

Environmental perturbation, grazing pressure and soil wetness jointly drive mountain tundra toward divergent alternative states

Patrick Saccone^{1*}, Tuija Pyykkonen¹, Anu Eskelinen^{1,2} and Risto Virtanen¹

¹Department of Biology, University of Oulu, PO Box 3000, Oulu FI-90014, Finland; and ²Department of Environmental Science and Policy, University of California Davis, One Shields Avenue, Davis, California 95616, USA

Summary

1. Plant communities are structured by complex interactions between multiple factors, which veil our understanding of the effects of environmental changes on communities and ecosystems. Besides the relative role of biotic and abiotic factors as community-structuring processes, addressing how they jointly affect the ecological resilience and resistance of plant communities is crucial to understand better the long-term response of communities facing global changes.

2. Here, we used the results from a long-term (23 years) perturbation experiment set up in Fennoscandian mountain tundra to test these mechanisms. The experiment consisted of a transplantation of twenty blocks of *Vaccinium myrtillus* heath vegetation including upper soil layer from a lower elevation tundra heath habitat to a snowbed habitat 150 m higher in elevation where *V. myrtillus* lies at its upper limit. In the snowbed with contrasting levels of soil wetness, half of the transplanted blocks were protected from mammalian herbivores.

3. Our results revealed that in addition to the important role of environmental conditions as a structuring force, the joint effects of multiple drivers resulted in divergent patterns in both plant functional composition and species diversity among transplanted communities. Under environmental perturbation (i.e. transplantation to snowbed), the heath vegetation was altered by grazing pressure that reduced the cover of shrubs (especially *V. myrtillus*). In grazed dry snowbed, a species-rich community with high functional type evenness and diversity developed. Reversely, in dry exclosures, *V. myrtillus* gained high dominance associated with only few graminoids and forbs. In wet snowbed conditions, shrubs tended to decline both in grazed plots and exclosures whereas bryophytes attained high abundance. Grazing promoted species richness while soil waterlogging tended to promote among-plot heterogeneity (β -diversity) which was highest in wet exclosures.

4. *Synthesis.* Our long-term experiment reveals that environmental perturbation, grazing and soil wetness exhibit joint effects that induce divergent trajectories of tundra plant communities. We suggest that a strong environmental perturbation triggers mountain tundra heath community to move away from its equilibrium state. The outcome of this shift depends on the interplay between grazing pressure and soil wetness that drive tundra plant communities toward divergent alternative states.

Key-words: alternative states, determinants of plant community diversity and structure, diversity, herbivory, joint effects, long-term experiment, multiple drivers, species abundance distribution, tundra shrubification

Introduction

The greening and shrubification of tundra are visible evidences of the immediate consequences of global change in arctic regions (Tape, Sturm & Racine 2006; Walker *et al.* 2006). The expected magnitude of tundra vegetation changes

in terms of functional composition and texture are suggested to have strong implications for the regional and global feedback with the climate and global changes (Cahoon *et al.* 2012; Lorant & Goetz 2012). However, recent studies reveal that the shrub expansion is also context-dependent and variable in space and time, underlining the importance of local environmental conditions that can mask or buffer the main expansion pattern (Elmendorf *et al.* 2012; Tape *et al.* 2012;

*Correspondence author. E-mail: patrick.saccone@gmail.com

Epstein, Myers-Smith & Walker 2013). Several studies from contrasting habitats also reveal that local conditions can mediate the response of communities to global change (Brooker 2006; Saccone *et al.* 2010; Kaarlejärvi, Eskelinen & Olofsson 2013; Liancourt *et al.* 2013), because community composition and functioning emerge from a complex interplay of processes involving both biotic and abiotic factors (Lortie *et al.* 2004). In this context, the evaluation of the long-term consequences of global change on arctic ecosystems requires a better understanding of the complex web of interactions and processes structuring tundra plant communities.

In low-productivity environments such as mountain tundra, environmental constraints are commonly considered as the main drivers of the composition of plant communities (Körner 2003). In cold tundra biomes, for instance, soil disturbances, air temperature or short growing season are suggested to function as strong filters of the species pool (Keddy 1992). At the same time, the importance of biotic factors (i.e. their impact relative to other processes) such as plant interactions or grazing as community structuring forces is expected to decrease along increasing environmental severity (Grime 2001; Brooker *et al.* 2005; Michalet *et al.* 2006; Lezama *et al.* 2014). As a result, tundra communities are dominated by stress-tolerant, long-lived species capable of withstanding strong inter-annual environmental variation and perturbations (Hudson & Henry 2010; Wahren *et al.* 2013).

On the other hand, there are theoretical studies which predict that grazing pressure exerts strong impacts on plant community composition (Noy-Meir 1975; Fretwell 1977; Oksanen *et al.* 1981), and that plant functional composition of tundra is primarily structured by grazing pressure (Oksanen 1990). Several studies from tundra regions emphasize that grazing pressure strongly affects plant community composition (Olofsson *et al.* 2009), plant species performance (Eskelinen 2008) and plant stoichiometry (Zamin & Grogan 2013). These studies suggest that the development of vegetation states in tundra could be sensitive to shifts in grazing pressure. In this vein, van der Wal (2006) has proposed that grazing pressure drives shifts of tundra plant communities between lichen-, moss- and grass-dominated alternative states. Indeed, several studies report alternative tundra vegetation states and propose that they are produced by the levels of grazing (Oksanen & Virtanen 1995; Zimov *et al.* 1995; Olofsson 2006; van der Wal & Hessen 2009). Moreover, some studies also highlight that the effects of grazing on tundra plant communities cannot be considered in isolation from several locally varying factors such as soil nutrient status (Eskelinen, Harrison & Tuomi 2012) and many abiotic conditions changing with an elevation gradient (Speed, Austrheim & Mysterud 2013).

Instead of viewing tundra plant communities driven solely by either abiotic or biotic factors, a more fruitful approach is to address the joint effects of multiple forces that may manifest themselves in different relative strengths depending on the context. Houseman *et al.* (2008) showed that multiple perturbations may have complex effects on community dispersion that are difficult to predict based on analysis of single factors and that lead to divergent alternative states. Such ideas are well

accommodated by the concept of alternative stable states (ASS; see Beisner, Haydon & Cuddington 2003 for a review) which proposes that a perturbation of community-structuring processes could move a community from a stable state to another by triggering a crossover a threshold point between two basins of attraction. These transitions are likely to depend on interacting abiotic and biotic forces. However, the responses of plant communities to multiple perturbations need to be studied over time scales where ecological processes have even a theoretical chance to reach a steady state (Schröder, Persson & De Roos 2005), especially in tundra ecosystems where most species are long-lived and harsh environmental conditions limit the growth of plants (Sonesson & Callaghan 1991; Grime 2001). Long-term experiments are the most appropriate tool to disentangle the interplay between biotic and abiotic factors acting in plant communities and to assess their consequences for multiple vegetation states (Tilman 1989).

Here, we report results from a 23-year experiment, established in 1989 in mountain tundra of Finnish Lapland, to test the mechanisms underlying the long-term effects of environmental perturbation and local processes on plant community composition and diversity, and development of alternative states. The experiment consisted of the transplantation of blocks (including soil and vegetation) of low elevation *Vaccinium myrtillus* heath vegetation to a snowbed site 150 m higher in elevation. This transplantation simulates strong perturbation of environmental conditions since the surrounding species pool, climate and hydrology, are altered. The blocks transplanted to the snowbed were assigned to a grazing pressure treatment in contrasting conditions of soil wetness. As environmental conditions are predicted to be important determinants of tundra plant assemblages, we expected that the environmental perturbation due to the transplantation to the snowbed would impose a considerable change in the transplanted communities. However, as local biotic and abiotic conditions are also predicted to play an important role in driving tundra community dynamics, we primarily hypothesized that grazing and soil wetness conditions would jointly affect the development of vegetation states and yield divergent community trajectories following environmental perturbation.

Materials and methods

STUDY SITE

The study was carried out on Mt. Jehkats at Kilpisjärvi in the north-western Finnish Lapland (69°01'N and 20°50'E). The mountain tundra at altitudes of 600–800 m above sea level (a.s.l.) is characterized by dwarf shrub heaths which are more fragmented above 800 m a.s.l. where sedge-grass meadows and snowbed type communities occur extensively (Oksanen & Virtanen 1995). *Vaccinium myrtillus*, a deciduous dwarf shrub, dominates heath vegetation on slope sites with intermediate snow persistence and it is usually absent from snowbed sites, where a short growing season likely limits plant growth (Wijk 1986; Sonesson & Callaghan 1991). In the study area, *V. myrtillus* heaths are common up to altitudes of about 700 m a.s.l. and occur sporadically up to altitudes of about 900 m a.s.l. (Oksanen & Virtanen 1995).

The gradient from the low elevation heath to the high elevation heath-snowbed mosaic represents a substantial change in the characteristics of physical environment. The aerial primary net production on heaths rich in *V. myrtillus* is about $294 \pm 41 \text{ g m}^{-2} \text{ year}^{-1}$, while that of snowbed sites rich in *Salix herbacea* is $65 \pm 23 \text{ g m}^{-2} \text{ year}^{-1}$ (Kyllönen 1988). In the snowbed site, snow cover remains till late June which is about 10 days later than in the heath site 150 m lower in the altitude (own observations). Soil nutrients in the heath and snowbed habitats are at about equal levels (Virtanen 1998).

The snowbed habitat is grazed by arviculids and reindeer (*Rangifer tarandus* (Smith 1827)) that are the most important grazers of the study area. The grey-sided vole (*Myodes rufocanus* (Sundevall 1846)) uses *V. myrtillus* as its main winter food (Kalela 1957). The moss and graminoid specialist Norwegian lemming (*Lemmus lemmus* (Linnaeus 1758)) exerts the strongest grazing impact on snowbed vegetation (Virtanen, Parviainen & Henttonen 2002) and can mechanically injure shrubs. Semi-domesticated reindeer induces a relatively heavy grazing and trampling pressure during the summer season (Oksanen & Virtanen 1995). The densities of arviculids fluctuated throughout the whole study period and two outbreaks of lemmings occurred (in 1998–99 Virtanen, Parviainen & Henttonen 2002; and in 2010–11 H. Henttonen, unpubl. data). The grazing pressure on low elevation heath habitat is lower than on the snowbed. On the one hand, reindeer preferably visit snowbed areas richer in sedge and grasses and, on the other hand, the density of arviculids is lower in the heath (H. Henttonen, unpubl. data).

EXPERIMENTAL DESIGN

In late June 1989, 30 $40 \times 50 \text{ cm}$ blocks of *V. myrtillus* heath vegetation including 5–10-cm thick layer of humus and mineral soil were dug out from the natural heath habitat lying at an altitude of 660 m a.s.l. and randomly allocated into different treatments. To be able to test for the transplantation and environmental perturbation effects, 10 blocks were transplanted within the original *V. myrtillus* heath and were used as control plots (C). The environmental perturbation consists in the transplantation of the remaining 20 blocks to a snowbed site of about $15 \times 30 \text{ m}$, 150 m higher in elevation. As a result, the blocks originating from the low elevation heath have been transplanted in a new habitat with a shorter growing season, a lower productivity level, harsher climatic conditions, higher grazing pressure, different hydrologic and topographic conditions and a different local species pool in the surrounding. Ten blocks within the snowbed site were protected from herbivores (E for enclosure) using metal mesh fences that were 60–70 cm in diameter, 60-cm high with 1-cm mesh size, and dug into the soil. The remaining 10 blocks were left grazed (G). Fences excluded small mammal herbivory and the clear contrast in average height of fenced ($15.9 \pm 1.04 \text{ cm}$) and grazed ($6.75 \pm 0.77 \text{ cm}$) communities attests that fences also strongly reduced but not fully excluded reindeer grazing (some herbivory marks on the top of taller plants) because of the open tops of the fences. Within the recipient snowbed, meso-topography induces differences in soil wetness which delimit relatively dry and wet soil areas characterized by *Kiaeria* and *Polytrichum* spp., and *Sphagnum* spp., respectively. We confirmed these recurrent field observations of soil wetness by gravimetric soil moisture measurements in mid-August 2012 (see Appendix S1 in Supporting Information) and the 20 snowbed blocks were split in dry (soil water content $64.9 \pm 4.9\%$ dry soil mass) and wet (soil water content $199.4 \pm 19.9\%$ dry soil mass) according to the significant differences between both groups

(see Appendix S1). Finally, the experimental design contained five treatments: control plots (C), grazed plots (G.dry) and exclosures (E.dry) on dry snowbed, and grazed plots (G.wet) and exclosures (E.wet) on wet snowbed.

COMMUNITY COMPOSITION AND DIVERSITY, AND STATISTICAL ANALYSES

In the central part of each block, a $0.125 \times 0.125 \text{ m}$ area was delimited and preserved from any other experimental manipulations during the 23 years of the experiment. This size of experimental plots was suitable given the small stature and number of vascular plants (2–15 cm and up to 16 species) and the high number of extremely small cryptogam species in the plots (1–2 mm and up to 22 species) that are traditionally considered as an important component of arctic vegetation and ecosystem functioning (e.g., van der Wal, van Lieshout & Looen 2001). Also, we recorded 88 different species in the 30 study plots (see Fig. 2 and Appendix S2), representing a large proportion (> 50%) of the local diversity, which suggest that the design captured most of the spatial heterogeneity in the system. In mid-August 2012, the abundance of each plant species was estimated using visual estimation method (Kent 2012) that was found the only feasible method to record very small cryptogam and many small vascular plant species. The nomenclature of the vascular flora, bryophytes and lichens follows Hämet-Ahti *et al.* (1998), Ulvinen, Syrjänen & Anttila (2002) and Vitikainen *et al.* (1997), respectively. Because different aggregation levels of the plant data may highlight different processes (Dorrepaal 2007), we also pooled species by functional type (PFT) and the aggregation commonly used in the studies of arctic vegetation, that is, graminoids, forbs, shrubs, lichens and bryophytes (based on Bruun *et al.* 2006) was used. Species richness and Shannon diversity index were calculated for each plot and β -diversity (Sørensen 1948) values were calculated to quantify divergence of community composition within each treatment.

We analysed the divergence of communities transplanted in the different treatments using Non-Metric Dimensional Scaling (NMDS) ordination. The ordinations were based on Bray-Curtis distances with Wisconsin double standardized and square-root transformed species and PFT cover data. The respective effects of experimental treatments, that is, environmental perturbation, grazing pressure, soil wetness and grazing pressure \times soil wetness interaction on community dissimilarities were evaluated using Permutational Multivariate Analyses of Variances Models (PERMANOVA, Anderson 2001) and their significance were assessed with 999 permutations. The differences in β -diversity among the five treatments were evaluated using Permutational Multivariate Dispersion Analyses Model (PERMDISP; Anderson, Ellingsen & McArdle 2006) and their significance was assessed with 999 permutations. We used 'adonis', 'metaMDS' and 'betadisper' functions in the VEGAN package (Oksanen *et al.* 2012) in R software (R Development Core Team 2013) to perform the PERMANOVA analyses, NMDS ordinations and PERMDISP analysis, respectively.

To analyse the effects of environmental perturbation, grazing pressure, soil wetness and grazing pressure \times soil wetness interaction on PFT, *V. myrtillus* and *S. herbacea* cover and on diversity indices we used two-way Generalized Linear Models (GLM) with a Gaussian error distribution and an identity link function. We used otherwise similar but one-way GLMs to test the difference among the five treatments (i.e. C, G.dry, G.wet, E.dry and E.wet) for each PFT cover and for diversity indices. In all analyses, data were square-root transformed to meet the assumptions of the homogeneity of variances and normality of errors. To test pairwise differences among treatments,

one-way GLMs were followed by *post-hoc* tests using 'ghlt' function in the MULTICOMP package (Horthon, Bretz & Westfall 2008) in R.

Results

In general, all three treatment factors, that is, environmental perturbation (transplantation to the snowbed), grazing pressure and soil wetness significantly affected the composition of transplanted communities, considering both species and functional type based comparisons (Table 1). Both NMDS

Table 1. Results of Permutational Multivariate Analyses of Variances (permanova) performed with environmental perturbation, soil wetness, grazing pressure and the soil wetness × grazing pressure interaction as explanatory variables on community cover matrix at the plant species level (a) and on community cover matrix with species pooled by plant functional type (b, PFT)

Source of variation	(a) Community (species)				(b) Community (PFT)			
	d.f.	F	R ²	P	d.f.	F	R ²	P
Environmental perturbation	1	6.78	0.17	0.001	1	16.43	0.29	0.001
Soil wetness (W)	1	3.15	0.08	0.002	1	7.55	0.13	0.001
Grazing pressure(G)	1	3.19	0.08	0.003	1	6.41	0.11	0.001
W × G	1	1.92	0.05	0.036	1	1.31	0.02	0.252
Residuals	25		0.62		25		0.44	

ordinations (Fig. 1) illustrate the PERMANOVA results (Table 1) and outline the divergence between the communities in response to the 23 years of experimental treatments.

THE EFFECT OF ENVIRONMENTAL PERTURBATION DUE TO THE TRANSPLANTATION TO SNOWBED

The clear separation along the first axis in both NMDS ordinations (Fig. 1) between the control plots (C) and those transplanted to the snowbed (G and E, dry and wet) corresponded to 17% and 29% of the total variation in species and functional composition, respectively, explained by the environmental perturbation treatment (Table 1).

The small value of β-diversity in the control communities (Table 2) indicated a relatively high level of homogeneity in this community with a dominant species (*V. myrtillus*), some co-dominant bryophyte species (e.g. *Dicranum* sp.) and shrubs (*Empetrum hermaphroditum*, *Phyllodoce caerulea* and *S. herbacea*), and several rare species (Figs 1a and 2a). In the snowbed site, *V. myrtillus* remained dominant or co-dominant species of the transplanted communities and reached comparable abundance to the original heath site (Fig. 2), while *S. herbacea* remained abundant only in dry conditions (Fig. 2 and Appendix S3). Reversely, *E. hermaphroditum*, *P. caerulea* and *Vaccinium vitis-idaea* were clearly negatively impacted by the transplantation to the snowbed, suggesting these species tolerate snowbed conditions poorly.

The environmental perturbation also affected the cover of graminoids, as reflected by their ingress in communities

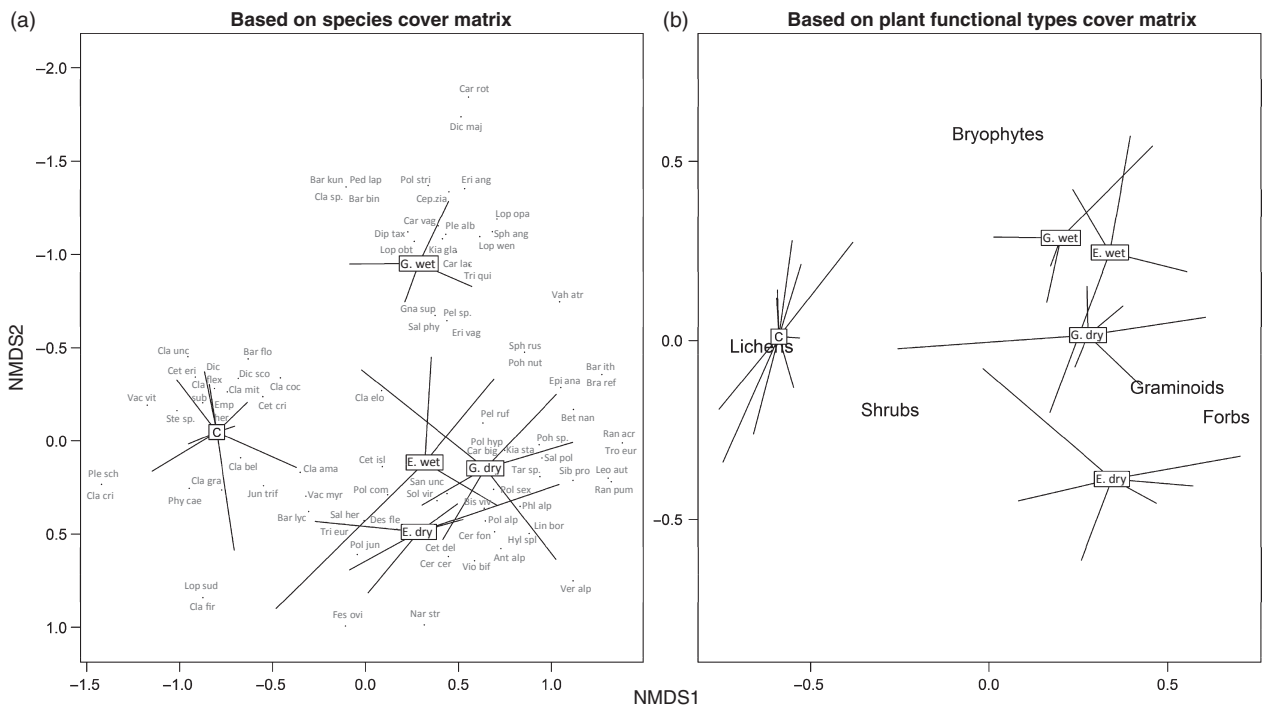


Fig. 1. Non-Metric Dimensional Scaling (NMDS) ordinations of plant community dissimilarity based on species cover (a) and on plant functional type (PFT) cover (b). Plot labels are drawn at the centroids of each group and plots are located at the end of segments. Abbreviated species names (see Appendix S1 for complete names) and plant functional types are additively plotted on the left (a) and right (b) ordination spaces, respectively. NMDS stress = 0.2 (a) and 0.09 (b), respectively.

transplanted to the snowbed site compared to their almost complete absence in the control communities (Figs 2 and 3b, Table 3). Some graminoid species attained especially high cover in the snowbed (Fig. 2), for example *Deschampsia*

Table 2. Mean \pm 1 SE of plant community diversity indexes

Treatments	Species richness	Shannon index	β -diversity
Control	11.4 \pm 0.64 b	1.62 \pm 0.06 b	0.51 b
Grazed plots			
Dry	18.5 \pm 2.22 a	2.33 \pm 0.18 a	0.53 ab
Wet	21.25 \pm 3.28 a	2.25 \pm 0.23 ab	0.59 ab
Exclosures			
Dry	9.33 \pm 1.36 b	1.58 \pm 0.23 b	0.57 ab
Wet	13.25 \pm 2.93 ab	1.74 \pm 0.25 ab	0.66 a
	***	*	*

Asterisks under species richness and Shannon index columns indicate significant differences among treatments tested by one-way Generalized Linear Models on square-root transformed data with Gaussian error distribution and an identity link function (** $P < 0.001$; * $P < 0.05$). Asterisk under β -diversity column indicates significant differences among treatments tested by Permutational Multivariate Dispersion Analyses (PERMDISP) model (* $P < 0.05$). Different letters indicate significantly different groups based on *post hoc* tests ($P < 0.05$). β -diversity index were calculated using the Sørensen index of dissimilarity (Sørensen 1948) at the treatment level.

flexuosa, which reached 12.5% of the total cover in the dry exclosures. We found similar pattern for forbs with a strong effect of environmental perturbation but also significant effects of soil wetness and grazing pressure (Table 3). Reversely, the total abundance of bryophytes was not affected by the environmental perturbation (Table 3). Finally, despite the low overall cover and subordinate status of lichens (only 7% of the total cover at the maximum, Figs 2 and 3e), they strongly characterised the control community in the NMDS ordination figure (Fig. 1b) and significantly decreased when transplanted from the heath to the snowbed (Table 3).

THE JOINT EFFECTS OF ENVIRONMENTAL PERTURBATION, GRAZING PRESSURE AND LOCAL SOIL WETNESS

The communities transplanted to the snowbed were scattered along the second axis of both NMDS ordinations and showed distinct patterns depending on whether the ordination was based on species or functional type data. In the ordination space for species cover data (Fig. 1a), the grazed wet plots (G.wet) were clearly isolated from the three other treatments. In contrast, in the ordination for PFT cover data (Fig. 1b), the dry exclosures (E.dry) were clearly separated from the three other treatments. Such discrepancy among both analyses

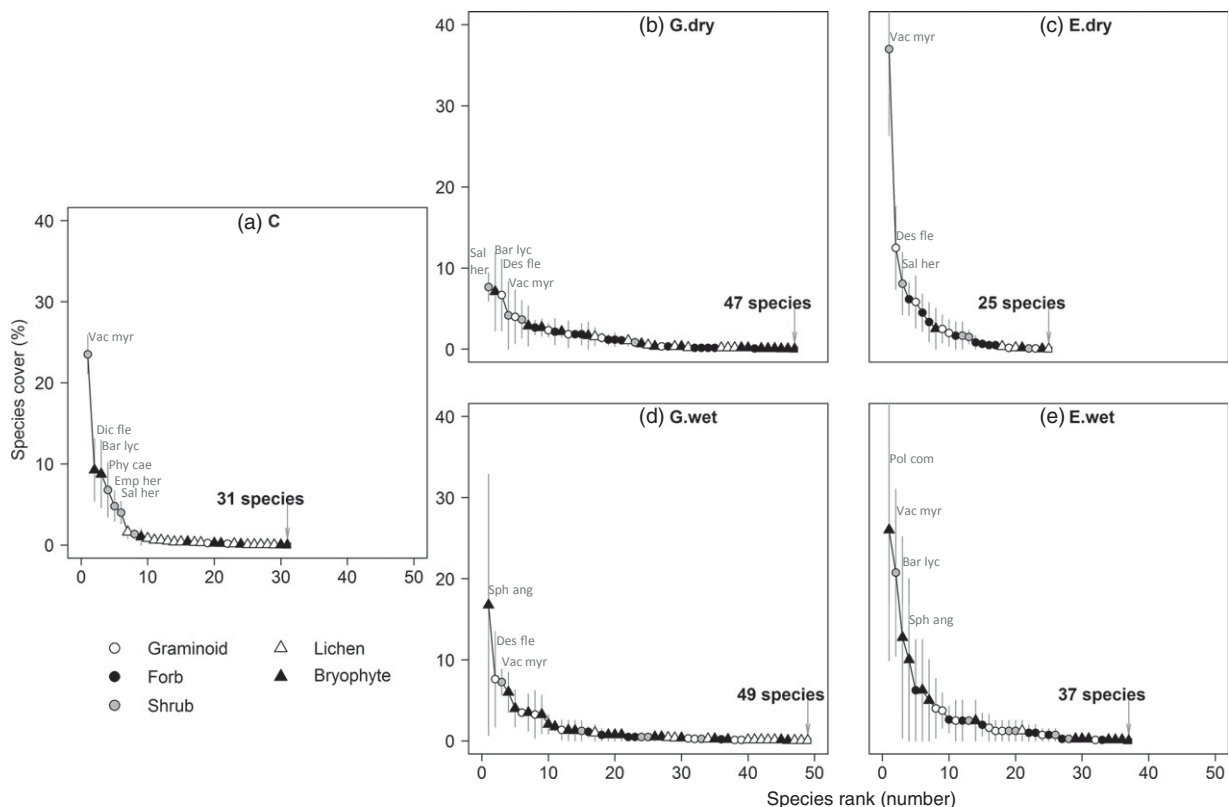


Fig. 2. Species Abundance Distribution curves by treatment. Mean \pm 1 SE of plant cover ranked by order of dominance. Arrows represented the number of species occurring at least once in the blocks of each treatment. Data symbols plotted at the mean values figured the plant functional type (PFT) of the species concerned. The abbreviated names of the most abundant species were adjoined to the error bars of corresponding point (see Appendix S1 for complete names).

Table 3. Results of the two-way Generalized Linear Models with environmental perturbation, soil wetness, grazing pressure and soil wetness \times grazing pressure interaction as explanatory variables, and the cover of each plant functional type as response variables

Source of variation	Resid. d.f.	Graminoids			Lichens		
		Resid. dev	<i>F</i>	<i>P</i>	Resid. dev	<i>F</i>	<i>P</i>
Null	29	128.67			40.90		
Environmental perturbation	28	44.71	50.05	< 0.0001	27.97	14.43	0.0008
Soil wetness (W)	27	43.76	0.56	0.4525	27.94	0.03	0.8644
Grazing (G)	26	43.37	0.23	0.6346	22.65	5.9	0.0226
W \times G	25	41.94	0.85	0.3644	22.41	0.27	0.6103

Source of variation	Resid. d.f.	Forbs			Bryophytes		
		Resid. dev	<i>F</i>	<i>P</i>	Resid. dev	<i>F</i>	<i>P</i>
Null	29	116.09			253.43		
Environmental perturbation	28	41.49	66.56	< 0.0001	251.63	0.35	0.5601
Soil wetness (W)	27	37.00	3.99	0.0565	161.42	17.48	0.0003
Grazing (G)	26	31.20	5.18	0.0317	150.87	2.04	0.1652
W \times G	25	28.02	2.84	0.1041	129.04	4.23	0.0503

Source of variation	Resid. d.f.	Shrubs		
		Resid. dev	<i>F</i>	<i>P</i>
Null	29	110.54		
Environmental perturbation	28	94.32	7.98	0.0092
Soil wetness (W)	27	85.81	4.19	0.0513
Grazing (G)	26	52.83	16.23	0.0005
W \times G	25	50.80	1.00	0.3261

Bold *P* values indicate significant effects of the explanatory variables.

could probably be attributable to the uneven distribution of species among functional types (see Appendix S2) and among treatments, and in particular to the number of bryophytes species occurring in abundance in wet conditions. Moreover, each functional type includes a wide range of species with different moisture preference ranging from rich liverwort assemblages to hygrophilic *Sphagnum* spp. in bryophytes or the generalist *D. flexuosa* and the stress-tolerant *Nardus stricta* in graminoids which lead to different ordinations of communities. Nonetheless, both ordinations shared the same treatment ranking along the second axis: G.wet, E.wet, G.dry and E.dry. To some extent, the second axes of both ordinations reflected grazing pressure and soil wetness gradients which explained between 8% and 13% of the total variation in species and functional composition respectively (Table 1).

Grazed plots on snowbed harboured richer communities (Table 2, Fig. 2b,d and see also Appendix S3), and they seemed to be more homogenous as shown by lower β -diversity (Table 2). After 23 years in the snowbed site, the shrub cover was strongly reduced by the grazing pressure and, to a lesser extent, by the environmental perturbation and the wet conditions (Fig. 3a, Table 3). Grazing reduced the dominance of shrubs and other potential dominants, and this favoured low-growing forbs, graminoids, lichens and bryophytes, leading to high evenness of functional types (Fig. 2b,d). The species abundance distribution (SAD) curves of grazed plots were flat showing a long tail of species with low cover and

the absence of any strongly dominating species. Specifically, there were 22 and 17 species covering more than 1% of the plot for G.dry and G.wet plots, respectively, whereas there was only nine species with >1% cover for C plots (Fig. 2).

The positive effect of the grazing pressure on diversity was greater in dry conditions with G.dry and E.dry communities having the highest and lowest Shannon index values, respectively (Table 2). This matched with a strong negative effect of grazing on *V. myrtillus* on the dry snowbed site (Fig. 2 and Appendix S3), implying that the dominance of *V. myrtillus* was associated with low species diversity. Indeed, *V. myrtillus* reached its highest cover in dry enclosures (37%, see Fig. 2) and shared the dominance with bryophytes and graminoids in both grazed and enclosures plots on the wet snowbed (Figs 1 and 2). Moreover, in dry enclosures 12 of the 13 species with a cover >1% were vascular plants, and forbs represented half of the subordinate species covering more than 0.5% of the plot (Fig. 2c).

The effect of the grazing pressure was less pronounced in communities transplanted to the wet snowbed where there was strong variation in the cover of most abundant species (see length of SE bars in Fig. 2). This finding coincided with patterns of β -diversity, which was highest in the wet snowbed plots (Table 2). The cover of bryophytes was affected by the interactive effects of grazing and soil wetness (Table 3): bryophytes abounded in wet conditions, remained abundant under grazing in dry conditions, and were very scarce in the dry ex-

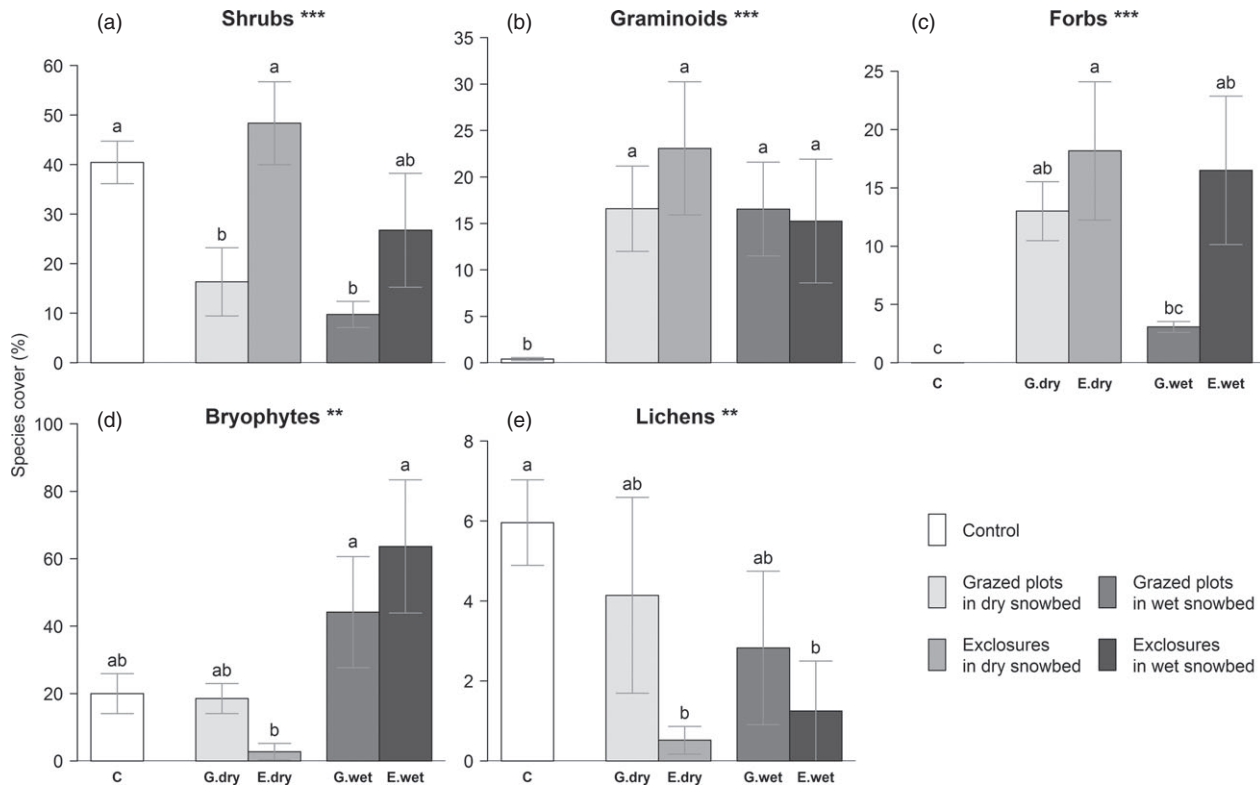


Fig. 3. Mean \pm 1 SE of plant functional type (PFT) cover in each treatment. Asterisks following PFT names indicate significant differences of cover among treatments tested by Generalized Linear Models (GLM) on square-root transformed data with Gaussian error distribution and an identity link function ($***P < 0.001$; $**P < 0.01$). Different letters indicate significantly different groups based on *post hoc* tests ($P < 0.05$).

closures (Fig. 3d). On individual species level, the ground layer of the original heath community was dominated by *Dicranum* spp. and *Barbilophozia* spp. which became largely replaced by hydrophilic mosses in the wet conditions, while *Barbilophozia* spp. persisted in the grazed dry plots (Figs 1 and 2). Specifically, *Sphagnum angustifolium* in the grazed wet plots reached 17% cover on average and *Polytrichum commune* in the wet exclosures reached 26% cover. Finally, while the cover of forbs was also negatively affected by the combined effects of grazing and high soil wetness (Fig. 3c), the cover and occurrence of lichens were only affected by the grazing pressure regardless of soil wetness (Table 3), with a strong negative effect of fencing (Fig. 2).

Discussion

The results of our long-term perturbation experiment show evidence for markedly distinct vegetation states developed in response to interactions of different treatments. This finding supports our hypotheses that the development of vegetation states is driven by joint effects of environmental filtering, local biotic and abiotic conditions. These joint effects of multiple drivers contrast with simple traditional ideas that abiotic constraints and environmental filtering alone would explain the majority of vegetation patterns and states in tundra, and they also do not suggest that mere top-down control by grazers would drive vegetation states regardless of abiotic

conditions. Our results rather support propositions stating that combinations of abiotic factors and biotic processes are crucial in the development of tundra vegetation states (see van der Wal 2006; Houseman *et al.* 2008). Below, we discuss the effects of the translocation to the snowbed as a general environmental perturbation and how it interacts with local grazing pressure and soil wetness to develop distinct assemblages. Furthermore, we discuss how their joint effects influence community trajectories and mechanisms underlying the development of alternative states in tundra vegetation.

CHANGES IN TRANSPLANT COMMUNITIES AND UNDERLYING PROCESSES

Seven years after the translocation, Virtanen (1998) noted a consistent decrease of the initially dominant shrub species (*V. myrtillus*) when transplanted to the snowbed, which was interpreted to reflect the importance of environmental conditions as the driving force in the tundra, according to the traditional view (Billings & Mooney 1968; Grime 2001). Other shrubs and herbaceous plants showed variable and often non-significant changes in response to the treatments which emphasized relatively high resistance of tundra heath communities to the 7-year treatment. Now after 23 years, a time span that largely exceeds the life time of most genets and/or ramets (Rixen *et al.* 2004; Nestby *et al.* 2011), this initial resistance was not evident any more, and strong and often contrasting

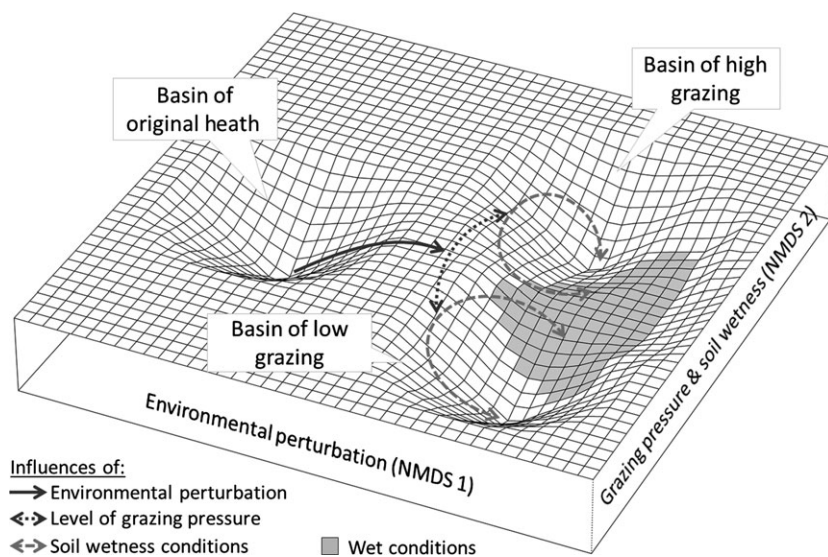


Fig. 4. Conceptual diagram based on the Non-Metric Dimensional Scaling ordinations on species and plant functional type (PFT) matrixes (Fig. 1) and convert in the way of the traditional topographic analogy of alternative stable states. We suggest that (i) environmental perturbation triggers the community to shift away from its original alternative stable state (solid dark grey arrow), then (ii) the level of grazing pressure determines the alternative basin of attraction (dotted dark grey arrows) and (iii) the soil wetness level locates the community within the basin (dotted light grey arrows).

species-specific responses of transplant communities to the treatments occurred. Some shrub species from the original heath virtually disappeared in the snowbed habitat, while the abundance of the some other species was mainly determined by the level of grazing and was also negatively affected by soil wetness. These findings demonstrate the transient status of the first results (Virtanen 1998) and that short and long-term outcomes of ecological processes can markedly differ (Tilman 1989; Schröder, Persson & De Roos 2005). Moreover, this strong role of grazing and the fact that its effects were more pronounced in dry snowbed conditions suggest that mere environmental filtering mechanisms (Keddy 1992), regarded as predominant in arctic and alpine systems (Grime 2001; Körner 2003) are not sufficient to exclude shrubs from snowbeds or to limit tundra shrubification. In contrast, our findings highlight the importance of grazing as an efficient biotic filter restricting the spread of dwarf shrubs to mountain tundra snowbeds (see also Olofsson *et al.* 2009), and that the outcome also depends upon soil wetness conditions and species concerned. Thus, environmental constraints, grazing and soil wetness may jointly filter shrub species from tundra snowbeds.

The second long-term consequence of the transplantation of communities to the snowbed was the strong contribution of graminoids and forbs in the new assemblages. Because graminoids and forbs are well established in the recipient site surrounding the transplant communities while they are nearly absent in the original *V. myrtillus* heath, such a result was expected. However, we found also that they established relatively equally in transplanted plots exposed to different treatments, even in exclosures with high shrub cover. This finding suggests that they are not strongly suppressed by shrub competitors in harsh snowbed conditions, which is consistent with ideas that the importance of competition could be low under severe environmental conditions (Brooker *et al.* 2005; see also Virtanen 1998). The graminoid PFT includes generalist species exhibiting life strategies which combine good competitive abilities with a tolerance to grazing pressure and wet soil

conditions (e.g., *D. flexuosa*, CSR, Grime 1988 or grazing tolerant-exploitative-competitive species, Oksanen 1990). In contrast, forbs present in the snowbed area may be less tolerant to soil waterlogging and may also become negatively impacted by thickening of the moss carpet (Gornall *et al.* 2011). It is also evident that the responses of forbs to grazing reflect marked species-specific differences. Relatively tall herbs such as *Solidago virgaurea* had fairly high cover in exclosures, whereas prostrate herbs such as *Epilobium anagallidifolium* were more characteristic in grazed plots. This is compatible with previous studies showing that tall forbs are sensitive to grazing whereas prostrate herbs are favoured by grazing because they can avoid it (Lavorel *et al.* 1997; Karlejärvi, Eskelinen & Olofsson 2013).

The finding that bryophytes were hampered by the reduction of grazing under dry conditions, where shrubs strongly dominated, while they benefitted from the reduction of grazing in wet conditions, is generally consistent with other studies showing a generally negative relationship between tundra shrubs and bryophytes (Pajunen, Oksanen & Virtanen 2011; Pajunen, Virtanen & Roininen 2012). But this also suggests that bryophyte abundance in tundra snowbeds is not merely determined by direct negative grazing impacts (Moen, Lundberg & Oksanen 1993; Virtanen, Henttonen & Laine 1997). Indeed, competition with vascular plants and soil wetness act in concert, and grazer-mediated impact on competition with vascular plants may be an important force dictating bryophyte responses.

Reversely to forbs and graminoids, lichens decreased in response to the transplantation to the snowbed which is in accordance with their well-known sensitivity to prolonged duration of snow and soil waterlogging (Benedict 1990; Bruun *et al.* 2006). Moreover, the additional decrease of lichens inside exclosures, where especially shrubs and forbs were abundant, agrees with previous studies suggesting that the development of dense vascular plant cover may suppress lichens (Cornelissen *et al.* 2001). However, in the high arctic tundra, an opposite result, that is increase of lichens and

decrease of deciduous shrubs, was observed in long-term exclosures in dry tundra sites (Johnson *et al.* 2011), which may indicate that the interactions between lichens and vascular plants are highly dependent on site conditions.

The positive effect of grazing on species richness (α -diversity) in our study matches with other evidences from mountain tundra habitats (Austrheim & Eriksson 2001; Speed, Austrheim & Myrnerud 2013). It is noteworthy, however, that other studies have shown contrasting results that vary from negative impact of grazing on diversity in nutrient-poor habitats (Proulx & Mazumder 1998) to positive impact in nutrient-rich conditions (Eskelinen, Harrison & Tuomi 2012) and sometimes the effect is negligible (Mayer *et al.* 2009; Johnson *et al.* 2011). Here, in accordance with the results reported by Olofsson (2006), the increase in species richness is associated with simultaneous decreases of shrub cover and β -diversity. Interestingly, such homogenization tendency was associated with high species richness, while the grazing homogenization hypothesis advocates that grazing promotes the dominance of some browsing-tolerant species (low species richness) which, in turn, reduces β -diversity (Rooney 2009). The shift in the shapes of the SAD curves from exclosures to grazed plots, that is, from short-tailed steep curves to long-tailed flat curves, resembles those encountered, for example, in very long-term nutrient addition treatments (May & McLean 2007). However, this latter example of niche differentiation dynamic (Silvertown 2004) was due to the increase of interspecific competition in resource-rich conditions while our results reflect the outcomes of processes where grazing limits any species from gaining dominance and subsequent niche release which may indicate that grazing functions as a stabilising force in the community (Adler, HilleRisLambers & Levine 2007).

Community heterogeneity (β -diversity) tended to be higher in wet snowbed conditions than in dry conditions which could reflect an engineering effect of the bryophyte mat in wet conditions able to harbour a large pool of subordinate species that are susceptible to vary in cover and identity between the plots, thus promoting heterogeneity. Thick bryophyte mats in cold and slightly disturbed tundra environments reduce soil temperatures and retain wetness, and this way slow down nutrient cycling and further promote development of mossy tundra (van der Wal, van Lieshout & Loonen 2001; Michel *et al.* 2012). As a result, the developing moss may modify the environmental conditions for subordinate species (Gornall *et al.* 2011) and in particular vascular plants. Indeed, we also found that high soil wetness had a negative effect on shrub abundance especially inside exclosures, which could act, together with moss engineering effects, as niche differentiation processes for subordinate species and result in greater community heterogeneity.

LONG-TERM DIVERGENCE AS AN EVIDENCE FOR ALTERNATIVE STATES?

Despite the lack of a clear or generally accepted definition (Fukami & Nakajima 2011), ASS represent a major conceptual

framework when addressing the relative importance of drivers of plant community composition (Beisner, Haydon & Cuddington 2003). In his application of the ASS concept to boreal and tundra ecosystems, van der Wal (2006) suggested that, along a gradient of increasing grazing pressure, trampling and selective feeding by reindeer induce a transition from lichen- to moss-dominated communities and that a transition from moss to graminoid tundra occurs due to greater tolerance of graminoids to repeated defoliation, enhancement of soil nutrients and increase in soil temperature. Specifically for tundra heath communities, he suggested that similar vegetation states resulting from increasing grazing pressure can be identified on the basis of replacement of lichens by mosses beneath shrubs, and by replacement of shrubs by grasses (see Olofsson *et al.* 2001; Olofsson, Stark & Oksanen 2004 for examples). In a recent study, Olofsson, Moen & Östlund (2010) found no clear support of the model proposed by van der Wal (2006) in boreal forest floors, but they revealed that the local occurrence of the community in a certain vegetation state may hinge on abiotic conditions such as hydrological status or topography. Our results support the idea that it may be overly simplistic to understand alternative states without such connections among the multiple drivers of plant communities.

Because our experiment tested the joint effects of three main driving forces of the tundra system over a long-term duration, we propose that placing our results in the theoretical framework of ASS may reveal new insights about alternative states of mountain tundra. van der Wal (2006) described alternative states of tundra ecosystems mainly by the dominant plant functional group. Here, our results suggest that the level of species richness and the relative abundance of plant functional types of a community could also reflect distinct attractors (stable points) for mountain tundra vegetation. Indeed, the strongest divergence appears in dry conditions between the species-rich grazed communities with high evenness of functional types and species-poor very lightly grazed (exclosures) communities with strongly unbalanced representation of PFTs. Grazing therefore appears to favour functional type evenness and species diversity. Since niche differentiation processes and forces favouring plant diversity and species coexistence are considered as stabilising forces (Chesson 2000), grazing might enhance the resilience of an alternative state. On the other hand, the unbalanced representation of PFTs within the very lightly grazed communities could also favour community stability because functionally poor communities could have a limited potential to switch from a basin of attraction to another (Didham, Watts & Norton 2005; Ives & Carpenter 2007). Thus reduced grazing and resulting dominance of competitive species might also form an alternative state. As a result, we suggest that the contrasting communities developed in grazed and ungrazed dry snowbed could represent attractor points of our studied system.

Since wet bryophyte-dominated communities show a high variability in species composition, they are still very likely to be far from any new equilibrium. Additionally, they are less divergent than the dry communities and harbour a large reservoir of species from different functional types which might

facilitate community switches among multiple states. For these reasons, we suggest that wet communities represent transient alternative states (*sensu* Fukami & Nakajima 2011) of one or the other grazing alternative basin. If bryophyte dominance can characterize some tundra alternative states (van der Wal 2006), this suggests that, in our system, soil wetness conditions may reduce the resilience of communities subject to contrasting level of grazing by maintaining high compositional heterogeneity.

We summarize these interpretations in a conceptual model (Fig. 4) where we suggest that the trajectories towards alternative states are oriented at different levels by the combinations of environmental perturbation, grazing pressure and soil wetness conditions. We propose that environmental perturbation triggers the community to shift away from the heath state equilibrium. Similarly to Hidding, Tremblay & Côté (2013) who found that the presence of herbivores, even during a limited period, can lead to alternative successional trajectories in the boreal forest, here grazing pressure level then drives the main trajectory toward high and low grazing alternative basins of attraction. Finally, local soil wetness conditions maintain alternative transient states of both low and high grazing basins of attraction. Considering multiple drivers of plant community states, the model highlights that the role of each single factor is not necessarily separable from the other factors and that their relative importance for community trajectories is subject to variation. For instance, it is possible that wet tundra snowbed could represent a basin of attraction *per se* (the hollowed 'wet' grey cells in the conceptual diagram, Fig. 4), but our transplant communities in wet conditions, even after 23 years of perturbation treatment, lie still in transient states with easy switching between alternative states.

Since clear and indisputable evidence of ASS may not really exist as stability is likely impossible to define (Ives & Carpenter 2007), we do not suggest that our findings represent the only possible outcome. Rather, we argue that these patterns identified after more than 20 years of experimental manipulations could help to better understand the role of the multiple drivers of the mountain tundra vegetation and the responses of these communities to environmental changes. Our results highlight that local biotic and abiotic factors could buffer or accelerate tundra responses to environmental change and the resulting shifts in vegetation, for example, current shrubification, and maintain alternative states.

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Data accessibility

Data available from the Dryad Digital Repository (Saccone *et al.* 2014).

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Supporting Information

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

Appendix S1. Mean \pm 1 SE of soil water content (% dry soil mass) in the three conditions of the experimental design: The original heath and the wet and dry areas of the snowbed.

Appendix S2. List of species observed in the experimental design with their abbreviated species names reported in the Figs 1a and 2, their attributed Plant Functional Type.

Appendix S3. Results of the two-way Generalized Linear Models (GLM) with environmental perturbation, soil wetness, grazing pressure and soil wetness \times grazing pressure interaction as explanatory variables, and the species richness, Shannon index and the cover of *Vaccinium myrtillus* and *Salix herbacea* (dominant shrubs of the system) as response variables.