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Current vegetation changes in an alpine late snowbed community in the south-eastern Alps (N-Italy)

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Abstract During the last decades, a significant warming was observed in the Alps, cascading into a decrease in snowfall and snow-cover duration. Within the alpine landscape, snowbed communities are regarded as especially vulnerable to the predicted warmer temperatures and earlier snowmelt time. Albeit snowbeds represent a prominent component of the tundra biome, the current vegetation dynamics of these habitats are not yet well understood. In this study, the changes of vascular species richness, co-occurrence, composition, and abundance were evaluated within a late snowbed in the south-eastern Alps. The study was based on a re-survey of 11 permanent plots after a 6-year period. Species richness and abundance significantly increased and species co-occurrence shifted toward higher species segregation. Moreover, the changes in species richness at different spatial scales were related to different environmental factors, and a change in the proportion between snowbed and non-snowbed plants was found. The results suggest an increasing importance of competitive interaction among species in determining the future structure and composition of this community. In conclusion, there is strong evidence that this snowbed community is not in equilibrium with the current climate, and that changes in floristic composition and functional processes of this habitat are underway.

Keywords Alpine tundra · Landscape biodiversity · Climate change · Invasion · Species richness · Vegetation dynamics

Introduction

Climate change will have multiple effects on species physiology, phenology, distribution, and interactions, ultimately leading to changes in the structure and composition of communities (e.g. Hughes 2000). The effects of climate change on vegetation may be especially pronounced in cold biomes (high latitude and altitude areas). Within these regions, climate is the main driver of biodiversity changes (Sala et al. 2000), and strong vegetation shifts are predicted due to elevated rates of both observed and projected warming (Gonzalez et al. 2010).

In the Northern Hemisphere, the last three decades were the warmest 30-year period of the last 1400 years, and, over the last two decades, the extent of the spring snow cover has continued to decrease (IPCC 2013). Moreover, the recent Representative Concentration Pathways scenarios for the end of the twenty-first century consistently forecast a further increase of global mean surface temperature and a further decrease of spring snow-cover area in the Northern Hemisphere (IPCC 2013).

In Europe, species distribution models for the twenty-first century predict marked levels of threat to cold-adapted high-mountain plants (Thuiller et al. 2005; Engler et al. 2011; Dullinger et al. 2012), due to a reduction or shift of species habitats. Considering that different habitats may be variously influenced by global warming (Grabherr et al. 1995),

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and that in alpine communities the vegetation dynamics induced by climate change are most obvious as an invasion process (Grabherr 2003), it is possible that species colonization will be faster within extreme habitats characterized by low plant production and high availability of space (Vittoz et al. 2009), such as snowbeds or high-mountain summits. However, while several studies have investigated the presence and nature of recent vegetation changes on mountain tops in the last years (e.g. Erschbamer et al. 2011; Michelsen et al. 2011; Fernández Calzado et al. 2012; Gottfried et al. 2012; Pauli et al. 2012; Venn et al. 2012; Gigauri et al. 2013), less is known about the current dynamic processes within alpine snowbed communities, representing a pronounced component of the tundra biome (Björk and Molau 2007).

Moss-dominated alpine snowbeds, which develop in sites with a long-lasting snow cover, are characterized by a scattered cover of a scanty number of low-competitive (Heegaard and Vandvik 2004) vascular species, which are limited by the length of the snow-free period (Carbognani et al. 2012) and by soil resources (Petraglia et al. 2013, 2014). Given these properties, late snowbed habitats may be regarded as particularly prone to vegetation dynamics, in particular in the face of climate change. Indeed, ecological theories predict that, in a changing climate, the rate of variation in vegetation structure and composition will be higher for communities characterized by a restricted number of species (Elton 1958), which follow the stress-tolerance strategy (Grime 2001), and are limited by soil resources (Tilman 1988). Moreover, the immigration rate of plants is expected higher in disturbed relative to undisturbed sites (Lenoir et al. 2010). From the physiological viewpoint, the length of the snow-cover period imposes a severe environmental stress to the plants, limiting the time available for biomass production. Nevertheless, the variation among years of the snow-cover period length may act as a disturbance factor. Indeed, despite snowbed species cannot be categorized as true “ruderals” (Molau 1993), the long-lasting snow cover can cause partial or total destruction of live and dead biomass, because the conditions under the snowpack may lead to high levels of plant respiratory depletion of carbohydrate reserves (Salisbury 1985; Auerbach and Halfpenny 1991) and plant litter decomposition (Baptist et al. 2010; Carbognani et al. 2014). These mechanisms, in our opinion, can be included in the definition of disturbance provided by Grime (2001). In addition, snowbeds also function as plant diaspore traps (Larsson and Molau 2001), and this feature may promote the invasion of species from adjacent communities.

Long-term studies (ranging from 25 to 70 years), showed that snowbeds are subjected to change in structure and composition both at high latitude and high altitude sites (Braun-Blanquet 1975; Virtanen et al. 2003; Daniëls et al. 2011; Kudo et al. 2011; Elumeeva et al. 2013; Sandvik and Odland 2014); these vegetation changes, related to variation in temperatures, snow cover, and soil moisture, are generally interpreted as consequences of climate change. However, the current dynamics of these habitats at a mid-term time scale (about 5 years) are hitherto far from being exhaustively known, despite its knowledge is essential for planning effective proactive conservation measures. To our knowledge, the only study reporting mid-term data on vegetation changes within snowbeds is that published by Sandvik et al. (2004), who found, after 5 years, a weak but significant increase in species richness and a stronger change in species abundance. Nevertheless, the study was carried out in south-western Norway, whereas similar data for mid-latitude snowbeds are until now completely lacking.

The aim of this study is to fill this gap by analyzing the occurrence and magnitude of the changes in vegetation properties within a late snowbed community dominated by the arctic-alpine moss *Polytrichastrum sexangulare* (Brid.) G.L. Smith. For this purpose, we analyzed the natural variation of vascular species richness, co-occurrence, composition, and abundance over a 6-year period in 11 permanent plots located in the high Gavia Valley (Rhaetian Alps, Italy). In particular, the following questions were tested:

1. Have there been detectable changes in the species-to-area relationship?
2. Is the variation of the species richness at different spatial scales influenced by the same environmental factors?
3. Has there been a shift from facilitation to competition among species?
4. Has the proportion between snowbed and non-snowbed species changed?
5. Does the direction and magnitude of plant abundance variation differ between species?

Materials and methods

Study area and sampling design

This study was carried out in the high Gavia Valley, a natural conservation area of about 10 km^2 located inside the Stelvio National Park on the Italian Rhaetian Alps (46°20–21′N 10°29–30′E, 2,445–3,360 m a.s.l.). Climatic features for the period 1950–2000 derived from WorldClim datasets (Hijmans et al. 2005) indicate for the Gavia Pass (2,651 m a.s.l.) a mean annual rainfall of 1,150 mm and a mean annual temperature of −1.4 °C, with an average maximum of 9.3 °C in the warmest month and an average minimum of −10.4 °C in the coldest one.

Eleven spatially separated snowbed stands dominated by the moss *Polytrichastrum sexangulare* were studied. They are part of a vegetation mosaic including *Carex curvula* grasslands, pioneer communities on rock faces and screes, mire and stream communities, and windswept espalier heaths. The baseline dataset was established in 2005, and in 2011 a re-survey of the original permanent plots was carried out.

Considering that the number of species at several spatial scales is essential to evaluate how diversity is structured spatially, that the species richness at different scales can be differently influenced by environmental variables (e.g. Waide et al. 1999), and that the proportion of species groups at different spatial scales may be informative on the structure and composition of vegetation, data from different spatial scales were collected. In particular, for each stand, the number of vascular species was counted in one plot, composed of 12 nested sub-plots with areas ranging from 15 × 15 cm to 1 × 1 m, with the same spatial arrangement described by Carbognani et al. (2012). Moreover, in each 1 × 1 m plot (hereafter called large spatial scale), species occurrence, as presence or absence, and abundance, as number of individuals and modules (i.e. reiterated pluricellular plant sub-units as ramets, rosettes, or shoots), were recorded in a 90 × 90 cm sub-plot, composed by 36 squared sub-units of 15 × 15 cm (hereafter called small spatial scale).

For each plot, the following environmental features were also recorded: elevation (in m a.s.l.), snowmelt time (in week of the year), stand area (in m^2), distance to the closest adjacent community (in m), area occupied by adjacent communities (within a radius of 50 m), and potential grazing (as distance in m from the closest summer stall). In addition, the aboveground net primary production (ANPP) was estimated as the product between individual or module density and production. Individual or module production of vascular plants were derived from published and unpublished data based on vegetation harvesting in the same snowbed stands in 2005 and 2006. We are aware that with this method of production estimate, we implicitly assume no change in time of plant population structure and individual or module production. Despite these assumptions may represent a potential bias, we consider such ANPP estimation as an acceptable proxy for species occupation of space.

The nomenclature of vascular plants and their classification as snowbed or non-snowbed species (based on the phytosociological optimum) are those of Aeschimann et al. (2004) (Table S1, Online Resource 1). We added to the list of snowbed species defined by Aeschimann et al. (2004) also *Veronica alpina*, because according to our experience in the study area, this *taxon* occurs mostly within snowbed communities (see also Pignatti and Pignatti 1958).

Data analyses

To analyze the species-to-area relationship generalized linear mixed-effect models (GLMMs), with a Poisson error structure and the logarithmic link function, were fitted to nested-plot data (setting in turn the smallest and the largest nested-plot areas as intercept term), with year of survey, nested-plot area (log-transformed), and their interaction as fixed effects and plot as random effect.

The influence of environmental factors on the variation of species richness after 6 years was separately tested at small and large spatial scales. Generalized additive mixed models (GAMs) and generalized linear models (GLMs) were, respectively, used for small and large scales. In GAM regression, which is a non-linear and non-parametric regression technique that does not require a priori functional specification of the relations between response and explanatory variables (Hastie and Tibshirani 1990), a random effect was included to account for the spatial hierarchical structure of plot sub-units. Firstly, maximal models (with a Poisson error structure and the logarithmic link function) were run, fitting the following explanatory variables: elevation, average snowmelt time during the study period, stand area, distance of the closer adjacent community, area occupied by adjacent communities, potential grazing, variation of ANPP between the two surveys, and initial species richness at the respective spatial scale (i.e. the species richness of the 2005 survey). In addition, for the small-scale difference in species richness, the variation of the number of species at the large scale between the two surveys was also included in the model as explanatory variable. Secondly, minimal adequate models were obtained with model simplification procedures, by progressive deletion from the maximal models of the least significant explanatory variables.

Species co-occurrence data in the 36 sub-units of the 90 × 90 cm sub-plots were also used to analyze the presence of competition (segregation) or facilitation (aggregation) among plant species in the two surveys. To this end, the C-score statistics (Stone and Roberts 1990), which quantifies the “checkerboardedness” in a species-by-sites presence–absence matrix (where sites are the sub-units, and a checkerboard unit is an elementary combination of two species and two sites such that the occurrence of the species are mutually exclusive), were used. Deviations from randomness of observed C-scores were evaluated by the comparison with simulated C-scores, resulting from 10,000 random co-occurrence models. To make the results of different plots and years comparable, the differences between observed C-scores and mean simulated C-scores were divided by the standard deviation of simulated C-scores. After this scaling, departures from 0 indicate deviations from randomness, with positive values indicating less co-occurrence (segregation due to competition) and negative values indicating more co-occurrence (aggregation due to facilitation). Finally, standardized C-scores of the two surveys were compared by means of the non-parametric Wilcoxon test.

The mean number of species in the 15 × 15 cm sub-units and the species number in the 1 × 1 m plots were used to test the differences in space (small and large spatial scale) and time (2005 and 2011 survey) of the proportion between snowbed and non-snowbed species. To assess the significance of the prevalence of species groups (snowbed and non-snowbed) and to take into account the different potential changes of the two spatial scales, for each spatial scale and survey, the proportion between snowbed and non-snowbed species was expressed as the log-transformed ratio of the respective number of species as follow:

$$\begin{aligned}&\text{Standardized proportion}\\&\quad=\log(\text{number of snowbed species}/\text{number of non}\\&\qquad\text{-snowbed species})\end{aligned}$$

Thus, a null standardized proportion indicates an equal number of snowbed and non-snowbed species, whereas significant departures from 0 denote the prevalence of snowbed species (positive values) or the prevalence of non-snowbed ones (negative values). These data were analyzed using linear mixed-effect models (LMMs), with standardized proportion between snowbed and non-snowbed species as response variable, spatial scale (small and large) and year (2005 and 2011) as fixed effects, and plot as random effect (the interaction term was dropped from the models because not significant). To test whether standardized proportions were significantly different from 0, models were re-run with each combination of spatial scales and years as baseline level.

Species abundance variation between the two surveys at small scale of the 16 most frequent species (which accounted for about 95 % of the total vascular production) was assessed with one-sample *t* test, considering the module density of the plot sub-units where species were present in 2005 and/or in 2011. In addition, for plants showing significant changes in abundance and with high frequency in plots (>90 %), the magnitude of variation among species was compared with a Wilcoxon test on the ratio between module density in 2011 and 2005, based on plot sub-units where species were present in both surveys.

The analyses were performed using the R statistical suite version 3.0.2 (R Core Team 2013) with the nlme (LMMs), lme4 (GLMMs), mgcv (GAMs), and vegan (C-score) libraries.

Results

Species-to-area relationship

After 6 years, the number of species showed a significant increase both at small (15 × 15 cm, $Z = 2.08$, $P = 0.038$) and large (1 × 1 m, $Z = 3.37$, $P = 0.001$) spatial scale, indicating a general increase in time of the species richness (Fig. 1). However, the spatial increase rate of species (i.e. the regression slope) did not significantly differ between the two surveys ($Z = -0.14$, $P = 0.886$), denoting similar changes of the species richness at different spatial scales.

Factors controlling species richness variation at different spatial scales

At small scale, the increase in species number was found negatively affected by the small-scale initial richness, positively influenced by both large-scale initial richness and large-scale variation of richness between the two surveys (Table 1), and maximum at intermediate increase of ANPP between the two surveys (Fig. 2). In contrast, at large scale, the increase in species number was found negatively influenced by the elevation ($Z = -2.72$, $P = 0.007$), while the other environmental features analyzed did not show significant relationships with the variation of species richness.

Species co-occurrence

The majority of the studied plots showed co-occurrence patterns of species not significantly different from randomness (10 and 9 plots in 2005 and 2011, respectively).

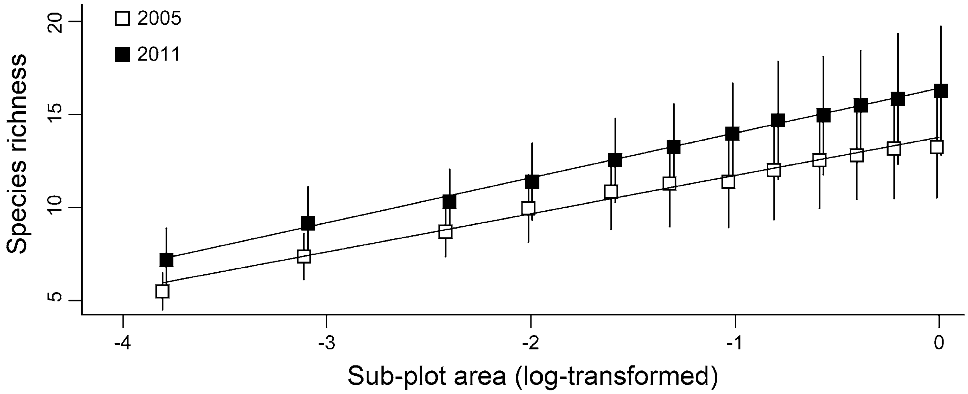

Fig. 1 Relationships between vascular species richness and log-transformed sub-plot area (in m^2) in 2005 (white symbols) and 2011 (*black symbols*). Values are mean ± SD

Table 1 Controlling factors of species richness variation between the two surveys (2005 and 2011) at small spatial scale (15 × 15 cm) resulting from generalized additive model with Poisson error structure

	Coeff ± SE	t	F	*P*
Parametric terms				
Small-scale initial richness	−0.597 ± 0.011	−14.198	201.59	<0.001
Large-scale initial richness	0.209 ± 0.017	3.052	9.31	0.002
Large-scale richness variation	0.265 ± 0.023	2.792	7.80	0.005
Smooth term				
ANPP variation	–	–	14.45	<0.001

Estimated effect (Coeff ± SE, in change of species number per unit changes of richness of explanatory variables), *t* value (t), F-statistic (F), and *P* value (*P*) of parametric and smooth terms are shown. The change of species richness between the 2005 and 2011 surveys is modeled (A) as function of the following parametric terms: (1) species number within the 15 × 15 cm sub-units in 2005 (Small-scale initial richness) (2) species number within the 1 × 1 m plots in 2005 (Large-scale initial richness), and (3) variation between the two surveys of the species number within the 1 × 1 m plots (Large-scale richness variation), and (B) as a smoothing function of the variation between the two surveys of aboveground net primary production in the 15 × 15 cm sub-units (ANPP variation)

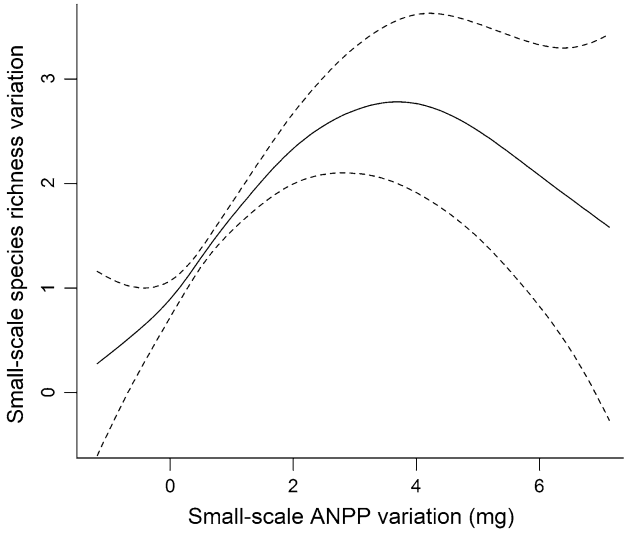

Fig. 2 Relationships between species richness variation after 6 years (2005–2011) at small spatial scale (15 × 15 cm) and the variation in the same period and at the same scale of aboveground net primary production (ANPP). Estimated smoothing curve (*solid line*), obtained considering the mean effects of the other explanatory variables (Parametric terms, Table 1), and 95 % confidence bands are shown

However, among those plots where non-random co-occurrence was detected, a significant species aggregation was found only in the 2005 survey, whereas significant species segregation was found only in the 2011 survey. Moreover, comparing the standardized C-scores of the two surveys (Fig. 3), a significant trend toward higher species segregation in time was found ($V = 4.0$, $P = 0.007$).

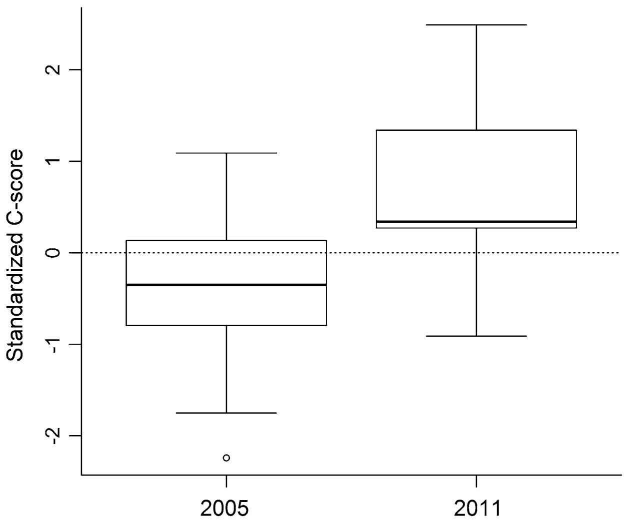

Fig. 3 Box plots of standardized C-scores (Stone and Roberts 1990) in the first (2005) and the second (2011) survey, with positive values indicating less species co-occurrence (segregation due to competition) and negative values indicating more co-occurrence (aggregation due to facilitation)

Proportion between snowbed and non-snowbed species

The standardized proportion between the number of snowbed and non-snowbed species showed significant differences both between small and large spatial scale ($t = -10.11$, $P < 0.001$) and between 2005 and 2011 ($t = -3.15$, $P = 0.004$), with a general decrease of snowbed species incidence proceeding in space and time (i.e. lower values of standardized proportion at larger scale and in the second survey, Fig. 4). Furthermore, while at small-scale snowbed species outnumbered non-snowbed ones in both the surveys (i.e. significant departures from 0 of standardized proportion, $t = 8.01$, $P < 0.001$ and $t = 5.69$, $P < 0.001$ in 2005 and 2011, respectively), at large scale no group was prevailing in any survey ($t = 0.57$, $P = 0.574$ and $t = -1.75$, $P = 0.090$ in 2005 and 2011, respectively).

Species abundances

A significant increase in module or individual density after 6 years was found for the majority of the species studied (Table 2), while no species showed a significant abundance decrease.

Among the most frequent species, the comparison of the ratios of module density between the two surveys showed the highest increase for the dwarf shrub *Salix herbacea* (Fig. 5).

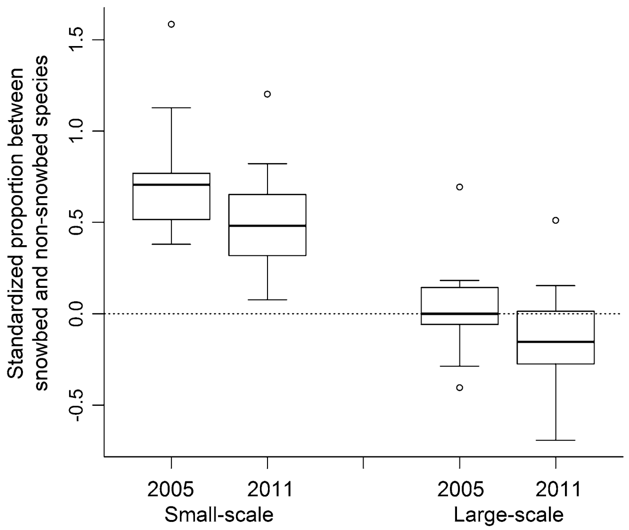

Fig. 4 Box plots of standardized proportion between the number of snowbed and non-snowbed species at small (15 × 15 cm) and large (1 × 1 m) spatial scale and in the first (2005) and the second (2011) survey, with positive values indicating the prevalence of snowbed species and negative values that of non-snowbed ones

Table 2 Species abundance changes between the 2005 and 2011 surveys, expressed as differences of module or individual density at small spatial scale (15 × 15 cm) for the 16 most frequent species

Species	Abundance change	*P* value	Species group
Agrostis rupestris	0.89 ± 0.17	<0.001	Non-snowbed
Alchemilla pentaphyllea	1.44 ± 1.09	0.233	Snowbed
Arenaria biflora	−0.02 ± 0.30	0.948	Snowbed
Cardamine alpina	−0.99 ± 1.00	0.345	Snowbed
Carex curvula	1.11 ± 0.25	0.004	Non-snowbed
Cerastium cerastoides	0.88 ± 0.26	0.009	Snowbed
Euphrasia minima	0.95 ± 0.33	0.018	Non-snowbed
Gnaphalium supinum	22.78 ± 4.95	<0.001	Snowbed
Leucanthemopsis alpina	3.07 ± 1.30	0.039	Non-snowbed
Poa alpina	2.75 ± 0.71	0.003	Non-snowbed
Primula glutinosa	0.42 ± 0.14	0.015	Non-snowbed
Salix herbacea	11.31 ± 1.77	<0.001	Snowbed
Sedum alpestre	−0.16 ± 0.30	0.610	Non-snowbed
Soldanella pusilla	2.70 ± 0.85	0.033	Snowbed
Taraxacum alpinum	0.04 ± 0.23	0.867	Non-snowbed
Veronica alpina	0.52 ± 0.77	0.516	Snowbed

Mean values (±SE) and levels of significance (from one-sample *t* test) are shown

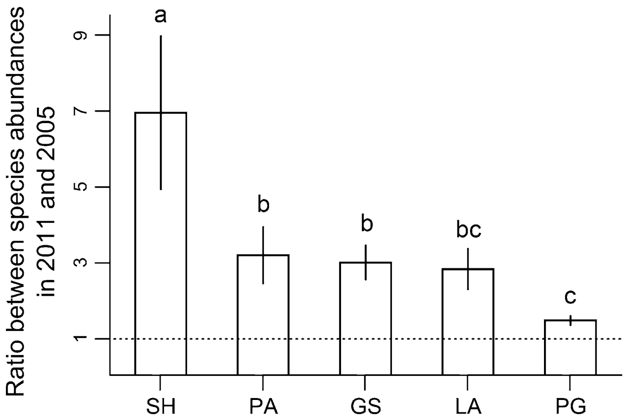

Fig. 5 Species abundance increase, expressed as ratio between module densities in 2011 and 2005. SH: *Salix herbacea*; PA: *Poa alpina*; GS: *Gnaphalium supinum*; LA: *Leucanthemopsis alpina*; PG: *Primula glutinosa*. Different letters refer to significant differences (from Wilcoxon test)

Discussion

To the best of our knowledge, this is the first study specifically devoted to mid-latitude moss-dominated late-snowbeds which analyzed the occurrence and magnitude of current mid-term changes in vegetation properties.

Considering the climatic features of the last 50 years recorded by the closest weather station at similar altitude (Fig. S1 and S2, Online Resource 2), characterized by a rather constant amount of annual precipitation coupled with a remarkable warming trend in the last three decades (and, consequently, a probable shorter snow-cover period due to a smaller snow/rain ratio and a faster snowmelt in spring), it seems convincing that the observed changes of this plant community are primarily due to the current climate changes.

Temporal and spatial changes in species richness

After 6 years, the vascular species richness increased (on average, about +25 % both at small and large scales), indicating that one of the most distinctive feature of this moss-dominated snowbed community, namely the low number of vascular plants, is changing. Interestingly, although the spatial increase rate of species showed significant differences both within and between alpine snowbeds in relation to the constant interannual differences in the snowmelt time (Carbognani 2011; Carbognani et al. 2012), the slopes of the species-to-area regressions did not differ between the 2005 and the 2011 survey (Fig. 1). This suggests that similar changes happened at small and large spatial scales, despite these variations of the number of species at different scales may be due to different processes. Indeed, the changes in species richness were due both to an expansion of already present species, more affecting the species number at small scale, and to an entry of new species, more probable with increasing spatial scale.

On average, the number of local species invasion was 4.0 ± 1.7 m^{-2}, about twice the value reported by Sandvik et al. (2004) for slightly larger snowbed plots in southwestern Norway; such a difference can derive, at least partially, from the higher species pools of mid-latitude alpine habitats, for which a higher species turnover in snowbeds is expected. However, this increase of species richness at the plot level may produce a general floristic homogenization of this habitat. Altogether, 25 plant species were found in the 11 plots in the first survey and 28 in the second survey (Table S1, Online Resource 1). This small change in the total number of species at the community level between the two surveys suggests that plots may become more similar to each other.

Scale-dependent controlling factor of species richness variation

Different environmental factors were found related to the change of the number of species at different spatial scales. Probably, at small scale, the change in species richness was influenced mainly by biotic factors, such as the species pool and the availability of space. Indeed, the increase of species richness was higher where: (1) at small scale the initial number of species was low and the ANPP variation was intermediate and (2) at large scale the initial number of species and the increase of species richness were high (Table 1; Fig. 2). Differently, at large scale, the change of species richness was found related to only one abiotic factor, namely elevation. Clearly, this significant influence may not mean a direct effect of the elevation *per se*, but instead might indicate the combined effects of several co-varying key environmental factors. Indeed, despite a limited variation of the environmental factors analyzed, lower elevation plots were basically located in snowbed stands characterized by (1) a smaller area, (2) a higher level of potential grazing, (3) an earlier snowmelt, and (4) a shorter distance from adjacent communities which take up a larger portion of the surrounding area (Table S2, Online Resource 1). Consequently, the higher increase of species richness found in lower elevation plots may ultimately be due to combined influences of higher temperatures, earlier snowmelt, and higher invasion capacity of adjacent habitats.

Increased interspecific competition

In 6 years, the spatial co-occurrence of vascular plants in this snowbed community showed a trend from species aggregation (Fig. 3, negative values) to species segregation (positive values), reflecting an increasing effect of interspecific competition in determining the spatial occurrence of plant species. This shift toward higher species segregation may be influenced by the increase of species richness, and, to a greater extent, due to the increase of species abundances. These thoughts suggest that a relaxation of environmental limiting factors, promoting an increase of the species number and primary production, can lead to a higher importance of negative biotic interactions in determining the future structure and composition of this plant community.

Changes in plant community composition

Notwithstanding the spatial and temporal increase of species richness was due to an increase both of snowbed and non-snowbed species (Table S3, Online Resource 1), differences in the proportion between these two group of species were found comparing both spatial scales and years (Fig. 4). These results reflect a decrease, both in space and time, of the importance of snowbed plants in forming the vegetation of this habitat, suggesting that changes in the floristic composition of this community are ongoing.

Increased species abundances

Among the 16 species under study, 10 showed a significant increase in abundance, and no species was found to decrease significantly (Table 2). The snowbed dwarf shrub *Salix herbacea* showed the strongest change in abundance (a sevenfold increase), but high abundance variations (threefold increases) were also found both for snowbed specialist (the forb *Gnaphalium supinum*) and alpine generalist (the graminoid *Poa alpina* and the forb *Leucanthemopsis alpina*) species (Fig. 5). These results indicate that, at least in the current phase, the dynamics of late snowbed vegetation are driven by an increase in abundance of both snowbed and non-snowbed species, probably due to a climate-induced release of environmental limiting factors. Moreover, within snowbed communities, changes in vegetation structure and composition can further influence plant species reproduction (Lluent et al. 2013) and nutrient cycles (Carbognani et al. 2014), with consequent feedbacks on the vegetation dynamics of these habitats.

Besides the strong increase of module density of *Salix herbacea* and *Gnaphalium supinum* found in our alpine site after 6 years, a general increase of the abundance of the above-mentioned snowbed species were reported over longer periods (2–3 decades) both for the Alps (Braun-Blanquet 1975) and for Northern Norway (Sandvik and Odland 2014). However, in different areas and at longer time scale, the same species declined significantly (Virtanen et al. 2003; Elumeeva et al. 2013). These contrasting results may depict dynamics in which species expansion or restriction is produced by the balance between the possible positive and negative effects of climate and vegetation changes. Probably, in the studied habitat, the current positive effects of a changing environment (e.g. warmer temperatures, longer growing season, more soil nutrient, facilitation among plants against herbivory or frost damage) overcome the negative effects (e.g. higher occurrence of frost events, summer drought, interspecific competition among plants for space and soil resources) for most of the species. Such observations highlight that, to predict the responses of snowbed species and communities in a changing environment, both positive and negative influences of changes in climatic parameters and biotic interactions must be taking into account.

Conclusion

In conclusion, this study showed a noticeable vegetation change over a 6-year period, that, in term of the growing season length, implies a quite limited time (<600 days in total). The changes in species richness, co-occurrence, composition, and abundance indicate that this late snowbed habitat is not in a stable equilibrium with the current climate. These variations in plant community properties within less than a decade suggest that rapid dynamics of snowbed vegetation, probably due to the ongoing climate change, is underway. In the future, the transformation of this plant community may cause both a strong alteration of functional processes within this habitat and a decrease of the alpine landscape biodiversity.

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