $= 0.13$, $p = 0.22$). It is therefore likely

that the lack of goodness-of-fit indices in SEM_{lat} is due to low sample size and not due to misspecification. The following results are therefore reported for the SEM_{lat} and can be compared with results from the SEM_{avg} in Table 2.

Overall, the SEM_{lat} demonstrated an impact of the timing of snowmelt on all trophic levels, with a positive slope effect on flowering phenology (beta-coefficient: $\beta = 0.80$, $p < 0.0001$), abundance in the subsequent year ($\beta = 1.2$, $p < 0.0001$), arthropod emergence phenology ($\beta = 0.78$, $p = 0.007$) and wader nest success ($\beta = 0.84$, $p = 0.018$). In other words, earlier snowmelt leads to earlier flowering, earlier arthropod emergence and a decrease in wader nest success in the concurrent years, together with a reduction in flower abundance in the subsequent year. Additionally, flowering phenology had a negative slope effect on the abundance of flowers in the subsequent year ($\beta = -1.6$, $p < 0.0001$), indicating that earlier flowering leads to an increase in the abundance of flowers in the following year. The combined direct effect of snowmelt on plant performance ($\beta = 1.2$) and indirect effect of snowmelt through plant phenology ($\beta = -1.28$) resulted in a very weak total effect of snowmelt on plant performance in the subsequent year ($\beta = -0.08$).

Plant flowering phenology displayed covariance with timing of arthropod emergence ($\beta = 0.96$, $p = 0.039$) and an effect on the abundance of arthropods in subsequent year ($\beta = 0.99$, $p = 0.001$). This indicates (1) that timing of flowering and timing of arthropod emergence are relatively synchronous, i.e. emerge at the same time relative to each other, and (2) that earlier flowering would be associated with a reduction in the arthropod abundance in subsequent year. Hence, arthropod abundance is indirectly affected by snowmelt through timing of plant flowering ($\beta = 0.79$), leading to a positive overall effect of snowmelt on arthropod abundance ($\beta = 1.6$), although this effect was displaced in time divided over two subsequent years (Fig. 3).

Lastly, arthropod emergence phenology was shown to have an effect on wader egg laying phenology ($\beta = 0.80$, $p = 0.012$), which in turn had an effect on wader nest success ($\beta = -0.79$, $p = 0.046$), indicating that earlier arthropod emergence leads to an earlier egg laying, which subsequently leads to increase in nest success. Thus, the timing of snowmelt was indirectly associated with wader egg laying phenology ($\beta = 0.62$) and wader nest success ($\beta = -0.49$), which results in a positive slope of the total effect of snowmelt on wader nest success ($\beta = 0.35$), indicating that earlier snowmelt potentially reduces the wader nesting success.

Disentangling the climate effects into direct and indirect effects (Table 3) showed that the climate effects on plant performance and wader performance were counteracted by biotic interactions, dampening the effects of snow melt. However, the climate effects on arthropod performance

Table 2 Comparison of beta-weights in the SEM with latent variables (SEM_{lat}) and SEM with averages (SEM_{avg})

	Snowmelt	Plant.Phe	Plant.PerT1	Arth.Phe	Arth.Per	Arth.PerT1	Wader.Phe	Wader.Per
SEM_{lat}								
Snow Melt	–	0.80**	1.2**	0.78**	0.78**	–	–	0.84*
Plant.Phe	–	–	−1.6**	~0.96*	–	0.99**	–	–
Plant.Per	–	–	–	–	–	–	–	–
Arth.Phe	–	~0.96*	–	–	–	–	0.80**	–
Arth.Per	–	–	–	–	–	–	–	–
Arth.PerT1	–	–	–	–	–	–	–	–
Wader.Phe	–	–	–	–	–	–	–	−0.79*
Wader.Per	–	–	–	–	–	–	–	–
SEM_{avg}								
Snow Melt	–	0.81**	0.63’	0.71**	0.58**	–	–	0.54*
Plant.Phe	–	–	−0.97**	~0.64*	–	0.68**	–	–
Plant.Per	–	–	–	–	–	–	–	–
Arth.Phe	–	~ 0.64*	–	–	–	–	0.65**	–
Arth.Per	–	–	–	–	–	–	–	–
Arth.PerT1	–	–	–	–	–	–	–	–
Wader.Phe	–	–	–	–	–	–	–	−0.53*
Wader.Per	–	–	–	–	–	–	–	–

Phe. is phenology, PerT1 is performance at time + 1, while Per is performance. Sign of numbers indicates an increase or decrease. Magnitude of numbers is indications of the size of change

’ $p < 0.07$; *$p < 0.05$; ** $p < 0.01$

were accentuated by the biotic interactions with plant phenology, leading to a larger climatic impact, than if only direct effects were considered.

Discussion

The current study presents a detailed analysis of a tritrophic Arctic food web. We found that the timing of snowmelt influences multiple components of the ecosystem and that the effect of timing of snowmelt propagates through the trophic system by biotic interactions, which is in accordance with findings of other studies (Meltofte et al. 2008b; Grabowski et al. 2013; Høye et al. 2013; Iler et al. 2013a). Additionally, we were able to disentangle the direct climate effects from indirect biotic effects and to demonstrate that climate effects on the performance of individual trophic levels were dampened by species phenology, suggesting an inert ecosystem resilience (Holling 1996). Based on our results, it is therefore likely that Arctic ecosystems are able to absorb at least some of the predicted perturbations from climate changes.

However, studies have shown that the timing of snowmelt is likely to drastically advance in the future (Overland et al. 2011). Iler et al. (2013a) suggested that some Arctic species are already reaching the limits of their phenological range capacity, supporting the notion on the existence of ecosystem thresholds in the Arctic (Post et al. 2009). Similarly, wader phenology in the current study was demonstrated not to be fully able to compensate for the adverse impact of earlier snowmelt on wader performance. Thus, although the current study suggests an inherent resilience to the advancing time of snowmelt, it is likely that the dramatic predicted temperature increases will push the ecosystem to the limits of its plasticity. Exceeding the limits of the plasticity of individual species can result in either sudden or gradual changes in species composition and/or abundance, depending on the species traits. The sum of the species responses is, thus, likely to be the ecosystem response, creating an ecosystem tipping point (Lenton 2012) or a gradual change in ecosystem composition and function. Predicting which ecosystem outcome is likely to occur is inherently difficult as all interactions within the ecosystem are to be taken into account and the relative importance of each interaction is to be estimated against ecosystem functioning and structure.

Intrinsic model dynamics

Our model showed that plant phenology responded to earlier snowmelt by advancing the timing of flower emergence accordingly. Other studies have documented cases where this response was nonlinear (Høye et al. 2007; Iler et al. 2013a), indicating limits to the plasticity of plants' phenological responses. It is therefore possible that further advance in snowmelt dates will not be paced accordingly in the timing of flowering, which in turn is likely to affect the abundance of flowers produced. Our model also indicated a very small total effect of climate on the abundance of flowers, because the direct effect of snowmelt was counteracted by the indirect effect mediated through flowering phenology. Flower abundance was reduced with the advancement of snowmelt dates possibly due to the increasing exposure to freezing events (Inouye 2008; Wheeler et al. 2015), but counteracted by the advancement in flowering dates which increased the length of the growing season. However, a potential future reduction in phenological response to snowmelt will reduce the total indirect effect of snow on flower abundance. This may subsequently increase the total effect of snow, resulting in a decrease in flower abundance with advancing snowmelt dates (Wheeler et al. 2015).

Our model also demonstrated a covariance between plant phenology and phenology of Muscidae and Chironomidae, likely through similar dependencies to climatic driver (Forrest and Thomson 2011). An earlier time of snowmelt directly reduced the abundance of arthropods, probably due to reduced soil moisture due to earlier reductions in melt-water supply. However, arthropod phenology did not appear to affect arthropod performance. Indirectly, the timing of snowmelt affected arthropod abundance in the subsequent year, mediated through a

Table 3 Table of direct and indirect effects of snowmelt on the selected components

Latent variable	Plant phenology	Plant performance	Arthropod phenology	Arthropod performance	Wader phenology	Wader performance
Direct	0.80	1.2	0.78	0.75	0	0.74
Indirect	0	−1.3	0	0.78	0.62	−0.45
Total	0.8	−0.1	0.78	1.53	0.62	0.29

Plant performance and arthropod performance show the combined effect on current and subsequent year. Direction of numbers indicates an increase or decrease. Magnitude of numbers is indications of the size of change

change in flowering phenology. Høye et al. (2013) suggested a differential phenological response to climate resulting in a "de facto" shortening of the flower season. It therefore seems that advances in timing of snowmelt are reducing arthropod abundances on two temporal scales. However, the total effect is difficult to estimate, because we found no direct density dependence in the arthropod abundance.

Likewise, timing of nest initiation of waders depended on the emergence of arthropods, which is typical for income like migrating Arctic waders, who rely on energy and nutrient sources acquired immediately prior to breeding for reproductive investment (Klaassen et al. 2001). The measure for arthropod phenology in our paper is indirectly a measure for the timing of food resources available for waders (Warnock and Gill 1996; Nettleship 2000; Macwhiter et al. 2002). Thus, arthropod phenology is a measure for how early waders can access and obtain a sufficient energy and nutrient supply for breeding initiation (Klaassen et al. 2001). Earlier emergence of arthropods enables waders to initiate breeding earlier, which is in line with the increase we found in wader performance as a consequence of earlier egg laying. It has been suggested that earlier egg laying may lead to increased egg predation from predators, such as the Arctic fox (Meltofte et al. 2007). However, it also increases the possibility for re-laying, which reduced the negative effects on the nest success of the waders (Meltofte et al. 2007). The current model showed a direct effect of snowmelt on the wader performance, with a reduction in nest success with advancing snowmelt dates, which resulted in a total reduction in nesting success in response to earlier snowmelt, possibly as a result of lower success of relaid clutches following, e.g. predation.

Using SEM to analyse ecosystems

The choice of SEM for the current study proved highly useful, since the use of latent variables made it possible to make more general conclusions. Additionally, the use of SEM facilitated more realistic statements about the interaction patterns in the system across trophic levels (Pugesek 2003), which could not be made on the same scale with conventional regression models. Additionally, the SEMs allow for the incorporation of previous knowledge on variable associations (Kline 2011), which is well suited to study areas like Zackenberg with continuous long-term monitoring and research. On the downside, SEMs require larger sample sizes than alternative multivariate methods (Hair et al. 2010) which was evident in the lack of goodness-of-fit in the initial latent variable model. However, refitting the model as a path analysis demonstrated the same ecosystem structure as the full SEM, indicating that the full SEM was justly specified, but lacked sample size to calculate goodness-of-fit indices.

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Compliance with ethical standards

Ethical statement All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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