OIKOS

Research Article

Predator density outweighs experimental warming effects on short-term carbon and nitrogen loss from arctic shrub litter

Nevo Sagi[1], **Anna M. Cress**[1], **Jennie R. McLaren**[2] **and Amanda M. Koltz**[1]

[1]Department of Integrative Biology, The University of Texas at Austin, Austin, TX, USA
[2]Department of Biological Sciences, The University of Texas at El Paso, El Paso, TX, USA

Correspondence: Nevo Sagi (nevo.sagi@austin.utexas.edu)

Oikos
2026: e11529
doi: 10.1002/oik.11529
Subject Editor: James D. Roth
Editor-in-Chief:
Paulo R. Guimaraes
Accepted 14 September 2025

Rapid climate change in the Arctic is altering biological communities and their subsequent effects on ecosystem functioning. For example, warming-induced shrub expansion accelerates biogeochemical cycles in part by increasing high-quality litter inputs. Likewise, warming may enable higher densities of wolf spiders, which are dominant invertebrate predators whose activities indirectly alter plant litter decomposition rates. Although shrubs and wolf spiders are responding to climate change simultaneously, it is unclear how more shrub litter and more spiders together will influence elemental cycling in Arctic ecosystems. To test how warming could influence these processes, we used a fully factorial mesocosm experiment to quantify effects of wolf spiders on litter decomposition of an expanding species of dwarf deciduous shrub *Betula nana* under ambient and warmed conditions. We found higher densities of wolf spiders were consistently associated with more litter mass loss, and more C and N release regardless of warming treatment, indicating biotic interactions may be a stronger driver of short-term *B. nana* litter decomposition than warming when wolf spiders are present. Our findings suggest the combined effects of warming-induced shifts in plant and arthropod communities may further accelerate C and N cycling, which could cause positive feedbacks on Arctic shrub expansion.

Keywords: climate change, decomposition, nutrient cycling, shrub expansion, trophic cascade, wolf spiders

Introduction

Global climate change is altering ecosystems and the communities that inhabit them in countless ways (Grimm et al. 2013). Although responses by different species may have interactive effects on ecosystem functioning (Thakur 2020, Vandvik et al. 2020, Wang et al. 2023), studies tend to focus on single species responses (Weiskopf et al. 2020) which limits our ability to capture overall effects of climate change (Tylianakis et al. 2008). Interactive effects of multi-species responses to climate change may be particularly pronounced in the Arctic, where warming has been fourfold faster than the global average (Rantanen et al. 2022). Organisms across all trophic levels are responding to

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this warming, ranging from plants to microbes to invertebrate and vertebrate animals (Deslippe et al. 2012, Bjorkman et al. 2018, Davidson et al. 2020, Høye et al. 2021). How multispecies responses affect ecosystem-level processes is highly relevant in this system, because Arctic soils store nearly half of the global pool of soil organic carbon (C) (Tarnocai et al. 2009, Schuur et al. 2015, Crowther et al. 2019). Therefore, changes in species interactions that affect release of this C to the atmosphere could exacerbate global climate change (Schuur et al. 2015, Xue et al. 2016).

Rapid climate change in the Arctic has driven major shifts in plant productivity, community composition and phenology (Jia et al. 2003, Bjorkman et al. 2020). In particular, many Arctic and subarctic ecosystems are experiencing deciduous shrub expansion. Shrub expansion into areas historically graminoid-dominated (Tape et al. 2006, Mekonnen et al. 2021) has been attributed to a combination of drivers, including permafrost thaw, changes in soil and microclimate, enhanced microbial activity, and associated increases in nutrient availability (Sturm et al. 2005, Tape et al. 2006, Myers-Smith et al. 2011, Thompson et al. 2017, Mekonnen et al. 2021, Dunleavy and Mack 2024). Areas with higher shrub densities have higher plant biomass but lower plant diversity as herbaceous and non-vascular vegetation are lost (Walker et al. 2006, Wilson and Nilsson 2009, Mod and Luoto 2016). Higher shrub densities may also lead to faster decomposition and higher turnover rates of carbon (C) and nitrogen (N) due to shrub litter having higher nitrogen content and lower C:N than some other tundra species (Hobbie 1996, Chapin and Shaver 1996, Hobbie and Gough 2004, DeMarco et al. 2014a, 2014b, McLaren et al. 2017; although see Cornelissen et al. 2007). Some studies suggest higher rates of nutrient cycling and associated microbial activity could offset C sequestering benefits of higher plant biomass in shrub-dominated areas (Jonasson et al. 1999, Weintraub and Schimel 2005) and result in positive feedback to climate change (Crowther et al. 2016).

Arctic climate change is also altering the life history traits, population dynamics, community composition, and biotic interactions of arthropod communities (Høye 2020). These changes include direct and indirect responses to warming and other aspects of climate change. Disentangling these various effects is challenging - yet essential - for predicting changes in community dynamics and ecosystem functioning. For example, warming directly affects organismal metabolism (Kordas et al. 2022), but it also enables shrub expansion, which alters the resources, habitat structure, and microclimate available to arthropods (Rich et al. 2013, Hansen et al. 2016, Asmus et al. 2018). In wolf spiders, one of the dominant invertebrate predators in the Arctic, responses to direct effects of warming may contrast with those of indirect effects on habitat-level changes. Specifically, although several studies suggest longer Arctic growing seasons will benefit wolf spiders by increasing their fecundity (Høye et al. 2009, 2020), shrub expansion may negatively affect spider populations by reducing their preferred open-tundra habitat (Rich et al. 2013, Hansen et al. 2016, Asmus et al. 2018).

How such direct and indirect responses to climate change play out is broadly relevant, because wolf spiders indirectly influence processes such as decomposition and nutrient cycling (Lensing and Wise 2006, Koltz et al. 2018b, 2024). Further, cascading effects of wolf spiders can vary depending on environmental context (Lensing and Wise 2006, Liu et al. 2015, Koltz et al. 2018b). For example, in the Arctic, higher wolf spider densities led to more decomposition of graminoid litter under ambient conditions but less decomposition under experimental warming (Koltz et al. 2018b). This switch in the effects of wolf spiders on decomposition was explained by an apparent weakening of spider predation pressure on their fungal-feeding Collembola prey under warming (Koltz et al. 2018b). Whether wolf spider activity similarly influences shrub litter decomposition has not been explored despite ongoing shrub expansion (Myers-Smith et al. 2011, Bjorkman et al. 2020) and potential future increases in wolf spider populations (Høye et al. 2009, 2020).

Deciduous shrubs and wolf spiders are widely distributed across the Arctic (Walker et al. 2005, Høye and Forchhammer 2008, Wyant et al. 2011, Koltz et al. 2018a) and have the potential to affect C and nutrient cycling (McLaren et al. 2017, Koltz et al. 2018b). Both groups also seem to be benefitting from climate change (Høye et al. 2009, 2020, Myers-Smith et al. 2011, Mekonnen et al. 2021). Together, this makes deciduous shrubs and wolf spiders an excellent model for testing the consequences of multiple warming-induced species responses on ecosystem processes. We investigated the extent to which warming and predators affect short-term decomposition and C and N loss from litter of an important species of expanding shrub in the North American Arctic. Specifically, we used a fully factorial field mesocosm experiment to test for potential interactive effects of wolf spiders and experimental warming on *Betula nana* leaf litter decomposition during a single Arctic summer. Given previously published findings from this experiment showing warming reversed wolf spider effects on graminoid litter decomposition (Koltz et al. 2018b, 2024), we expected to observe similar effects on shrub litter decomposition. Specifically, we expected increasing wolf spider densities to be associated with more *B. nana* litter decomposition under ambient conditions but less decomposition under the experimental warming treatment.

Material and methods

Site description

We conducted our experiment near Toolik Field Station (68°38′N, 149°43′W, elevation 760 m) on the North Slope of Alaska during June-July 2012. The mean annual temperature of this area is −10°C and annual precipitation ranges between 200–400 mm per year. Our experimental plots were located in moist acidic tundra, which is the dominant habitat type on the North Slope of Alaska (Raynolds et al. 2006, North Slope Science Initiative 2013). The vegetation community is dominated by the sedge *Eriophorum vaginatum*

with deciduous *Betula nana* and evergreen *Rhododendron palustre*, *Vaccinium vitis-idaea* shrubs in roughly equal abundance and mosses forming nearly continuous cover (Shaver and Chapin III 1991, Williamson et al. 2024).

Experimental set-up

We used a fully factorial mesocosm experiment to experimentally test for interactive effects of wolf spider density and warming on *Betula nana* litter decomposition. We focused on this dominant expansive deciduous shrub species because its leaves comprise a large fraction of surface litter in shrub dominated areas, including at our own study site (DeMarco et al. 2014a, 2014b). Five blocks were distributed in a homogenous area of moist acidic tundra, with each block containing a plot for each of the six experimental treatments. The 1.5-m^2 mesocosms were constructed using aluminum flashing that was buried approximately 20 cm belowground and stood 20 cm aboveground. Wolf spiders are not adept climbers, so these conditions were sufficient to contain the wolf spiders, surface-active detritivore community, and the belowground detritivore community. Mesocosms were assigned one of three wolf spider density treatments: low density, control density, and high density. Control densities simulated natural wolf spider densities (approximately 1.1 spider per m^2) based on field surveys conducted in an area adjacent to our experimental plots. For low density plots, we removed all wolf spiders prior to the start of the experiment and maintained the treatment by periodically removing stray wolf spiders that had entered the plots throughout the course of the experiment. High density treatments received enough wolf spiders to double the density of control plots at the beginning of the experiment and subsequently received additional wolf spiders throughout the summer if densities declined. We used visual surveys at the end of the field season to confirm that plot-level wolf spider densities varied according to their pre-assigned treatments (ANOVA: $F_{2,27} = 21.85$, $p = < 0.0001$), with average densities in high-density plots being 3.3 ± 0.47 wolf spiders, control plots 1.8 ± 0.20 wolf spiders, and low-density (removal) plots with 0.3 ± 0.213 wolf spiders each (Koltz et al. 2018b). In the year of our experiment, the wolf spider community in this habitat type around Toolik Lake was dominated by a single species (>95%), *Pardosa lapponica* (Koltz and Wright 2020).

Half of the mesocosms were experimentally warmed using ITEX open-topped warming chambers (OTCs), which are a common experimental method for passive warming in tundra ecosystems. This approach typically increases mean daytime air temperature by 1–2°C (Marion et al. 1997, Hollister and Webber 2000, Dollery et al. 2006, Alatalo et al. 2016, Christiansen et al. 2017, Hollister et al. 2023) and surface temperature by 1.27°C (Healey et al. 2016). OTCs were positioned over the mesocosm plots during the summers of 2011 and 2012 immediately after snow melt (Koltz et al. 2018b). In both years, the experimental warming treatment was in place from approximately mid-June to early August. To account for potential effects of experimental warming on soil moisture, we measured soil moisture at each litter bag location at the beginning, middle, and end of the field season using a HydroSense portable soil moisture probe (Campbell Scientific). We found there were no significant differences in average soil moisture ($t = 0.833$, $df = 87$, p-value = 0.407) between experimentally warmed and control plots.

Litter decomposition, carbon loss and nitrogen loss

We used litter bags to measure how experimental warming and wolf spiders affect litter mass loss, C loss, and N loss using *Betula nana* leaves that were collected locally from live shrubs in July 2010, air dried, and stored indoors at room temperature in paper bags. Prior to deployment in June 2012, *B. nana* leaves were dried at 50°C for 48 h, weighed and loaded into 8 × 8 cm litterbags with approximately 0.75 g litter. The litter content of each bag was recorded individually. The initial litter mass in each litterbag sufficed for the duration of our short-term experiment (Parker et al. 2018, Aguirre et al. 2024) without the risk of overexploitation by decomposers. Litter bags had 3 mm mesh size to allow access by microarthropods. We deployed three replicate litter bags at evenly spaced locations within each plot in early June 2012. This approach was used to avoid artifacts derived from the specific locations of the litterbags within plots, while providing redundancy in case of litterbag loss during the experiment. Litter bags were incubated for six weeks before being collected in late July 2012. This timeframe was chosen to capture the effects of wolf spiders on decomposition during their peak activity period. One litter bag was lost from a high spider density, ambient temperature plot, so that plot only had two replicates. After the 6-week incubation period, we removed litter from bags, cleaned off the debris, weighed and dried it at 60°C for 72 h, and weighed it again to estimate percent mass loss and litter moisture content. Litter was then ground and C and N content measured at the Duke Environmental Stable Isotope Laboratory (DEVIL) using a Carlo-Erba NA1500 elemental analyser feeding a Thermo Finnigan Delta Plus XL continuous flow mass spectrometer system. The % C and N contained within each sample were converted to mass based on the pre- or post-decomposition (initial and final respectively) sample weight and then % of C, N, and total mass remaining were calculated as follows:

$$\%\ \text{remaining} = \frac{[\%_{w/w}]_f \times \text{mass}_f}{[\%_{w/w}]_i \times \text{mass}_i} \times 100$$

where $\%_{w/w}$ represent mass percent of the element in a sample, whereas f and i represent final and initial values.

Analyses

We used linear mixed effects models (LMMs) to test for effects of the warming treatment, wolf spider density treatment, and their potential interaction on % litter mass remaining, % C remaining, and % N remaining. Each model included litter moisture content as a covariate and plot nested in block as

random factors. In all analyses, the interaction term between wolf spider density and the warming treatment was found to be non-significant; consequently, we removed it from all models, resulting in the following model structure:

DV ~ Spider Density + Warming

+ Litter Moisture + (1 | Block / Plot)

where DV is the dependent variable (i.e. % remaining mass, C or N). The intercept was set as the low spider density and ambient temperature treatments. The % remaining litter mass data were log-transformed to meet the normality of residuals model assumption. We used the 'nlme' package (Pinheiro et al. 2025) in R for all analyses.

Results

We found significant and consistent treatment effects of wolf spider density on litter mass loss, litter C loss and litter N loss. Specifically, higher wolf spider densities were associated with less remaining litter mass, litter C and litter N (i.e. higher loss of all three variables) (Fig. 1, Table 1). Our model results indicate the experimental warming treatment did not significantly affect litter mass, C or N loss (Table 1). However, although there were no significant interactive effects of wolf spider density and the experimental warming treatments, we did observe that under low wolf spider densities only, there was a trend towards higher litter mass, C and N loss in warm compared to control plots (Fig. 1). Higher litter moisture content was also associated with significantly more litter mass loss and more litter C loss (Table 1).

Discussion

Rapid warming in the Arctic is hastening elemental cycling by enhancing soil decomposer activity (Feng et al. 2020) and litter biomass and quality through shrub expansion (DeMarco et al. 2014a). Our results suggest wolf spiders may further accelerate these processes through their trophic interactions that regulate decomposer communities. Specifically, our findings show predator densities can outweigh effects of experimental warming on short-term shrub litter decomposition, C- and N-release (Fig. 1). This work resonates with other research showing wolf spiders indirectly influence decomposition (Lensing and Wise 2006, Liu et al. 2016, Koltz et al. 2018b) and plant-available soil N (Koltz et al. 2018b, Wilder et al. 2024), suggesting this widespread invertebrate predator may play an underappreciated role in driving C and N cycling that could contribute to positive feedbacks on shrub expansion.

Our findings align with a growing body of work showing wolf spider activity is associated with more decomposition in a range of terrestrial ecosystems (Lawrence and Wise 2000, Lensing and Wise 2006, Liu et al. 2016, Koltz et al. 2018b). Although experimental warming did not alter wolf spiders influence on short-term decomposition in this study (Table 1), others have pointed to the context-dependency of these types of effects (Lensing and Wise 2006, Liu et al. 2015, Koltz et al. 2018b). For example, in temperate deciduous and alpine forest sites, wolf spiders and other large invertebrate predators had a positive effect on tree leaf litter decomposition under low rainfall, but a negative effect under high rainfall (Lensing and Wise 2006, Melguizo-Ruiz et al. 2020). The opposite was found in a tropical forest, where wolf spiders enhanced leaf litter decomposition in ambient conditions but slowed it under drought (Liu et al. 2015).

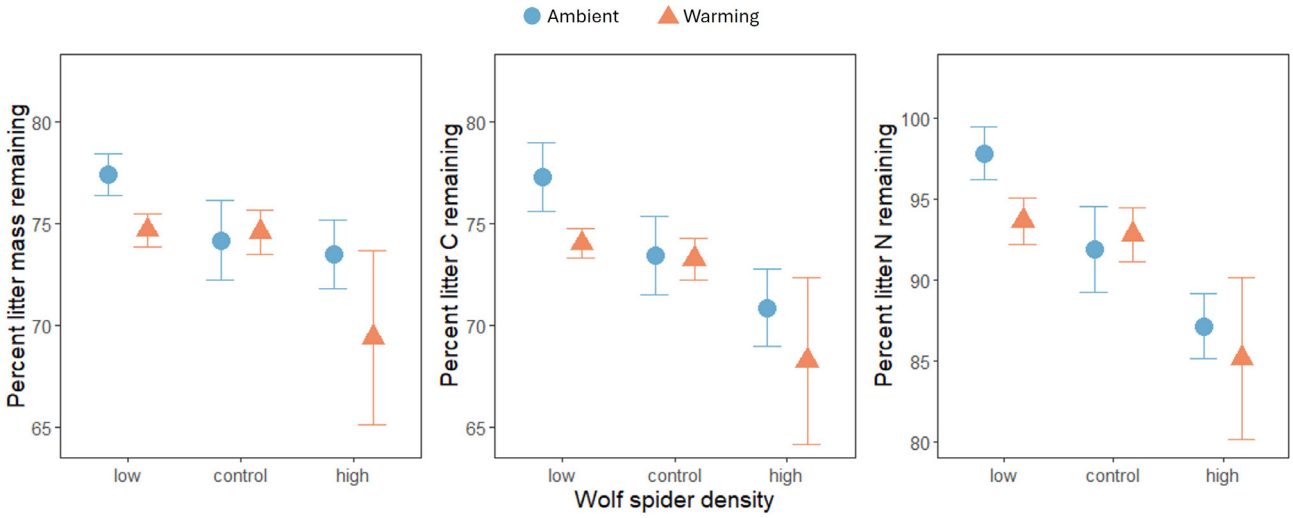


Figure 1. Effects of wolf spider density on percent mass remaining (left), percent carbon remaining (center) and percent nitrogen remaining (right) from *Betula nana* litter. Litter was incubated over six weeks in the Arctic tundra under ambient (blue circles) and experimentally warmed (orange triangles) conditions. Error bars represent SE.

Table 1. Results of linear mixed models testing the effects of wolf spider density, experimental warming and litter moisture on remaining litter mass, C and N. The intercept was defined as low spider density and ambient temperature. Significant effects (p-value < 0.05) are denoted in bold.

	Value	SE	df	t-value	p-value
Litter mass remaining (log-transformed)					
(Intercept)	4.592	0.120	58	38.36	**< 0.0001**
Spider density (control)	−0.022	0.029	22	−0.73	0.47
Spider density (high)	−0.071	0.030	22	−2.39	**0.026**
Warming	−0.032	0.024	22	−1.33	0.20
Litter moisture	−0.004	0.002	58	−2.08	**0.042**
Litter C remaining					
(Intercept)	94.601	6.912	58	13.69	**< 0.0001**
Spider density (control)	−2.166	1.702	22	−1.27	0.22
Spider density (high)	−5.742	1.722	22	−3.34	**0.003**
Warming	−1.794	1.400	22	−1.28	0.21
Litter moisture	−0.259	0.098	58	−2.65	**0.0103**
Litter N remaining					
(Intercept)	96.897	9.038	58	10.72	**< 0.0001**
Spider density (control)	−3.373	2.226	22	−1.52	0.14
Spider density (high)	−9.587	2.251	22	−4.26	**0.0003**
Warming	−1.755	1.830	22	−0.96	0.35
Litter moisture	−0.005	0.128	58	−0.04	0.97

Previously published results from this same experiment in the Arctic tundra after two summers showed more graminoid litter decomposition occurred with higher wolf spider densities but only under ambient temperatures; warming reversed this pattern and resulted in less decomposition when more spiders were present (Koltz et al. 2018b). These interactive effects of wolf spiders and warming were likely driven by changes in abundances of their Collembola prey (Koltz et al. 2018b) and possibly also in microbial community composition (Koltz et al. 2024). Given that Collembola densities varied among the experimental warming plots (Koltz et al. 2018b) but short-term shrub litter decomposition did not over the same period, the trophic cascade responsible for shrub litter decomposition here is still unclear. Characterizing the composition of the shrub litter-associated microbial communities may have provided further insights into the mechanism through which the spiders indirectly affected decomposition.

Although invertebrate activity is often slower in the Arctic due to cold conditions, we show wolf spider effects on shrub litter decomposition were detectable after a single summer. Wolf spiders have been found to influence decomposition on a similarly short timescale in a temperate forest (Lawrence and Wise 2000). However, it took 14 months to detect wolf spider and warming effects on belowground graminoid litter in our same experimental plots in the Arctic (Koltz et al. 2018b, 2024). Previous work has suggested high resource quality of shrub litter could strengthen trophic interactions and enhance top–down control on decomposition (Thakur and Eisenhauer 2015). If so, the short-term effects of wolf spiders on shrub but not graminoid litter decomposition may be partially attributed to detrital resource quality. Together, differing results between graminoid and shrub litter suggest multiple potential mechanisms for spider-induced trophic cascades in tundra ecosystems that may be influenced by the nutritional quality of basal resources. Further exploration of the shrub litter decomposer community could shed light on the differential mechanisms by which spiders regulate shrub and graminoid litter cycling.

In our study, short-term experimental warming did not affect leaf litter decomposition of *B. nana*, which is a highly decomposable (McLaren et al. 2017) and expanding shrub species. These findings corroborate those from a recent meta-analysis showing warming hastens decomposition of grass but not leaf litter from woody plants in cold environments such as the Arctic tundra (Schwieger et al. 2025). This meta-analysis also noted more decomposable litter (i.e. litter that decomposes faster under ambient conditions) seems to be less sensitive to warming in cold regions (Schwieger et al. 2025). One reason for this pattern may be that higher resource abundance under shrubs compared to open-tundra habitats may support more copiotroph-dominated microbial communities (Wallenstein et al. 2007, Adamczyk et al. 2020) that are better adapted to decomposing high quality shrub litter. Such differences in the microbial decomposer community could also affect the strength of potential top–down effects by consumers. Future research would benefit from testing the sensitivity of shrub- versus graminoid-based detrital food webs to warming and clarifying differences in the trophic pathways that influence decomposition.

Our results suggest if wolf spider densities increase with warming as predicted (Høye et al. 2009, 2020, Viel et al. 2022, Wehner et al. 2023), their predation effects could further exacerbate accelerated C and N cycling with continued shrub expansion (Walker et al. 2006, Sistla et al. 2013). However, how the combination of warming and shrub expansion will affect wolf spider populations – and their ultimate impacts on ecosystem functioning – is unclear. Which arthropod groups benefit from warming depends on their physiological capacity to withstand higher temperatures but also their habitat specificity (Bowden et al. 2018, Høye et al.

2021, Sørensen et al. 2024). Indeed, some groups, including wolf spiders, seem to benefit from direct effects of warming and earlier snowmelt (Høye 2020). On the other hand, warming-induced shrub encroachment can negatively affect arthropods by reducing plant diversity (Koch et al. 2015), modifying habitat structure (Greaves et al. 2015), increasing the litter layer (Rich et al. 2013), and changing microclimatic conditions (Hansen et al. 2016, Asmus et al. 2018). For example, previous studies in Arctic Alaska have shown lower wolf spider densities in shrub patches compared with open tundra (Rich et al. 2013, Hansen et al. 2016, Asmus et al. 2018). Shrub expansion may therefore reduce wolf spider densities given their preference for open habitats. The ultimate role of wolf spiders as key regulators of biogeochemical cycles in the warming Arctic will depend on their population sizes, vegetation community dynamics and spatial overlap between wolf spiders and plant functional types. Future work should aim to combine long-term monitoring of vegetation, decomposer and wolf spider assemblages with manipulative experiments to quantify how variation in both wolf spiders and shrubs influence C and nutrient dynamics in tundra habitats.

Our findings also highlight the importance of including biotic interactions when considering how changes in abiotic conditions affect ecosystem processes. Although we did not find interactive effects of wolf spider density and warming on shrub litter decomposition, there was a trend toward more *B. nana* decomposition in the warm plots compared to the controls when spiders had been removed (Fig. 1). Effects of warming in those spider removal plots were roughly on par with effects of including control-level densities of wolf spiders in either ambient or warmed plots. Other recent studies have emphasized how the exclusion of certain animal groups, such as herbivores, can result in under- or overestimations of global change effects on tundra ecosystems (Yu et al. 2011, Rastetter et al. 2022). Inclusion of predation effects that regulate both herbivory and decomposition could further refine these types of models to help achieve more accurate estimations of changes in C and N cycling under various conditions (Schmitz and Leroux 2020, Bianchi et al. 2021).

Our investigation focused on wolf spiders effects on short-term decomposition of *B. nana* shrub litter during the summer season. Short-term decomposition experiments capture the breakdown of mostly labile compounds and largely miss decomposition of more recalcitrant material (Sun et al. 2024). However, large fractions of litter carbon and nitrogen are recycled during this early stage (Blok et al. 2016, Parker et al. 2018, Malhotra et al. 2018). Effects of experimental warming on decomposition may take more time to accrue than direct biotic effects (Schwieger et al. 2025). The results from this short-term study are therefore not indicative of longer-term effects of warming or spiders on shrub litter decomposition. Variation in leaf litter chemistry between different shrub species (Vowles and Björk 2019) may further affect the strength of top–down effects by spiders or other invertebrates. Although not addressed here, shrub canopies also alter the physical environment by providing thermal buffering and could affect decomposer communities and decomposition rates across cold and warm seasons (Aguirre et al. 2021, 2024). Studies that explore the role of detrital food webs in driving short- versus longer-term decomposition across seasons, habitats and plant species would contribute to a more nuanced understanding of the conditions under which invertebrate predators influence litter C and N cycling in Arctic ecosystems.

Our results demonstrate that activity by a dominant invertebrate predator can outweigh effects of experimental warming on early-stage decomposition of a common and expanding shrub species. As temperatures continue to rise in the Arctic, species big and small are being affected. The ways in which these species respond – and how their responses affect species interactions – could have unexpected consequences. In particular, we show that compounding impacts of larger wolf spider populations (Høye et al. 2020) and increasing shrub

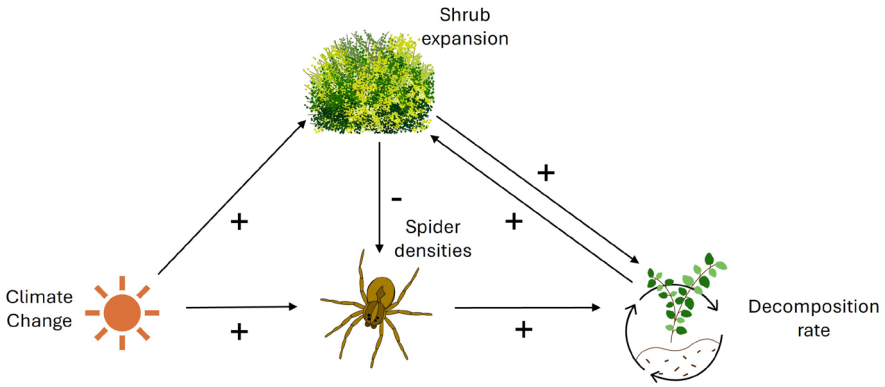


Figure 2. A conceptual framework of the interactions between climate change, shrub expansion, changes in wolf spider densities and decomposition, synthesizing our results with previous findings in Arctic tundra ecosystems. Climate change, including rapid warming, indirectly enhances litter decomposition by stimulating the expansion of shrubs that produce high quality litter and by benefitting wolf spiders, which accelerate shrub litter decomposition through trophic cascades. The hastened nutrient release from decomposing shrub litter under high spider densities may enhance soil nutrient availability which in turn, might promote further shrub expansion. However, how these dynamics may play out at broader scales under shrub expansion is unknown given wolf spiders' preference for open habitats.

litter availability (Mekonnen et al. 2021) could potentially accelerate nutrient cycling (Fig. 2). Although the Arctic has historically been considered to be driven by bottom–up processes, this research contributes to a growing body of work revealing that top–down effects of vertebrates and invertebrates alike contribute to the functioning of tundra ecosystems (Ims and Fuglei 2005, Schmidt et al. 2017, Koltz et al. 2022, Barbero-Palacios et al. 2024).

Acknowledgements – The authors thank Kiki Contreras, Samantha Walker, Jason Stuckey, PolarTREC teachers Nick LaFave and Nell Kemp, and the staff of Toolik Field Station for assistance in the field. *Funding* – Funding for this research was supported by grants to AMK by the U.S. National Science Foundation (grants 1210704 and 1106401); National Geographic Committee on Research and Exploration, Conservation, Research, and Education Opportunities International; Alaska Geographic; the Lewis and Clark Fund; Western Ag Solutions; and the Arctic Institute of North America. NS was supported by BARD, the United States - Israel Binational Agricultural Research and Development Fund, Vaadia-BARD Postdoctoral Fellowship Award No. FI-643-2024; and by a postdoctoral fellowship from the Planning and Budgeting Committee of the Council for Higher Education of Israel.
Conflict of interest – The authors declare no conflict of interest.

Author contributions

Nevo Sagi: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Anna M. Cress**: Conceptualization (supporting); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Jennie R. McLaren**: Investigation (supporting); Writing – review and editing (supporting). **Amanda M. Koltz**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Supervision (lead); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9p8cz8www (Sagi et al. 2025).

References

Adamczyk, M., Perez-Mon, C., Gunz, S. and Frey, B. 2020. Strong shifts in microbial community structure are associated with increased litter input rather than temperature in High Arctic soils. – Soil Biol. Biochem. 151: 108054.

Aguirre, D., Benhumea, A. E. and McLaren, J. R. 2021. Shrub encroachment affects tundra ecosystem properties through their living canopy rather than increased litter inputs. – Soil Biol. Biochem. 153: 108121.

Aguirre, D., Benhumea, A. E. and McLaren, J. R. 2024. Shrub effects on the decomposition microenvironment and changes in litter quality have opposing effects on litter decomposition. – Soil Biol. Biochem. 195: 109472.

Alatalo, J. M., Jägerbrand, A. K. and Molau, U. 2016. Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. – Sci. Rep. 6: 21720.

Asmus, A. L., Chmura, H. E., Høye, T. T., Krause, J. S., Sweet, S. K., Perez, J. H., Boelman, N. T., Wingfield, J. C. and Gough, L. 2018. Shrub shading moderates the effects of weather on arthropod activity in arctic tundra. – Ecol. Entomol. 43: 647–655.

Barbero-Palacios, L. et al. 2024. Herbivore diversity effects on Arctic tundra ecosystems: a systematic review. – Environ. Evid. 13: 6.

Bianchi, T. S., Aller, R. C., Atwood, T. B., Brown, C. J., Buatois, L. A., Levin, L. A., Levinton, J. S., Middelburg, J. J., Morrison, E. S., Regnier, P., Shields, M. R., Snelgrove, P. V. R., Sotka, E. E. and Stanley, R. R. E. 2021. What global biogeochemical consequences will marine animal–sediment interactions have during climate change? – Elem. Sci. Anthr. 9 00180.

Bjorkman, A. D. et al. 2018. Plant functional trait change across a warming tundra biome. – Nature 562: 57–62.

Bjorkman, A. D., García Criado, M., Myers-Smith, I. H., Ravolainen, V., Jónsdóttir, I. S., Westergaard, K. B., Lawler, J. P., Aronsson, M., Bennett, B., Gardfjell, H., Heiðmarsson, S., Stewart, L. and Normand, S. 2020. Status and trends in Arctic vegetation: evidence from experimental warming and long-term monitoring. – Ambio 49: 678–692.

Blok, D., Elberling, B. and Michelsen, A. 2016. Initial stages of tundra shrub litter decomposition May be accelerated by deeper winter snow but slowed down by spring warming. – Ecosystems 19: 155–169.

Bowden, J. J., Hansen, O. L. P., Olsen, K., Schmidt, N. M. and Høye, T. T. 2018. Drivers of inter-annual variation and long-term change in High-Arctic spider species abundances. – Polar Biol. 41: 1635–1649.

Chapin, F. S. and Shaver, G. R. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. – Ecology 77: 822.

Christiansen, C. T., Haugwitz, M. S., Priemé, A., Nielsen, C. S., Elberling, B., Michelsen, A., Grogan, P. and Blok, D. 2017. Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. – Global Change Biol. 23: 406–420.

Cornelissen, J. H. C. et al. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. – Ecol. Lett. 10: 619–627.

Crowther, T. W. et al. 2016. Quantifying global soil carbon losses in response to warming. – Nature 540: 104–108.

Crowther, T. W., van den Hoogen, J., Wan, J., Mayes, M. A., Keiser, A. D., Mo, L., Averill, C. and Maynard, D. S. 2019. The global soil community and its influence on biogeochemistry. – Science 365: eaav0550.

Davidson, S. C. et al. 2020. Ecological insights from three decades of animal movement tracking across a changing Arctic. – Science 370: 712–715.

DeMarco, J., Mack, M. C. and Bret-Harte, M. S. 2014a. Effects of arctic shrub expansion on biophysical vs biogeochemical drivers of litter decomposition. – Ecology 95: 1861–1875.

DeMarco, J., Mack, M. C., Bret-Harte, M. S., Burton, M. and Shaver, G. R. 2014b. Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. – Ecosphere 5: art72.

Deslippe, J. R., Hartmann, M., Simard, S. W. and Mohn, W. W. 2012. Long-term warming alters the composition of Arctic

soil microbial communities. – FEMS Microbiol. Ecol. 82: 303–315.
Dollery, R., Hodkinson, I. D. and Jónsdóttir, I. S. 2006. Impact of warming and timing of snow melt on soil microarthropod assemblages associated with Dryas-dominated plant communities on Svalbard. – Ecography 29: 111–119.
Dunleavy, H. R. and Mack, M. C. 2024. Nonlinear responses of ericaceous and ectomycorrhizal Arctic shrubs across a long-term experimental nutrient gradient. – Ecosphere 15: e4888.
Feng, J. et al. 2020. Warming-induced permafrost thaw exacerbates tundra soil carbon decomposition mediated by microbial community. – Microbiome 8: 3.
Greaves, H. E., Vierling, L. A., Eitel, J. U. H., Boelman, N. T., Magney, T. S., Prager, C. M. and Griffin, K. L. 2015. Estimating aboveground biomass and leaf area of low-stature Arctic shrubs with terrestrial LiDAR. – Remote Sens. Environ. 164: 26–35.
Grimm, N. B., Chapin III, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. A., Schimel, J. and Williamson, C. E. 2013. The impacts of climate change on ecosystem structure and function. – Front. Ecol. Environ. 11: 474–482.
Hansen, R. R., Hansen, O. L. P., Bowden, J. J., Treier, U. A., Normand, S. and Høye, T. 2016. Meter scale variation in shrub dominance and soil moisture structure Arctic arthropod communities. – PeerJ 4: e2224.
Healey, N. C., Oberbauer, S. F. and Hollister, R. D. 2016. Examination of surface temperature modification by open-top chambers along moisture and latitudinal gradients in arctic Alaska using thermal infrared photography. – Remote Sens. 8: 54.
Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. – Ecol. Monogr. 66: 503–522.
Hobbie, S. E. and Gough, L. 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. – Oecologia 140: 113–124.
Hollister, R. D. and Webber, P. J. 2000. Biotic validation of small open-top chambers in a tundra ecosystem. – Global Change Biol. 6: 835–842.
Hollister, R. D. et al. 2023. A review of open top chamber (OTC) performance across the ITEX Network. – Arct. Sci. 9: 331–344.
Høye, T. T. 2020. Arthropods and climate change – arctic challenges and opportunities. – Curr. Opin. Insect Sci. 41: 40–45.
Høye, T. T. and Forchhammer, M. C. 2008. Phenology of high-arctic arthropods: effects of climate on spatial, seasonal, and inter-annual variation. – In: Meltofte, H. et al. (eds), Advances in ecological research. High-arctic ecosystem dynamics in a changing climate. Academic Press, pp. 299–324.
Høye, T. T., Hammel, J. U., Fuchs, T. and Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. – Biol. Lett. 5: 542–544.
Høye, T. T., Kresse, J.-C., Koltz, A. M. and Bowden, J. J. 2020. Earlier springs enable high-Arctic wolf spiders to produce a second clutch. – Proc. R. Soc. B 287: 20200982.
Høye, T. T., Loboda, S., Koltz, A. M., Gillespie, M. A. K., Bowden, J. J. and Schmidt, N. M. 2021. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. – Proc. Natl Acad. Sci. USA 118: e2002557117.
Ims, R. A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – BioScience 55: 311–322.
Jia, G. J., Epstein, H. E. and Walker, D. A. 2003. Greening of arctic Alaska, 1981–2001. – Geophys. Res. Lett. 30: 2003GL018268.
Jonasson, S., Michelsen, A. and Schmidt, I. K. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. – Appl. Soil Ecol. 11: 135–146.
Koch, B., Edwards, P. J., Blanckenhorn, W. U., Walter, T. and Hofer, G. 2015. Shrub encroachment affects the diversity of plants, butterflies and grasshoppers on two Swiss subalpine pastures. – Arct. Antarct. Alp. Res. 47: 345–357.
Koltz, A. M. and Wright, J. P. 2020. Impacts of female body size on cannibalism and juvenile abundance in a dominant arctic spider. – J. Anim. Ecol. 89: 1788–1798.
Koltz, A. M., Asmus, A., Gough, L., Pressler, Y. and Moore, J. C. 2018a. The detritus-based microbial-invertebrate food web contributes disproportionately to carbon and nitrogen cycling in the Arctic. – Polar Biol. 41: 1531–1545.
Koltz, A. M., Classen, A. T. and Wright, J. P. 2018b. Warming reverses top–down effects of predators on belowground ecosystem function in Arctic tundra. – Proc. Natl Acad. Sci. USA 115: E7541–E7549.
Koltz, A. M., Gough, L. and McLaren, J. R. 2022. Herbivores in Arctic ecosystems: effects of climate change and implications for carbon and nutrient cycling. – Ann. N. Y. Acad. Sci. 1516: 28–47.
Koltz, A. M., Koyama, A. and Wallenstein, M. 2024. Warming alters cascading effects of a dominant arthropod predator on fungal community composition in the Arctic. – mBio 15: e0059024.
Kordas, R. L., Pawar, S., Kontopoulos, D.-G., Woodward, G. and O'Gorman, E. J. 2022. Metabolic plasticity can amplify ecosystem responses to global warming. – Nat. Commun. 13: 2161.
Lawrence, K. L. and Wise, D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. – Pedobiologia 44: 33–39.
Lensing, J. R. and Wise, D. H. 2006. Predicted climate change alters the indirect effect of predators on an ecosystem process. – Proc. Natl Acad. Sci. USA 103: 15502–15505.
Liu, S., Chen, J., Gan, W., Schaefer, D., Gan, J. and Yang, X. 2015. Spider foraging strategy affects trophic cascades under natural and drought conditions. – Sci. Rep. 5: 12396.
Liu, S., Chen, J., Gan, W., Fu, S., Schaefer, D., Gan, J. and Yang, X. 2016. Cascading effects of spiders on a forest-floor food web in the face of environmental change. – Basic Appl. Ecol. 17: 527–534.
Malhotra, A., Moore, T. R., Limpens, J. and Roulet, N. T. 2018. Post-thaw variability in litter decomposition best explained by microtopography at an ice-rich permafrost peatland. – Arct. Antarct. Alp. Res. 50: e1415622.
Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. N., Svoboda, J. and Virginia, R. A. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. – Global Change Biol. 3: 20–32.
McLaren, J. R., Buckeridge, K. M., van de Weg, M. J., Shaver, G. R., Schimel, J. P. and Gough, L. 2017. Shrub encroachment in Arctic tundra: Betula nana effects on above- and belowground litter decomposition. – Ecology 98: 1361–1376.
Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C.

and Grant, R. F. 2021. Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. – Environ. Res. Lett. 16: 053001.
Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., Wise, D. H. and Moya-Laraño, J. 2020. Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. – J. Anim. Ecol. 89: 334–346.
Mod, H. K. and Luoto, M. 2016. Arctic shrubification mediates the impacts of warming climate on changes to tundra vegetation. – Environ. Res. Lett. 11: 124028.
Myers-Smith, I. H. et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. – Environ. Res. Lett. 6: 045509.
North Slope Science Initiative 2013. NSSI landcover GIS data: Landcover/Vegetation mapping for north slope of Alaska - north slope science catalog.
Parker, T. C., Sanderman, J., Holden, R. D., Blume-Werry, G., Sjögersten, S., Large, D., Castro-Díaz, M., Street, L. E., Subke, J.-A. and Wookey, P. A. 2018. Exploring drivers of litter decomposition in a greening Arctic: results from a transplant experiment across a treeline. – Ecology 99: 2284–2294.
Pinheiro, J., Bates, D. and R Core Team 2025. nlme: linear and nonlinear mixed effects models. – https://CRAN.R-project.org/package=nlme
Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. and Laaksonen, A. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. – Commun. Earth Environ. 3: 1–10.
Rastetter, E. B., Griffin, K. L., Rowe, R. J., Gough, L., McLaren, J. R. and Boelman, N. T. 2022. Model responses to CO2 and warming are underestimated without explicit representation of Arctic small-mammal grazing. – Ecol. Appl. 32: e02478.
Raynolds, M. A., Walker, D. A. and Maier, H. A. 2006. Alaska arctic tundra vegetation map. – U.S. Fish and Wildlife Service.
Rich, M. E., Gough, L. and Boelman, N. T. 2013. Arctic arthropod assemblages in habitats of differing shrub dominance. – Ecography 36: 994–1003.
Sagi, N., Cress, A., McLaren, J. R. and Koltz, A. 2025. Data from: Predator density outweighs experimental warming effects on short-term carbon and nitrogen loss from arctic shrub litter. – Dryad Digital Repository, https://doi.org/10.5061/dryad.9p8cz8www.
Schmidt, N. M., Hardwick, B., Gilg, O., Høye, T. T., Krogh, P. H., Meltofte, H., Michelsen, A., Mosbacher, J. B., Raundrup, K., Reneerkens, J., Stewart, L., Wirta, H. and Roslin, T. 2017. Interaction webs in arctic ecosystems: determinants of arctic change? – Ambio 46: 12–25.
Schmitz, O. J. and Leroux, S. J. 2020. Food webs and ecosystems: linking species interactions to the carbon cycle. – Annu. Rev. Ecol. Evol. Syst. 51: 271–295.
Schuur, E. Schuur, E. A., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C. and Vonk, J. E. 2015. Climate change and the permafrost carbon feedback. – Nature 520: 171–179.
Schwieger, S. et al. 2025. Environmental conditions modulate warming effects on plant litter decomposition globally. – Ecol. Lett. 28: e70026.
Shaver, G. R. and Chapin III, F. S. 1991. Production: biomass relationships and element cycling in contrasting arctic vegetation types. – Ecol. Monogr. 61: 1–31.
Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R. and Schimel, J. P. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. – Nature 497: 615–618.
Sørensen, J. G., Noer, N. K., Kristensen, T. N. and Bahrndorff, S. 2024. Acclimation to moderate temperatures can have strong negative impacts on heat tolerance of arctic arthropods. – Funct. Ecol. 38: 1549–1561.
Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J. and Romanovsky, V. E. 2005. Winter biological processes could help convert arctic tundra to shrubland. – BioScience 55: 17–26.
Sun, T., Dong, L., Zhang, Y., Hättenschwiler, S., Schlesinger, W. H., Zhu, J., Berg, B., Adair, E. C., Fang, Y. and Hobbie, S. E. 2024. General reversal of N-decomposition relationship during long-term decomposition in boreal and temperate forests. – Proc. Natl Acad. Sci. USA 121: e2401398121.
Tape, K., Sturm, M. and Racine, C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. – Global Change Biol. 12: 686–702.
Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P. Mazhitova, G. and Zimov, S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. – Global Biogeochem. Cycles 23: 2008GB003327.
Thakur, M. P. 2020. Climate warming and trophic mismatches in terrestrial ecosystems: the green–brown imbalance hypothesis. – Biol. Lett. 16: 20190770.
Thakur, M. P. and Eisenhauer, N. 2015. Plant community composition determines the strength of top–down control in a soil food web motif. – Sci. Rep. 5: 9134.
Thompson, J. A., Zinnert, J. C. and Young, D. R. 2017. Immediate effects of microclimate modification enhance native shrub encroachment. – Ecosphere 8: e01687.
Tylianakis, J. M., Didham, R. K., Bascompte, J. and Wardle, D. A. 2008. Global change and species interactions in terrestrial ecosystems. – Ecol. Lett. 11: 1351–1363.
Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H. and Goldberg, D. E. 2020. Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. – Proc. Natl Acad. Sci. USA 117: 22858–22865.
Viel, N., Mielec, C., Pétillon, J. and Høye, T. T. 2022. Multiple reproductive events in female wolf spiders *Pardosa hyperborea* and *Pardosa furcifera* in the Low-Arctic: one clutch can hide another. – Polar Biol. 45: 143–148.
Vowles, T. and Björk, R. G. 2019. Implications of evergreen shrub expansion in the Arctic. – J. Ecol. 107: 650–655.
Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A. and Team, T. other members of the C. 2005. The circumpolar Arctic vegetation map. – J. Veg. Sci. 16: 267–282.
Walker, M. D. et al. 2006. Plant community responses to experimental warming across the tundra biome. – Proc. Natl Acad. Sci. USA 103: 1342–1346.
Wallenstein, M. D., McMahon, S. and Schimel, J. 2007. Bacterial and fungal community structure in Arctic tundra tussock and shrub soils. – FEMS Microbiol. Ecol. 59: 428–435.
Wang, J., Grimm, N. B., Lawler, S. P. and Dong, X. 2023. Changing climate and reorganized species interactions modify community responses to climate variability. – Proc. Natl Acad. Sci. USA 120: e2218501120.

Wehner, A., Hein, N., Beckers, N., Dobbert, S., Pape, R. and Löffler, J. 2023. Early snow melt and diverging thermal constraints control body size in arctic–alpine spiders. – Biol. J. Linn. Soc. 138: 1–13.

Weintraub, M. N. and Schimel, J. P. 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. – BioScience 55: 408–415.

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., Morelli, T. L., Morisette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F. and Whyte, K. P. 2020. Climate change effects on biodiversity, ecosystems, ecosystem services and natural resource management in the US. – Sci. Total Environ. 733: 137782.

Wilder, S. M., Barnes, C. L., Smith, G., Youssef, N. H. and Hawlena, D. 2024. Spider waste enhances soil nutrient content, soil respiration, and plant growth. – Funct. Ecol. 39: 140–153.

Williamson, N., Suchocki, M. and Gough, L. 2024. Soil nutrient availability affects tundra plant community composition and plant–vole interactions. – Arct. Antarct. Alp. Res. 56: 2356276.

Wilson, S. D. and Nilsson, C. 2009. Arctic alpine vegetation change over 20 years. – Global Change Biol. 15: 1676–1684.

Wyant, K. A., Draney, M. L. and Moore, J. C. 2011. Epigeal spider (Araneae) communities in moist acidic and dry heath tundra at Toolik Lake, Alaska. – Arct. Antarct. Alp. Res. 43: 301–312.

Xue, K., Yuan, M., M., Qin, Y., Deng, Y., Cheng, L., Wu, L., He, Z., Van Nostrand, J. D., Bracho, R., Natali, S., SCHUUR, E. A. G., Luo, C., Konstantinidis, K. T., Wang, Q., Cole, J., Tiedje, J., Luo, Y. and Zhou, J. R. 2016. Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming. – Nat. Clim. Change 6: 595–600.

Yu, Q., Epstein, H. E., Walker, D. A., Frost, G. V. and Forbes, B. C. 2011. Modeling dynamics of tundra plant communities on the Yamal Peninsula, Russia, in response to climate change and grazing pressure. – Environ. Res. Lett. 6: 045505.