ARCTIC ECOLOGY

Large herbivore diversity slows sea ice–associated decline in arctic tundra diversity

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Biodiversity is declining globally in response to multiple human stressors, including climate forcing. Nonetheless, local diversity trends are inconsistent in some taxa, obscuring contributions of local processes to global patterns. Arctic tundra diversity, including plants, fungi, and lichens, declined during a 15-year experiment that combined warming with exclusion of large herbivores known to influence tundra vegetation composition. Tundra diversity declined regardless of experimental treatment, as background growing season temperatures rose with sea ice loss. However, diversity declined slower with large herbivores than without them. This difference was associated with an increase in effective diversity of large herbivores as formerly abundant caribou declined and muskoxen increased. Efforts that promote herbivore diversity, such as rewilding, may help mitigate impacts of warming on tundra diversity.

Without efforts to mitigate carbon emissions, 2°C warming above the preindustrial baseline is expected to precipitate rapid extinctions across multiple taxa and biomes (*1*, *2*). Notably, the relatively species-poor Arctic is already 2°C warmer than this baseline seasonally and will exceed this threshold annually decades sooner than anywhere else on Earth (*3*). Despite such rapid warming, plant diversity responses to climate change in the Arctic are ostensibly inconsistent and difficult to predict (*4*, *5*), perhaps in part because of heterogeneity in abiotic conditions including soil moisture and nutrient availability across the Arctic and the limitations this imposes on tundra plant responses to warming (*6*).

Although warming itself is a major driver of ecological change in the Arctic (*7*), associated declines in sea ice extent and seasonal melt onset (*8*–*10*) also pose direct and indirect consequences, including threats to Indigenous livelihoods based on wildlife harvest (*11*) and husbandry (*12*). For instance, sea ice decline may alter biodiversity in adjacent terrestrial systems through effects on temperature and precipitation that influence the abundance and distribution of local species (*13*–*15*). Indirectly, sea ice decline has also been linked to rain-on-snow events and shrubification of tundra, both of which are associated with declines in abundance of reindeer and caribou (both *Rangifer tarandus*) (*12*, *16*). Such consequences may be reciprocally important to tundra vegetation dynamics because large herbivores influence patterns of vegetation abundance and community composition across multiple spatial and temporal scales in the Arctic (*17*, *18*). Moreover, vertebrate herbivores mediate numerous vegetation responses to climate change (*19*), including plant diversity loss under warming (*20*) (Fig. 1). Accordingly, conservation of herbivores and rewilding of lost herbivore assemblages have emerged as novel mitigation strategies for effects of climate change in many biomes, including the rapidly warming arctic tundra (*19*, *21*–*23*).

To investigate interactive effects of warming and herbivory on community composition of arctic tundra, including plants, fungi, and lichens, we initiated a large-scale herbivore exclusion and warming experiment in 2002 near Kangerlussuaq, Greenland (*24*) (figs. S1 and S2). The experiment ran continuously for 15 years (concluding in 2017) and included annual nondestructive sampling of tundra community diversity (*24*). The site is one of

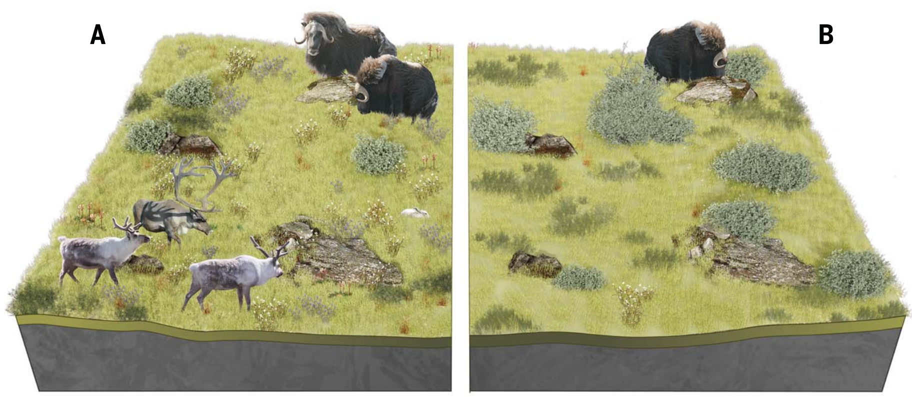

Fig. 1. Conceptualization of potential interactions between warming and large herbivore diversity and abundance in arctic tundra vegetation dynamics motivating this study. Both panels depict arctic tundra under climatic warming. (**A**) represents a scenario in which warming occurs with an abundant and diverse assemblage of large herbivores (in this case caribou and muskoxen) and (**B**) represents a scenario in which warming occurs with a sparse and species-poor assemblage of large herbivores. The arrows indicate differences in arctic tundra composition under warming that might arise with a decline in large herbivore diversity and abundance (upper arrow) or an increase in large herbivore diversity and abundance (lower arrow). Hence, from (A) to (B) a lower or declining diversity or abundance of large herbivores, or their complete absence, may facilitate a warming-induced increase in deciduous shrub height and abundance, decline in graminoids and forbs, and a consequent reduction in tundra diversity. Conversely, from (B) to (A) greater or increasing diversity or abundance of large herbivores may constrain a warming-induced increase in deciduous shrub height and abundance, thereby maintaining tundra diversity by promoting the persistence of graminoids and forbs that might otherwise be outcompeted or interfered with by shrubs for space, light, or soil nutrients. This study combined long-term experimental warming and herbivore exclusion with monitoring of background variation in abiotic conditions and herbivore diversity and abundance to investigate such interactions. [Artwork by SciStories]

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the few locations in the Arctic tundra biome with multiple species of large herbivores (*19*), caribou and muskoxen (*Ovibos moschatus*). After the first five years of the experiment, we reported that both caribou and muskoxen influenced tundra community responses to the experimental treatments (*25*). Ongoing work at the site revealed associations between sea ice extent and several components of the system, including local spring warming (*26*) and increasing shrub abundance (*27*). The long-term nature of the experiment was therefore conducive to monitoring natural changes in abiotic conditions and herbivore abundance (*24*) presumed important to tundra community composition and diversity dynamics (Fig. 1) and ultimately presented an opportunity to investigate their interactions with the experimental treatments.

Patterns of tundra diversity decline

Effective species number of plants, fungi, and lichens (i.e., True Simpson's diversity, hereafter tundra diversity) (*24*) declined across the study site under all experimental treatments as the 15-year experiment progressed (Fig. 2, top row; see also fig. S3). However, rates of tundra diversity decline differed across experimental treatments at both the plot and site scale (table S1). Tundra diversity declined nearly twice as fast under herbivore exclusion as under grazing, most slowly under grazing with experimental warming and, at the site scale, most rapidly under herbivore exclusion with warming (Fig. 2 and table S1).

The decline in tundra diversity across all experimental treatments suggests a common abiotic driver whereas different rates of decline under grazing versus herbivore exclusion suggest mediation of that abiotic driver by herbivory. We examined relationships among declining tundra diversity and local precipitation and temperature during the growing season (May through July; hereafter May-July), as well as both Arctic-wide sea ice extent (ASIE) and regional Baffin Bay sea ice extent (BBSIE) (*24*). Growing season mean ASIE was the best overall predictor of interannual variation in tundra diversity at the site whereas July (peak growing season) temperature was the best local predictor (table S2). Moreover, ASIE outperformed BBSIE (tables S2 and S3). Associations between May-July ASIE and tundra diversity were positive across all experimental treatments, both at the plot scale and across the study site (Fig. 2 and tables S3 and S4), indicating that tundra diversity declined with diminishing ASIE during the growing season. Moreover, associations between May-July ASIE and tundra diversity were stronger under herbivore exclusion than under grazing and weakest under grazing with experimental warming (Fig. 2 and tables S3 and S4). Peak growing season (July) temperature effects on tundra diversity were negative across all experimental treatments (tables S3 and S4), indicating a decline in tundra diversity with local warming. These associations varied only marginally among treatments at both the plot and site scales (tables S3 and S4, respectively), but were significantly weaker under grazing than under herbivore exclusion at the plot scale (table S3).

Abiotic drivers of tundra diversity decline: Relation of local weather to sea ice decline

Linking sea ice decline and local tundra community dynamics requires, at a minimum, examining associations among sea ice and local abiotic conditions. During the experimental period (2002 to 2017), Arctic mean annual temperature increased by nearly 1°C (*3*), ASIE declined by 1.34 million km^2 (*28*), and peak annual growing season (July) mean temperature at the study site increased by >1°C (*29*). Of the candidate local abiotic predictors of tundra diversity decline considered here (*24*), the only ones significantly related to May-July ASIE during the experimental period were mean daily temperature and mean daily maximum temperature in July, the latter of which was also the single best local abiotic predictor of variation in tundra diversity (tables S2 and S5). Both of these variables were also correlated with July ASIE (tables S5), the second-best individual predictor of variation in tundra diversity (table S2). Additionally, July mean and maximum temperatures were more highly correlated with ASIE than with BBSIE in both July and May-July (table S6), and multivariate models testing competing abiotic predictors (*24*) revealed the dominant effect of May-July ASIE (table S7). In all cases, July temperature variables were negatively correlated with ASIE, suggesting that declining spring and summer ASIE promotes local July warming. Additional analyses

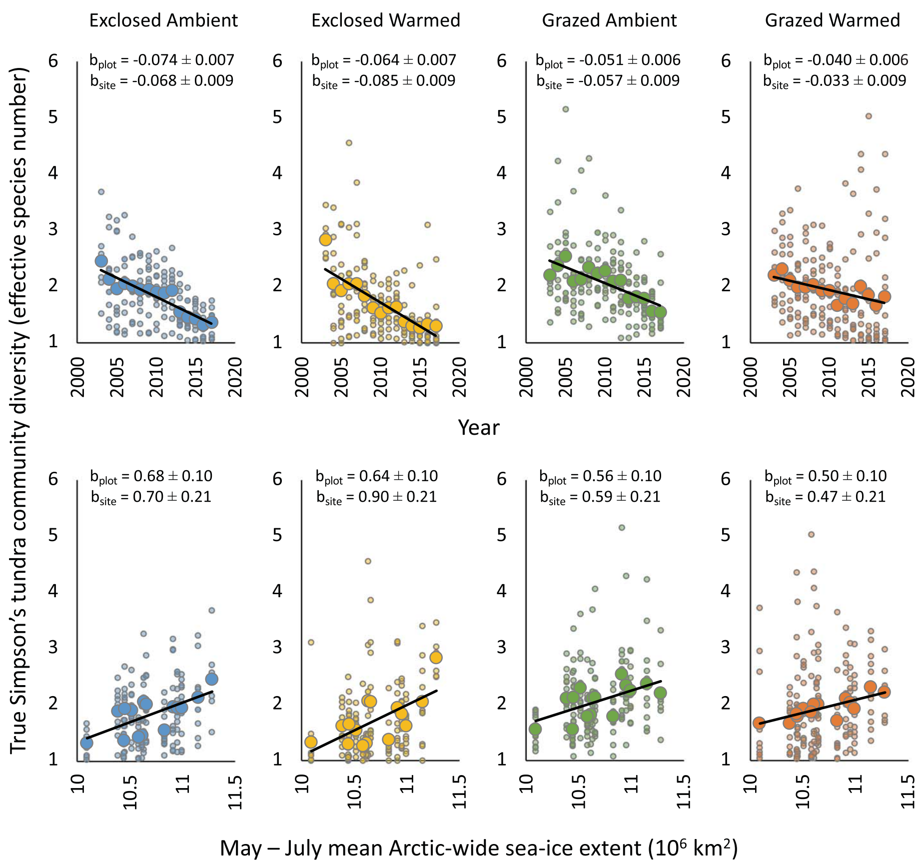

Fig. 2. Arctic tundra diversity trends and associations with sea ice decline. Decline in arctic tundra community diversity (True Simpson's diversity, or effective species number) across treatments over the course of a 15-year field experiment near Kangerlussuaq, Greenland, 2003 to 2017 (upper row) and association with declining Arctic-wide sea ice extent during the annual growing season (May through July) (bottom row). Panels in the upper row show plot-scale (small, pale symbols; n = 174 for exclosed plots and n = 189 for grazed plots) and site-scale (large, dark symbols; n = 15 in all cases) community diversity during each year of the experiment. Panels in the bottom row show plot- and site-scale community diversity in relation to mean Arctic-wide sea ice extent during the annual growing season (May-July). Trend lines are fit to site-scale mean values. Plot- and site-scale trends and sea ice coefficients (b ± 1SE) were significant for all treatments (*24*).

indicate that this relationship operates through effects of synoptic-scale air mass configurations that increase the frequency of easterly winds over the study area in July during low sea ice years (figs. S4 and S5).

Mediation of tundra diversity responses to the experiment by large herbivore diversity and abundance

Greater rates of decline in tundra diversity under herbivore exclusion than under grazing, and stronger associations between abiotic conditions and declining tundra diversity on exclosed than on grazed plots, suggest a role of vertebrate herbivores in mediating sea ice effects at this site. Hence, we examined the response of tundra diversity to our experiment in relation to background variation in large herbivore diversity (or abundance) and May-July ASIE over the course of the experiment (*24*). At the inception of this experiment, local caribou abundance was 20 times that of muskoxen but declined throughout the experiment whereas muskox abundance more than tripled (*30*) (Fig. 3, upper panels). Opposing abundance trends of these two species resulted in an increase in effective species number (True Simpson's diversity) of large herbivores from a low of approximately 1 to a high of 1.7 between 2003 and 2017 (Fig. 3). Across the arctic tundra biome, local richness of large herbivores typically ranges from 0 to 2 species (*19*), so the magnitude of the increase in herbivore diversity over the course of this experiment is comparable to extant biome-wide variation in large herbivore diversity (but not density, which is comparatively low at this site) (*24*, *31*).

Tundra diversity responses to the experimental treatments were unrelated to May-July ASIE but were strongly related to variation in large herbivore diversity over the course of the experiment (table S7) (Fig. 4). The exclosure effect on tundra diversity on warmed plots was negatively associated with large herbivore diversity, whereas the warming effect on tundra diversity on grazed plots was positively associated with large herbivore diversity (Fig. 4). Both relationships indicate that a large herbivore diversity index above an effective species number of ~1.5 promoted greater tundra diversity on grazed versus exclosed plots, and on warmed versus ambient plots under grazing. Hence, although tundra diversity declined across the study site in association with trends in background abiotic conditions, the concurrent increase in large herbivore diversity likely facilitated a slower decline and greater overall tundra diversity on grazed and experimentally warmed plots than on plots under any other experimental treatment combination. This was especially evident in the latter years of the experiment when herbivore diversity was greatest (Fig. 2, top row, small symbols).

Tundra diversity responses to the experiment were also more strongly related to variation in large herbivore diversity than to variation in caribou or muskox abundance individually [table S8; see table S9 for analyses that also considered arctic hares (*Lepus arcticus*; fig. S6), which were not significant].

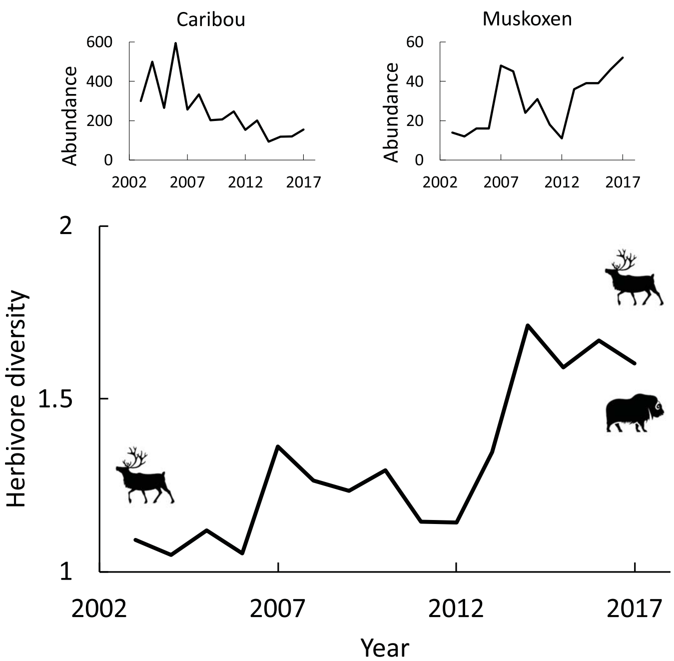

Fig. 3. Dynamics of large herbivore abundance and diversity at the study site near Kangerlussuaq, Greenland. Increase in large herbivore diversity (True Simpson's diversity, or effective species number) (*24*) at the study site near Kangerlussuaq, Greenland (2003 to 2017; linear regression b = 0.06 ± 0.01, t = 5.02, P < 0.001). Upper panels show annual maximum abundances of caribou and muskoxen observed at the site used to calculate True Simpson's diversity of the large herbivore assemblage (*24*, *30*). Caribou and muskox silhouettes in the lower panel are intended to illustrate a shift from dominance of effective species number by caribou at the beginning of the 15-year tundra warming and herbivore exclusion experiment to contributions of both species to effective species number by the end of the experiment.

Moreover, tundra diversity responses to the experiment were differentially associated with variation in caribou versus muskox abundance (table S8), likely reflecting distinct influences of the two herbivores on tundra taxa (fig. S7). For instance, the exclosure effect on warmed plots was positively associated with caribou abundance but negatively associated with muskox abundance (Fig. 4). Consequently, the slower sea ice–associated decline in tundra diversity under grazing with warming eventually resulted in greater tundra diversity under this treatment than under herbivore exclusion with warming (Fig. 2). This difference developed even as caribou abundance declined and muskoxen increased at the study site. Moreover, the strength of the effect of the warming treatment on tundra diversity on grazed plots increased with increasing muskox abundance at the site but not with caribou abundance (Fig. 4). This suggests distinct interactions of the two herbivores with warming, further emphasizing the potential for variation in diversity of the herbivore assemblage to influence tundra community responses to background abiotic change (Fig. 1).

Contributions of individual tundra taxa to tundra diversity

Finally, we sought to determine which taxa contributed most to variation in tundra diversity under each experimental treatment combination (*24*) (fig. S8). Tundra diversity declined with increasing abundances of deciduous shrubs (Fig. 5A) and, consistent with other findings (*32*), shrub abundance at the Kangerlussuaq site increased with both herbivore exclusion and warming (*33*). The decline in tundra diversity with increasing shrub abundance occurred under all treatments but was strongest under exclosed ambient conditions and weakest under grazed warmed conditions (Fig. 5A and table S10). Contributions of shrub increases to declining diversity were, moreover, generally weaker under herbivory than under herbivore exclusion (Fig. 5A and table S10). Deciduous shrubs were also the only functional group contributing to tundra diversity decline as they became more common (*33*) during the experiment (Fig. 5B).

Tundra diversity decline appears, therefore, attributable mainly to increases in the two most common species at the site: dwarf birch and gray willow, the abundances of which are constrained by herbivory and promoted by warming, respectively (*18*). The abundances of both species also co-vary negatively at the site with sea ice extent (*27*). The role of large herbivore diversity in this suite of interactions likely derives from the distinct yet complementary seasonal presence and behavioral-foraging impacts of caribou and muskoxen. The impact of migratory caribou on vegetation at the site is likely limited mainly to growing

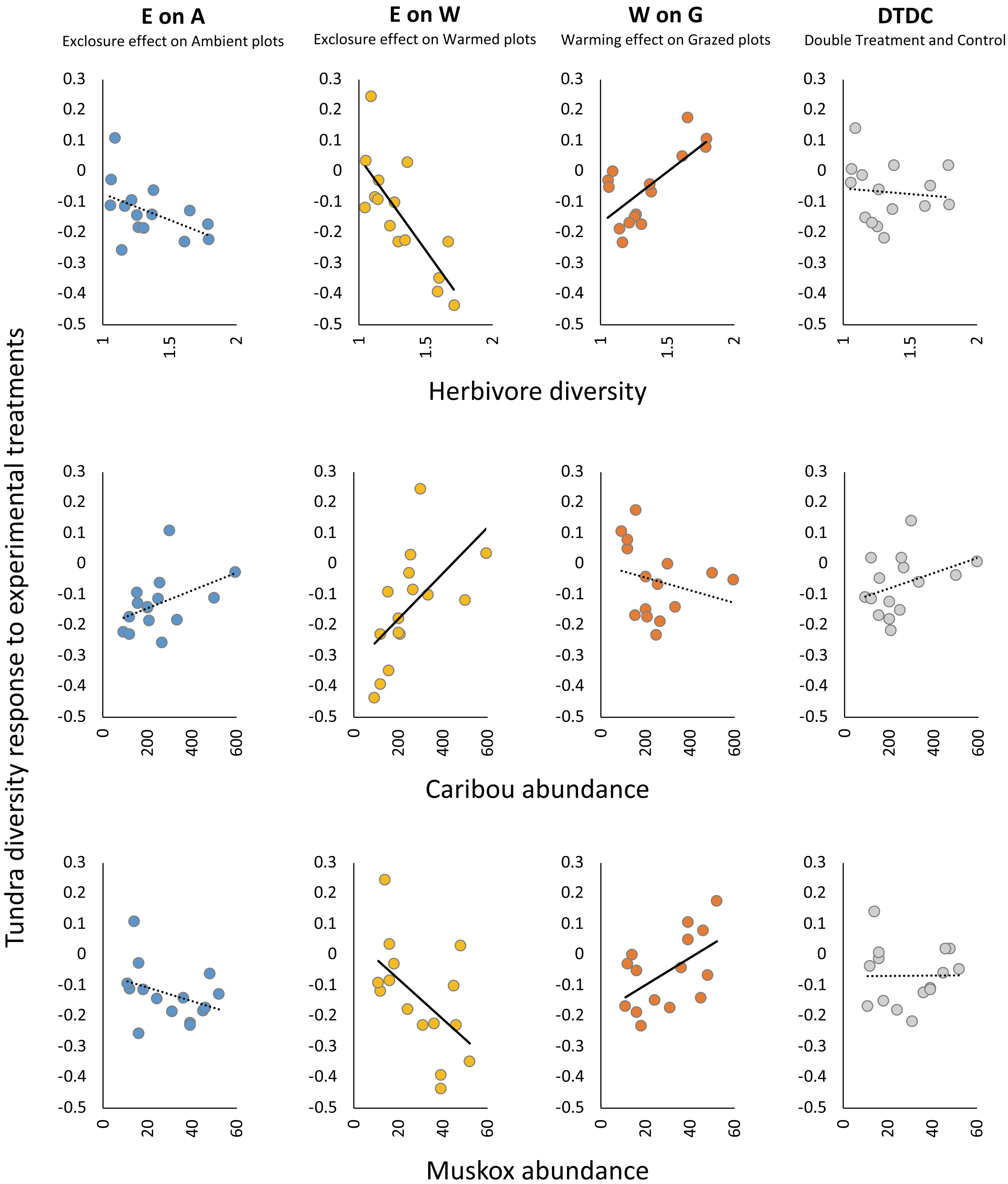

Fig. 4. Arctic tundra diversity responses to experimental manipulations in relation to background variation in herbivore diversity, caribou abundance, and muskox abundance. Variation in the magnitude of annual experimental treatment effects on tundra community diversity, quantified as delta-corrected log response ratios (*24*), in relation to interannual variation in large herbivore diversity (upper row), abundance of caribou (middle row), and abundance of muskoxen (bottom row) at the study site near Kangerlussuaq, Greenland, 2003 to 2017. Shown are the exclosure effect on ambient plots (E on A), for which positive (negative) values indicate that tundra diversity was greater (lower) on exclosed plots than on grazed plots under ambient conditions; the exclosure effect on warmed plots (E on W), for which positive (negative) values indicate that tundra diversity was greater (lower) on exclosed plots under warming than on grazed plots under warming; the warming effect on grazed plots (W on G), for which positive (negative) values indicate that tundra diversity was greater (lower) on warmed plots under grazing than on ambient plots under grazing; and the double treatment double control effect (DTDC), for which positive (negative) values indicate that tundra diversity was greater (lower) on exclosed warmed plots than on grazed ambient plots. Solid and dashed lines indicate significant and nonsignificant relations, respectively; multivariate generalized linear model Wald Chi-Square values and significance tests for each relationship are reported in table S8.

season herbivory whereas that of resident muskoxen is annual (fig. S8). Moreover, behavioral and rumen content analyses of the two species in the area indicate that they exhibit distinct intra- and interseasonal preferences for dwarf birch and gray willow (*34*–*36*) (fig. S8). Such differences, although in some ways subtle, may foster a "portfolio effect" (*37*) of heterogeneous herbivore impacts on tundra community composition, buffering responses to climate change that might otherwise develop more quickly in concert with changes in herbivore abundance in a single large herbivore system.

Implications for ongoing climate change impacts on tundra diversity and rewilding

Biodiversity loss is projected to be one of the most likely and ecologically consequential outcomes of climate change (*1*, *2*, *38*). In addition to cultural and economic impacts to humans (*39*, *40*), biodiversity loss will affect key ecological properties, including community stability and ecosystem function (*41*). Recent assessment reports have indicated that polar ecosystems have experienced the greatest impacts of climate change on biodiversity over the past century (*39*), that climate change impacts experienced by Indigenous Peoples and local communities are greater in tundra habitats than in any other biome (*40*), and that there is a "high to very high" risk of imminent biodiversity loss in the Arctic with ongoing climate change (*42*). Our results likewise signal potential adverse consequences for tundra biodiversity of sea ice loss and warming.

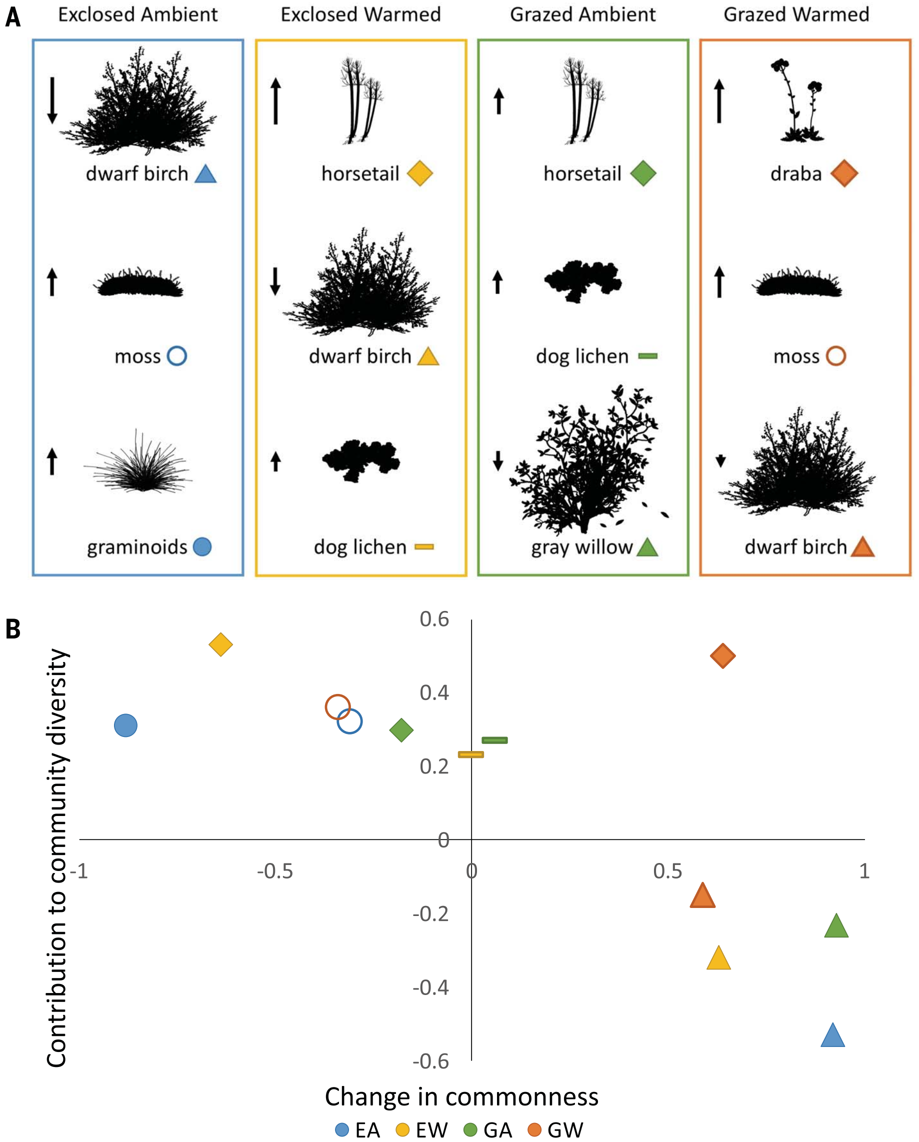

Fig. 5. Taxa contributing most to variation in arctic tundra diversity under long-term experimental warming and large herbivore exclusion. (**A**) Species or taxa contributing most to variation in tundra community diversity (*24*) at the plot scale under each experimental treatment combination at the study site near Kangerlussuaq, Greenland, 2003 to 2017. Black arrows indicate the direction and magnitude of contributions of each species or taxon to tundra diversity and are scaled according to the values of the standardized linear coefficients quantifying their individual contributions to variation in tundra diversity (*24*). Taxa are arranged within each treatment from top to bottom in order of decreasing contributions to tundra diversity. (**B**) Magnitude of the contribution of individual taxa to tundra diversity [standardized linear model coefficient; (*24*)] in relation to changes in their commonness [abundance-weighted occurrence; (*33*)] over the course of the experiment. Positive *y*-axis values indicate that increases in the abundance of a taxon enrich tundra diversity, and negative values indicate that increases in abundance of a taxon reduce tundra diversity. Positive *x*-axis values indicate that a taxon has become more common under that experimental treatment, whereas negative values indicate that a taxon has become rarer under that treatment, over the duration of the experiment (*33*). Experimental treatment abbreviations in the lower panel are as follows: EA, exclosed ambient; EW, exclosed warmed; GA, grazed ambient; and GW, grazed warmed. Common names refer to the following species, genera, or families: dwarf birch (*Betula nana*), moss (*Aulacomnium* sp.), graminoids (Gramineae), horsetail (*Equisetum* sp.), dog lichen (*Peltigera* sp.), gray willow (*Salix glauca*), and draba (*Draba* sp.).

The extent to which management or conservation of large herbivores might slow or possibly reverse tundra diversity losses in the Arctic is difficult to generalize from our results. However, other recent work has also indicated both warming-driven losses of arctic plant diversity and mediation or reversal of such losses by large herbivores (*20*), and additional evidence suggests that herbivore reintroductions or replacements may prevent or reverse ecosystem state shifts resulting from the loss of herbivore diversity (*43*). Hence, our results may have relevance to discussions of nature-based solutions (*44*) to climate change impacts such as rewilding of the Arctic to mitigate tundra diversity losses associated with woody plant encroachment (*22*, *45*) (Fig. 1). Our study demonstrates that climate-driven vegetation diversity decline may be mediated by an increase in large herbivore diversity, even at the modest level of increase seen here. Efforts focused on maintenance or enhancement of large herbivore diversity may therefore under certain conditions help mitigate climate change impacts on at least one important element of ecosystem health and function: tundra diversity.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.add2679
Materials and Methods
Supplementary Text
Figs. S1 to S8
Tables S1 to S10
References (*51–64*)
MDAR Reproducibility Checklist

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Large herbivore diversity slows sea ice–associated decline in arctic tundra diversity

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Editor's summary
Arctic tundra is experiencing rapid climate change, including warming temperatures and loss of sea ice. Plants and herbivores are both affected by these abiotic changes. Post *et al*. examined the effects of climate change and herbivory on the diversity of tundra plants, fungi, and lichens using a 15-year warming and herbivore exclusion experiment. They found that diversity decreased over time across all treatments, which was mainly explained by losses of sea ice with ambient warming. However, herbivores tempered this decline in plots where they were not excluded, particularly under experimental warming. The two herbivores studied, caribou and muskoxen, had different effects on the understory, with a positive effect of increasing muskoxen (and thus herbivore diversity) on tundra diversity. —Bianca Lopez