

Herbivory and nutrient limitation protect warming tundra from lowland species' invasion and diversity loss

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Abstract

Herbivory and nutrient limitation can increase the resistance of temperature-limited systems to invasions under climate warming. We imported seeds of lowland species to tundra under factorial treatments of warming, fertilization, herbivore exclusion and biomass removal. We show that warming alone had little impact on lowland species, while exclusion of native herbivores and relaxation of nutrient limitation greatly benefitted them. In contrast, warming alone benefitted resident tundra species and increased species richness; however, these were canceled by negative effects of herbivore exclusion and fertilization. Dominance of lowland species was associated with low cover of tundra species and resulted in decreased species richness. Our results highlight the critical role of biotic and abiotic filters unrelated to temperature in protecting tundra under warmer climate. While scarcity of soil nutrients and native herbivores act as important agents of resistance to invasions by lowland species, they concurrently promote overall species coexistence. However, when these biotic and abiotic resistances are relaxed, invasion of lowland species can lead to decreased abundance of resident tundra species and diminished diversity.

Keywords: abiotic resistance, biotic resistance, colimitation, community-weighted mean traits, establishment limitation, grazing, multiple interacting global changes, range shift

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Introduction

As a result of global climate warming, high altitude and latitude systems are expected to undergo dramatic shifts in plant community assembly and diversity (Walker *et al.*, 2006; Thuiller *et al.*, 2008; La Sorte & Jetz, 2010; Elmendorf *et al.*, 2012a). Warm-adapted species originating from lower altitudes and latitudes are migrating up and northward to track climate change (Lenoir *et al.*, 2008; Chen *et al.*, 2011; Kelly & Goulden, 2012; Dogue *et al.*, 2015). This invasion of novel competitors may strongly impair the performance of species currently occupying high elevation/latitude systems (Alexander *et al.*, 2015) and pose a threat to biodiversity (Sala *et al.*, 2000; Thuiller *et al.*, 2005; Bellard *et al.*, 2012). However, up- and northward migration of lowland invaders can also increase, at least temporarily, the size of species pool of tundra ecosystems and thereby increase diversity (Gottfried *et al.*, 2012; Pauli *et al.*, 2012). To be able to forecast these range expansions and contractions, and resulting diversity change, it is critical to understand under which conditions warm-adapted invaders outcompete

cold-adapted residents and diminish tundra diversity, and what factors make tundra ecosystems more resistant to invasions and diversity loss.

Plant interspecific interactions, soil nutrient scarcity and herbivory by native consumers are among the strongest forms of biotic and abiotic resistances for invasions (Davis *et al.*, 2000; Maron & Vilá, 2001; Levine *et al.*, 2004; Heard & Sax, 2013; ESKELINEN & Harrison, 2014) and are also key factors regulating recruitment, community assembly and diversity of resident communities (Huntly, 1991; Tilman & Pacala, 1993; Olff & Ritchie, 1998). These all could interact with climate change (Tylianakis *et al.*, 2008; HilleRisLambers *et al.*, 2013; Post, 2013; Brown & Vellend, 2014). For example, climate warming can facilitate recruitment of both residents and invaders in temperature-, but not soil moisture-, limited ecosystems (Rustad *et al.*, 2001; Walck *et al.*, 2011; Hoyle *et al.*, 2013) and thereby increase overall diversity; however, these direct beneficial impacts on diversity can be tempered or reversed by indirect negative effects through altered species interactions if warming leads to enhanced biomass and more intense competition (Klein *et al.*, 2004; Olsen & Klanderud, 2014; Alexander *et al.*, 2015). If warming benefits also the resident species, increase in the intensity of competition may also strengthen the biotic resistance of

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communities and ecosystems to invasions (Levine *et al.*, 2004) and mitigate the positive effects of ameliorated climatic conditions on invasions (Eskelinen & Harrison, 2014). In addition, scarcity of soil nutrients is one of the strongest forms of abiotic resistance to invasions (Davis *et al.*, 2000; Polce *et al.*, 2011; Eskelinen & Harrison, 2014) and may make individual plants and communities less responsive to warmer temperatures (Klanderud & Totland, 2005). In particular in high altitude/latitude areas, low availability of soil nutrients is likely to colimit plant growth response to temperature. Herbivores can also act as major drivers of biotic resistance of communities for invasions, if invading species are more susceptible to herbivores than residents (Maron & Vilá, 2001; Levine *et al.*, 2004; Heard & Sax, 2013). Alternatively, by consuming vegetation biomass, grazing mammals can also mitigate the biomass increasing effects of climate warming (Post & Pedersen, 2008; Kaarlejärvi *et al.*, 2013, 2015; but see Spence *et al.*, 2014), which should alleviate microsite limitation and maintain diversity of resident vegetation (Huntly, 1991; Olff & Ritchie, 1998; Eskelinen *et al.*, 2016). The counteracting role of herbivory could be even more important in nutrient-rich habitats where competition for light is likely to be stronger (Borer *et al.*, 2014).

Plant functional traits have been successfully used to forecast how different species will respond to climate change (Soudzilovskaia *et al.*, 2013; Alexander *et al.*, 2015; Eskelinen & Harrison, 2015) and can thus help predict warming impacts on residents vs. warm-adapted invaders. Fast-growing, resource-demanding traits (i.e., tall stature, high SLA and tissue nitrogen concentration; Fargione & Tilman, 2002; Wright *et al.*, 2004; Reich, 2014; Diaz *et al.*, 2016) can render species more responsive to resource enhancements and improve their competitive ability in resource-rich, light-limited conditions. However, these same traits can also make species more palatable and visible to herbivores and therefore more susceptible to grazing (Fargione & Tilman, 2002; Diaz *et al.*, 2007; Evju *et al.*, 2009; Eskelinen *et al.*, 2012). The opposite slow-growing and resource-conservative traits should confer tolerance to low-resource conditions and help avoiding herbivory at the cost of poor competitive ability in high-resource and high-biomass conditions (Fargione & Tilman, 2002). As species originating from lower altitudes/latitudes are likely adapted to higher temperatures, nutrient levels and biomass (i.e., stronger competition for light) than species occupying resource-poor tundra (Körner, 2003; Sundqvist *et al.*, 2013), fast-growing traits should be more common among them. Fast-growing traits should be beneficial in assisting invasions into open tundra under warmer climate, especially into nutrient-rich habitats experiencing little grazing. In

contrast, species from resource-poor tundra should do relatively worse in resource-rich conditions, due to more intense competition for light, and should benefit from biomass-reducing grazing. However, the extent to which plant traits can explain species' up- and northward migrations is still largely unknown.

In temperature-limited systems, a simple prediction is that warming will allow warm-adapted species to invade, outcompete cold-adapted residents and diminish diversity of tundra species. However, this prediction ignores the potential roles of nutrient limitation, herbivory and competition with residents, which may reduce or reverse the effects of warming. Furthermore, it also ignores the fact that higher temperature alone could facilitate recruitment and thereby increase diversity, as long as warm-adapted competitors do not outcompete the residents. We assessed (i) whether mammalian herbivory, soil nutrient availability and alleviation of competition (biomass removal) alter the effects of warming on invasions of lowland species and recruitment of residents, (ii) how these responses influence total community species richness, and (iii) what is the role of plant traits in mediating invasions/recruitment success. To study these, we released a tundra ecosystem from migration limitation by adding seeds of 12 lowland and 13 tundra species to a full-factorial warming, fertilization, herbivore exclusion and biomass removal experiment and followed the establishment of seeded species for 5 years.

We predicted that (i) warming should increase the establishment of lowland species (exhibiting fast-growing syndrome) especially in nutrient-amended conditions, while herbivory should decrease their success. In contrast (ii), warming and fertilization should decrease the establishment of tundra species (exhibiting slow-growing syndrome) due to increased competition, while herbivory should increase their success. We also predicted that (iii) warming, especially in the absence of competitors (i.e., in biomass removal plots), would increase the number of species establishing from seed; however, fertilization and the absence of herbivores (which should both lead to biomass increase) should mitigate or cancel these positive impacts on richness.

Materials and methods

Study system and experimental site

Our experiment was carried out in Kilpisjärvi, NW Finnish Lapland (69.055°N, 20.887°E), on the south-western slope of Mt. Iso-Jehkats at an altitude of 750 m (Kaarlejärvi *et al.*, 2013). Our study site of roughly 50 × 100 m is a species-rich (up to 13 vascular plant species per 25 × 25 cm² area) treeless tundra meadow, dominated by grasses and forbs (e.g., *Deschampsia flexuosa*, *Festuca ovina*, *Potentilla crantzii*, *Viola biflora*,

Thalictrum alpinum, *Astragalus alpinus*). In this area, treeline lies at 600–650 m a.s.l. and is formed by mountain birch [*Betula pubescens* Ehrh. subsp. *czerepanovii* (N.I. Orlova) Hämet-Ahti]. This area is an important summer grazing area for semidomesticated reindeer (*Rangifer tarandus tarandus*), which are released to the area by local reindeer herders at the end of June and return to the winter grazing area at the beginning of August (Heikkinen *et al.*, 2005). In summers 2010 and 2011, ca. 1500 reindeer grazed within a summer grazing area of ca. 90 km² (corresponding to a density of roughly 17 animals per km²) (Kaarlejärvi *et al.*, 2013). During the past decades, the amount of reindeer in our study area has considerably varied (Eskelinen & Oksanen, 2006). Reindeer is a generalist herbivore reducing vegetation biomass; however, it can also strongly select for palatable plants and affect species composition (e.g., Olofsson *et al.*, 2002; Kaarlejärvi *et al.*, 2013; Eskelinen *et al.*, 2016). Other mammalian herbivores present in the area are Norwegian lemmings (*Lemmus lemmus* L.) and gray-sided voles (*Clethrionomus rufocanus* Sund.), which can cut stems of vascular plants and create small open patches, having considerable impact on vegetation during their peak years (Virtanen *et al.*, 1997). Mountain hares (*Lepus timidus* L.) are encountered occasionally.

Experimental design

In August 2009, we established 56 plots of 0.8 × 0.7 m at our experimental site. Plots were randomly assigned to the following treatments in a full-factorial design: (i) mammalian herbivore exclusion, (ii) fertilization, (iii) warming, or as controls, resulting in seven replicates per treatment combination. Each of the 56 main plots was further split into two 0.25 × 0.25 m subplots, one of which was assigned to a biomass removal treatment and the other was left intact.

For the herbivore exclusion treatment, we erected circular enclosures 160 cm in diameter, 100 cm high, dug to a depth of 15 cm into the soil and made of galvanized net with a mesh size of 10 × 10 mm around the grazer exclusion plots. Our herbivore exclusion treatment excluded all mammalian herbivores including reindeer, hares, voles and lemmings and tests the role of mammalian herbivory in tundra areas in general. However, it also mimics a possible scenario that reindeer (and other mammals) are absent or exhibit very low densities for a limited time period. For the fertilization treatment, we applied fast-dissolving NPK fertilizer (16-9-22) mixed with 1 l of water from a nearby stream over the fertilized plots twice per growing season (mid-June and end of July), resulting in an addition of 9.6 g N, 5.4 g P and 13.2 g K m⁻² on the fertilized plots annually. The same amount of water (without fertilizer) was also applied to the unfertilized plots. Our nutrient addition treatment was testing the importance of nutrient limitation in general. It also mimicked variation in soil nutrient concentrations between habitats and between tundra areas of low vs. high anthropogenic nutrient enrichment (e.g., some alpine tundra areas in heavily impacted regions; Galloway *et al.*, 2004; Dentener *et al.*, 2006). In addition, herbivores and climate warming can also increase soil nutrient availability (Olofsson *et al.*, 2001; Rustad *et al.*, 2001; Natali *et al.*, 2012).

For the warming treatment, we used ITEX (International Tundra Experiment) hexagonal open-top chambers (hereafter OTC) with a maximum basal diameter of 146 cm. While voles and lemmings can move in and out of the chambers, OTCs can at least partly act as grazing barriers for reindeer and prevent their grazing (Moise & Henry, 2010; E.K. and J.O. pers. obs.). Thus, to achieve full-factorial experiment where all mammalian herbivores could equally access all grazed (unfenced) plots, we removed the OTCs during the 1-month period when reindeer were present in the area (i.e., in July). To ensure that reindeer potentially straying from the main herd did not confound our design, we established a temporary reindeer fence around the whole experimental area every year when the OTCs were placed back (i.e., in the end of July). This temporary fence was removed every year when reindeer were released back to the area and our OTCs were removed (i.e., in the end of June). Our warming treatment therefore simulated spring and autumn warming (i.e., April–June and August–October) and extended the length of the growing season at both ends; this is when lower temperatures are likely to constrain growth the most and warming should have the biggest impact. The OTCs increased air temperature on average by 1.92 °C in June (mean ± SE in controls and in OTCs 11.20 ± 0.59, *n* = 4, and 13.12 ± 0.25, *n* = 4, respectively) and by 1.23 °C in August 2011 (mean ± SE in controls and in OTCs 9.68 ± 0.21, *n* = 4, and 10.91 ± 0.49, *n* = 2, respectively). Greater temperature increase by OTCs at both ends of growing season than in the middle of the growing season corresponds well with the predictions for our study region (Kivinen *et al.*, 2012).

For the biomass removal treatment (simulating competition reducing disturbance), we hand-clipped all above-ground live biomass and litter from the biomass removal subplots in August/September 2009. We repeated the biomass removal treatment in 2010 and 2011; however, care was taken not to disturb any of the seeded species occurring in the plots (and therefore biomass removal treatment was only partial in these years). After 2011, seeded species were fully grown and it was not possible to clip any unseeded residents without disturbing the seeded species. Although our biomass removal treatment was designed to test the impact of competition at the time of seed arrival and germination, it also mimicked natural heavy disturbance created by lemmings during their peak years or intensive trampling by reindeer.

Seed addition

We chose 25 common plant species in our study region of which 12 were common and typical for above-treeline communities (called 'tundra species') and 13 species had their main altitudinal distribution below the treeline (called 'lowland species'). The division of the species into lowland and tundra species was done based on their current occurrence in the field in our study region. Tundra species represent species that are presently common and abundant above treeline in Fennoscandia (Benum, 1958; Oksanen & Virtanen, 1995; Virtanen *et al.*, 1999) and also occur at our study site. Many of these species can, however, also be found at lower altitudes.

Lowland species represent species that are not found at our study site, are mainly found in the below-treeline forests and meadows and only occasionally enter above-treeline tundra (Benum, 1958; Olofsson *et al.*, 2002; Virtanen *et al.*, 2010). Single sporadic individuals of two of the lowland species were, however, found at our study plots (*Geranium sylvaticum*, *Trollius europeus*), but both at very low abundances. These two species have their altitudinal optimum in below-treeline communities where they belong to dominant species pool (Benum, 1958; Olofsson *et al.*, 2002; Virtanen *et al.*, 2010). Tundra species thus represent resident species that are already present at the site, and lowland species represent species that could potentially migrate from lower altitudes, establish at the site and become dominant under warmer climate.

The seeded species represented different growth forms (grasses, forbs, N-fixers, dwarf shrubs) and traits (see Table S1). Seeds of all species were collected in fall 2009 (for the 2009 sowing) and in 2010 (for the 2010 sowing) from Kilpisjärvi area. All species germinated either in laboratory or in the field (Table S1). Seed mixtures of 50 seeds per species were individually prepared to all subplots, and each subplot therefore received the same number of seeds per species. The mixture of seeds of 25 species was evenly distributed over all subplots, both with and without biomass removal treatment, in mid-September 2009 just before the first snowfall of the year. We repeated the seed addition in mid-September 2010 because germination was relatively low after the first sowing and to ensure that the seeds experienced the full range of altered environmental conditions brought by the experimental treatments. During sowing, we prevented accidental seed spread using a cardboard box around each seeded subplot. After seed addition, vegetation was gently shaken to facilitate settling of seeds to the ground.

Traits of the seeded species

We measured plant height (cm), specific leaf area (SLA, leaf area in mm² per g dry mass) and foliar carbon-to-nitrogen ratio (C : N; based on % C and N in plant leaves) for the seeded species (Table S1) following the standard protocol by Pérez-Harguindeguy *et al.* (2013). Trait data were collected from 10 naturally occurring individuals per species from the study region in summer 2014. We used community-weighted mean trait values (CWM traits; Garnier *et al.*, 2004) to describe how seeded community trait composition changed in response to the experimental treatments. For each trait, each species' relative abundance in the seeded community in 2014 was multiplied by that species' trait value and summed across species to give a community-weighted mean value in each plot. A high CWM trait value therefore indicates a community that is dominated by species with high values of that trait.

Community measurements

We sampled subplots for seeded species community composition at the end of July/the beginning of August in 2014. The cover of all seeded species in all subplots was estimated visually by the same trained and experienced person with a

minimum estimate threshold of 0.1%. We were especially careful to detect and identify even small seedlings of the seeded species. We also used these cover values to calculate community-weighted mean trait values for the communities.

To get biomass estimates for the main plots (within which the biomass removal treatment was nested), we used a modified point intercept method (Jonasson, 1988) with 108 evenly spaced sampling points in 25 × 50 cm subplots (separate from but next to the seeded plots). At each point, a pin was lowered to the ground and the number of contacts with all vascular plant species was recorded. We used the sum of all contacts of all vascular plant species as a proxy for total community biomass. This method correlates well with true biomass (Jonasson, 1988) and is widely used as a nondestructive method to estimate biomass (see, e.g., Post & Pedersen, 2008; Eskelinen *et al.*, 2012; Kaarlejärvi *et al.*, 2015).

Statistical analyses

To test the effects of herbivore exclusion, fertilization, warming and biomass removal on the success of seeded lowland and tundra species, we applied linear mixed-effects models (LME; Pinheiro & Bates, 2000). The cover of lowland and tundra species, total species richness of seeded species and species richness of seeded lowland and tundra species were response variables (each in their own separate models), and herbivory, fertilization, warming, biomass removal and their interactions were fixed explanatory variables. We included the hierarchical experimental design in each model by nested random effects where biomass removal treatment (subplot) was nested within the other treatments (plot). We used *F*-tests to assess the significance of the experimental treatments and their interactions (Pinheiro *et al.*, 2015). The heteroskedasticity of variances and normality of errors were checked using model diagnostic plots (Crawley, 2007), and the response variables were square-root-transformed or log-transformed as necessary (see Table 1). Transformed data met homogeneity and normality assumptions.

To test whether plant functional traits mediated seeded community responses to herbivore exclusion, fertilization, warming and biomass removal, we first applied nonmetric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity measure and square-root-transformation with Wisconsin double standardization (Oksanen *et al.*, 2016) for the seeded communities. We then assessed the significance of the correlations between seeded communities (NMDS ordination) and plant functional traits (calculated using community-weighted mean trait values for the seeded species in 2014) using 999 permutations. Significances of experimental treatments on the seeded communities were assessed using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with Bray–Curtis dissimilarity measure and 999 permutations.

We also used correlations to look at relationships between cover of seeded tundra and lowland species, between species richness of the seeded species and total community biomass, and between the ratio of tundra-to-lowland species cover and species richness of the seeded species.

Table 1 Results of linear mixed-effects models where species richness (total, tundra and lowland) and cover (tundra and lowland) of seeded species were used as response variables (each in their own model), and herbivore exclusion, fertilization, warming, biomass removal and their interactions were used as explanatory variables

Source of variation	Total species richness		Tundra species richness		Lowland species richness		Tundra cover		Lowland cover	
	F	P	F	P	F	P	F	P	F	P
Exclosure	29.1	<0.0001	18.8	0.0001	5.2	0.0271	40.0	<0.0001	4.4	0.0388
Fertilization	87.0	<0.0001	63.3	<0.0001	12.4	0.0009	130.9	<0.0001	27.5	<0.0001
Warming	8.6	0.0043	1.4	0.2476	5.2	0.0271	9.5	0.0028	3.8	0.0540
Biomass removal	20.1	<0.0001	20.5	<0.0001	29.9	<0.0001	0.6	0.4421	5.8	0.0178
E × F	8.0	0.0057	0.5	0.4859	6.7	0.0126	0.3	0.6147	2.2	0.1382
E × W	<0.1	0.9273	0.2	0.6418	<0.1	0.7572	0.4	0.5322	4.1	0.0459
E × BR	4.8	0.0307	2.7	0.1066	10.5	0.0022	0.1	0.7221	0.1	0.7394
F × W	5.7	0.0195	1.7	0.2041	2.4	0.1266	2.3	0.1303	4.0	0.0494
F × BR	3.0	0.0857	15.3	0.0003	<0.1	1.000	0.4	0.5345	0.2	0.6339
W × BR	1.0	0.3171	2.1	0.1567	0.7	0.4222	1.1	0.3064	0.4	0.5405
E × F × W	8.0	0.0057	2.3	0.1347	3.5	0.0682	2.8	0.0992	0.8	0.3611
E × F × BR	<0.1	1.0000	<0.1	0.8380	<0.1	0.8405	2.1	0.1489	<0.1	0.8758
E × W × BR	0.5	0.4663	1.1	0.3092	0.4	0.5466	1.1	0.3009	<0.1	0.9859
F × W × BR	1.8	0.1735	2.7	0.1066	2.0	0.1631	0.3	0.5754	2.0	0.1618
E × F × W × BR	4.0	0.0472	8.3	0.0060	2.6	0.1120	<0.1	0.8602	<0.1	0.8951

In the models, biomass removal was nested within other treatments. *df* = 1.90. E, exclosure; F, fertilization; W, warming; and BR, biomass removal. Significant ($P \leq 0.05$) results are in bold and marginally significant ($P < 0.1$) results are in italics.

We used the function 'lme' in package nlme (Pinheiro *et al.*, 2015) for LME and the functions 'vegdist' for Bray–Curtis dissimilarity, 'metaMDS' for NMDS, 'envfit' for fitting and testing significance of vectors/factors in NMDS ordination, and the function 'adonis' for PERMANOVA, all in package vegan (Oksanen *et al.*, 2016), in R statistical software (R Development Core Team 2015 version 3.2.3).

Results

Species' cover and traits

Seeded lowland and tundra species' cover showed opposite responses to many treatments (Fig. 1), and we also identified a strong negative correlation between lowland and tundra species cover ($r = -0.731$, $t_{14} = -4.0$, $P = 0.0013$, Fig. 2). Overall, lowland species cover was lowest in grazed-only, and grazed and warmed plots, where tundra species had high cover and high in fertilized-exclosed and fertilized-warmed plots, where the cover of tundra species was lowest (Fig. 1). These contrasting responses were also associated with clear trait differences (Fig. 3).

Warming alone did not increase lowland species cover; however, warming and fertilization together exhibited a synergistic, positive impact on lowland species (in line with our prediction), indicating colimitation by temperature and soil nutrients ($W \times F$ interaction, Table 1, Fig. 1). Both fertilization and herbivore exclusion alone also increased lowland cover,

suggesting that nutrient scarcity and grazing hamper lowland species establishment (in line with our prediction; positive main effects of F and E, Table 1, Fig. 1). Surprisingly, warming effects on lowland cover also depended on herbivore exclusion; we saw no effect inside exclosures but found a positive effect in grazed plots ($W \times E$ interaction, Table 1, Fig. 1). In line with our prediction, the cover of lowland species was positively associated with community-weighted traits representing fast-growing syndrome, especially height but also SLA and low C : N. Both lowland species' cover and these traits were also associated with the combined herbivore exclusion, fertilization and warming treatment (NMDS and PERMANOVA results; Fig. 3).

In contrast to our second prediction, warming alone had a positive impact on tundra species cover, while, in accordance with our prediction, both fertilization and herbivore exclusion had negative effects on their cover (Table 1, Fig. 1). The cover of tundra plants was highest in warmed-only plots (in both grazed and ambient nutrient conditions, Fig. 1), suggesting that tundra species benefit from warmer conditions especially when grazers are present and when soil nutrient supply remains low (although $W \times E \times F$ interaction was not significant; $P = 0.0992$, Table 1). In our trait analyses, tundra species cover was negatively associated with height and positively with the C : N ratio and warming (NMDS and PERMANOVA results; Fig. 3).

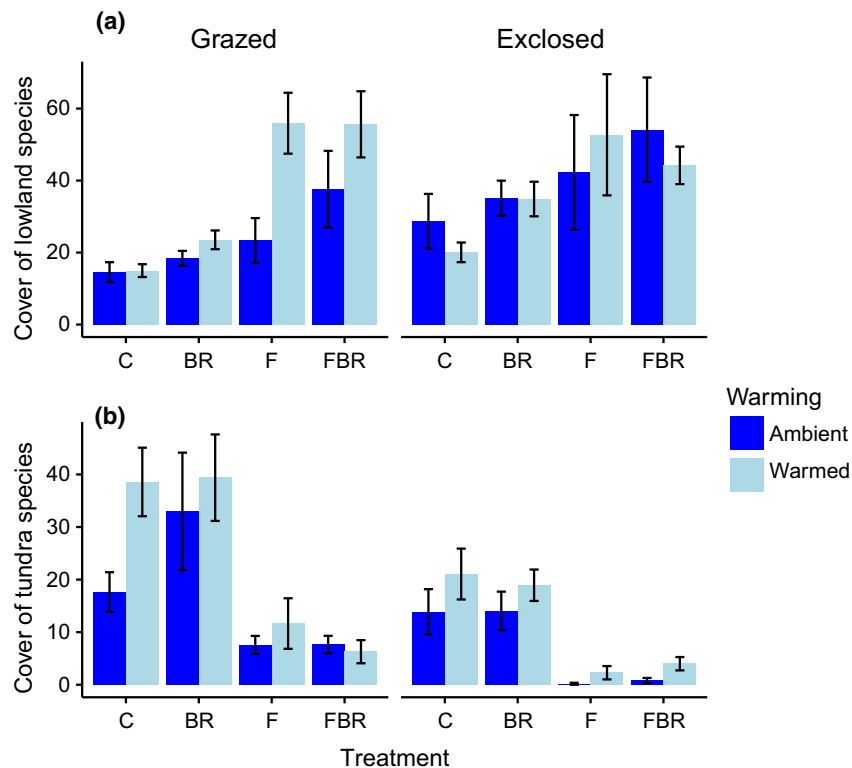


Fig. 1 (a) The cover of seeded lowland species and (b) the cover of seeded tundra species (mean \pm SE) with respect to different combinations of biomass removal, warming and fertilization in exclosed and grazed plots in 2014. Note the different axis scales in different subfigures. C, control; BR, biomass removal; F, fertilization; and FBR, fertilization and biomass removal.

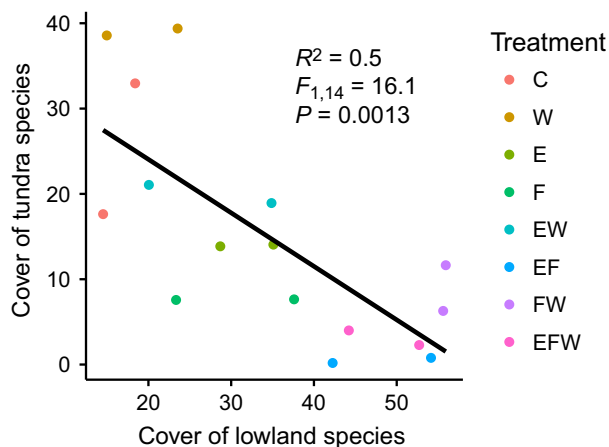


Fig. 2 Relationship among tundra species cover and lowland species cover. Individual points represent means per treatment combination (see Fig. 1). The fitted line is a linear regression.

Species richness

Species richness of seeded lowland and tundra plants was relatively similar to each other and corresponded to total seeded richness responses to the treatments (see Table 1, Fig. S1), and we therefore only report total

species richness response here. As we predicted (Prediction 3), warming increased total seeded species richness in the absence of competitors (i.e., in biomass removal plots); however, fertilization and herbivore exclusion canceled this positive impact (significant $W \times BR \times E \times F$ interaction, Table 1, Fig. 4). Species richness peaked in warmed and grazed plots from which biomass had been removed and which were not fertilized, while the lowest species richness was encountered in exclosed and fertilized plots without biomass removal, irrespective of warming (Fig. 4). In particular, tundra species were nearly absent from fertilized and exclosed nonbiomass removal plots (Fig. S1).

The ratio of tundra-to-lowland species cover exhibited a strong positive relationship to species richness ($r = 0.58$, $t_{110} = 7.6$, $P < 0.0001$, Fig. 5): the dominance of tundra species (i.e., high tundra: lowland ratio) was associated with high species richness, whereas the dominance of lowland species was associated with low species richness. There was also a negative correlation between total seeded richness and total community biomass ($r = -0.555$, $t_{54} = -4.9$, $P < 0.0001$, Fig. S2).

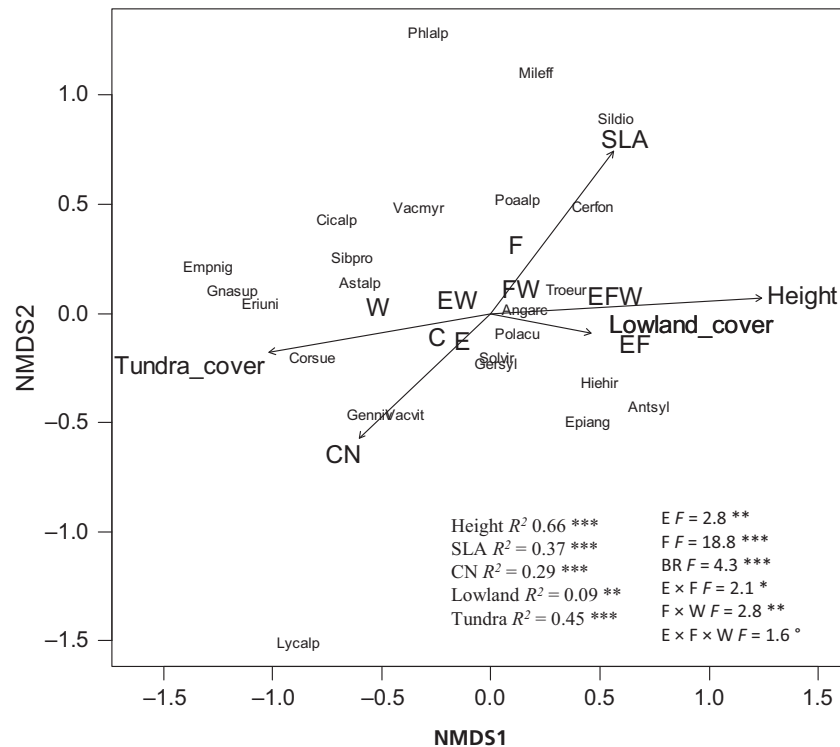


Fig. 3 Nonmetric multidimensional scaling ordination plot illustrating the effects of warming, fertilization, herbivore exclusion, and their interactions on the seeded community composition (measured as Bray–Curtis dissimilarities on square-root-transformed data and with Wisconsin standardization). The treatment labels show weighted class centroid of each treatment combination. The arrows show the direction of correlations among CWM traits [C : N ratio (CN), height, SLA], the total cover of lowland and tundra species, and the seeded species ordination. The length of each arrow is proportional to the strength of its correlation to the seeded species community. Significances of the correlations were assessed using permutational tests (R^2 values indicate the goodness of fit of each fitted vector), and the significances of experimental treatments on the seeded community were assessed using PERMANOVA. Biomass removal treatment is not shown because, even though it had significant main effect on the seeded community, it grouped in the middle of the ordination space with no clear connection to any traits or species, and because it did not interact with any other treatments. C, control; W, warming; F, fertilization; FW, fertilization and warming; E, exclusion; EW, exclusion and warming; EF, exclusion and fertilization; and EFW, exclusion, warming and fertilization. Significance codes: 0.001 ***, 0.01 **, 0.05 *, <0.1 °.

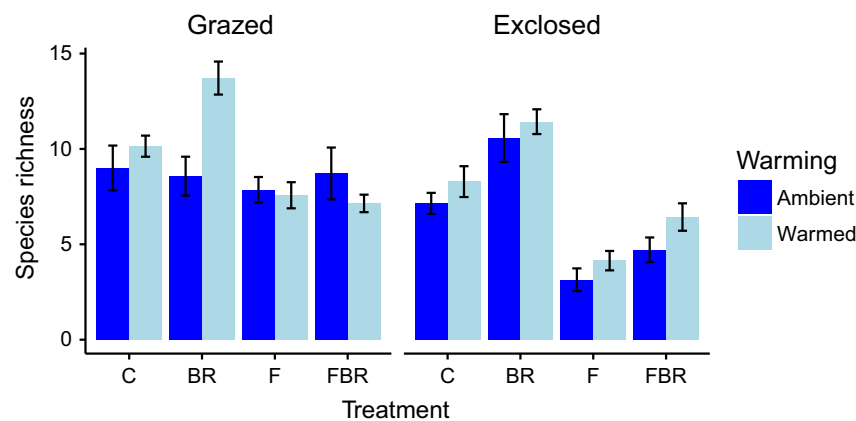


Fig. 4 Species richness of the seeded species (including both lowland and tundra species) (mean \pm SE) with respect to different combinations of biomass removal, warming and fertilization in exclosed and grazed plots in 2014. C, control; BR, biomass removal; F, fertilization; FBR, fertilization and biomass removal.

Discussion

As migration limitation can delay tundra community responses to climate warming, observations linking current temperatures to concurrent shifts in species' ranges and results from warming experiments with resident species may not provide accurate predictions of the long-term impacts of climate change (Alexander *et al.*, 2015). We released above-treeline tundra ecosystem from this migration limitation and show that the ability of lowland species to proliferate and expand their distributions to open tundra is to a greater extent determined by biotic and abiotic resistance by native herbivorous consumers and scarcity of soil nutrients than warmer conditions. In addition, we also demonstrate that once these resistances have been relaxed, introduction of novel species from lower altitudes can lead to depression of resident tundra species and diminished overall species richness.

Our finding that successful establishment of lowland species introduced to open tundra was strongly limited by native herbivores and low soil nutrient availability, but was little affected by warming alone, is consistent with growing body of evidence emphasizing the fundamental role of mammalian herbivores and soil nutrients in controlling plant performance and productivity in tundra ecosystems (Post & Pedersen, 2008; Eskelinen *et al.*, 2012; Gough *et al.*, 2012; Speed *et al.*, 2010; Kaarlejärvi *et al.*, 2013). This control often precedes the control by temperature (Klanderud & Totland, 2005; Post & Pedersen, 2008; Wang *et al.*, 2012; Kaarlejärvi *et al.*,

2013, 2015). We also found that after relaxing nutrient limitation, warming did exhibit a positive impact on lowland species establishment, demonstrating the importance of soil nutrients in dictating lowland species' responses to warmer climate in this naturally nutrient-poor system with low anthropogenic nutrient enrichment. However, these results also suggest that habitats with naturally fertile soils or those experiencing high nutrient deposition could be especially vulnerable to lowland species' invasions.

In line with a recent study showing that alpine plants suffer from increased competition under warmer climate when novel competitors from lower altitudes can track changing climate (Alexander *et al.*, 2015), we found a strong negative correlation among the success of tundra and lowland species: when lowland species suffered from herbivory and nutrient scarcity, species typical for tundra thrived. Conversely, when removal of biotic and abiotic resistance allowed lowland species to attain dominance, tundra species suffered. Therefore, paralleling with studies that show negative effect of exotic invaders on native species in general (Vilà *et al.*, 2011), our findings suggest that those conditions that promote success of lowland invaders will lead to declined abundance of resident tundra species.

Tundra species clearly benefitted from warming, even in the presence of resident competitors, implying that neither warmer temperatures nor competition with current residents hamper their success. This result agrees with the observation that extinctions due to climate change are rarely caused by direct negative physiological responses (Cahill *et al.*, 2012; but see White *et al.*, 2014). How high altitude and latitude species will experience warmer climates may therefore depend on a combination of abiotic and biotic conditions that determine the success of their novel competitors, rather than the direct effect of warmer environment on themselves.

We identified height of the seeded species most strongly connected to the successful invasion of lowland plants to the plots that were fertilized and from where herbivores had been excluded. These were also the plots where vegetation biomass was highest (Fig. S2), associated with strongest light limitation (Kaarlejärvi *et al.*, unpublished results) and strongest benefit from being able to grow tall and compete for light (Tilman, 1988). Plant height is often attributed to increased success under resource enhancements that increase productivity (e.g., Suding *et al.*, 2005; Yang *et al.*, 2011; Eskelinen & Harrison, 2015), and it has also been found to predict vulnerability to grazers (Diaz *et al.*, 2007; Evju *et al.*, 2009; Forrestel *et al.*, 2015). Our results suggest that soil nutrients and consumer pressure interact to affect the benefit obtained from being

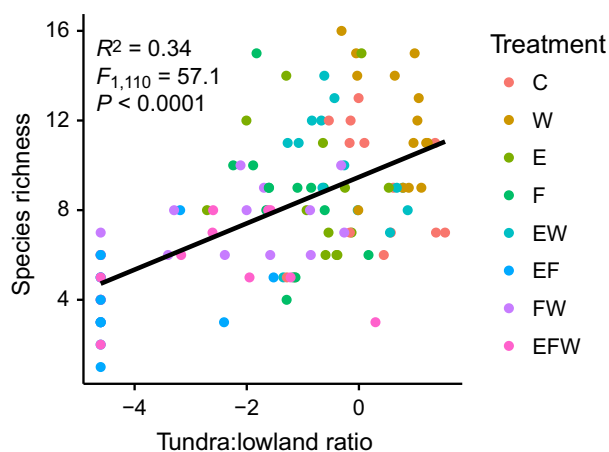


Fig. 5 Relationship between total seeded species richness and ratio of tundra-to-lowland species cover (on log-scale) in different treatment combinations. The fitted line is linear regression. C, control; W, warming; F, fertilization; FW, fertilization and warming; E, exclosure; EW, exclosure and warming; EF, exclosure and fertilization; EFW, exclosure, fertilization and warming. Biomass removal treatment is not shown.

tall: while height helps lowland species establishment in nutrient-rich conditions, it also exposes them to herbivory, allowing tall lowland species to benefit from greater soil nutrient availability more in the absence of grazers (Fargione & Tilman, 2002). At the same time, height did not make lowland invaders more successful in warmed-only conditions, probably because biomass in general remained low (Fig. S2) and being able to grow tall did not improve species' competitive performance and invasion success in such conditions (Carboni *et al.*, 2016). Our data suggest that, after successful arrival, being able to grow tall in resource-rich conditions can help lowland invaders establish, and that successful establishment depends critically on soil nutrient availability and herbivore pressure, rather than temperature.

One of our key findings is that while warming alone (in the biomass removal plots) increased overall species richness of seeded species, promoting establishment of nearly 15 species, its positive impact was canceled by fertilization and exclusion of native mammalian herbivores. On average, less than five species were able to establish when addition of soil nutrients coincided with the absence of herbivory. Furthermore, decline in species richness was strongly associated with dominance of lowland species, suggesting that invasion of lowland species suppressed overall diversity. Several important inferences can be made from these results. First, warming can facilitate number of species germinating from seed in cool and moist ecosystems where temperature but not soil moisture limit plant growth, which is in accordance with findings from earlier studies (Rustad *et al.*, 2001; Milbau *et al.*, 2009; Walck *et al.*, 2011; Hoyle *et al.*, 2013; but see Shevtsova *et al.*, 2009). This implies that, at least temporarily, tundra can become richer because warming benefits recruitment of both tundra and lowland species. Our result therefore supports observations of increased diversity of high altitude and latitude plant communities during the past decades with warmer climate (Klanderud & Birks, 2003; Virtanen *et al.*, 2010; Stöckli *et al.*, 2011; Pauli *et al.*, 2012). Second, in line with previous studies (Klein *et al.*, 2004; Olsen & Klanderud, 2014), our results show that competition with surrounding plants becomes stronger with warming and that this negative impact can repeal the positive impact of warming. Warming may therefore increase species richness mainly in disturbed sites. Third, our results illustrate how mammalian grazers and soil nutrients simultaneously impact richness of recruiting species; the positive impact of grazing mammals (Eskelinen *et al.*, 2016) can alleviate the negative impact of fertilization (Stevens *et al.*, 2004). Overall, these findings highlight strong conditionality

of climate warming effects on species richness by herbivores, soil nutrients and plant competition: warmer climate increases richness via recruitment only in conditions where competition with the residents is relaxed (e.g., in disturbed sites), where herbivores keep vegetation open and in habitats with relatively low nutrient availability.

Last, we demonstrate that conditions which allow lowland species to invade and become dominant in tundra are also those that strongly reduce the overall number of species being able to recruit and establish from seed. We are among the first to provide direct experimental evidence of a mechanistic link between successful establishment of lowland invaders and simultaneously diminished number of recruiting species. We also reveal a dual impact of herbivory and scarcity of soil nutrients: while acting as important agents of abiotic and biotic resistance for invasions (Levine *et al.*, 2004; Pearson *et al.*, 2011; Heard & Sax, 2013), they concurrently function as important drivers promoting species coexistence and diversity (Olff & Ritchie, 1998; Borer *et al.*, 2014; Eskelinen & Harrison, 2015).

To conclude, our results demonstrate that the establishment of tall invaders from lower altitudes and latitudes can be severely constrained by nutrient scarcity and native mammalian herbivores, while these same factors benefit resident tundra species. On the other hand, once these biotic and abiotic resistances have been relaxed, lowland species' can rapidly take over assembly dominance and exclude resident tundra species – a process that leads to a declined diversity. Overall, our results highlight that biotic and abiotic filters unrelated to climate warming can be equally or more important than temperature in dictating distributional shifts of novel invaders. Our findings may help explain unexplained variation in species' range shifts and community responses to warming, reported by many studies (Lenoir *et al.*, 2010; Chen *et al.*, 2011; Elmendorf *et al.*, 2012b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Species richness of seeded tundra species and species richness of lowland species with respect to different combinations of biomass removal, warming and fertilization in grazed and exclosed plots in 2014.

Figure S2. Relationship between total species richness of the seeded species and total biomass estimate.

Table S1. Main distributional optimum and traits of the seeded species.