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Herbivory mediates the long-term shift in the relative importance of microsite and propagule limitation

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Summary

1. Microsite and propagule limitation are predicted to jointly influence plant community assembly and diversity, with shifts in their relative contributions under different ecological conditions. Mammalian herbivory can also exhibit strong impact on community assembly and diversity. However, to date few studies have considered how herbivory might interact with propagule and microsite limitation and how herbivory might alter their relative importance. Even fewer studies have examined how these processes manifest over time to influence community assembly.

2. In fenced and grazed tundra communities that varied in soil moisture, we manipulated propagule limitation by adding seeds of 14 species and manipulated microsite limitation through a one-time disturbance treatment which reduced resident community biomass. We then followed these communities for 11 years to assess the long-term impacts of these processes on community assembly and richness.

3. Herbivory interacted with soil moisture to promote long-term establishment of seeded species: seed addition increased species richness and this effect persisted over 11 years but only in grazed plots, and in drier conditions. Seed addition and herbivory also interacted to drive community composition. Disturbance initially resulted in greater richness and community divergence, but the effect weakened over time, whereas the effects of herbivory in general strengthened.

4. *Synthesis.* Our results show that herbivory interacts with environmental conditions to mediate the relative importance of microsite and propagule limitation on community assembly; however, its impacts may only become detectable over longer time-scales. Moreover, our results suggest that herbivory may be a key biotic modulator of community assembly in low-productivity ecosystems and that incorporating trophic interactions (such as herbivory) into hypotheses about community assembly may provide a better understanding of the relative importance of different assembly mechanisms.

Key-words: assemblage structure and diversity, biotic filtering, determinants of plant community diversity and structure, herbivory, long-term experiment, plant recruitment, seed limitation, species immigration

Introduction

Recruitment is a key process driving plant community assembly (Grubb 1977; Harper 1977; Tilman & Pacala 1993). Propagule and microsite limitation are two key drivers of plant recruitment and are therefore fundamental to understanding local community structure and diversity (Eriksson & Ehrlén 1992; Tilman 1997; Zobel *et al.* 2000; Myers & Harms 2009). Propagule limitation occurs when successful recruitment is constrained by limited seed production or dispersal of species in a landscape (Nathan & Muller-Landau 2000; Levine & Murrell 2004). Microsite limitation, on the other hand, occurs when successful recruitment is constrained by the availability of microsites suitable for germination and establishment, and is jointly influenced by both biotic and abiotic environmental factors. For example, microsite limitation can result from competitive suppression of immigrants by the resident vegetation or a lack of disturbances that create competition-free safe sites for germination (Stevens *et al.* 2004; Tilman 2004; Maron *et al.* 2012), as well as unfavourable soil moisture or nutrient levels (Xiong

*Correspondence author: E-mail: anu.eskelinen@idiv.de *et al.* 2003; Stevens *et al.* 2004; Myers & Harms 2011). Importantly, there is a growing consensus that propagule availability and microsite availability jointly regulate assemblage structure and dynamics (Clark *et al.* 2007; Myers & Harms 2009; Aicher, Larios & Suding 2011; Olsen & Klanderud 2014).

Recent theoretical and empirical studies suggest that the relative contributions of propagule and microsite limitation to community dynamics should vary predictably along ecological gradients (Foster *et al.* 2004; Tilman 2004; Brooker *et al.* 2008; Dickson & Foster 2008). Specifically, propagule limitation and abiotic microsite limitation (local environmental filtering) should contribute most to community assembly at low productivity, while biotic microsite limitation (competitive interactions) should contribute more as productivity and community biomass increase (Huston 1999; Zobel *et al.* 2000; Foster 2001; Foster *et al.* 2004; Tilman 2004). However, none of these studies consider how mammalian herbivores can potentially shift the relative contribution of propagule and microsite limitation on plant community assembly.

Herbivores are known to have strong impact on plant productivity and biomass (Oksanen *et al.* 1981; Huntly 1991; Olff & Ritchie 1998; Gough, Ramsey & Johnson 2007; Hillebrand *et al.* 2007; Eskelinen, Harrison & Tuomi 2012; Borer *et al.* 2014). Importantly, by altering community biomass herbivores may alter the relative contribution of propagule and microsite limitation for a given community. Under low grazing pressure and especially in highly fertile conditions, microsite limitation (competitive interactions) should be the dominant driver of community assembly as the absence of herbivory enhances resident community biomass and light limitation (Bakker *et al.* 2006; Borer *et al.* 2014). In contrast, propagule limitation should predominate under high grazing pressure where continuous removal of resident community biomass maintains communities open for colonization. Besides reducing biomass and competition for light, herbivores can reduce microsite limitation by creating opportunities for colonization. For example, strong localized grazing events (e.g. vole and lemming outbreaks), soil-disturbing activities (e.g. burrowing) by small mammalian herbivores and intensive trampling by large mammalian herbivores can create competition-free safe sites favouring germination and seedling emergence, thereby promoting diversity (Olff & Ritchie 1998; Bakker & Olff 2003; Bagchi, Namgail & Ritchie 2006; Davidson, Detling & Brown 2010; Nystuen *et al.* 2014). Under strong microsite limitation (e.g. in highly fertile conditions), more continuous disturbance may be needed to break barriers for successful species establishment (Tilman 2004). In the long term, grazing on adult plants may play a different role by selecting species based on their grazing tolerance and palatability, thereby affecting species composition, dominance relationships and diversity (Oksanen 1990; Huntly 1991; Olff & Ritchie 1998; Howe, Brown & Zorn-Arnold 2002). Herbivory could therefore control both plant colonization and establishment, and mediate the relative importance of propagule limitation vs. microsite limitation.

Here, we tested the idea that herbivory mediates the relative effects of propagule limitation and biotic microsite limitation (competitive interactions) on plant community assembly in two community types (wet and dry snowbed tundra). We performed the study in a low-productivity tundra ecosystem, where mammalian herbivores exhibit strong impact on individual plant performance, community biomass, composition and diversity (e.g. Aunapuu *et al.* 2008; Post & Pedersen 2008; Speed *et al.* 2010; Eskelinen, Harrison & Tuomi 2012; Gough *et al.* 2012; Kaarlejärvi, Eskelinen & Olofsson 2013; Olofsson *et al.* 2014). We examined the success of 14 plant species sown into fenced and grazed plots with wet and dry soils, and with and without experimental disturbance, over 11 years. We hypothesized that herbivory alleviates microsite limitation by removing competing resident vegetation and thus shifts the community towards being more propagule limited. Specifically, we predicted that (i) adding seeds increases seedling colonization and species richness; (ii) the positive impact of seed addition on seedling colonization and long-term seedling establishment is greater in the presence of herbivores; (iii) the impact of herbivory becomes stronger over time; (iv) the impact of a strong localized one-time disturbance (simulated by clipping) weakens over time. As soil moisture, in general, can have substantial impact on seedling colonization (Xiong *et al.* 2003; Foster & Dickson 2004; Myers & Harms 2011) and is also an important determinant of tundra community structure and diversity (Billings & Mooney 1968; Saccore *et al.* 2014), we additionally explored the influence of soil moisture on seedling colonization and establishment.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

The study was carried out on the eastern slope of Mt. Jehkats in Kilpisjärvi (69°01′N, 20°50′E), NW Finnish Lapland. The study site is located at an altitude of 820 m a.s.l., ca. 200 m above treeline. This site has a short growing season (c. 2–3 months) with a mean annual temperature of c. −2 °C (monthly mean ranging from +5 to +10 °C in the growing season) and an average annual precipitation of 400–500 mm, with about 50% falling as snow. The vegetation in this area consists of heath and meadow snowbed vegetation (Oksanen & Virtanen 1995), dominated by dwarf willow (*Salix herbacea*), prostrate herbs (e.g. *Sibbaldia procumbens, Veronica alpina, Epilobium anagallidifolium*), snowbed graminoids (e.g. *Agrostis mertensii*, *Carex bigelowii*) and bryophytes (e.g. *Polytrichastrum alpinum*). The main mammalian herbivores in the study site are reindeer (*Rangifer tarandus* L.) and Norwegian lemming (*Lemmus lemmus* L.), whereas field voles (*Microtus agrestis* L., *M. oeconomus* Pallas) and grey-sided voles (*Myodes rufocanus* Sund.) occur mainly during peak years. Our study area is an important summer grazing area for reindeer, which graze in the area from June to August (Heikkinen *et al.* 2005). In 2010–2011, ca. 1500 reindeer grazed in Kilpisjärvi area (of ca 90 km^2), corresponding to a density of ca 17 reindeer per km^2 (Kaarlejärvi, Eskelinen & Olofsson 2013). However, reindeer densities vary between years and have overall decreased since 1980s in the larger region to which our study area belongs (Eskelinen & Oksanen 2006). Lemming and vole population densities have been relatively low with moderate lemming peaks taking place between 1998 and 2000 and between 2008 and 2011 (see Eskelinen &

Virtanen 2005; Virtanen, Henttonen & Laine 1997; Kaarlejärvi, Eskelinen & Olofsson 2013).

To test how the relative importance of propagule limitation and microsite limitation is influenced by herbivory, we established twenty permanent vegetation plots of 25 × 25 cm in a snowbed plant community in 1989. The plots were distributed across an area of about 20 × 30 m. In 1989, circular fences were placed around half (10) of the plots. The fences were made of a metal with a 1 cm mesh size, and the exclosures were ca. 50 cm in diameter, 50 cm high and dug into the soil. Fences excluded small mammalian herbivory and strongly reduced but did not fully exclude reindeer grazing (some evidence of herbivory on the tops of taller plants) because of the open tops of the fences. Fenced plots were randomly interspersed among unfenced plots. The fences were rather small, open at the top, and did not impact snow accumulation and time of snow melt (A. Eskelinen and R. Virtanen, personal observations during multiple years). Their shading effects are also likely to be small. The plot positions also differed in soil moisture as some of the plots were located in small depressions where water level was higher. Our yearly observations of soil moisture differences among plots were quantified by measuring gravimetric soil moisture in mid-August 2012. The plots were split in dry (soil water content 64.9 ± 4.9 g g dry soil^{-1}, mean ± SE) and wet (soil water content 199.4 ± 19.9 g g dry soil^{-1}, mean ± SE), resulting in four (wet) and six (dry) replicates per soil moisture level by fenced/grazed combinations. We set the soil moisture threshold between dry and wet soils at 100 (wet > 100 > dry). In general, wet plots supported much greater proportion of mosses than dry plots (Saccore *et al.* 2014). All experimental plots (both grazed and fenced plots) were previously used in a transplantation experiment in which *Vaccinium myrtillus* heath vegetation from lower altitudes was transplanted to an upper elevation (Virtanen 1998). In 2001, both vascular plant biomass and litter mass were greater in fenced than in the unfenced plots, with 217 g m^{-2} of vascular biomass in fenced plots and 108 g m^{-2} in unfenced plots, and with 91 g m^{-2} of litter mass in fenced plots and 33 g m^{-2} in unfenced plots (Eskelinen & Virtanen 2005). By using these long-term herbivore exclosures that differed from grazed plots already at the start of the seeding experiment, we were able to investigate the impact of long-term reduction of grazing pressure, including increased live and dead biomass and changed species composition, on the relative importance of seed and microsite limitation.

In August 2001, we established a factorial seeding experiment in the existing twenty plots, both inside and outside fences (grazed plots). We subdivided the centre 25 × 25 cm area of each plot into four 12.5 × 12.5 cm subplots and applied the following treatments to these subplots: (i) seeding, (ii) disturbance to remove biomass, (iii) seeding and disturbance, and (iv) control (neither seeding nor disturbance). This size of subplots was suitable given the small stature and number of vascular plants (up to 16 species of 2–10 cm tall in a 12.5 × 12.5 cm subplot, see, e.g. Zobel *et al.* 2000 and Graae *et al.* 2011 for similar-sized plots). Altogether, there were 80 subplots of which 40 were fenced and 40 were grazed, and ten replicates per treatment combination (including interactions among exclosure treatment and seeding and disturbance). When we accounted for the different soil moisture levels, we ended up having four (wet) and six (dry) replicates per treatment combination per soil moisture level.

For the seeding treatment, we selected fourteen perennial species: eight of the species originated from tundra snowbed communities (*Anthoxanthum alpinum*, *Carex lachenalii*, *Epilobium anagallidifolium*, *Phyllodoce caerulea*, *Poa alpina*, *Sibbaldia procumbens*, *Taraxacum* sp. and *Veronica alpina*), while six originated from lower elevation (below treeline) communities and only occurred sporadically at the study site (*Antennaria dioica*, *Cerastium fontanum*, *Gnaphalium norvegicum*, *Ranunculus acris*, *Solidago virgaurea* and *Trollius europaeus*). Seeds of all species were field collected in September 2001 from areas close to Mt. Jehkats. The germination rates of the seeds for each species were tested in laboratory and were generally high (A. Eskelinen and R. Virtanen unpublished data, for germination in the field see Table S1, Supporting Information). A mixture of 50 seeds per species was manually added into each seeding treatment subplot at the very end of September prior to the first snowfall of the year (see Eskelinen & Virtanen 2005 for details). By adding a relatively high number of seeds per species, we did not attempt to mimic the amount of natural seed rain but to ensure that seed availability would not constrain the establishment of any of the seeded species (Foster & Tilman 2003). During sowing, accidental seed spread was prevented using a cardboard box around each seeded subplot. The disturbance treatment was implemented by harvesting above-ground vascular plant biomass, mosses, lichens and litter with scissors at ground level. To avoid disturbing soil and microbial communities, we left the soil surface intact and did not pull away any bases of cut plant stems or remove microscopic liverworts (< 5 mm) that covered most of the soil surface (i.e. there was very little or no bare soil exposed). Therefore, our disturbance treatment did not create bare soil but mimicked natural vole and lemming disturbance. In our system, lemmings and voles often cut stems of vascular plants and bryophytes, creating small-scale open patches without disturbing soil (Virtanen, Henttonen & Laine 1997). Most of the vascular biomass had regrown by the end of the second or third growing season after applying the disturbance treatment; however, for dwarf shrubs and mosses, it took several years to recover (A. Eskelinen, pers. observ.).

From 2002 to 2007, in late July-early August, we counted the number of seedlings of each seeded species in each subplot. In 2007, the seedlings started to resemble adult plants, and we thereafter recorded the % cover of seeded as well as resident plants. The goal of this study was to examine the net effects of propagule addition on community diversity and assembly over long time period and under various experimentally controlled contingencies, an approach chosen by many other community-level studies (see, e.g., Tilman 1997; Zobel *et al.* 2000; Foster & Tilman 2003; Dickson & Foster 2008; Foster *et al.* 2011), and thus, we did not collect demographic data.

STATISTICAL ANALYSES

All statistical analyses were carried out using R Statistical Software 3.1.2 (R Development Core Team 2014). For the analyses, we pooled abundance/richness of the seeded species and did not test any individual species responses. We analysed the effects of seeding, disturbance, fencing, soil moisture, and their interactions (fixed explanatory variables) on species establishment (i.e. seedling number and species cover) and richness (i.e. seedling richness and total species richness [including seeded and other vascular species]) in the subplots using linear mixed-effects models (LME; Pinheiro & Bates 2000) in package lme4 (function lmer; Bates *et al.* 2014). We limited the statistical analyses to a subset of years to avoid multiple analyses, and separately analysed the following years: 2002 (number of seedlings, species richness of seedlings) and 2012 (cover of seeded species and total vascular cover, species richness of seeded species and total vascular richness). The complete 11-year time series of species richness and abundance is available in Supplementary Information. We included the hierarchical experimental design in each model by nested random effects where seeding and disturbance treatments (subplots) were nested within the fencing treatment (plot). We limited the analyses to three-way interactions to reduce the risk of over-parameterization and used *F*-tests with Satterthwaite approximation in the package 'lmerTest' to assess the significance of the factors (Kuznetsova, Brockhoff & Bojesen Christensen 2014). When necessary, the response variables were either log or square root transformed to reduce heteroscedasticity and improve normality (see Table 1 for detailed information). Transformed data fulfilled the variance homogeneity and normality assumptions, which were checked using model diagnostic plots (Crawley 2007). We also run all models of seedling and species numbers using Poisson error structure with the function 'glmer' in package lme4, but we found that normal errors (even without any transformations) better met the assumptions of normality and variance homogeneity than respective models with Poisson error, and we therefore only report results from the lmer-models with normal errors. However, the results from the different models were qualitatively similar.

To analyse the effects of seeding, disturbance, fencing and soil moisture on seeded and whole community compositions, we applied permutational multivariate analysis of variances (PERMANOVA, Anderson 2001) and NMDS (non-metric multidimensional scaling) ordinations on 2002 and 2012 community data sets, both years separately. Both PERMANOVA and NMDS ordinations were based on Bray–Curtis dissimilarities and 999 permutations (number of seedlings in 2002 and plant cover in 2012). For these analyses, we used 'adonis' and 'metaMDS' functions in the vegan package (Oksanen *et al.* 2014).

Results

Supporting our first prediction, the one-time seed addition increased the number of seedlings and seeded species richness in 2002, and this effect remained significant even after 11 years (in 2012); seeding increased the cover of seeded species, seeded species richness and total community richness (including resident and seeded species, Table 1, Figs 1–3, see also Figs S1 and S2). The one-time seed addition also promoted community divergence over the long-term, as shown by significant impact of propagule addition on seeded and whole community composition in 2012 (PERMANOVA results, Table S2, Fig. 4, Fig. S3).

Supporting our second prediction that herbivory alleviates microsite limitation and shifts the community towards propagule limitation, we found that the positive impact of seeding on seeded species richness and total community richness in 2012 was much greater in grazed than fenced plots especially in dry conditions (seeding × fencing interaction, Figs 1 and 3, Table 1). Moreover, herbivory also modified the impact of seeding on seeded community composition (seeding × fencing interaction in PERMANOVA in 2012, Table S2, Fig. S3). Interestingly, the impact of seeding on seeded species richness was much more pronounced in dry than in wet plots (seeding × soil moisture interaction, Fig. 1, Table 1) and attained highest value in seeded dry plots that were exposed to grazing (marginally significant seeding × fencing × soil moisture interaction, Table 1, Fig. 1). In contrast, the cover of seeded species was highest in fenced dry plots (seeding × fencing and seeding × fencing × soil moisture interactions, Table 1, Fig. 2), showing the generally negative impact of herbivory on species' cover. Seeding had no significant impact on total plant cover in 2012.

Consistent with our third prediction, we found that the impact of herbivory became stronger with time (Table 1, Figs 1 and 2). Furthermore, total plant cover was only

Table 1. Summary statistics of linear mixed-effects (LME) models for seeded species richness (2002 and 2012), seedling number of seeded species (2002), cover of seeded species (2012) and total vascular cover (2012). Seeding (S), disturbance (D), fencing (F), soil moisture (M) and their interactions were treated as fixed factors in all models. The nested design of the experiment was included in the models as nested random effects, where the four subplots (receiving disturbance, seeding or a combination of these) were nested within plots (which were either fenced or not and exhibited different soil moisture levels)

Source of variation	2002		2012			
	Richness of seeded sp.	Seedling number	Cover of seeded sp.	Richness of seeded sp.	Total cover	Total richness
Fencing	$F_{1,16} = 4.3$*	ns	ns	ns	$F_{1,16} = 35.7$***	ns
Disturbance	$F_{1,49} = 35.4$***	$F_{1,49} = 83.2$***	ns	ns	ns	ns
Seeding	$F_{1,49} = 266.4$***	$F_{1,49} = 264.3$***	$F_{1,49} = 18.3$***	$F_{1,49} = 76.1$***	ns	$F_{1,49} = 33.0$***
Moisture	ns	ns	ns	$F_{1,16} = 5.6$*	$F_{1,16} = 14.1$**	ns
F × D	ns	ns	ns	ns	ns	ns
F × S	$F_{1,49} = 7.4$**	$F_{1,49} = 4.9$*	$F_{1,49} = 6.1$*	$F_{1,49} = 12.6$***	ns	$F_{1,49} = 4.7$*
F × M	ns	$F_{1,16} = 4.4$*	ns	$F_{1,16} = 7.0$*	$F_{1,16} = 5.1$*	ns
D × S	$F_{1,49} = 9.7$**	$F_{1,49} = 13.0$***	ns	$F_{1,49} = 8.8$**	ns	$F_{1,49} = 5.7$*
D × M	ns	ns	ns	ns	ns	ns
S × M	ns	$F_{1,49} = 22.3$***	ns	$F_{1,49} = 5.7$*	ns	ns
F × D × S	ns	ns	ns	ns	ns	ns
F × D × M	ns	ns	ns	ns	ns	ns
F × S × M	ns	ns	$F_{1,49} = 6.7$*	$F_{1,49} = 3.3^{\S}$	ns	ns
D × S × M	ns	ns	ns	ns	ns	ns

For clarity, the values for non-significant main effects or interactions are not shown. sp, species; ns, non-significant on the level $P < 0.06$. Significance codes: < 0.001***; < 0.01**; ≤ 0.05*; ≤ 0.07§. Cover of seeded species in 2012 was log + 0.1 transformed, total cover in 2012 and seeded species richness in 2002 and 2012 were untransformed, while seedling number in 2002 and total richness in 2012 were square root transformed for the analyses.

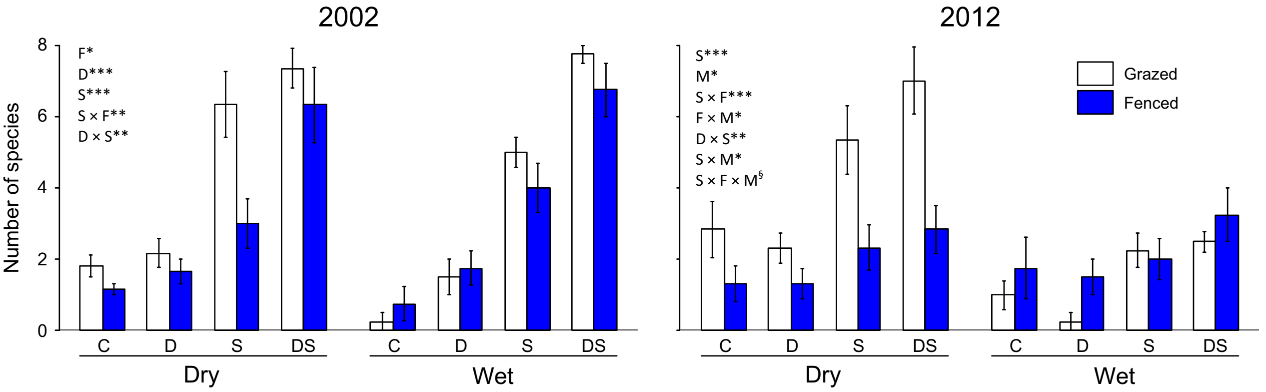

Fig. 1. Mean ± 1 SE of species richness of seeded species in 2002 and 2012 (the first and last years of the experiment) in different treatment combinations. For complete time series including all study years see Fig. S1. Significance codes ($P < 0.001$***; $P < 0.01$**; $P \leq 0.05$*; $P \leq 0.07^{\S}$) are summary statistics of linear mixed-effects (LME) models for seeded species richness (2002 and 2012) where seeding (S), disturbance (D), fencing (F), soil moisture (M) and their interactions were treated as fixed factors. For complete model information, see Table 1. Treatment codes on *x*-axis: C = control plots; D = disturbed plots; S = seeded plots; SD = seeded and disturbed plots; Dry = dry plots; Wet = wet plots.

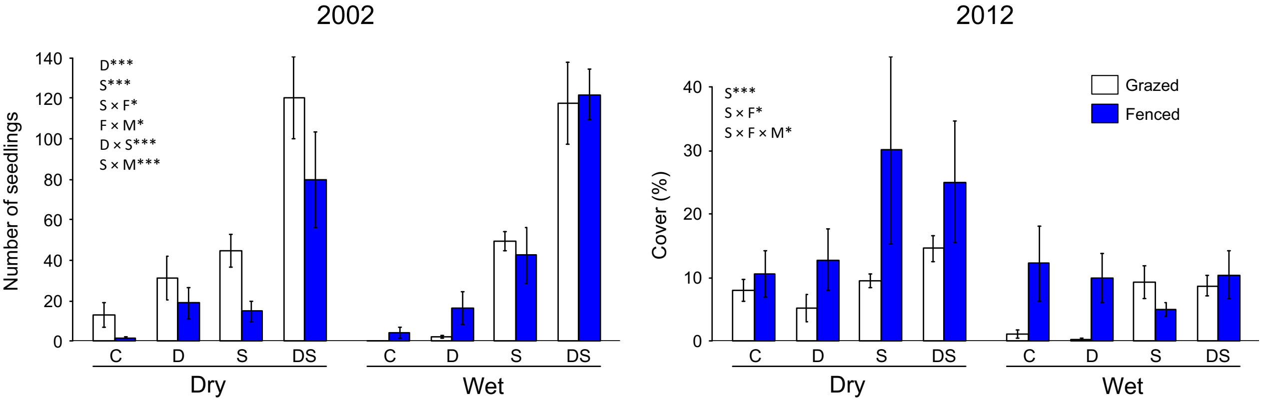

Fig. 2. Mean ± 1 SE of number of seedlings of seeded species in 2002 and the cover (%) of seeded species in 2012 in different treatment combinations. For complete time series including all study years see Fig. S2. In 2002, seedling number was counted while in 2012 plant cover was estimated. Significance codes ($P < 0.001$***; $P < 0.01$**; $P \leq 0.05$*) are summary statistics of linear mixed-effects (LME) models for number of seedlings of seeded species (2002) and cover of seeded species (2012) where seeding (S), disturbance (D), fencing (F), soil moisture (M) and their interactions were treated as fixed factors. For complete model information, see Table 1. Treatment codes on *x*-axis: C = control plots; D = disturbed plots; S = seeded plots; SD = seeded and disturbed plots; dry = dry plots; wet = wet plots.

influenced by fencing and soil moisture with the greatest cover in fenced dry plots (main effects of soil moisture and fencing, and fencing × soil moisture interaction, Table 1, Fig. 3). Moreover, fencing and soil moisture exhibited more significant impacts on community composition in 2012 than in 2002 (PERMANOVA results, Table S2, Fig. 4, Figs S3 and S4).

Consistent with our fourth prediction, the effects of one-time disturbance weakened over time. There was no significant main effect of one-time disturbance treatment on total plant cover, total species richness, cover of seeded species and seeded species richness in 2012, even though both seeded species richness and seedling number were highly significantly influenced by disturbance in 2002 (Table 1). Moreover, the initial significant main effect of disturbance on the seeded community composition in 2002 disappeared with time and had no significant effect 11 years after the initiation of the experiment (i.e. 2012, Table S2, Fig. 4, Figs S3 and S4). However, even though the impact of one-time disturbance alone weakened over time, it helped the establishment of seeded species in the long term: the positive impact of seeding on seeded species richness in 2012 was greatest in disturbed subplots (disturbance × sowing interaction, Table 1, Fig. 1).

Discussion

Our results show that mammalian herbivory can modulate the contribution of propagule and microsite availabilities in governing community composition and diversity. In an 11-year seed addition experiment, we found that a one-time seed addition increased plant species richness and that this effect persisted after 11 years. However, in line with our prediction, over time this impact was increasingly contingent on grazing

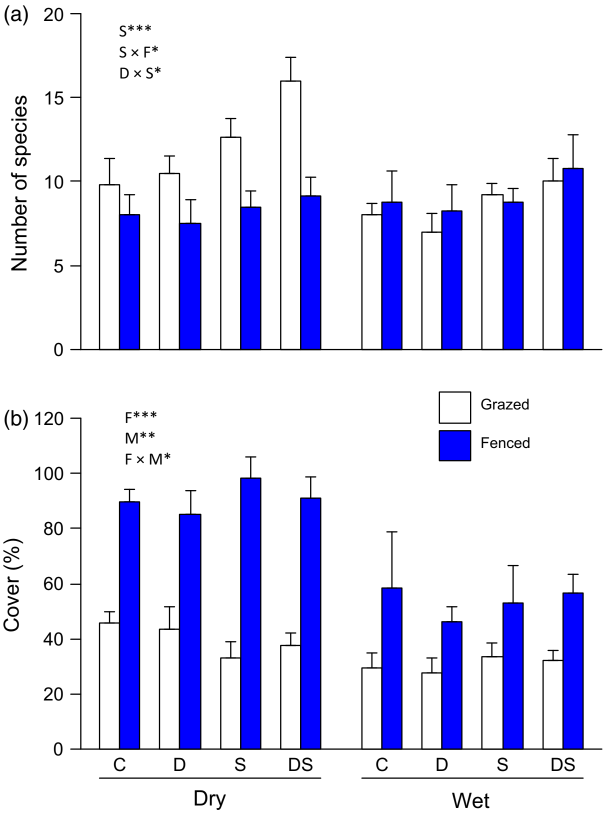

Fig. 3. Mean ± 1 SE of (a) total species richness (i.e. number of all vascular species including both seeded and resident species) and (b) total per cent cover of vascular plants (including both seeded and resident species) in response to 11-year treatments. Significance codes ($P < 0.001$***; $P < 0.01$**; $P \leq 0.05$*) are summary statistics of linear mixed-effects (LME) models for total species richness and cover (2012) where seeding (S), disturbance (D), fencing (F), soil moisture (M) and their interactions were treated as fixed factors. For complete model information see Table 1. Treatment codes on x-axis: C = control plots; D = disturbed plots; S = seeded plots; SD = seeded and disturbed plots; dry = dry plots; wet = wet plots.

with very few seeded species left inside herbivore exclosures after 11 years. Furthermore, the initially strong effect of disturbance on species colonization weakened, and the main and interactive effects of environmental conditions and grazing pressure on the establishment of individual seeded species and community composition increased over time. These findings emphasize the importance of considering the different aspects of regeneration niche, i.e. seed germination, seedling establishment and maturation of plants (Grubb 1977; Harper 1977; Grime 2001), and underscore the fundamental role of herbivory in impacting these different stages. Moreover, our results highlight the importance to use long-term approaches when investigating interacting impacts of propagule limitation, biotic and environmental filtering on plant recruitment and community assembly (Clark *et al.* 2007; Myers & Harms 2009; Erfmeier, Hantsch & Bruelheide 2013; Olsen & Klanderud 2014).

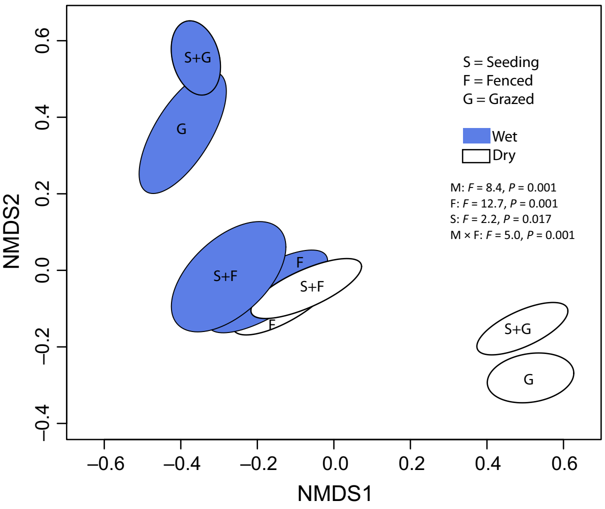

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of the whole vascular plant community (including seeded and resident species) in 2012, and its relationship with experimental treatments and soil moisture. The ordination was based on Bray–Curtis dissimilarities on square-root-transformed data and with Wisconsin standardization. The ellipses show class standard errors for each factor, and the labels show the class centroids for each treatment combination. We slightly moved the label positions for fenced-only treatments to clarify the presentation. Only those factors that were significant in permutational multivariate analyses of variances (PERMANOVA) are shown, and therefore, disturbance treatment is not shown. *F*- and *P*-values are summary statistics of PERMANOVA (see Table S2) with seeding (S), fencing (F), soil moisture (M) and their interactions as explanatory variables.

Grazing favoured the establishment of seeded species and also interacted with propagule limitation such that propagule supply facilitated long-term success of the seeded species much more when grazers were present. Thus, our results suggest that analogous to the influence of productivity (due to soil resource availability; Foster *et al.* 2004; Dickson & Foster 2008), grazing exhibits a strong effect on the relative importance of propagule and microsite limitation for plant community assembly and provides a mechanism by which natural communities can shift from being mainly microsite to propagule limited. In our study, plant biomass was much higher inside fences already at the beginning of the experiment (Eskelinen & Virtanen 2005), implying that constant removal of biomass by herbivores alleviated competition for light and space in a way that favoured long-term establishment of the immigrants. Our findings are in line with earlier studies, suggesting that herbivores are important for plant community structure via their impacts on recruitment processes in general (Huntly 1991; Olff & Ritchie 1998; Maron & Crone 2006; MacDougall & Wilson 2007; Clark, Poulsen & Levey 2012) and with theoretical and empirical studies predicting/showing strong grazing impacts on vegetation biomass and community dynamics in low-productivity environments (e.g. Oksanen *et al.* 1981; Post & Pedersen 2008; Speed *et al.* 2010; Eskelinen, Harrison & Tuomi 2012; Gough *et al.* 2012; Olofsson *et al.* 2014; Saccore *et al.* 2014). Building on this body of research, our results are a novel demonstration of how herbivores control the balance between microsite and propagule limitation and how this control can translate to plant assembly dynamics.

The initial positive effect of disturbance on seedling colonization [mimicking strong localized grazing events that create temporary gaps to the vegetation, such as lemming outbreaks (Nystuen *et al.* 2014) or occasional trampling] implies that competition with established vegetation represents a strong limitation for plant recruitment even in low-productivity environments such as tundra, as found also in other studies (e.g. Eskelinen & Virtanen 2005; Gough 2006; Olofsson & Shams 2007; Eskelinen 2010; Klanderud 2010; Dullinger & Hülber 2011; Graae *et al.* 2011). This result is in line with other studies showing the importance of gap creation as an important mechanism by which herbivores can affect initial seed germination and seedling emergence (Bakker & Olff 2003; Bagchi, Namgail & Ritchie 2006). In our study, the effect of disturbance on community richness was still present 11 years after its application, but only when combined with seeding. These results suggest that local small-scale disturbances can have long-term effect on plant communities if the disturbance is coupled with propagule arrival. However, the impact of this one-time artificial disturbance alone disappeared with time as the resident community recovered, highlighting that more continuous disturbance (e.g., large mammalian grazing, frequent burrowing and intensive trampling) engendering recurrent competition-free resource pulses (Tilman 2004) would be needed to break biotic resistance by the resident vegetation.

Besides opening space for seed germination and seedling emergence, herbivores can influence plant recruitment dynamics by several mechanisms including dispersing seeds, seed predation and seedling herbivory (Bakker & Olff 2003; MacDougall & Wilson 2007; Clark, Poulsen & Levey 2012; Maron *et al.* 2012). Although these mechanisms were not investigated in our study, they could all impact the balance between propagule and microsite limitations also in our study system. Moreover, the size of the herbivores can also play crucial role in dictating the magnitude and direction of herbivore impacts (Bakker & Olff 2003; Bakker *et al.* 2006). In our study system, however, all three species primarily impact the community through the removal of above-ground plant biomass rather than through burrowing or other soil-disturbing activities even though reindeer, lemmings and voles, at least partially, consume different components of the plant community (i.e. reindeer target taller and larger plants, lemmings eat mosses, voles cut stems of all vascular plants; Moen, Lundberg & Oksanen 1993; Virtanen, Henttonen & Laine 1997; Olofsson *et al.* 2004; Kaarlejärvi, Eskelinen & Olofsson 2013). Although we cannot separate the specific mechanisms by which small and large mammalian herbivores impact plant communities with our experimental design, our results provide insights into the net effect of the herbivore community on the balance between microsite and propagule limitation and suggest that this net effect is primarily driven by the relaxation of above-ground competition.

In addition to showing the importance of herbivory, our results also revealed that the impact of grazing on plant recruitment can depend on local environmental conditions; the long-term impact of seeding on species richness was much greater in dry and grazed conditions than in wet and grazed conditions. In general, our findings are in line with other studies that highlight the importance of soil moisture influencing short-term colonization success (Xiong *et al.* 2003; Foster & Dickson 2004; Myers & Harms 2011; Dybzinski & Tilman 2012). These studies show either negative or positive impact of moisture on seed germination, the direction of the impact likely depending on how water-limited the system is – does water limit growth or does excess water availability impede growth (like in our system). However, our study provides a novel demonstration that the long-term establishment success of immigrating species is contingent on a combination among biotic and abiotic conditions, and may be attained only under a balance between grazing pressure and soil moisture. In our study, wet and ungrazed conditions did not impede short-term seedling emergence but started having negative impact only in the long term. These communities were covered by a thick layer of robust bryophytes typical for tundra (*Polytrichum* spp., *Sphagnum* spp.; Saccore *et al.* 2014), which may have hampered the long-term establishment of seeded species. Our finding is in line with other studies from tundra showing that wet conditions, often with abundant bryophytes, disfavour growth of vascular plants (Gornall *et al.* 2011). It is possible that lemming grazing is less intense in wet snowbed patches where they cannot effectively graze in winter, allowing development of thick moss carpets that hamper seedling emergence and establishment. Taken together, our results suggest that a potential feedback between grazing and soil moisture may limit recruitment and persistence of vascular plants in tundra snowbeds (see also Sandvik & Odland 2013).

Conclusions

Understanding the relative influences of propagule and microsite availabilities on recruitment dynamics is especially important under multiple global change factors, where changing environmental conditions and disturbance regimes have the potential to considerably change their relative contributions, with important ramifications on the whole community and ecosystem dynamics (Huntley 1991; Tylianakis *et al.* 2008; Wardle *et al.* 2011; Maron *et al.* 2014). While seed addition experiments are frequently used to investigate the role of plant recruitment in immigration, invasions and determination of local diversity, very few studies have continued to monitor plant recruitment long enough to determine whether or not populations were successfully established (Turnbull, Crawley & Rees 2000; but see Foster & Tilman 2003; Olsen & Klanderud 2014). Our study is among the first that have followed the effects of seed addition for more than ten years and enough long time for the added species to establish, and highlights the fundamental importance of propagule limitation in plant community assembly. Our results also underscore the importance of long-term approaches when investigating constraints on plant recruitment as factors favouring short-term colonization may greatly differ from those benefitting long-term establishment. Moreover, our results demonstrate the overriding importance of mammalian herbivory in dictating both plant colonization and establishment, and imply that mammalian herbivory, by reducing microsite limitation via competition with the resident community, can modulate the relative contribution of propagule and microsite availabilities in governing community composition and diversity. Thus, grazing may be a key biotic driver controlling recruitment dynamics, and can function as an important ecological filter that dictates species immigration from the species pool.

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Data accessibility

Data associated with this paper are available from the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.710ng (Eskelinen *et al.* 2016).

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Supporting Information

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

Figure S1. Figure showing the number of seeded species during all study years.

Figure S2. Figure showing the number of seedlings of seeded species during all study years.

Figure S3. NMDS ordination figure illustrating the treatment effects on the seeded community composition in 2012.

Figure S4. NMDS ordination figure illustrating the treatment effects on the seeded community composition in 2002.

Table S1. Table showing the number of seedlings for each seeded species with respect to fencing, seeding, disturbance and their interactions in 2002 and 2003.

Table S2. Table showing results from PERMANOVA for seeded species community in 2002 and 2012, and for the whole community in 2012.