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Herbivory and warming interact in opposing patterns of covariation between arctic shrub species at large and local scales

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A major challenge in predicting species' distributional responses to climate change involves resolving interactions between abiotic and biotic factors in structuring ecological communities. This challenge reflects the classical conceptualization of species' regional distributions as simultaneously constrained by climatic conditions, while by necessity emerging from local biotic interactions. A ubiquitous pattern in nature illustrates this dichotomy: potentially competing species covary positively at large scales but negatively at local scales. Recent theory poses a resolution to this conundrum by predicting roles of both abiotic and biotic factors in covariation of species at both scales, but empirical tests have lagged such developments. We conducted a 15-y warming and herbivore-exclusion experiment to investigate drivers of opposing patterns of covariation between two codominant arctic shrub species at large and local scales. Climatic conditions and biotic exploitation mediated both positive covariation between these species at the landscape scale and negative covariation between them locally. Furthermore, covariation between the two species conferred resilience in ecosystem carbon uptake. This study thus lends empirical support to developing theoretical solutions to a long-standing ecological puzzle, while highlighting its relevance to understanding community compositional responses to climate change.

Arctic | *Betula nana* | climate change | *Salix glauca* | species distributions

A readily observable phenomenon in nature is the tendency for the distributions of potentially competing species to covary positively at large spatial scales but negatively at small scales (1, 2). This scale dependence in patterns of species covariation is a defining phenomenon in ecology (3), and a classic illustration of it derives from MacArthur's observations of *Dendroica* sp. warblers in mixed forests of the northeastern United States (1) and related theoretical work (4, 5). However, while opposing patterns of species covariation at large and local scales are ubiquitous, assigning causality to interacting drivers of such patterns in natural systems is challenging. Originally, theory explained this phenomenon as a product of distinct types of drivers of species abundance and distribution at large versus local scales. According to this framework, regional factors, such as climate, determine species' distributions over large scales, while biotic interactions such as exploitation and interference determine presence, absence, and relative abundances of species at local scales (5–10). Hence, species with similar resource demands should, and often do, overlap spatially (covary positively) at broad scales as their distributions track abiotic niche requirements such as favorable climatic conditions (11). Meanwhile, the same species should, and often do, covary negatively at smaller spatial scales, where local biotic interactions such as competition, interference, niche complementarity, or exploitation by consumers or pathogens promote exclusion or segregation (5, 12–14). More recent theoretical developments have, however, highlighted the potential for roles of both types of

drivers in patterns at both scales (7, 15, 16). Understanding whether, and how, climate and biotic interactions simultaneously influence species' covariation at large and local scales has been repeatedly identified as a key challenge in improving predictions of species' distributional and biodiversity responses to climate change (15, 17, 18).

In contrast to progress in theory, field experimental tests of such potential interactions between biotic and abiotic factors in opposing patterns of species covariation at large and local scales have been lacking (14), in part because of the challenges inherent in conducting sufficiently controlled field experiments over suitably long time scales (19, 20). Consequently, novel empirical support for the role of, for example, biotic interactions in large scale patterns of species covariation has been strictly observational (21). Application of more robust empirical tests of predictions deriving from recent theory on this topic may also improve understanding of the consequences of patterns of species covariation at opposing spatial scales for important aspects of ecosystem function (22), including carbon exchange (23–26). Here, we present results of a 15-y warming and herbivore-exclusion experiment conducted at a remote arctic field site aimed at investigating influences of both drivers on patterns of covariation between two dominant shrub species at local and large spatial scales. The experimental design targets temperature

Significance

Whether climatic conditions or biotic interactions determine species abundances and distributions has been a persistent question in ecology. Furthermore, its answer has long been considered scale-dependent, with climate presumably constraining abundance and distributions at large scales and species interactions determining them at local scales. We conducted a 15-y field experiment to test more recent theory that predicts abiotic conditions and biotic interactions can shape patterns of species covariation at both large and local scales. Our results affirm this prediction, offering insights that will help improve predictions of species' distributional responses to climate change.

Author contributions: E.P. and C.P. designed research; E.P., S.M.P.C., J.T.K., C.P., and P.F.S. performed research; E.P., S.M.P.C., and P.F.S. analyzed data; and E.P., S.M.P.C., J.T.K., C.P., and P.F.S. wrote the paper.

The authors declare no competing interest.

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as the abiotic limiting factor and herbivory (and associated ancillary effects) as the biotic limiting factor (*Methods*).

The two focal shrub species in this study, dwarf birch (*Betula nana*) and gray willow (*Salix glauca*), hereafter “birch” and “willow,” respectively, are the most abundant plant species at our study site in low-arctic Greenland (27), and their functional role in ecosystem CO₂ exchange far exceeds that of any other vascular plant species at the site (28, 29). Furthermore, the two species are codominant across much of the Arctic (Fig. 1) (30, 31), but some experimental evidence indicates that *Betula* has the capacity to outcompete *Salix* at local scales in the Arctic due to its greater developmental plasticity and ability to invest rapidly in stem growth (32). Hence, although annual sampling throughout the duration of our experiment has assessed aboveground dynamics of all components of the plant community (*Methods*), our focus here is on patterns of covariation between birch and willow. Although birch is generally more common than willow across the study site (*SI Appendix*), the two species share similar distributions across the site, occur mainly on low to mid elevation slopes and plateaus, and predictably avoid arid steep slopes and stagnant mesic or saturated lowlands and fens (Fig. 1*B*). Each of the two species readily forms monospecific “shrub islands” at the local scale (Fig. 1*C* and *SI Appendix*, Fig. S3).

Results and Discussion

General Abundance Responses to the Experimental Treatments. The two shrub species responded differentially to the herbivore-exclusion and warming treatments over the 15-y course of the experiment. Local birch abundance (pin intercepts per plot; *Methods*) nearly doubled in response to the exclosure treatment (exclosed mean = 53.9 ± 1.81 vs. grazed mean = 29.5 ± 1.67 ; $F_{1, 695} = 99.9$, $P < 0.001$) but did not respond to the warming treatment (warmed mean = 42.1 ± 1.72 vs. ambient mean = 41.3 ± 1.7 ; $F_{1, 695} = 0.11$, $P = 0.74$). There was no significant interaction between the exclosure and warming treatments for birch ($F_{1, 695} = 0.18$, $P = 0.67$). Local willow abundance, in contrast, did not respond to the exclosure treatment itself (exclosed mean = 23.6 ± 1.73 vs. grazed mean = 23.9 ± 1.59 ; $F_{1, 695} = 0.02$, $P = 0.88$) but responded significantly to the interaction between the exclosure and warming treatments ($F_{1, 695} = 16.6$, $P < 0.001$). Moreover, willow abundance nearly doubled in response to the warming treatment (warmed mean = 29.3 ± 1.64 vs. ambient mean = 18.2 ± 1.65 ; $F_{1, 695} = 23.9$, $P < 0.001$). The significant interaction between the exclosure and warming treatments for willow resulted in willow abundance increasing to a greater extent with warming inside the exclosures (exclosed ambient mean = 13.3 ± 2.39 , exclosed warmed mean = 33.8 ± 2.39)

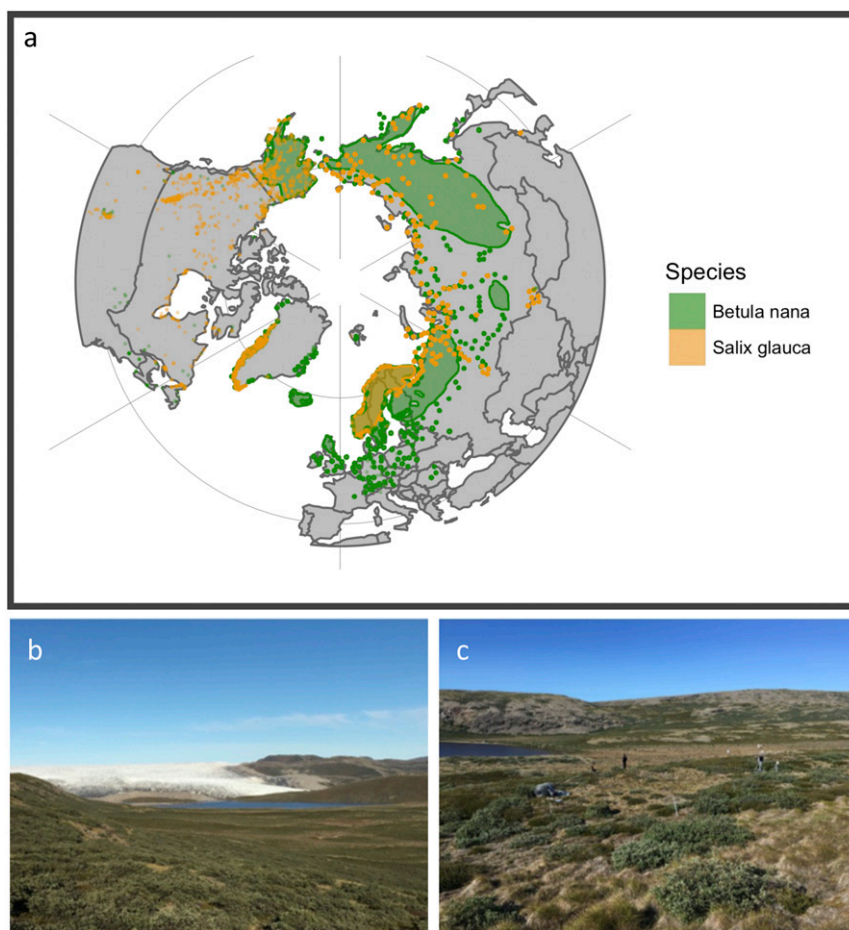


Fig. 1. (A) Circum-Arctic distributions of the two focal shrub species, dwarf birch (*B. nana*) and gray willow (*S. glauca*). Shaded polygons were derived from published range maps (30, 65). Point locations were derived from occurrence records (66–68) and the GBIF data portal (www.gbif.org). (B and C) Landscape and local scale views of patterns of covariation between the two species at the study site near Kangerlussuaq, Greenland. (B) South-facing hillside and lowland plains at the study site illustrating cooccurrence of dwarf birch (*B. nana*) and gray willow (*S. glauca*) at the landscape scale. (C) Monospecific shrub islands of each species are evident at smaller plot scales at the study site. In both photographs, birch appears dark or olive green, while willow appears lighter green. Image credit: E.P.

than outside the exclosures (grazed ambient mean = 23.0 ± 2.25 , grazed warmed mean = 24.9 ± 2.24).

Patterns of Species Covariation at the Landscape Scale. At the larger landscape scale over the 15-y duration of the experiment, abundances of the two shrub species covaried positively across treatments; however, the strength of this positive covariation was mediated by experimental warming and herbivore exclusion (Fig. 2A). Under exposure to herbivory, birch and willow occurred at nearly equal abundance across the landscape, whether warmed (Fig. 2A, purple) or not (Fig. 2A, green). However, herbivore exclusion rapidly promoted landscape-scale dominance by birch, which increased to approximately six times that of willow (Fig. 2A, blue). Warming further mediated this imbalance: while birch abundance did not increase with warming beyond the maximum achieved in response to herbivore exclusion, willow abundance on warmed, exclosed plots (Fig. 2A, orange) increased approximately threefold compared to willow abundance on ambient, exclosed plots (Fig. 2A, blue). Linear regression coefficients of landscape-scale total abundance of willow vs. birch did not differ from parity under herbivory, whether ambient ($b = 0.99 \pm 0.15$) or warmed ($b = 1.10 \pm 0.13$) (Fig. 2A, Inset). In contrast, regression coefficients for the relationships between landscape-scale total abundance of willow vs. birch in the absence of herbivory were <1 under both ambient conditions ($b = 0.15 \pm 0.02$) and warming ($b = 0.55 \pm 0.04$) (Fig. 2A, Inset). Furthermore, the 95% CIs of the coefficients for the exclosed ambient (0.11 to 0.19) and exclosed warmed (0.47 to 0.63) treatments did not overlap 1, indicating dominance by dwarf birch under those treatments. In contrast, 95% CIs of the grazed treatments, whether ambient (0.69 to 1.29) or warmed (0.84 to 1.36), did overlap 1, indicating parity between the two species under grazed conditions. A complementary analysis using a generalized linear model (GLM) to assess covariation between landscape-scale total mean abundances of the two species by treatment (see *Methods* for details and rationale) revealed a significant interaction between the exclosure treatment, warming treatment, and birch abundance on willow abundance ($F_{4, 52} = 58.4$, $P < 0.001$). Similar to the results of the linear regressions,

GLM coefficients of the relationship between willow and birch abundance under exposure to herbivory did not differ from parity whether ambient ($b = 1.04 \pm 0.13$) or warmed ($b = 1.14 \pm 0.14$) but were significantly <1 when exclosed from herbivory, whether ambient ($b = 0.13 \pm 0.06$) or warmed ($b = 0.54 \pm 0.05$) (SI Appendix, Fig. S1). Hence, at the landscape scale, herbivory promoted cooccurrence of willow and birch, removal of herbivory facilitated dominance by birch, and warming constrained the degree of birch dominance by promoting greater willow abundance above that under ambient conditions in the absence of herbivory. These results thus indicate that singular and interactive effects of both biotic (herbivory) and abiotic (temperature) factors can and do drive large-scale patterns of shrub species covariation at this site.

Patterns of Species Covariation at the Local Scale. At the local, plot scale, abundances of birch and willow covaried negatively, and visual inspection of the data together with a comparison of goodness-of-fit statistics indicated that they did so nonlinearly (Fig. 2B; nonlinear regression $R^2 = 0.25$ vs. linear regression $R^2 = 0.20$). As with patterns of positive covariation between the two species at the landscape scale, patterns of negative covariation between them at the local scale were strongly mediated by the herbivore-exclusion and warming treatments. Nonlinear regression models (*Methods* and Eq. 1) for each of the four treatment combinations revealed that the strongest negative association between the two species at the local scale was evident on exclosed warmed plots (model coefficient ± 1 SE: $b_{EW} = 84.6 \pm 5.39$; $F_{2,172} = 192.8$, $P < 0.001$), while the weakest was observed on grazed ambient plots ($b_{GA} = 23.5 \pm 6.19$; $F_{2,187} = 44.7$, $P < 0.001$), with comparable relationships on exclosed ambient ($b_{EA} = 38.5 \pm 5.10$; $F_{2,172} = 46.4$, $P < 0.001$) and grazed warmed ($b_{GW} = 37.7 \pm 6.80$; $F_{2,187} = 48.8$, $P < 0.001$) plots (Fig. 2B, Inset). Hence, these results indicate interactive roles of the focal abiotic and biotic drivers in patterns of species covariation at the local scale but in a somewhat divergent manner from their roles at the landscape scale. While herbivory under ambient conditions facilitated cooccurrence at both local and landscape scales, warming in the absence of herbivory promoted exclusion at the

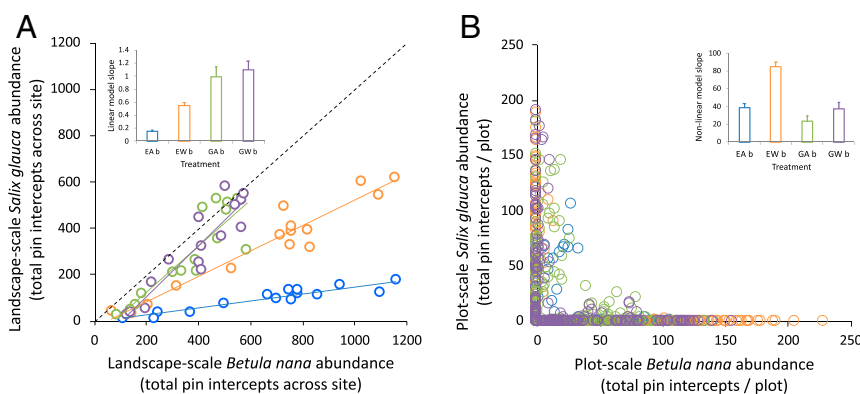


Fig. 2. Opposing patterns of covariation between gray willow (*S. glauca*) and dwarf birch (*B. nana*) at the landscape and local scales at the study site near Kangerlussuaq, Greenland. (A) Landscape-scale positive covariation between abundance of gray willow (*S. glauca*) and dwarf birch (*B. nana*) across the study site. Shown are total annual peak aboveground abundance (number of point frame pin intercepts summed across all plots at the scale of the study site) (27, 56) of each species by treatment: blue, exclosed ambient (EA) ($R^2 = 0.89$, $P < 0.001$); orange, exclosed warmed (EW) ($R^2 = 0.92$, $P < 0.001$); green, grazed ambient (GA) ($R^2 = 0.77$, $P < 0.001$); and purple, grazed warmed (GW) ($R^2 = 0.77$, $P < 0.001$). The dashed line indicates parity between the two species, i.e., a slope coefficient of 1. Inset shows linear regression coefficients for each treatment. Each point represents 1 y of data for each treatment. (B) Plot-scale negative covariation between gray willow (*S. glauca*) and dwarf birch (*B. nana*) within the study site. Shown are the annual peak abundances of each species on each plot (total number of point frame pin intercepts per plot) by treatment: blue, EA ($R^2 = 0.25$, $P < 0.0001$); orange, EW ($R^2 = 0.59$, $P < 0.0001$); green, GA ($R^2 = 0.07$, $P < 0.0001$); and purple, GW ($R^2 = 0.14$, $P < 0.0001$). Inset shows treatment-specific model coefficient estimates (± 1 SE) (see *Patterns of Species Covariation at the Landscape Scale*) (95% CIs: $b_{EA} = 28.5$ to 48.6; $b_{EW} = 73.9$ to 95.2; $b_{GA} = 11.2$ to 35.7; $b_{GW} = 24.3$ to 51.1). The strongest inverse relationship between the two species occurred on exclosed warmed plots, while the weakest occurred on grazed ambient plots (see *Patterns of Species Covariation at the Local Scale*). Each point represents 1 y of data for each plot within each treatment.

local scale while constraining the degree of exclusion at the landscape scale.

Monospecific Dominance versus Mixed-Species Cooccurrence. Corroborating evidence for such interactive effects of biotic and abiotic factors in local-scale patterns of covariation in shrub abundances is further apparent in time series of the proportion of mixed-species plots under each treatment over the course of the 15-y experiment (Fig. 3). While the proportion of mixed-species plots fluctuated under the exclosure treatment, whether ambient (Fig. 3A) or warmed (Fig. 3B), there were no trends in their occurrence over 15 y. In contrast, the proportion of mixed-species plots increased under exposure to herbivory and slightly more so under ambient conditions (Fig. 3C; $b_{GA} = 0.019 \pm 0.005$, 95% CI = 0.009 to 0.029) than under warmed conditions (Fig. 3D; $b_{GW} = 0.012 \pm 0.005$, 95% CI = 0.002 to 0.022). Hence, herbivory promoted the development of mixed-species assemblages suggestive of coexistence at the local scale over the course of the experiment, and yet warming slightly constrained this influence. An ancillary analysis also revealed a significant positive association between muskox abundance and willow abundance on grazed plots under both ambient and warmed conditions (SI Appendix), possibly reflecting an increase in stem bifurcation and density as a result of release from apical dominance under browsing (*sensu* ref. 33). Because birch are generally more abundant across the study site, the increase in mixed-species plots under exposure to herbivory might therefore relate at least partially to an increase in muskox abundance at the site over the course of the experiment (SI Appendix). While it is possible that our sampling method may not have been sufficient to detect trace abundances (e.g., a single stem) of either species at the initiation of the experiment, thus potentially misclassifying plots as truly monospecific, we do not anticipate that this would materially affect the interpretation of trends reported here.

Significant treatment effects on the abundance at which each species became monospecific dominant (i.e., excluded the other species) at the local scale were revealed by von Bertalanffy curves (Methods) fit to plot-scale data on the proportion of total shrub abundance comprising either birch (Fig. 4A) or willow (Fig. 4B). For birch, exclusion of willow occurred at significantly lower abundances on warmed plots than on ambient plots,

regardless of exposure to herbivory (Fig. 4C). For willow, exclusion of birch also occurred at the lowest local abundance on warmed plots and at significantly lower abundance on exclosed warmed than on grazed warmed plots (Fig. 4D). For both species, cooccurrence with the other species was maintained at the highest abundances on grazed ambient plots (Fig. 4C and D). The spatial scale of the transition between cooccurrence and monospecific exclusion of one species by the other also differed by species across the entire study site (SI Appendix, Figs. S3–S5).

Relations to Soil Water Content and Soil Temperature. To assess mechanistic factors contributing to the contrasting patterns of species' responses to the warming and exclosure treatments at the two scales, we examined data collected previously at the site on volumetric soil water content (SWC) and soil temperature (ST) at 5 cm depth (34, 35). Across treatments, SWC declined significantly with increasing ST (Fig. 5), and this relationship was described slightly better by a log-linear model ($R^2 = 0.42$, $P < 0.001$) than by a linear model ($R^2 = 0.39$, $P < 0.001$) (Methods). Within treatments, GLMs revealed that the magnitude of the decline in SWC with increasing ST was strongest on ambient plots, whether exclosed or grazed, and weakest on warmed plots, whether exclosed or grazed (Fig. 5, *Inset*). Because the warming and exclosure treatments elicited strong, and in some respects opposing, species-specific abundance responses, we suspect that the relationships in Fig. 5 reflect indirect responses of above-ground abundance to these treatments (36).

To test this, we compared the strength of associations between aboveground abundance of birch or willow and 1) SWC and 2) ST at 5 cm depth (34, 35). We applied a linear mixed-effects model to the data, with either SWC or ST as the response; treatment and species as fixed factors; and shrub species-specific aboveground abundance and year as covariates, with day of year nested within year. Hence, coefficients emerging from these models are scaled to unit aboveground abundance and thus comparable between species and across treatments. This analysis revealed significant, negative associations between increasing shrub abundance and SWC for both species across all treatment combinations except for birch on grazed warmed plots and willow on grazed ambient plots (Fig. 6). Models for ST revealed nonsignificant, positive associations with increasing shrub abundance for both species across all treatments, except for willow on exclosed warmed plots, which was significant (Fig. 6). Most notably, the pattern that emerged across all treatment combinations and both species (Fig. 6) suggests that willow tends to either occupy warmer and drier soils than birch, possibly revealing a dimension of niche partitioning between the two species, or that willow tends to promote/maintain warmer and drier soil conditions than birch. Regardless, larger-scale cover distributions suggest both species avoid the wettest and driest regions of the landscape (SI Appendix, Fig. S3).

Consequences of Species Covariation for Ecosystem Function. To examine the functional consequences of transitions between cooccurrence and spatial segregation of birch and willow, we analyzed plot-scale chamber-based measurements of ecosystem-atmosphere CO_2 exchange made during the 2008 and 2009 growing seasons (34) (Methods). This analysis revealed that, under low vapor pressure deficit (VPD), willow-dominated plots are characterized by greater gross ecosystem photosynthesis (GEP) than birch-dominated plots (SI Appendix, Fig. S6 and Table S3). However, with increasing VPD, birch- and willow-dominated plots converge upon a common level of GEP, until, at high VPD, birch-dominated plots begin to show greater GEP than willow-dominated plots (SI Appendix, Fig. S6). These results highlight important functional differences between birch- and willow-dominated plots that likely stem from a combination of unique physiological traits inherent to each species and our finding that willows tend to occupy warmer

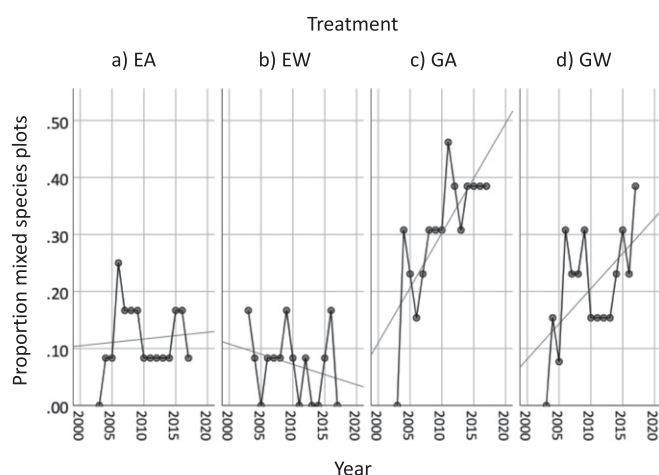


Fig. 3. Time series of the proportion of the total number of experimental plots containing both shrub species (i.e., mixed-species plots) by treatment across the 15-y experiment. Trends, indicated by gray linear regression lines, were not significant for the (A) exclosed ambient (EA) or (B) exclosed warmed (EW) treatments ($R^2_{EA} = 0.01$, $P = 0.76$; $R^2_{EW} = 0.07$, $P = 0.35$) but were significant for the (C) grazed ambient (GA) ($R^2_{GA} = 0.57$, $P = 0.001$) and (D) grazed warmed (GW) ($R^2_{GW} = 0.31$, $P = 0.03$) treatments.

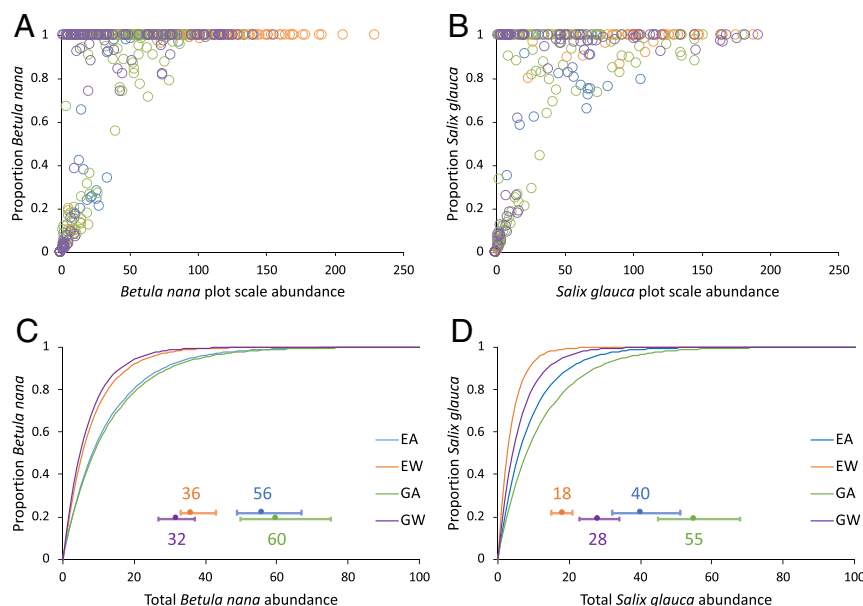


Fig. 4. Relations between plot-scale abundance and the proportion of total shrub abundance per plot comprising *B. nana* (A) or *S. glauca* (B), color coded by treatment (blue: excluded ambient [EA]; orange: excluded warmed [EW]; green: grazed ambient [GA]; purple: grazed warmed [GW]). von Bertalanffy curves fit to the data in A and B are shown in C and D for *B. nana* and *S. glauca*, respectively. Horizontal bars in C and D show 95% CIs around point estimates (dots and associated numeric values) of the abundance at which each species reaches monospecific dominance (defined in *Methods*) at the local scale, as estimated from the coefficients from each treatment-specific curve fit to the data in A and B. Nonoverlapping (CIs) are considered significantly different at $P < 0.05$ (*Methods*). Coefficients of determination, F statistics, and significance values for von Bertalanffy curves are as follows for *B. nana*: $R^2_{EA} = 0.73$, $F_{2, 172} = 2,347.7$, $P < 0.0001$; $R^2_{EW} = 0.94$, $F_{2, 172} = 4,056.8$, $P < 0.0001$; $R^2_{GA} = 0.75$, $F_{2, 187} = 864.2$, $P < 0.0001$; $R^2_{GW} = 0.84$, $F_{2, 187} = 1,385.8$, $P < 0.0001$. Coefficients of determination, F statistics, and significance values for von Bertalanffy curves are as follows for *S. glauca*: $R^2_{EA} = 0.91$, $F_{2, 172} = 1,038.7$, $P < 0.0001$; $R^2_{EW} = 0.97$, $F_{2, 172} = 4,630.8$, $P < 0.0001$; $R^2_{GA} = 0.79$, $F_{2, 187} = 679.0$, $P < 0.0001$; $R^2_{GW} = 0.84$, $F_{2, 187} = 914.9$, $P < 0.0001$.

and drier soils than birch. This suggests that the spatial segregation of birch and willow likely confers resilience to landscape-scale CO_2 uptake under moisture-limiting conditions, which are becoming increasingly common in this arctic landscape (37).

Conclusions

Biome-scale patterns of arctic shrub expansion or contraction, and associated tundra greening or browning, are highly variable across the Arctic and difficult to attribute to universal drivers such as climate change (38–42). Nonetheless, multiple recent site-specific studies that have taken into account influences of herbivory, whether explicitly or implicitly, argue strongly for its interaction with abiotic factors such as nutrient availability, moisture availability, or temperature in arctic shrub dynamics (37, 43–46). While comparatively uncommon and challenging to sustain, long-term field experiments can be sufficient, and may be necessary, to disentangle complex interactions between biotic and abiotic factors in the structure and dynamics of natural communities (19, 36, 47). This study uniquely highlights the potential offered by such approaches in addressing long-standing and fundamental questions in ecology concerning the roles of biotic and abiotic factors in patterns of species' distributions and abundance at disparate spatial scales, while also highlighting empirically the functional consequences of landscape-scale species distributions (11).

Methods

Study Site, Experimental Design, and Data Collection. The study site encompasses ~25 hectare (ha) located 20 km northeast of the village of Kangerlussuaq, Greenland, 160 km inland from the Davis Strait and 5 km west of Russell Glacier, a terminus of the Greenland Ice Sheet (48). The surrounding area has an extensive history of importance to indigenous peoples as a caribou hunting corridor and was designated as a United Nations Educational, Scientific and Cultural Organization World Heritage Site, Aasivissuit-Nipisat, by the United Nations in 2018.

We employed a cross-factorial experiment designed to test for effects of herbivore exclusion and warming, and their interaction, on plant species-specific abundance and community composition. The experiment was designed to facilitate quantification of abundance and compositional responses at multiple spatial scales: sampling was conducted on <2-m² plots (described in more detail at the end of this section) nested randomly within 800-m² subsites located randomly within the 25-ha site.

The herbivore-exclusion treatment was implemented in mid-June 2002 with the installation of three, 800-m² enclosures constructed of woven wire fencing and steel t-posts (49). Enclosures were removed at the end of the growing season in 2017. The enclosure treatment was intended to prevent grazing, trampling, and other ancillary effects of herbivore presence, such as soil compaction and fecal and urinary nutrient inputs by caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) at sublandscape scales that could be integrated across the landscape scale of the study site. Voles and lemmings, which can exert considerable influence on tundra vegetation composition (50), do not occur at the study site. Abundances of both caribou and muskoxen have varied substantially throughout the duration of the experiment, with caribou having declined from a peak density of ~24 adults per hectare in 2006 to ~6 adults per hectare in 2017 and muskoxen having increased from a density of ~0.5 adults per hectare at the start of the experiment to a peak density of ~2 adults per hectare by the end of the experiment (37, 48). While we have regularly observed both species of herbivores feeding on both species of shrubs at the site, including occasional observations of caribou and muskoxen feeding from inside nonexcluded warming chambers, the seasonal timing of herbivory by caribou and muskoxen and shrub responses to tissue removal by them likely differ. For instance, both caribou and muskoxen strip leaves from both birch and willow at the site during the growing season but may occasionally also tear apical stems from willow and break birch stems while leaf stripping. This action can kill stems of both shrub species and reduce their abundance. In contrast, muskoxen, which are resident year-round in the study area, may also browse stems of both shrub species in autumn, winter, and early spring prior to growth initiation, releasing stems from apical dominance. Such browsing action outside the growing season may result in production of more numerous shoots from axillary and adventitious buds during the ensuing growing season, increasing shrub canopy density or abundance by promoting a highly reticulated "broom" morphology, especially in willow

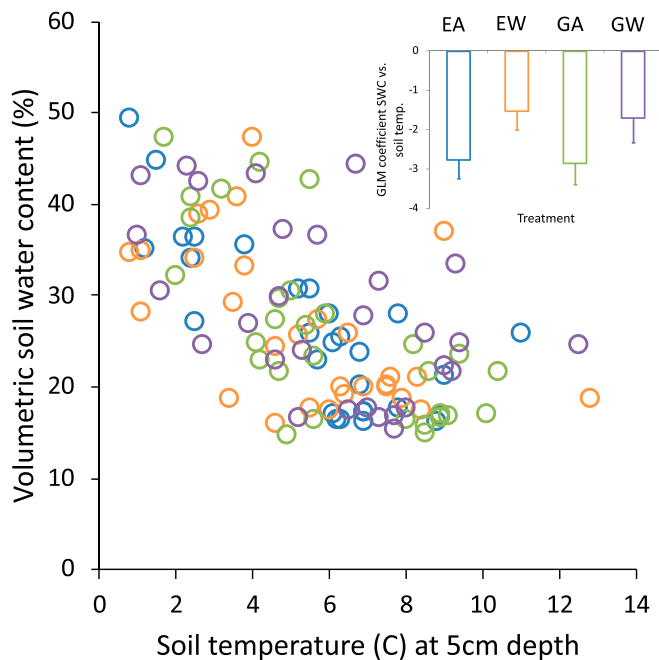


Fig. 5. Plot-scale measurements of volumetric SWC integrated over 0 to 15 cm depth (percentage water) and ST at 5 cm depth by treatment (blue: excluded ambient [EA]; orange: excluded warmed [EW]; green: grazed ambient [GA]; purple: grazed warmed [GW]). Inset shows GLM coefficients, b (± 1 SE), of SWC vs. ST for each treatment: $b_{EA} = -2.78 \pm 0.46$ (Wald $\chi^2 = 36.4$, $df = 1$, $P < 0.001$); $b_{EW} = -1.54 \pm 0.48$ (Wald $\chi^2 = 10.2$, $df = 1$, $P = 0.001$); $b_{GA} = -2.86 \pm 0.55$ (Wald $\chi^2 = 27.4$, $df = 1$, $P < 0.001$); $b_{GW} = -1.70 \pm 0.63$ (Wald $\chi^2 = 7.30$, $df = 1$, $P = 0.007$). Measurements were conducted at midday on two dates during mid and late summer in 2008 (June 18 and July 24) and on three dates during mid and late summer in 2009 (June 11, June 17, and August 4). Each point represents a single paired measurement in either year for a plot within a treatment (34, 35).

(31, 33). Unlike muskoxen, most of the caribou utilizing the study site migrate to the area in early to mid May and depart annually around late June and early July, with only a few males remaining resident year-round (51–53). Hence, caribou herbivory on both shrub species is restricted almost exclusively to the growing season and is therefore likely destructive (54, 55). In *SI Appendix, Analysis of Effects of Background Variation in Weather and Herbivore Abundances on Shrub Responses to the Warming Treatment*, we describe analyses investigating potential differential effects of variation in abundances of caribou and muskoxen over the course of this experiment on willow and birch abundance responses to the warming treatment.

The experimental warming treatment was implemented in early May 2003 and, like the enclosure treatment, ended in late July 2017. The warming treatment was applied annually from early May through the time of vegetation abundance sampling in mid to late July each year, after which warming chambers were removed and stored away until reapplication the following May (27, 56). The warming treatment used passive, open-topped warming chambers designed to minimize unwanted side effects, including interference with herbivory, evaporation, and precipitation (57, 58). Annual application of the warming treatment involved placement of 12 chambers inside and 13 chambers outside of enclosures; a comparable number of ambient plots, which received no warming treatment and were of the same dimensions as the base of the warming chambers, were established inside (12 plots) and outside (13 plots) of enclosures. Two of the enclosures and adjacent grazed sites each received three warmed and ambient plots; the third enclosure had six warmed and ambient plots, and its adjacent grazed site had seven warmed and ambient plots. Thus, the total number of plots by treatment combination was 12 excluded ambient plots, 12 excluded warmed plots, 13 grazed ambient plots, and 13 grazed warmed plots.

Warming chambers were constructed according to the standards and specifications of the International Tundra Experiment (ITEX) (57) using ultraviolet-neutral glazing material. We used recommendations in the ITEX manual (58) and a related metaanalysis of tundra vegetation responses to experimental warming following the ITEX protocol (59) to determine

sufficient sample sizes. As stated above, chambers were installed on warmed plots in early May each year and removed again each field season at the time of annual sampling. All plots, whether experimentally warmed or ambient, were circular, measured 1.5 m in diameter, and comprised a total area of 1.77 m². Locations of both treatment (warmed) and control (ambient) plots were selected at random within and outside of enclosures apart from the following conditions: plot bounds were positioned so as to be entirely inclusive of shrub individuals, i.e., we avoided positioning plots in a manner that would, for instance, capture only lateral stems of multiple individuals rather than the individuals themselves (49). No plot was positioned closer than 2 m from another plot or from the edge of an enclosure whether inside or outside of that enclosure. Thermal data loggers recording surface air temperature, together with soil moisture hygrometers, were paired with warming chambers and ambient control plots; these indicated that the warming treatment significantly elevated mean daily surface temperature by 1.5 to 3.0 °C across plots and produced a nonsignificant reduction in soil moisture content (27, 60).

Each of the 50 plots contained four hollow aluminum anchors embedded into the soil at each of the 4 cardinal corners of the plot. During nondestructive, annual sampling of aboveground vegetation abundance, the legs of a vertically adjustable, transparent Plexiglas table-top point frame measuring 0.25 m² with 20 randomly located 2-mm holes were placed into these anchors to ensure consistent orientation of the sampling frame. A 1-m steel welding pin was lowered through each hole in the Plexiglas top of the sampling frame, and every contact of the pin with shrub leaves or stems was recorded (as was abundance of every plant species or functional group contacted by the pin). While sampling, the 0.25-m² footprint of the point frame was centered within each 1.77-m² plot to minimize potential bias due to edge effects. Point-frame sampling of shrub abundance (27, 49, 56) was conducted annually over a 1- to 3-d period at the seasonal peak of aboveground abundance during mid to late July in most years and did not differ among treatments (*SI Appendix, Fig. S2*). The exceptions were in 2006, when sampling was conducted on June 14, and in 2003 and 2011, when sampling was conducted on August 14 and between August 16 and 17, respectively.

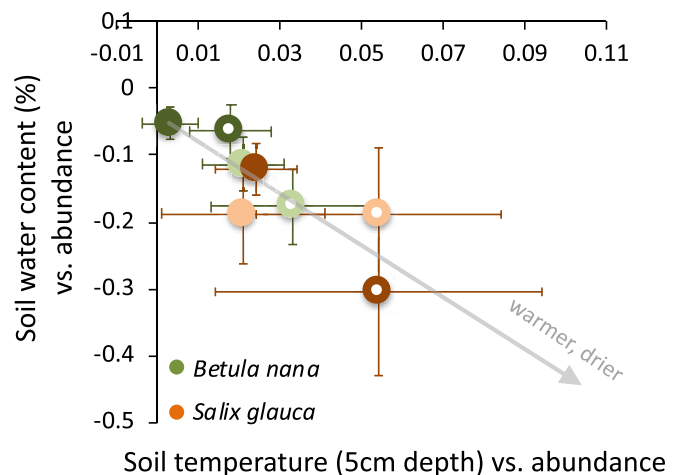


Fig. 6. Coefficients (± 1 SE) of GLMs of the association between shrub abundance and SWC (y axis) and ST (x axis). Coefficients for birch are shown in green, and those for willow are shown in orange. Open symbols are grazed, closed symbols are excluded, pale symbols are ambient, and dark symbols are warmed. The gray trend line is fit through the pooled coefficient estimates and indicates the direction of increasingly warm, dry conditions. SWC vs. abundance significance tests are as follows for birch: excluded ambient (EA): Wald $\chi^2 = 7.55$, $df = 1$, $P = 0.006$; excluded warmed (EW): Wald $\chi^2 = 4.38$, $df = 1$, $P = 0.04$; grazed ambient (GA): Wald $\chi^2 = 9.50$, $df = 1$, $P = 0.002$; grazed warmed (GW): Wald $\chi^2 = 2.50$, $df = 1$, $P = 0.11$. SWC vs. abundance significance tests are as follows for willow: EA: Wald $\chi^2 = 6.01$, $df = 1$, $P = 0.01$; EW: Wald $\chi^2 = 8.65$, $df = 1$, $P = 0.003$; GA: Wald $\chi^2 = 2.91$, $df = 1$, $P = 0.09$; GW: Wald $\chi^2 = 5.69$, $df = 1$, $P = 0.02$. ST vs. abundance significance tests are as follows for birch: EA: Wald $\chi^2 = 2.95$, $df = 1$, $P = 0.09$; EW: Wald $\chi^2 = 0.21$, $df = 1$, $P = 0.65$; GA: Wald $\chi^2 = 3.74$, $df = 1$, $P = 0.05$; GW: Wald $\chi^2 = 2.15$, $df = 1$, $P = 0.14$. SWC vs. abundance significance tests are as follows for willow: EA: Wald $\chi^2 = 0.82$, $df = 1$, $P = 0.37$; EW: Wald $\chi^2 = 3.89$, $df = 1$, $P = 0.05$; GA: Wald $\chi^2 = 2.61$, $df = 1$, $P = 0.11$; GW: Wald $\chi^2 = 1.98$, $df = 1$, $P = 0.16$.

The general timing of sampling each year was beyond our control and dependent upon the timing of availability of air transport to and from Kangarlussuaq. Statistical measures were taken as described in *General Abundance Responses to the Experimental Treatments* to account for any variation in shrub abundances due to differences in sampling dates among years. Hence, to the extent possible, annual sampling has been methodologically consistent, nondestructive, minimally invasive, and conducted with a consistent orientation of the point frame each year from 2003 through 2017. Shrub abundance data are archived online at the Arctic Data Center (data identifier bf007eae-f9f5-454c-ab34-990da909e56d).

General Abundance Responses to the Experimental Treatments. To assess general abundance responses of both shrub species to the experimental treatments, we used GLMs. Models included the enclosure and warming treatments, and their interaction, as fixed effects; plot nested within site as a random effect; and day of year of sampling nested within year as a random effect. We included plot nested within site to account for the experimental design and day of year of sampling nested within year of sampling to account for differences among years in the timing of sampling. Models were run separately for birch and willow. The response variable in each model was total plot-specific point frame pin intercepts of birch or willow. Treatment effects and their interactions were considered significant at $P \leq 0.05$; all tests were two-tailed. Statistical code for this analysis is included in *SI Appendix, A) Analysis of General Shrub Abundance Responses to Experimental Treatments*.

Patterns of Species Covariation at the Landscape Scale. There is no generally agreed upon standard definition of landscape vs. local scales in ecology, but we assume it is reasonable to define the scale of the study site, which encompasses ~25 ha, as landscape, and the scale of experimental plots, which encompass < 2 m², as local. To assess landscape-scale (i.e., square-kilometer) relationships between abundances of the two shrub species, we used two, complementary approaches. In the first, we fit linear regression models to the treatment-specific annual sums of willow abundance across all plots encompassing the entire study site vs. the same treatment-specific sums for birch. To determine whether the slopes of the relationships for each treatment differed from 1 (i.e., parity), we used an approximation of the two-tailed t test to compare the 95% CIs of each slope estimate to 1 (61). This approach quantifies sampled total abundances of each species under each treatment combination across the landscape area manipulated by the experiment. However, it potentially also reduces interplot or intersite variability in shrub abundances across the landscape scale, thus highlighting both conceptual and analytical challenges inherent in quantifying landscape-scale relationships using plot-sampled data. Conceptually, true landscape-scale abundance should comprise the aggregation of abundances measured at any unit smaller than the landscape, in our case, plots. Analytically, however, plot-scale estimates of abundance are population samples, and variation among them should, therefore, be taken into account in using them to derive larger-scale abundance estimates. To incorporate such variability, we employed an alternative approach using a separate set of two successive GLMs. In the first, we included the plot-sampled total pin intercepts of each shrub species as the dependent variable; the enclosure and warming treatments as fixed factors; year as a fixed factor; plot nested within site as a random factor; and an interaction term combining the enclosure treatment, warming treatment, and year. This interaction term was used to derive mean species-specific shrub abundance for each treatment combination in each year of the experiment. In this model, we did not include a term for day of year of sampling nested within year for two reasons. First, abundances of both shrub species were sampled simultaneously within each year, so day-of-year variation was considered unimportant in this context. Second, the interaction term enclosed/grazed $\times$ warmed/ambient $\times$ year was necessary for deriving the estimated marginal (EM) mean abundances of each shrub species by treatment for each year of the experiment for the next stage in this analysis, and inclusion of year as part of an additional, nested term would pose the possibility of biasing the EM means. Once the annual mean abundances of each shrub species under each experimental treatment combination were obtained, we used them in a second GLM of treatment-specific abundance relationships between the two species. This second model quantified landscape-scale mean total abundances of the two shrub species in relation to one another. In this model, mean annual treatment-specific willow abundance was included as the response variable, while the predictor variables included the enclosure and warming treatments as fixed factors and an interaction term for the enclosure treatment, warming treatment, and mean annual treatment-specific birch abundance. This approach allowed for an evaluation of the significance of the association between landscape-scale willow and birch abundances by

treatment, as well as slope (i.e., coefficient) estimates of the relationship between the landscape-scale abundances of the two shrubs by treatment. We report results of both the linear regression and general linear modeling approaches, which were in agreement (*Results and Discussion*). While there may be no a priori reason to assign one species or the other as the dependent or independent variable in these regression models and those described in *Patterns of Species Covariation at the Local Scale*, we settled on this approach because birch is generally more abundant across the study site (*SI Appendix*). Predictors and interaction terms were considered significant at $P \leq 0.05$; all tests were two-tailed. Statistical code for the GLMs used in this analysis is included in *SI Appendix, B) Derivation of Landscape-Scale Annual Mean Total Shrub Abundance by Treatment and C) Analysis of Landscape-Scale Annual Mean Total Abundance of Willow vs. Birch by Treatment*.

Patterns of Species Covariation at the Local Scale. To assess local scale (i.e., square-meter plot-scale) relationships between abundances of the two shrub species, we fit nonlinear regressions of the following form to the treatment-specific, plot-scale annual total pin hits of willow vs. plot-scale total pin hits of birch:

$$Y = a + b(\exp(-X)). \quad [1]$$

In Eq. 1, Y = plot-scale abundance of willow, X = plot-scale abundance of birch, a = the model intercept, and b = the model slope quantifying the decay in abundance of willow with increasing abundance of birch. Models for each treatment were considered significant if $b \neq 0$ based on a two-tailed $P \leq 0.05$. Pairwise slope comparisons among treatments were considered significantly different at $P \leq 0.05$ based on a two-tailed approximation of the t test derived from nonoverlapping 95% CIs (61).

Analysis of Relations between Species Abundance and Transitions from Mixed-Species Cooccurrence to Monospecific Dominance at the Local Scale. To quantify treatment effects on the abundance at which each shrub species transitioned between mixed-species cooccurrence and monospecific dominance, we fit a modified von Bertalanffy equation (62) to the treatment-specific plot-scale proportional abundance of willow or birch and total plot-scale abundance of the same respective species:

$$Y = 1 - \exp(-a(X-b)). \quad [2]$$

In Eq. 2, Y = plot-scale proportion of willow or birch, X = plot-scale abundance of willow or birch, a = the model intercept, and b = the model slope quantifying the approach to unity or complete dominance of shrub abundance by the focal species. When solved for X at $Y = 1$, Eq. 2 permits estimation of the abundance at which each of the shrub species excludes the other as well as estimation of associated 95% CIs. However, because this relationship approaches 1 asymptotically, we used empirically derived model coefficients to solve for X at $Y = 0.99$. We then compared 95% CIs of the estimate of X among treatments within each species to determine differences among treatments in the abundance at monospecific dominance. Nonoverlapping 95% CIs were considered significantly different (at $P \leq 0.05$) based on the two-tailed t test approximation (61). We emphasize here and in the analyses described in *Patterns of Species Covariation at the Landscape Scale* and *Patterns of Species Covariation at the Local Scale* that this test is distinct from falsely concluding that overlapping CIs indicate a lack of significant difference (63). A complementary assessment of species-specific spatial scales of transition between cooccurrence and monospecific dominance was conducted as described in *SI Appendix*.

Relations to SWC and ST. As part of a previous project at the site, we measured volumetric SWC (0 to 15 cm depth) and ST (5 cm depth) at the same set of plots during the 2008 and 2009 growing seasons (34, 35). *SI Appendix, Table S1* shows mean growing season (May through July) temperature and total precipitation for the experimental period (2002 to 2017) and the 2 y during which SWC and ST were measured. This comparison indicates that the 2008 growing season was 0.85 °C warmer and the 2009 growing season was 0.49 °C cooler than the growing season average for the experimental period (8.62 $\pm$ 0.20 °C), and the 2008 growing season was 7 mm drier and the 2009 growing season was 17 mm drier than the growing season average for the experimental period (43 $\pm$ 6.78 mm). We used the CURVEFIT procedure in SPSS Version 26 to determine whether the relationship between pooled SWC and ST was better fit by a linear or a nonlinear model. This procedure provides output statistics comparing coefficients of determination and F statistics for competing linear and logarithmic models. The two models performed comparably well (linear model: $R^2 = 0.39$, $F_{1, 114} = 73.0$, $P < 0.001$; logarithmic model: $R^2 = 0.42$, $F_{1, 114} = 81.9$, $P < 0.001$), and we opted for

linear models in the next phase of this analysis. Subsequently, we used treatment-specific generalized linear models (GLIMs) of SWC vs. ST with a normal probability distribution and identity link function. Year was included as a fixed factor to account for any potential difference in the relationship between SWC and ST in the 2 y of sampling. Models were significant for all treatments, indicating a negative association between SWC and ST in all cases (likelihood ratio χ^2 statistics, degrees of freedom [df] = 2 in all cases: exclosed ambient = 26.9, $P < 0.0001$; exclosed warmed = 14.0, $P = 0.001$; grazed ambient = 21.2, $P < 0.0001$; grazed warmed = 8.80, $P = 0.01$). For only the exclosed warmed treatment was year a significant factor (Wald $\chi^2 = 3.86$, $df = 1$, $P = 0.05$).

To explain patterns of species cooccurrence or segregation and exclusion mechanistically, we investigated the manner in which SWC and ST varied with abundance of each shrub species and how any such variation differed among experimental treatment combinations. To do this, we used two sets of GLIMs, one with SWC as the dependent variable and the other with ST as the dependent variable. In each set of models, we specified a normal probability distribution with an identity link function, birch or willow plot-scale abundance as the independent variable, and day of year by year as a covariate to account for potential influences of sampling date and year. Because we were interested in species-specific relationships, we classified plots as birch plots if birch abundance > willow abundance and as willow plots if willow abundance > birch abundance. The model for SWC vs. species X treatment was significant (likelihood ratio $\chi^2 = 16.9$, $df = 8$, $P = 0.03$), while the model for ST vs. species X treatment was not (likelihood ratio $\chi^2 = 8.16$, $df = 8$, $P = 0.42$). Significance ($P \leq 0.05$) of individual model coefficients (slope estimates) for each species X treatment combination was determined based on two-tailed Wald χ^2 tests with $df = 1$ in all cases; P values are reported in the legend of Fig. 6. Coefficients (± 1 SE) for SWC models were plotted against coefficients for ST models to derive the generalized relationship in Fig. 6.

Consequences of Species Covariation for Ecosystem Function. Ecosystem CO_2 exchange data, collected and processed as part of an earlier aspect of the warming $\times$ enclosure experiment (34), were paired with corresponding point-frame leaf abundance measurements made during the early and mid growing seasons of both 2008 and 2009. Early season point-frame data were paired with CO_2 flux data from the nearest weekly measurement. Midseason point-frame data were paired with both the preceding and the following CO_2 flux dates, as species abundance is more temporally stable near mid-season. Linear mixed-effects models were constructed with GEP estimated

at photosynthetic photon flux densities (PPFD) of 600 and 1,000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ as the dependent variables. Plot-level CO_2 fluxes at these PPFD levels were estimated by measuring CO_2 flux on clear, sunny days and manipulating the range of light levels at each plot on each measurement date in the field (34). Atmospheric vapor-pressure deficit (VPD) within the measurement chamber, birch leaf abundance, and willow leaf abundance were included as main effects. Sampling date nested within a unique plot identifier served as the random effect. Interactions between VPD and birch leaf abundance and between VPD and willow leaf abundance were included in the model to test for differences in the response of each species to increasing evaporative demand.

Aerial Imagery-Based Supplemental Methods Assessing the Adequacy of Our Experimental Design to Investigate Scale-Dependent Patterns of Species Covariation. We also provide a detailed [SI Appendix](#) that assesses the adequacy of our experimental design for detection of transitions between monospecific dominance and mixed-species cooccurrence at the plot scale. The supplemental analyses are intended to address potential concerns over whether the spatial scale of our plot-based measurements of abundance are potentially biased toward detection of monospecific dominance of one species or the other. Using high-resolution (0.025 m), low-altitude (~ 100 m) aerial kite photography and subsequent cover classifications, we conclude that the experimental design is adequate to assign treatment causality in patterns of species covariation at both the plot and landscape scales ([SI Appendix](#)).

Data Availability. Shrub abundance data have been deposited in the Arctic Data Center (data identifier bf007eae-f9f5-454c-ab34-990da909e56d) (64).

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