Warming reverses top-down effects of predators on belowground ecosystem function in Arctic tundra

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Predators can disproportionately impact the structure and function of ecosystems relative to their biomass. These effects may be exacerbated under warming in ecosystems like the Arctic, where the number and diversity of predators are low and small shifts in community interactions can alter carbon cycle feedbacks. Here, we show that warming alters the effects of wolf spiders, a dominant tundra predator, on belowground litter decomposition. Specifically, while high densities of wolf spiders result in faster litter decomposition under ambient temperatures, they result, instead, in slower decomposition under warming. Higher spider densities are also associated with elevated levels of available soil nitrogen, potentially benefiting plant production. Changes in decomposition rates under increased wolf spider densities are accompanied by trends toward fewer fungivorous Collembola under ambient temperatures and more Collembola under warming, suggesting that Collembola mediate the indirect effects of wolf spiders on decomposition. The unexpected reversal of wolf spider effects on Collembola and decomposition suggest that in some cases, warming does not simply alter the strength of top-down effects but, instead, induces a different trophic cascade altogether. Our results indicate that climate change-induced effects on predators can cascade through other trophic levels, alter critical ecosystem functions, and potentially lead to climate feedbacks with important global implications. Moreover, given the expected increase in wolf spider densities with climate change, our findings suggest that the observed cascading effects of this common predator on detrital processes could potentially buffer concurrent changes in decomposition rates.

Arctic | predator | decomposition | aboveground–belowground | trophic interactions

Despite general agreement that species interactions will be affected by climate change (1, 2), surprisingly few studies have explored the ways in which climate-modified trophic cascades might affect ecosystem functioning (reviewed in ref. 3). Individual and population-level responses to altered climatic conditions could have cascading effects that either amplify or dampen the impacts of existing trophic cascades on ecosystems. However, interactive effects between climate change and these population-level responses could also lead to completely new community structures with subsequent impacts on function. It is increasingly apparent that changes in community-scale dynamics can influence important ecosystem processes, such as productivity, nutrient cycling, and decomposition (4, 5). Thus, understanding how global change will shape both community interactions and function is important when predicting the effects of future climate change.

Shifts in aboveground–belowground trophic interactions due to climate change are particularly relevant in the Arctic, a region that is warming rapidly (6) and stores a large amount of soil organic carbon (C) (7, 8). Rapid warming is facilitating increased belowground microbial respiration from thawing permafrost more than it is increasing plant uptake of C, thereby causing the Arctic to become a source of atmospheric C and accelerating

the rate of global climate change (9). Prior studies have assessed the feedbacks between the Arctic terrestrial ecosystem and climate change by measuring the balance between plant community and microbial responses to warmer temperatures (reviewed in ref. 10). The extent to which these responses may be affected by interactions with organisms at other trophic levels, which are also responding to warming (e.g., detritivores, herbivores, pollinators, predators), has been largely overlooked (but see refs. 11–13 for discussion of effects of vertebrate herbivores on plant communities under warming). In particular, there has been little consideration of how changes in trophic interactions between belowground microbes and their associated consumers, which are both sensitive to warming (14–19), will affect ecosystem functioning in the Arctic (but see refs. 14, 20).

The composition and activity of microbial communities are often modified by soil micro- and macroinvertebrates (5), which are themselves regulated by higher level predators, such as surface-dwelling spiders (21). At our study site in the Alaskan Arctic, wolf spiders are extremely abundant at the soil surface (22, 23) and outweigh larger mammalian predators, such as wolves, by several orders of magnitude (*SI Appendix*), making them one of the dominant predators of the tundra community. In temperate forests and agroecosystems, wolf spider predation has indirect effects on key ecosystem processes, including plant productivity (24), nutrient cycling (25, 26), and decomposition (27–29). As in temperate systems, Arctic wolf spiders are generalist feeders that prey upon herbivores, detritivores, and other

Significance

Organisms' responses to climate change can result in altered species interactions, with cascading effects on communities and ecosystems. Understanding these processes is especially relevant in the rapidly warming Arctic, where faster decomposition of stored soil carbon is expected to result in positive carbon feedbacks to the atmosphere. We provide evidence that warmer temperatures alter the cascading effects of wolf spiders, an abundant and widespread predator, on ecosystem functioning. Specifically, we find that warming tends to reverse the effect of high spider densities on fungal-feeding Collembola and ultimately leads to slower decomposition rates. Our work demonstrates that climate change can alter the nature of predator effects on decomposition, resulting in unexpected changes in ecosystem function with potentially important global implications.

predators (30–32), suggesting that they could indirectly influence these processes in the Arctic as well. While experimental work has failed to detect changes in plant performance due to Arctic wolf spider predation on herbivores (33), more recent work suggests that these predators may obtain the majority of their energy from detritivorous prey [e.g., Collembola (22)], and therefore are more likely to have measurable indirect effects on processes such as decomposition and nutrient cycling. Currently, Arctic wolf spiders are responding to earlier snowmelt dates brought on by climate change by becoming larger (34) and hence more fecund (35). Because bigger and more abundant spiders could exert stronger predation pressure on belowground prey, these changes could have important consequences for microbial activity and nutrient cycling in the tundra.

Arctic wolf spiders and the food web to which they belong provide us with an ideal system to study how trophic interactions might alter the predicted effects of climate change on ecosystem functioning. Here, we explore the role of Arctic wolf spiders in mediating the response of the belowground community to warming. Specifically, using a fully factorial experimental design, we investigated the extent to which warming and the expected associated increase in wolf spider densities can impact lower trophic levels, decomposition rates, and soil nutrients over two summers in a well-studied area of moist acidic tundra in northern Alaska. Over the second summer, we measured densities of Collembola and oribatid mites, two of the dominant detritivore groups (22); microbial biomass (fungal and bacterial); and abundances of surface-active and soil-dwelling intermediate predators (i.e., other than wolf spiders) that could either serve as alternative prey for wolf spiders or influence detritivore densities. To assess belowground function, we measured decomposition and nitrogen (N) loss from litter. We also measured soil nutrient availability to identify the potential indirect effects that wolf spiders may have on plant nutrient uptake.

Although we measured various components of the belowground arthropod food web, our hypotheses of potential cascading effects of wolf spiders were based upon the premise that Collembola, in particular, are an important prey item of wolf spiders (31). Thus, we expected to see a direct negative effect of wolf spiders on Collembola such that Collembola densities would decrease when more wolf spiders were present (hypothesis 1). Collembola activity can affect decomposition rates directly through consumption of detritus or indirectly through consumption of the microbial community. At our site, Collembola likely consume primarily fungi, which have a larger role in decomposition and nutrient cycling in comparison to bacteria (36). Therefore, we expected that lower Collembola densities would release fungi from predation and would indirectly result in faster microbial decomposition of litter (hypothesis 2). Because cascading effects of top predators on soil nutrient availability can be context-dependent with positive, neutral, or negative effects (e.g., refs. 37–40), we did not have a priori expectations about soil nutrient responses to higher densities of wolf spiders. Based upon previous reports that warmer temperatures increased wolf spider activity (41) and likely increased overall predation rates (42), we expected that the overall effects of wolf spiders on the structure and function of the detrital community would be strengthened by warming (hypothesis 3).

Results

We maintained 1.5-m-diameter experimental mesocosms over two consecutive summers in the northern Alaska tundra to measure the effects of wolf spider densities on belowground community structure and function. We manipulated wolf spider densities in the mesocosms at the beginning of each summer and actively maintained density levels throughout the season. Half of the plots were warmed using International Tundra Experiment (ITEX) open-topped passive warming chambers (OTCs) (43).

Wolf spider density treatments included low density, control density, and high density; high-density treatments had approximately twice the densities of the average early season densities from the control treatments. Warming treatments were either ambient temperature or warmed.

Given the pace at which the Arctic is warming and the fact that wolf spider densities may be higher in the future, our primary interest for this experiment was in capturing potential interactions between the wolf spider density and warming treatments. We used a series of mixed effects models to investigate these potential interactive treatment effects on belowground community structure and function. In each model, either average soil moisture or litter moisture content was included as a fixed effect and experimental block was included as a random effect. Post hoc tests (e.g., Tukey) are not available for general linear mixed models with interaction terms; thus, for those models that showed significant interactive effects on the response variable, we split the models by ambient temperature and warming treatments to investigate pairwise differences under the three spider density treatments (low, control, or high).

Effects of Wolf Spider Density and Warming on Community Structure.
To explore treatment effects on community structure, we focused on several important groups within the belowground food web, including Collembola, oribatid mites, predatory mites, and other soil-dwelling and surface-active intermediate predators (including centipedes; unidentifiable juvenile spiders; and other small spiders from the Dysderidae, Thomisidae, Linyphiidae, and Gnaphosidae families). Among these groups, Collembola, in particular, are key prey for wolf spiders (31). Through their consumption of detritus and fungi, Collembola and oribatid mites alter soil processes, such as decomposition and nutrient cycling (44); therefore, both have important functional roles within the tundra ecosystem (22). Our analyses of treatment effects on these organisms relied on individual mixed effects models, where the response variable was the average density of a given microarthropod group (i.e., Collembola, oribatid mites, predatory mites, soil-dwelling intermediate predators) from samples taken from the upper organic layer of soil in June and July of the second experimental summer. In the Collembola model only, Collembola order (Entomobrymorpha, Poduromorpha, and Symphypleona) was included as a fixed effect and random effects included study plot nested within experimental block.

We found that there was a significant interactive effect of the wolf spider density and warming treatments on Collembola densities (Fig. 1A and Table 1). Plots across all treatments also
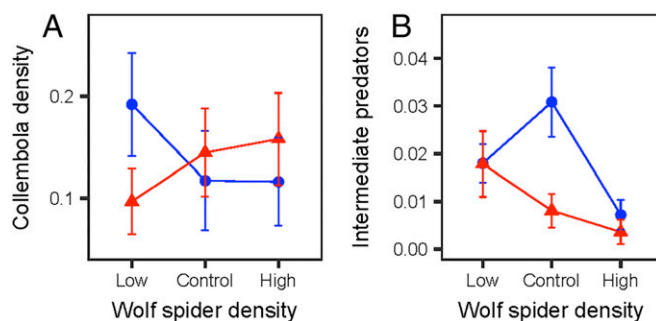

Fig. 1. Interactive treatment effects of altered wolf spider densities and warming on Collembola densities (A; individuals per cubic centimeter) and surface-active intermediate predators (B; log average total abundance per plot) within the experimental plots. Blue circles are from ambient temperature plots, and red triangles are from the experimentally warmed plots. Points are mean treatment effects, and error bars are SEs. Full model results are shown in Table 1 and SI Appendix, Table S5.

Table 1. Effects of wolf spider density and warming treatments on community structure

Response	Fixed effects terms	Estimate	SE	df	t	P
Collembola	Intercept	0.243	0.029	77	8.225	0.000
	Soil moisture	−0.001	0.001	77	−1.887	0.063
	Control SD	−0.050	0.033	77	−1.520	0.133
	High SD	−0.048	0.033	77	−1.454	0.150
	Warming	−0.064	0.033	77	−1.930	0.057
	Poduromorpha	0.006	0.023	77	0.249	0.804
	Symphypleona	−0.155	0.023	77	−6.832	0.000
	Control SD × warming	0.085	0.046	77	1.843	0.069
	High SD × warming	0.098	0.046	77	2.132	0.036
Oribatid mites	Intercept	0.982	0.202	19	4.863	0.000
	Soil moisture	−0.008	0.004	19	−1.936	0.068
	Control SD	0.107	0.251	19	0.425	0.675
	High SD	−0.203	0.253	19	−0.802	0.433
	Warming	−0.186	0.252	19	−0.739	0.469
	Control SD × warming	0.180	0.355	19	0.509	0.617
	High SD × warming	0.286	0.353	19	0.810	0.428
Predatory mites	Intercept	0.134	0.044	19	3.036	0.007
	Soil moisture	0.001	0.001	19	1.118	0.278
	Control SD	−0.095	0.055	19	−1.730	0.100
	High SD	−0.051	0.055	19	−0.924	0.367
	Warming	−0.069	0.055	19	−1.253	0.226
	Control SD × warming	0.093	0.077	19	1.202	0.244
	High SD × warming	0.106	0.077	19	1.380	0.184
Intermediate predators (soil-dwelling)	Intercept	0.005	0.002	19	2.786	0.012
	Soil moisture	0.000	0.000	19	−0.505	0.620
	Control SD	0.000	0.002	19	0.035	0.972
	High SD	0.001	0.002	19	0.247	0.808
	Warming	−0.001	0.002	19	−0.343	0.735
	Control SD × warming	−0.002	0.003	19	−0.677	0.506
	High SD × warming	0.001	0.003	19	0.409	0.687
Intermediate predators (surface-active)	Intercept	0.026	0.008	19	3.384	0.003
	Soil moisture	0.000	0.000	19	−2.003	0.060
	Control SD	0.017	0.009	19	1.806	0.087
	High SD	−0.006	0.010	19	−0.627	0.538
	Warming	0.004	0.010	19	0.465	0.647
	Control SD × warming	−0.028	0.013	19	−2.113	0.048
	High SD × warming	−0.009	0.013	19	−0.641	0.529
Fungal biomass	Intercept	1.668	1.881	16	0.886	0.389
	Soil moisture	0.121	0.047	16	2.563	0.021
	Control SD	−0.513	2.210	16	−0.232	0.819
	High SD	0.673	2.228	16	0.302	0.767
	Warming	0.677	2.187	16	0.309	0.761
	Control SD × warming	−2.266	3.051	16	−0.743	0.468
	High SD × warming	−4.330	3.160	16	−1.370	0.190
Bacterial biomass	Intercept	−0.009	0.017	18	−0.495	0.626
	Soil moisture	0.001	0.000	18	1.838	0.083
	Control SD	−0.008	0.021	18	−0.379	0.709
	High SD	−0.002	0.022	18	−0.091	0.929
	Warming	−0.009	0.021	18	−0.416	0.683
	Control SD × warming	0.009	0.030	18	0.295	0.772
	High SD × warming	0.058	0.030	18	1.924	0.070

Mixed effects model results of community response variables, as predicted by wolf spider density (SD; reference category: low SD), warming (reference category: ambient temperature), and average soil moisture. All community response variables were measured in the field during the second summer of experimental treatment. Collembola, oribatid mites, predatory mites, and soil-dwelling intermediate predators were extracted from the upper organic soil layer; densities (individuals per cubic centimeter of soil) are expressed as the average from the June and July sampling periods. Surface-active intermediate predator abundance is the average total abundance from several bouts of live pitfall trapping. Fungal and bacterial biomass (mg per gram of soil) were sampled from the upper organic soil layer. Model results with the reference category for the wolf SD treatment as the control SD are shown in *SI Appendix*, Table S5.

contained significantly fewer Collembola from the order Symphypleona than from the orders Entomobryomorpha ($P < 0.0001$; Table 1) and Poduromorpha ($P < 0.0001$). Average soil moisture was a marginally significant predictor of Collembola densities, whereby plots with lower soil moisture trended toward having more Collembola ($P = 0.063$; Table 1).

SI Appendix, Table S2 contains the mean ± SE of Collembola density by treatment.

As a post hoc test to investigate the pairwise interactive treatment effects on Collembola, we ran separate models for the Collembola data under ambient temperatures and under warming using a Bonferroni correction ($P_{\text{critical}} = 0.01\bar{6}$; *Materials and Methods*). At this level, there was not enough power to detect differences in Collembola densities between the three wolf spider density treatments (*SI Appendix*, Table S4). However, we did observe that the addition of wolf spiders tended to reduce Collembola densities under ambient conditions, as might be expected if wolf spiders were consuming Collembola (Fig. 1*A* and *SI Appendix*, Table S4). In experimentally warmed plots, there was the opposite trend: Plots with high wolf spider densities tended to have more Collembola than plots with lower wolf spider densities (Fig. 1*A* and *SI Appendix*, Table S4).

We did not find significant interactions between the wolf spider density and warming treatments on densities of any of the other measured groups of soil-dwelling microarthropods, including oribatid mites, predatory mites, and intermediate predators (Table 1 and *SI Appendix*, Tables S2 and S5). Moreover, none of these groups showed significant variation in association with either of the experimental treatments when models were simplified by eliminating nonsignificant terms on a one-by-one basis. Soil moisture had a marginally negative effect on oribatid mites but was not related to densities of predatory mites or soil-dwelling intermediate predators (Table 1).

Several other surface-active, intermediate predators within this community (including crab spiders, linyphiid spiders, unidentifiable juvenile spiders, and centipedes; hereafter referred to as intermediate predators) could serve as either alternative prey for wolf spiders or predators of Collembola. We therefore fitted a separate mixed effects model to explore the treatment effects on the average total abundance of these surface intermediate predators throughout the second summer season. We found that the average number of surface intermediate predators observed in our plots was also subject to interactive treatment effects in our experiment (Fig. 1*B* and Table 1; mean abundances by treatment are shown in *SI Appendix*, Table S2). Again, we ran separate models using a Bonferroni correction ($P_{\text{critical}} = 0.01\bar{6}$) to explore the pairwise effects of the wolf spider density treat-ments in ambient temperature and warmed plots. Although there was not enough power to detect treatment differences here either, we found that regardless of warming treatment, as wolf spider density increased, there tended to be fewer intermediate predators (all *P* values >0.0167; Fig. 1*B* and *SI Appendix*, Table S4). The exception to this was in ambient temperature plots with control densities of wolf spiders, which tended to have more intermediate predators than those from the other wolf spider treatments (Fig. 1*B* and *SI Appendix*, Table S4).

Similar models to those described above did not detect any significant differences in belowground fungal or bacterial biomass under the warming or wolf spider density treatments (all *P* values >0.07; Table 1; mean biomass by treatment is shown in *SI Appendix*, Table S2). Fungal biomass was higher in plots with higher soil moisture (Table 1).

Effects of Wolf Spider Density and Warming on Decomposition, Litter N, and Available Soil Nutrients. We used litter bags to measure the effects of wolf spiders and warming on litter decomposition and litter N loss using locally collected leaves of the dominant plant, *Eriophorum vaginatum*. To isolate where wolf spiders might have the largest indirect effects, one litter bag was placed on the soil surface and another was buried in the litter layer just below the moss surface (*ca.* 5–10 cm) in each plot. Litter bags were collected 14 mo after the experimental start date, at which point remaining litter was weighed and analyzed for total N content. We also measured treatment effects on available soil N, phosphorus (P), and potassium (K) using ion exchange membranes that were incubated over 6 wk during the second summer of the experiment. We fitted linear mixed effects models to estimate interactive treatment effects of wolf spider density and warming on litter decomposition (percent litter mass remaining from initial amount); litter percent N (in relation to initial litter N content); and total available soil N [total N, ammonium (NH_4^+), and nitrate (NO_3^-)], P, and K. Litter moisture content was included as a covariate in the litter-related models, while average soil moisture was used instead in the soil nutrient models; experimental block was included as a random effect in all models.

Within the litter layer, we found that there were significant interactive treatment effects of wolf spider density and warming on decomposition (Fig. 2*A*, Table 2, and *SI Appendix*, Table S2). Under ambient temperatures and at high spider densities, we

Table 2. Effects of altered wolf spider densities and warming on belowground litter decomposition and litter N

Response	Fixed effects terms	Estimate	SE	df	t	P
Mass remaining, %	Intercept	98.03	5.74	19	17.07	0.000
	Litter moisture content, %	−0.36	0.08	19	−4.84	0.0001
	Control SD	3.58	2.54	19	1.41	0.175
	High SD	−6.34	2.57	19	−2.47	0.0232
	Warming	−8.14	2.52	19	−3.23	0.0044
	Control SD × warming	4.82	3.51	19	1.37	0.186
	High SD × warming	15.01	3.54	19	4.24	0.0004
N remaining, %	Intercept	111.81	13.95	19	8.02	0.000
	Litter moisture content, %	−0.35	0.18	19	−1.90	0.073
	Control SD	1.30	5.98	19	0.22	0.830
	High SD	8.20	6.06	19	1.35	0.192
	Warming	10.27	5.935	19	1.73	0.0997
	Control SD × warming	−8.66	8.28	19	−1.05	0.309
	High SD × warming	−16.14	8.34	19	−1.94	0.068

Mixed effects model results of belowground ecosystem function response variables, as predicted by wolf spider density (SD; reference category: low SD), warming (reference category: ambient temperature), and average litter moisture content. The decomposition rate is expressed as percent litter mass remaining in proportion to initial mass. Litter N is percent N remaining in litter in relation to initial N content of litter. Litter bags were buried below the tundra litter layer and underwent 14 mo of experimental treatment. Model results with control SD as the reference category for the wolf spider treatment are shown in *SI Appendix*, Table S5.

observed faster litter decomposition rates. However, experimentally warmed plots with high spider densities experienced less litter decomposition than those with low spider densities. Higher litter moisture content was also associated with faster decomposition in the litter layer. When models were split using only ambient temperature or warmed plots to investigate pairwise effects of the wolf spider density treatments, we found that the rate of belowground decomposition was significantly affected by wolf spider densities under both temperature treatments (*SI Appendix*, Table S4). Specifically, under ambient temperature, decomposition was significantly faster in plots with high densities of wolf spiders than in those with control densities of wolf spiders ($P = 0.0103$; Fig. 2A and *SI Appendix*, Table S4). Under warming, decomposition was significantly slower under control and high wolf spider densities than under low wolf spider densities (control/low $P = 0.0041$, high/low $P = 0.0034$; Fig. 2A and *SI Appendix*, Table S4). There were no significant treatment effects on N loss or gain from the belowground litter bags (Fig. 2B and Table 2).

We did not observe any treatment effects on litter decomposition or litter N content at the soil surface. Similarly, variation in surface decomposition and litter N was not related to litter moisture content (*SI Appendix*, Table S1). A possible explanation for these results is that decomposition at the soil surface is driven by variations in biotic and abiotic conditions (45) that were not captured through our measurements in the soil and litter layers.

However, our results did indicate that increasing wolf spider densities resulted in higher availability of soil N (Fig. 2C and *SI Appendix*, Tables S2 and S3). Specifically, plots with high wolf spider densities showed a trend toward having higher levels of total N than those with low wolf spider densities (*SI Appendix*, Table S3a). This pattern was driven by significantly higher levels of soil NH_4^+ in plots with high wolf spider densities than in those with low wolf spider densities (Fig. 2C and *SI Appendix*, Table S3a); there was no difference in soil NH_4^+ between plots with control and low or control and high wolf spider densities (all $P_{critical}$ values >0.0167; *SI Appendix*, Table S3). Neither total N nor NH_4^+ was related to the warming treatment. Moreover, we did not find any effects of wolf spider density or warming on soil available NO_3^-, P, or K (*SI Appendix*, Tables S2 and S3). Soil moisture was positively and significantly associated with availability of total N and NH_4^+ (*SI Appendix*, Table S3) and marginally negatively correlated with soil P ($P = 0.0129$; *SI Appendix*, Table S3a).

Effect Sizes of Treatments on Belowground Community and Ecosystem Function. We compared the mean effect sizes of high wolf spider densities relative to low wolf spider densities for several key response variables (Collembola, belowground litter decomposition, percent litter N remaining, and soil available NH_4^+). Effect sizes were estimated under ambient temperatures and warming by calculating the $\log_{10}$ (X_a/X_b) effect magnitudes for each ex-

perimental block, where X_a and X_b are the values for a given response variable when spider densities are high or low, respectively (46, 47). We found that having high densities of wolf spiders resulted in mean $\log_{10}$ effect magnitudes of -0.739 to 0.422 under ambient temperatures and -0.219 to 0.581 under experimental warming relative to those plots with experimentally reduced wolf spider densities (Fig. 3B). Warming caused opposite responses to high wolf spider densities for most response variables. The exception was soil NH_4^+, which increased under high wolf spider densities, irrespective of the warming treatment.

Discussion

A central goal of ecological and environmental research is to understand how climate change is affecting biological communities and ecosystem functioning. Wolf spiders inhabit nearly every terrestrial habitat and are among the globally dominant groups of spiders in terms of local abundance and diversity (48, 49). The cascading effects of these predators on detrital food webs and decomposition may be a common phenomenon across many ecosystems (e.g., refs. 26, 28, 50), suggesting that responses by wolf spiders to environmental disturbances such as climate change could have widespread ecosystem-level effects. We have shown here that in the Arctic, an ecosystem that is rapidly warming and where changes in biogeochemical cycling have disproportionate effects on global processes (51), wolf spiders indirectly alleviate the effects of warming on decomposition rates. Specifically, we found that experimentally increasing wolf spider densities tended to reduce densities of belowground Collembola, with associated increases in litter decomposition and soil available N (NH_4^+). However, the direction of these effects was, in general, reversed under experimental warming (a conceptual model is shown in Fig. 3A). Increasing wolf spider densities did not have measurable effects on the densities of any of the other common members of the soil community (i.e., oribatid mites, predatory mites, soil-dwelling intermediate predators) under ambient temperature or warming. Therefore, we interpret our findings as warming mediating the direct, and potentially indirect, effects of wolf spiders on Collembola, which subsequently influences decomposition. Higher densities of wolf spiders were also associated with higher soil N availability irrespective of the warming treatment, suggesting that these predators have an indirect influence on primary production as well. Given that wolf spiders comprise a large portion of animal biomass across much of the Arctic (52) (*SI Appendix*), these impacts could scale across the region.

As has been previously documented in other ecosystems (5, 53), aboveground tundra predators can have important indirect effects on the functioning of the belowground community. The findings of our experiment suggest that under ambient conditions, moist tundra exhibits a classic trophic cascade, where high
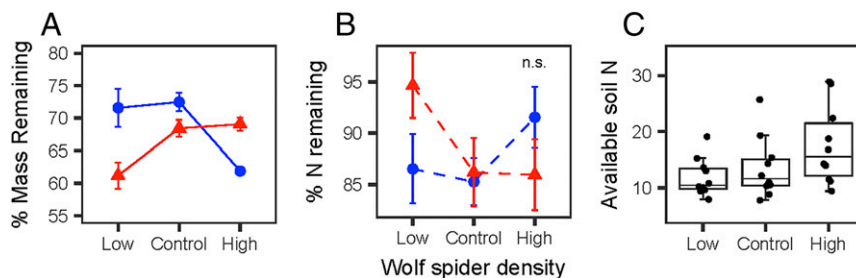

Fig. 2. Effects of altered wolf spider densities and experimental warming on decomposition in the litter layer (A; percent litter mass remaining from the initial amount), percent N remaining in litter (B; in relation to initial N content of litter), and total available soil N (C; milligrams of NH_4^+ per 10 cm^{-2}) over the peak 6-wk summer season. Blue circles are from ambient temperature plots, and red triangles are from the experimentally warmed plots. Points are mean treatment effects, and error bars are SEs. Solid lines in A represent a significant interaction between the treatments, and dotted lines in B indicate a non-significant interaction. Full model results are shown in Table 2 and *SI Appendix*, Tables S3 and S5.

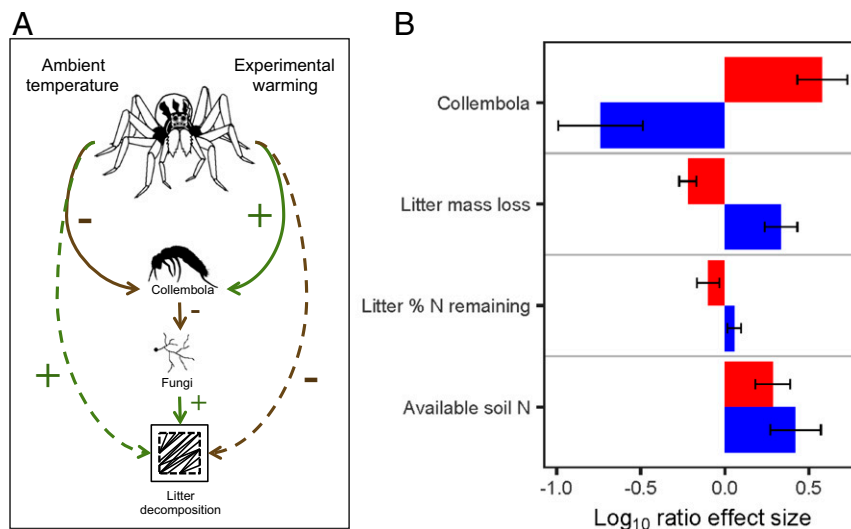**Fig. 3.** (*A*) Conceptualization of the hypothesized pathways by which warming alters the cascading effects of wolf spiders on decomposition via fungivorous Collembola. Solid lines denote direct effects of the wolf spiders, and dashed lines indicate indirect effects of the wolf spiders. Positive trophic effects are shown in green, and negative effects are shown in brown. (*B*) Mean ($\pm$SE) effect sizes of high wolf spider densities on Collembola, decomposition (belowground litter mass loss), percent N remaining in litter, and available soil N (total milligrams of NH_4^+ per 10 cm^{-2}) under ambient temperatures (shown in blue) and experimental warming (shown in red) across the five experimental blocks. The $\log_{10}$ ratios are comparisons between plots with low vs. high densities of wolf spiders; positive log ratios$_{10}$ indicate a positive effect of high wolf spider densities on the response variable.

densities of a top predator (wolf spiders) tend to suppress intermediate consumers (Collembola; Fig. 1*A*), which presumably releases the fungal community from predation, and indirectly results in faster litter decomposition (Fig. 2*A*). While the effects of increasing wolf spider densities on Collembola densities were not strong, they nevertheless corresponded to important changes in decomposition. Collembola can influence decomposition and nutrient cycling via their consumption of both detritus and fungal decomposers (e.g., ref. 44). The pattern of faster decomposition that we observed under modest declines in Collembola densities suggests that in this system, Collembola primarily affect decomposition indirectly via consumption of the microbial community. Otherwise, the trend toward lower Collembola densities should have corresponded to slower, not faster, decomposition rates. Similarly, the slower decomposition rates observed under warming and high wolf spider densities may be explained by the slightly higher densities of Collembola exerting stronger predation pressure on fungal decomposers under that treatment. The effects of actively hunting spiders can vary depending on moisture availability in temperate (29, 54) and tropical systems (55). This study was conducted in moist acidic tundra, which is the dominant ecosystem type in the Alaskan Arctic (56) and is also common in many subarctic areas (57); the extent to which our findings may be generalized to drier tundra habitats warrants further study.

Notably, despite previous work suggesting that predators are more likely to regulate processes in belowground food webs dominated by bacteria and bacteria-consuming organisms (39, 58), our findings suggest that trophic cascades also occur in systems where the fungal energy channel (i.e., fungi, fungal feeders) is responsible for the majority of nutrient cycling. The changes to the function of the belowground community (i.e., decomposition, soil N) that were brought about by higher wolf spider densities in our experiment are similar in magnitude to other documented trophic cascades by invertebrate predators on plant biomass (e.g., ref. 47) (Fig. 3*B*). As such, these results suggest that trophic cascades initiated by generalist predators that derive substantial energy from belowground systems can be equal to those in aboveground systems (59).

Our results suggest a change in both the strength and the nature of wolf spider effects under warming. We found that reduced numbers of predators could still suppress prey populations (as observed in the low wolf spider density treatment), possibly due to higher predator activity rates under warming (42). However, the unexpected positive trend in Collembola densities (and concurrent decline in decomposition) as wolf spider densities increased suggests that in some cases, climate change may not simply alter the strength of top-down effects but could, instead, induce different types of trophic cascades altogether (29, 55, 60, 61) (Fig. 3). At least two possible scenarios may explain the increasing, albeit weak, trend in Collembola with increasing wolf spider densities under warming. First, although we did not observe changes in the Collembola community at the order level, warming could have caused turnover in Collembola species composition (62) or ecologically relevant traits (63), which would likely have consequences for the functional roles of these animals (64). In plots with high wolf spider densities, intensified predation on preferred Collembola species may have released less palatable species (65) from competition and enabled them to reach higher abundances under warming. Alternatively, under elevated wolf spider densities, warming-associated increases in spider activity could result in more frequent antagonistic interactions with other predators (66). Strong predator–predator interactions or even intraguild predation, which is fairly common in this system (22), can relax the collective effect of predator communities, resulting in increased prey populations and weaker trophic cascades (67, 68). Under warming, we observed that numbers of intermediate predators declined as wolf spider densities increased (Fig. 1*B*). The reduction in intermediate predators corresponds to a progressive increase in Collembola, suggesting that under warming, wolf spiders may have preferentially preyed upon intermediate predators, effectively releasing Collembola from predation by both groups.

Our results lead us to believe that the differential effects of wolf spiders on decomposition under warming are mediated by trophic interactions with Collembola (Fig. 1*A*) and possibly also related to interactions with other predators (Fig. 1*B*). As species-level data for the Collembola and potential changes in wolf spider diets are not available for our experimental plots, it is

possible that the apparent shift in community-level effects of wolf spiders under warming was driven by an alternative mechanism. However, among the six organismal groups that we measured within this food web (including all major soil microarthropod groups), Collembola and intermediate predators were the only ones for which there were interactive treatment effects. Importantly, the trends in altered Collembola densities with increasing wolf spider densities were negatively related to the changes we observed in decomposition rates in both ambient and warmed plots. Overall, our results highlight the importance of accounting for changes in species interactions between and within trophic guilds (i.e., predator–prey interactions and predator–predator interactions) for predicting ecosystem responses to climate change.

Wolf spiders also influenced N cycling in this N-limited ecosystem, suggesting an important link between predators and plant nutrient availability in the tundra. We observed higher availability of total soil N, driven by increasing levels of NH_4^+, with increasing wolf spider densities (Fig. 2C). Higher availability of soil N may reflect increased N excretion by stressed prey when exposed to high predator densities (69) or microbial predation by microarthropods, which can result in remobilization of excess nutrients (ref. 70 and references therein). It is unclear whether the mechanism for higher soil N under high spider densities was the same or different under ambient temperatures and warming. Moreover, it remains to be seen whether such an increase in soil N would provide more of a benefit to the microbes or plants in N-limited tundra ecosystems, but previous work in our study region found that increased nutrient availability resulted in a net ecosystem loss of C despite increases in plant productivity (71).

Tundra decomposition rates and C losses are likely to increase under warming (e.g., ref. 72), yet we show that predators may indirectly dampen some of these impacts. While populations of many northern species are projected to decline under climate change (73), wolf spiders may actually benefit from warmer Arctic temperatures (34). Given that close to half of the world's terrestrial C is stored in the Arctic permafrost (7, 51), slight changes in regional C dynamics, even those driven by predators as small as the wolf spider, could have disproportionate effects on the global C cycle (72). The results of this study therefore highlight the importance of considering trophic interactions in efforts to understand ecosystem responses to global change and suggest that those studies that do not consider species interactions (particularly top-down effects of predators) may potentially miscalculate the projected effects of warming on decomposition and nutrient cycling.

Materials and Methods

Study System and Experimental Design. Our study took place from early June 2011 through late July 2012 near Toolik Field Station (68°38′N and 149°43′W, elevation = 760 m), a well-studied area of moist acidic tundra (74) on the North Slope of Alaska. The mean annual temperature at Toolik is −10 °C, with the majority of positive temperatures occurring during the summer months (average July temperature is 14 °C), and the annual precipitation is 200–400 mm (75). We explored the effects of wolf spider density and warming on community composition, litter decomposition, litter N loss, and available soil nutrients through a fully factorial field experiment. Mesocosms were circular, 1.5 m in diameter, and enclosed with aluminum flashing that was buried 20 cm belowground and stood 20 cm above the soil surface to contain the belowground community and wolf spiders, who are not skilled climbers. Plots were distributed across five blocks and randomly assigned to one of the six spider density/warming treatments. For the warming treatment, we placed ITEX OTCs over half of the plots during the summer seasons only. The ITEX method typically increases mean air temperature within the OTCs by 1–2 °C (43).

Wolf spider density treatments included the following: (i) low, (ii) control, and (iii) high density. At the beginning of each summer, we removed all possible wolf spiders from low-density plots and added spiders to high-density plots such that they would have approximately twice the early season average density of control plots, which was 1.1 wolf spiders per square

meter. We continued to check and remove individuals from the removal plots throughout each summer. Visual inspection and live pitfall trapping at the end of the summer seasons verified that we successfully manipulated wolf spider densities during both summers of the experiment. In 2011, the mean and SE values of wolf spider densities within each plot over a series of three 24-h live pitfall trapping bouts (July 20–22, 2011) were 0.8 ± 0.22 wolf spiders in high-density plots, 0.167 ± 0.075 wolf spiders in control plots, and 0.20 ± 0.10 wolf spiders in low-density plots. ANOVA and post hoc Tukey tests for these 2011 data showed that the average number of spiders was significantly higher in high-density plots than in control ($P = 0.0145$) and removal ($P = 0.021$) plots but that catches did not differ between control and removal plots ($P = 0.986$). At the end of the second summer, we visually surveyed each plot to get a more complete count of the total number of wolf spiders per plot (as opposed to pitfalls, which catch a smaller subset of spiders present) and found that wolf spider densities differed significantly according to their preassigned treatments (ANOVA: $F_{2,27} = 21.85$, $P = <0.0001$); low-density (removal) plots had an average of 0.3 ± 0.213 wolf spiders, control plots had 1.8 ± 0.20 wolf spiders, and high-density plots had 3.3 ± 0.47 wolf spiders each.

Sampling of Community Composition. We sampled the belowground community by taking soil samples of the upper soil organic layer (average sample volume = 176 cm³) in each plot on two midseason dates (June 20 and July 17, 2012). Microarthropods were removed through heat extraction using Berlese–Tullgren funnels (BioQuip Products) into 90% ethanol over a period of 5 d. Groups that were present in at least 70% of our soil samples included Collembola, which were identified to order (Entomobrymorpha, Poduromorpha, and Symphypleona); oribatid mites; and predatory mites. There were also some intermediate predators in the soil samples (centipedes; unidentifiable juvenile spiders; and other small spiders from the Dysderidae, Thomisidae, Linyphiidae, and Gnaphosidae families). Although none of these predator types were present in abundance, at least one intermediate predator was caught in 73% of the soil samples. These animals are likely predators to the detritivore groups and could potentially be prey to wolf spiders; due to their low numbers in the soil samples, we did not differentiate among different soil-dwelling intermediate predators but, instead, used a measure of the total density of these predators. In all subsequent analyses of soil-dwelling microarthropods, we used the average densities from the June and July samplings.

To measure treatment effects on other intermediate predators that could affect detritivore densities, particularly Collembola, and/or be prey to wolf spiders (e.g., surface-active crab spiders, linyphiid spiders, juvenile spiders, centipedes), we used live pitfall traps over several dates during the second summer season (June 13–15, June 29, July 9, July 11, and July 20–23). Live traps were checked daily; surface-active intermediate predators and other bycatch were immediately returned to their respective experimental plots. Counts were corrected by the number of live pitfall traps within each plot and expressed as the average number of surface-active intermediate predators caught per plot over the summer.

Fungal biomass and bacterial biomass were estimated using epifluorescent microscopy techniques (76) from 5-g soil samples that were collected from the upper organic layer at the conclusion of the experiment in late July. Fungal samples were stained with Calcofluor fluorescent brightener (77) and read between 334-nm and 365-nm wavelengths. Bacterial samples were stained with 5-(4,6 dichlorotriazin-2-yl) aminofluorescein and read at a 490-nm wavelength. We estimated active fungal biomass as 10% of the total fungal biomass (78).

Measures of Decomposition and Nutrient Availability. We measured decomposition rates and litter N loss in the experimental plots using litter bags that were filled with standing dead leaves of the dominant plant, *E. vaginatum*, that were collected from an area adjacent to our experimental plots in June 2010. Litter was dried at 40° C for 48 h, mixed, and subsampled for litter bag preparation. Litter bags were 8 × 8 cm with a 3-mm mesh size on the top and bottom to allow access by most arthropods, and each bag contained 1.5 g of litter. Subsamples of the initial litter mixture were ground and processed for total N content using a CE Elantech Flash EA 1112 Elemental Analyzer (CE Elantech, Inc.) at Duke University.

We deployed a pair of litter bags in each plot during mid-June 2011 by placing one litter bag on the soil surface and burying the other in the lower litter layer under the moss surface (*ca.* 5–10 cm). We collected both litter bags in August 2012 (14 mo) after the experimental start date and manually removed accumulated soil, ingrown moss and roots, and microarthropods from the decomposed leaves before drying them at 40° C for 72 h. Litter bag contents were weighed to determine proportional mass loss from the initial

litter, and subsamples were ground and analyzed for percentage of N as described above.

We used ion exchange membranes (Plant Root Simulator probes; Western Ag Innovations, Inc.) to measure treatment effects on available soil N, P, and K. Three cation-exchange and three anion-exchange resin membranes were inserted at equal spacing within each plot in June 2012 and incubated 3 wk before collection. The initial probes were replaced with a second set of probes that were similarly incubated for an additional 3 wk. Probes were analyzed by Western Ag Innovations, Inc. for NO_3^-; NH_4^+; and total N, P, and K. Nutrient supply rates are expressed as the total over these two periods.

Moisture Availability. Experimental warming can reduce soil moisture, which can affect litter decomposition (e.g., refs. 79, 80), microarthropod abundances (e.g., ref. 62), and microarthropod effects on decomposition (81). To account for this, we took measures of soil moisture at three locations within each plot at the beginning, middle, and end of the 2012 summer season using a HydroSense portable soil moisture probe (Campbell Scientific). Those data indicated that the warming treatments had no effect on average soil moisture content (mixed effects model: df = 24, t = 0.683, P = 0.501; mean ± SE values of soil moisture in ambient plots were 34.31 ± 6.57 and 37.37 ± 4.81 in warmed plots). Furthermore, we did not observe effects of the warming treatment on percent moisture content within litter bags, although the moisture content of surface litter was significantly lower than that of litter from bags that were buried in the litter layer (mixed effects model of litter moisture content as the response variable, with warming treatment and litter bag location as fixed effects and experimental block as a random effect; intercept = 78.75 ± 4.54, df = 53, t = 17.36; warming = 1.46 ± 4.78, df = 53, t = 0.306, P = 0.761; surface = −50.99 ± 4.78, df = 53, t = −10.68, P < 0.0001); the results of a test of potential interactive effects between the warming treatment and litter bag location were also nonsignificant.

Analyses. We used linear mixed effects models estimated through the lmer function of the nlme package (82) in R (83) to investigate the influence of our treatments and their potential interactive effects (spider density × warming) on the relevant response variables. Spider density was treated as a categorical variable (low density, control, high density), and treatment block was included as a random effect. Average percent moisture from the nine measures of soil moisture was also included as a continuous independent predictor. We fitted separate models for the average densities of each of the soil arthropod groups (Collembola, oribatid mites, predatory mites, and soil-dwelling intermediate predators) from the June and July samplings, as well as the average total abundance of surface-active intermediate predators from the dry pitfall traps and biomasses of fungi and bacteria from the upper organic horizon. Soil animal densities (per cubic centimeter) and abundances of surface-active intermediate predators (per plot) were log-transformed following the technique of Osborne (84) to conform to the assumptions of linear models. In the Collembola model, Collembola order (i.e., Entomobrymorpha, Poduromorpha, Symphypleona) was included as a fixed effect and study plot nested within experimental block was included as a random effect. Bacterial biomass in one plot was 399 standard deviations (SDs) above the mean biomass of other plots within the same treatment, and was thus excluded from analyses. Similarly, fungal biomass estimates from three plots were between 12 and 24 SDs above the other biomass measures in those treatments, and were therefore also excluded from analyses.

We individually assessed the interactive effects of the spider density and warming treatments on decomposition, litter N content, and available soil nutrients (N, P, and K). Litter moisture content was included as a covariate in the litter-related models, while average soil moisture was included in the soil nutrient models. Decomposition rate was expressed as cumulative mass loss over the 14 mo of the experiment, and the percent gain or loss in litter N was expressed as the percent difference from the initial N content.

Post hoc tests (e.g., Tukey) are not available for linear mixed effects models with interactions; therefore, we investigated the direction of significant interaction effects by running separate models for data under ambient temperature and warming treatments. From these models, we evaluated the significance of pairwise differences in wolf spider density using Bonferroni correction ($P_{critical}$ = 0.05/3 = 0.016).

Finally, we estimated the mean (±SE) effect sizes of wolf spiders on several key response variables (Collembola, belowground litter decomposition, percent litter N remaining, and soil available NH_4^+) under ambient conditions and warming across all experimental blocks. To do this, we calculated the $\log_{10}$ (X_a/X_b) effect magnitude for each response variable within a given experimental block, where X_a and X_b are the values for a given response variable when spider densities are high or low, respectively (46, 47).

All data used in the analyses described above are archived by the LTER Network Data Portal (85).

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