

Changes in snowbed vegetation as a response of climatic variability: a case study

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ABSTRACT

Monitoring a snowbed vegetation transect after nine years revealed small changes in species composition. The set of vegetation groups remained the same, but we observed some shifts in the boundaries between them. Snowbed specialists showed a trend to reduce their space occupancy and moved towards the area of thickest snowpack, whereas some grassland species settled on the spaces left. Such changes could be related to the noticeable irregularities in the thermal and rainfall regimes occurred during this period.

Key words: Pyrenees, monitoring, plant communities, climate change

Changements dans la végétation des combes à neige en réponse à la variabilité climatique : une étude de cas

RÉSUMÉ

Le suivi d'un transect de végétation de combe à neige après neuf ans révèle des légers changements en la composition des espèces. L'ensemble des groupes végétaux reste le même, mais nous avons observé certains changements dans leurs limites. Les espèces spécialistes des combes à neige montrent une tendance à réduire leur occupation de l'espace et à se localiser vers la zone centrale de la combe à neige, tandis que certaines espèces des pelouses s'installent dans les espaces libérés. De tels changements pourraient être liés à des irrégularités notables des températures et des précipitations pendant cette période.

Mots-clés : Pyrénées, suivi des communautés végétales, changement climatique

Cambios en la vegetación de los neveros como respuesta a la variabilidad climática: un caso de estudio

RESUMEN

El seguimiento de un transecto de vegetación de nevero revela pequeños cambios en la composición de las especies después de nueve años. El conjunto de los grupos de vegetación sigue siendo el mismo, pero observamos algunos cambios en sus límites. Los taxones especialistas de neveros mostraron una tendencia a reducir la ocupación del espacio situándose hacia la zona más interior del nevero donde la nieve permanece más tiempo, mientras que algunas especies pratenses avanzaron también más hacia el centro. Tales cambios podrían estar relacionados con las notables irregularidades térmicas y pluviométricas ocurridas durante este período.

Palabras clave: Pirineos, monitoreo de comunidades vegetales, cambio climático

I. Introduction

In alpine environments, the highly pronounced microrelief results into sharp floristic and ecological gradients (JOHNSON & BILLINGS 1962), which in snowbeds are mainly caused by the duration and thickness of snow cover (GALEN & STANTON

1995) and, to a lesser extent, by the distribution of melting water and by the soil organic matter content (STANTON *et al.* 1994). Snowbed specialists (or chionophilous species) benefit from thermal insulation by snow during winter and spring (LLUENT 2007), and from water and nutrient supply during

the growing season (BOWMAN 1992, LLUENT 2007). However, these favourable conditions for growth are constrained by a short growing season due to a long-lasting snowpack. Snowbed species are adapted to complete their life cycle in a short period of time and to receive a limited amount of energy during the growing season (LLUENT 2007, ILLA *et al.* 2011).

Snowbeds occupy fragmented and reduced areas in alpine ranges, and many of their characteristic species have their southern distribution limits in the Pyrenees. In the context of climate change, evidences show how glaciers are experiencing a clear retreat in mountain areas (HAEBERLI & BENISTON 1998), and all models suggest that during the current century winter snow will significantly diminish (BENISTON *et al.* 2003, LÓPEZ-MORENO *et al.* 2009). It is expected that climate change will affect the Pyrenees through important climatic irregularities (LÓPEZ-MORENO *et al.* 2009, ENGLER *et al.* 2011), which can change environmental conditions in snowbeds. In a context of reduced snowpack and an increased growing season, low-competitive chionophilous specialists may be excluded from snowbeds by surrounding grassland species, more abundant and competitive (HEEGAARD & VANDVIK 2004, BJÖRK & MOLAU 2007, SCHÖB *et al.* 2008). Thus, snowbed species and communities are very vulnerable and threatened in all alpine areas, and most evidently in the Pyrenees due to their geographic situation.

Nowadays, few studies are aimed to investigate if changes are occurring in snowbed vegetation, and at which speed they proceed. With the aim to survey vegetation changes and assess their magnitude in snowbeds, during the period 2003-2007 we established some permanent transects along the snowmelt

gradient in the National Park of Aigüestortes i Estany de Sant Maurici (LLUENT *et al.* 2006), in order to perform periodic surveys of snowbed vegetation.

The main objective of this work was to check whether the distribution of species and communities has changed in a snowbed transect first studied in 2003. We hypothesize that climatic irregularity affecting the Pyrenees these last years may have allowed some degree of colonisation of snowbed communities by grassland species, and pushed chionophilous species to the snowiest areas in the snowmelt gradient.

II. Methods

1. Study area and sampling design

The snowbed studied is situated on the northern slope of port de Ratera, at 2,540 m a.s.l. in the peripheral area of Aigüestortes i Estany de Sant Maurici National Park (Fig. 1), in the Catalan Pyrenees.

Climatic conditions in the nearest alpine meteorological station (la Bonaigua, 2266 m a.s.l.) are characterized by relatively low temperatures (mean annual temperature 3.1 °C) and high precipitation (mean annual rainfall of 1146 mm; Fig. 2 left). Data obtained from the last ten years (2003 and period 2008-2012) show rainfall irregularities mainly during summer, which has on average decreased (Fig. 2 right; Table 1). The critical period for snowbed vegetation regarding rainfall is mid- to late-summer, concretely July and especially August, when snow has already melted and snowbed plants do not benefit from snowmelt water.

The transect studied follows the snowmelt gradient: it begins in the grassland outside the snowbed (which experiences usual

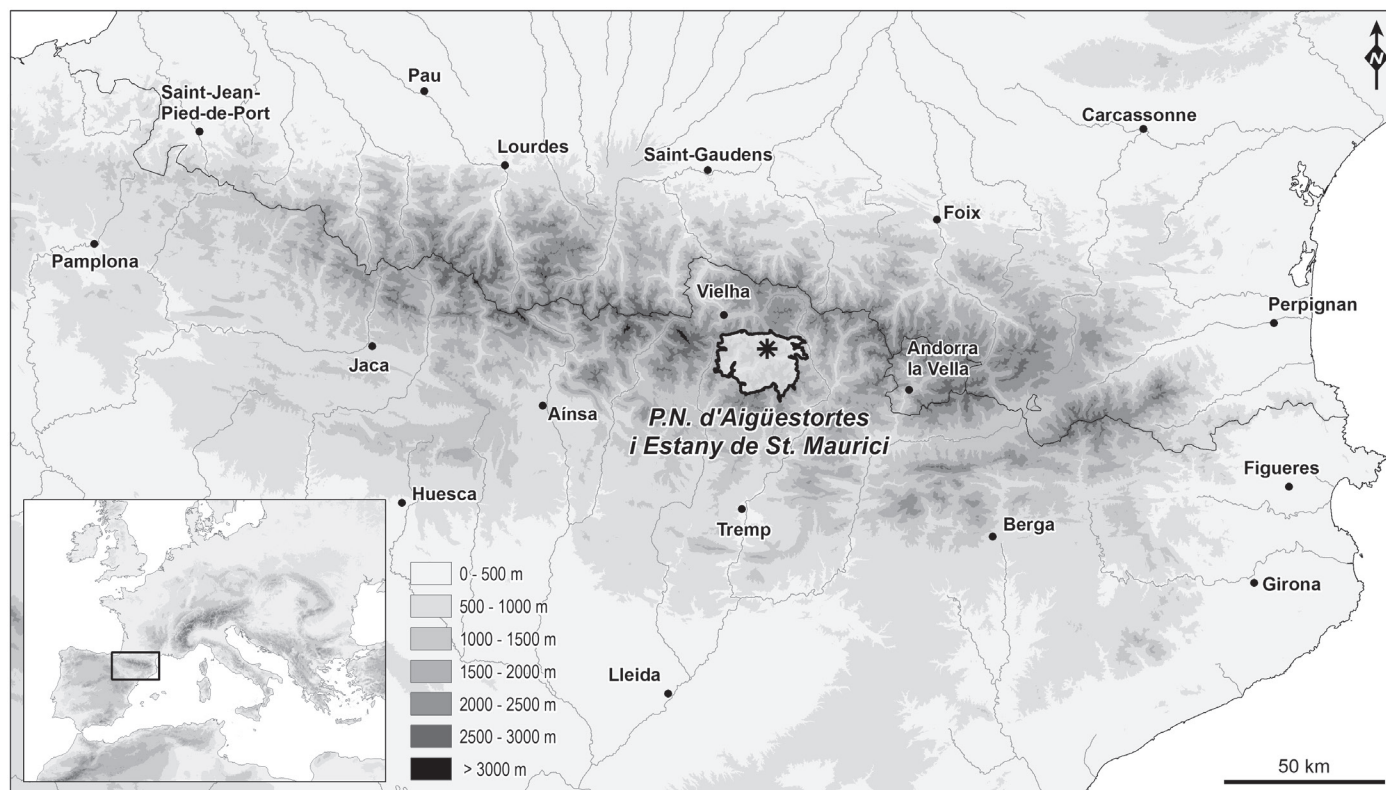


Fig. 1. Situation of Aigüestortes i Estany de Sant Maurici National Park (delimited with a dark line) and the snowbed studied (asterisk).

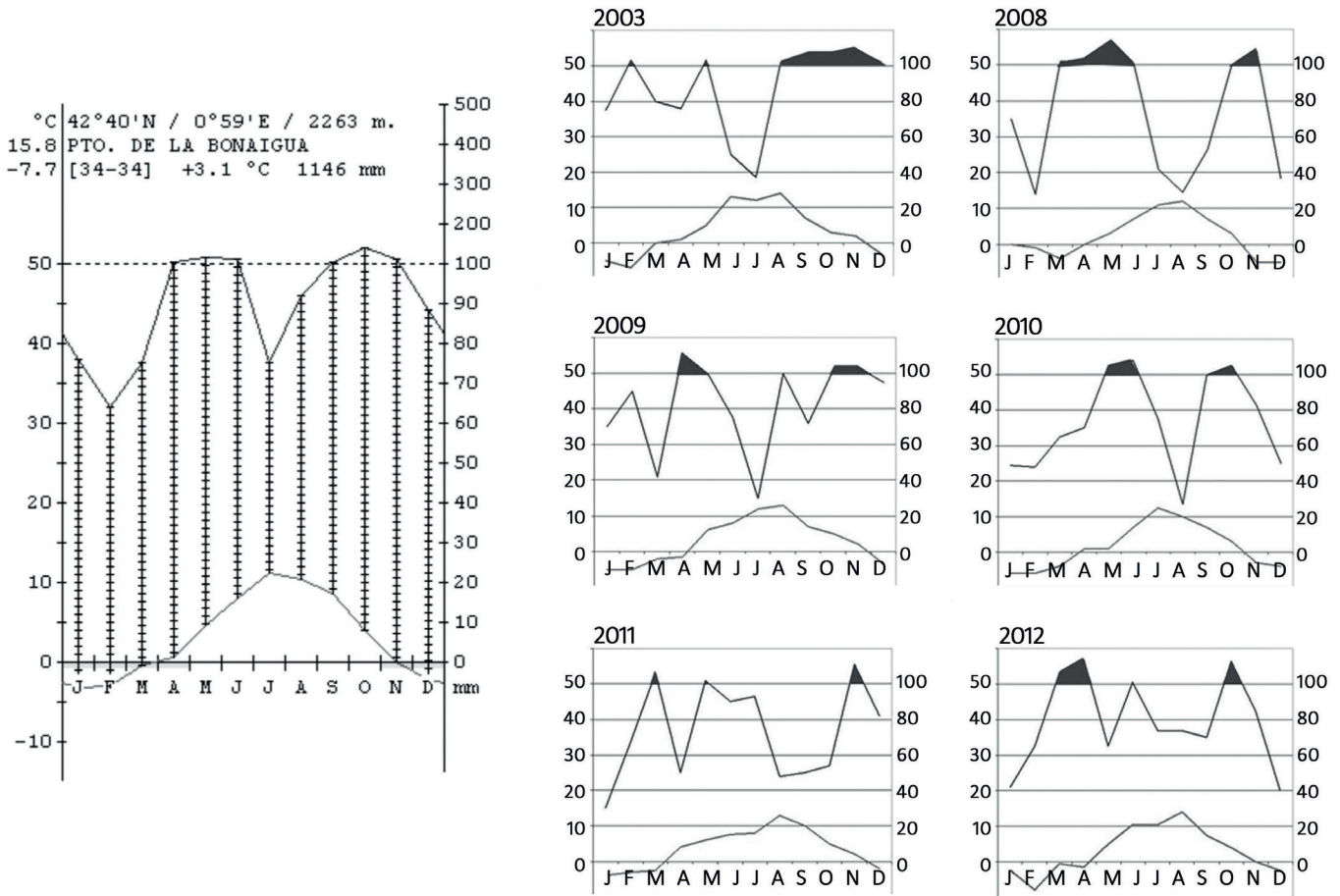


Fig. 2. Ombrothermal diagrams from la Bonaigua station, near the transect studied; reference diagram (left obtained from <https://webs.ub.edu/~infcif/index.html>) and annual diagrams for years 2003, 2008, 2009, 2010, 2011 and 2012 (right).

	Reference diagram	2003	2008	2009	2010	2011	2012
June	105	50	110	75	184	90	107
July	78	35	45	35	75	95	73
August	92	115	37	100	27	48	73
July-August rainfall	170	150	82	135	102	143	146

Table 1. Summer rainfall (mm) in the meteorological station of la Bonaigua (2266 m a.s.l.) of the reference ombrothermal diagram (Fig. 2 left) and for years 2003 and the period 2008-2012 (Fig. 2 right). Data generated by the authors from raw data obtained from Institut Meteorològic de Catalunya. Data from period 2004-2007 were not available.

conditions of alpine snowpack) and finishes in the snowbed core (where vegetation experiences increased snowpack conditions). The transect is 14 meters long and has a total of 70 subsamples. The methodology used is the same followed by LUENT *et al.* (2006). Concretely, at every 20 cm length we recorded a vegetation subsample setting a frame of 10 x 50 cm perpendicular to the direction of the transect. In each subsample we recorded all vascular plant and bryophyte species found and their cover, divided into 3 classes: 1 <10%, 2 between 10 and 50%, 3 > 50%. Sampling was performed during the optimal vegetation period (late July to mid-August) in years 2003 and 2012. Plant nomenclature follows BOLÒS *et al.* (2005).

2. Statistical analyses

To look for differences in the distribution of subsamples into groups and in the structure of transitions between groups, we performed the same analyses that LUENT (2007). Concretely, we classified subsamples into groups with the non-hierarchical clustering technique Fuzzy C-means (BEZDEK 1987). This method classifies subsamples according to their floristic composition and gives them a membership value between 0 and 1. Low membership values in one subsample mean that it belongs simultaneously to two or more groups, and is then considered as a transition between groups.

We first created a rectangular matrix for each year, where

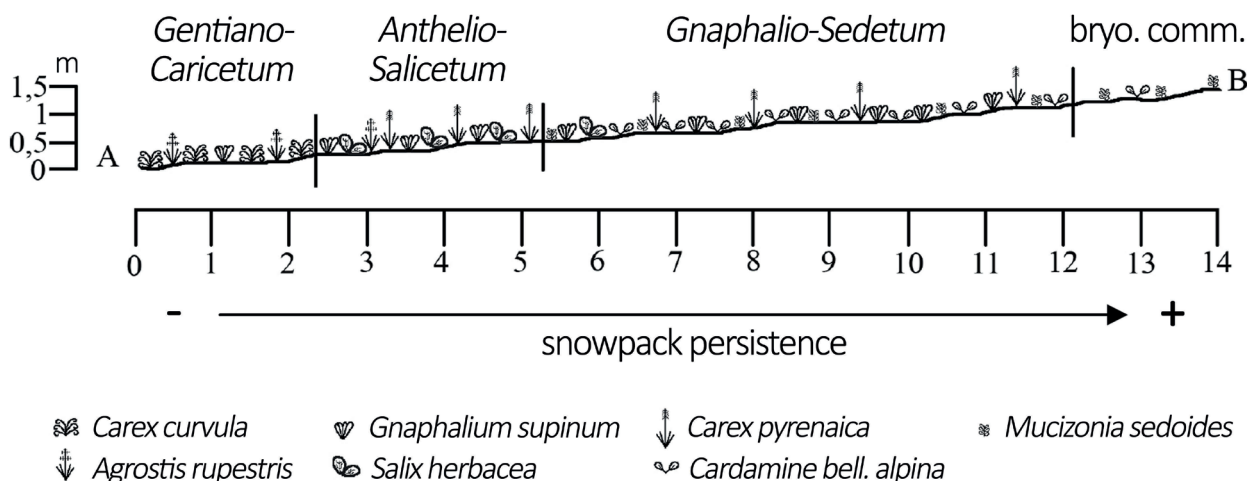


Fig. 3. Situation of the different plant communities (with the most abundant species) along the transect, following the snowmelt gradient. A- starting point of the transect; B- endpoint of the transect; scale in meters (figure obtained from LLUENT 2007).

columns were species and rows were subsamples. Data were transformed with the Hellinger distance (RAO 1995), which uses the cover values to compute the distance between objects. Then we performed the fuzzy analysis with a fuzziness value of 1.2 (it is the highest value with which membership values of 1 can be obtained, but it is also useful in detecting transitional samples). We performed different partitions, and retained the best according to the Dunn coefficient partition (DUNN 1976). Once we obtained the total number of groups, we checked whether the different species discriminate between them by computing the ϕ -fidelity of each species to each group (CHYTRÝ *et al.* 2002). We considered a threshold value of $\phi=0.3$, whose statistical significance is $p < 0.05$ for datasets with more than 46 samples and $p < 0.01$ for datasets with more than 61 samples (de Cáceres 2005). All analyses were performed with the program Ginkgo in the package VegAna (BOUXIN 2005, DE CÁCERES 2005).

To look for trends in the frequency of species along the transect, we computed a frequency index for each species. We subtracted the total number of subsamples where a species was present in a given group in 2003 to the total number of subsamples where it was present in the same section of the transect in 2012. Positive values meant an increase and negative values a decrease of the frequency of species along the section of the transect included in the group analysed. To know if there were differences between the different vegetation groups and between the sets of species with different habitat specificity (i.e. grassland species and snowbed specialists), we performed a general two-way ANOVA. Afterwards, we also performed individualised one-way ANOVAs for each vegetation group in order to look for differences between the sets of species at group level. These analyses were conducted with R (R Development Core Team 2016).

III. Results

Vegetation groups resulting from the Fuzzy-C-means analyses were four, the same that were evidenced in 2003, and corresponded to the same plant communities identified by LLUENT (2007). Concretely, following the snowmelt gradient from the earliest snow-melting end to the latest snow-melting

end, the first group identified corresponded to the *Carex curvula* subsp. *curvula* grassland (*Gentiano-Caricetum curvulae* Nègre 1969), the second group to the chionophilous *Salix herbacea* carpet (*Anthelio-Salicetum herbacea* Br.-Bl. 1948), the third group to the chionophilous community of small snowbed hemicryptophytes (*Gnaphalio-Sedetum candollei* Br.-Bl. 1948) and the last group to the bryophyte community dominated by *Brachythecium glaciale* (Fig. 3).

The distribution of these different communities on the snowmelt gradient was similar between years, although some minor variations were detected in subsamples corresponding to the transition area between them (Fig. 4). The most noticeable differences were that the boundary area between *Gentiano-Caricetum* and *Anthelio-Salicetum* increased at expenses of the second community, that the transition between *Anthelio-Salicetum* and *Gnaphalio-Sedetum* became more defined, and that the border between *Gnaphalio-Sedetum* and bryophyte community moved slightly towards the end of the snowmelt gradient.

The fidelity of species to each vegetation group (or community) also showed some differences (Table 2). In *Gentiano-Caricetum curvulae* faithful species were characteristic taxa of this grassland in both years, except *Anthelia juratzkana*, a snowbed specialist liverwort which had been associated with this group in 2003, but belonged to *Anthelio-Salicetum herbaceae* in 2012, as it would be expected. *Gnaphalio-Sedetum candollei* and bryophyte community showed the most apparent changes. In 2003 the only species that showed fidelity to the bryophyte community was the moss *Brachythecium glaciale*, while in 2012 also *Cerastium cerastoides* and *Cardamine bellidifolia* subsp. *alpina* had significant fidelity for this vegetation group. The case of this last species proves that snowbed vegetation is experiencing important changes: in 2003 it was the species with the highest fidelity for *Gnaphalio-Sedetum candollei*, whereas in 2012 it appeared as significantly faithful (although it had lower fidelity values) to both *Gnaphalio-Sedetum* and the bryophyte community.

The set of species found along the transect for 2003 was 36,

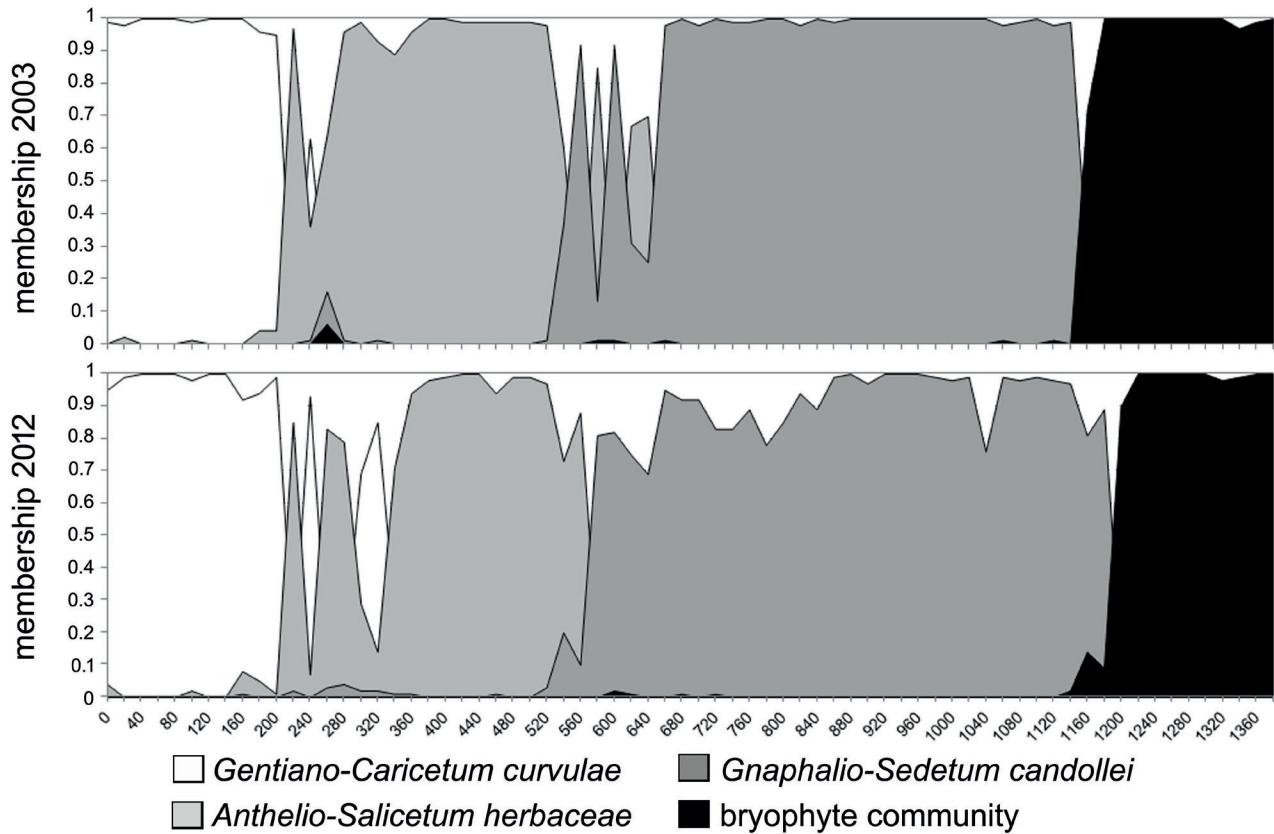


Fig. 4. Distribution of subsamples into the vegetation groups for years 2003 and 2012.

	<i>Gentiano-Caricetum</i>		<i>Anthelio-Salicetum</i>		<i>Gnaphalio-Sedetum</i>		<i>Bryophyte community</i>	
	2003	2012	2003	2012	2003	2012	2003	2012
<i>Carex curvula curvula</i>	0.95	0.82	-0.21	-0.09	-0.38	-0.45	-0.22	-0.2
<i>Primula integrifolia</i>	0.63	0.71	0.3	0.21	-0.51	-0.56	-0.33	-0.26
<i>Polytrichum piliferum</i>	0.61	0.13	-0.17	0.12	-0.22	-0.15	-0.13	-0.07
<i>Gentiana acaulis alpina</i>	0.59	0.66	0.35	0.32	-0.54	-0.6	-0.31	-0.28
<i>Phyteuma hemisphaericum</i>	0.59	0.58	0.35	0.39	-0.54	-0.57	-0.31	-0.31
<i>Agrostis rupestris</i>	0.57	0.49	0.24	-0.12	-0.39	-0.04	-0.36	-0.36
<i>Leontodon pyrenaicus pyrenaicus</i>	0.54	0.45	-0.05	0.27	-0.24	-0.4	-0.17	-0.27
<i>Anthelia juratzkana</i>	0.5	0.1	0.23	0.31	-0.41	-0.16	-0.24	-0.25
<i>Poa alpina alpina</i>	0.42	-0.03	-0.11	-0.27	-0.37	0.32	0.19	-0.11
<i>Luzula spicata montsignatica</i>	0.26	0.34	-0.07	-0.09	-0.1	-0.15	-0.05	-0.07
<i>Pedicularis kernerii</i>	0.09	0.34	0.03	-0.09	-0.02	-0.15	-0.1	-0.07
<i>Plantago maritima alpina</i>	-0.02	0.08	0.78	0.67	-0.48	-0.44	-0.28	-0.26
<i>Sibbaldia procumbens</i>	-0.15	-0.17	0.62	0.32	-0.27	0.03	-0.24	-0.21
<i>Euphrasia gr. minima</i>	0.36	0.25	0.59	0.19	-0.55	0.08	-0.35	-0.62
<i>Salix herbacea</i>	0.23	0.22	0.55	0.39	-0.32	-0.12	-0.45	-0.55
<i>Nardus stricta</i>	-0.09	-0.18	0.53	0.62	-0.26	-0.17	-0.2	-0.28
<i>Cardamine bellidifolia alpina</i>	-0.42	-0.36	-0.6	-0.45	0.73	0.33	0.19	0.47
<i>Mucizonia sedoides</i>	-0.38	-0.24	-0.45	-0.25	0.7	0.39	0	0.01
<i>Veronica alpina</i>	-0.37	-0.37	-0.24	-0.32	0.61	0.72	-0.14	-0.22
<i>Carex pyrenaica</i>	-0.49	-0.45	0.36	0.09	0.55	0.63	-0.65	-0.49
<i>Polytrichum sexangulare</i>	-0.39	-0.4	0.19	0.3	0.44	0.3	-0.39	-0.32
<i>Gnaphalium supinum</i>	0.21	-0.2	0.28	0.17	0.36	0.37	-1	-0.51
<i>Taraxacum alpinum</i>	-0.16	-0.17	-0.22	-0.17	0.36	0.09	-0.04	0.27
<i>Sagina saginoides</i>	-0.29	-0.4	-0.24	-0.27	0.34	0.48	0.13	0.1
<i>Cerastium cerastoides</i>	-0.41	-0.23	-0.16	-0.15	0.3	0.05	0.2	0.36
<i>Oreochloa disticha blanka</i>	-0.16	-0.15	-0.02	-0.16	0.27	0.34	-0.16	-0.12
<i>Arenaria biflora</i>	-0.16	-0.02	0.05	-0.23	0.27	0.33	-0.25	-0.18
<i>Brachythecium glaciale</i>	-0.2	-0.2	-0.26	-0.21	-0.34	-0.36	0.95	1

Table 2. Fidelity values of species to the different groups of vegetation in years 2003 and 2012. Dashed lines separate faithful species belonging to the different vegetation groups in 2003. Grey background highlights significant values ($\phi \geq 0.3, p < 0.05$).

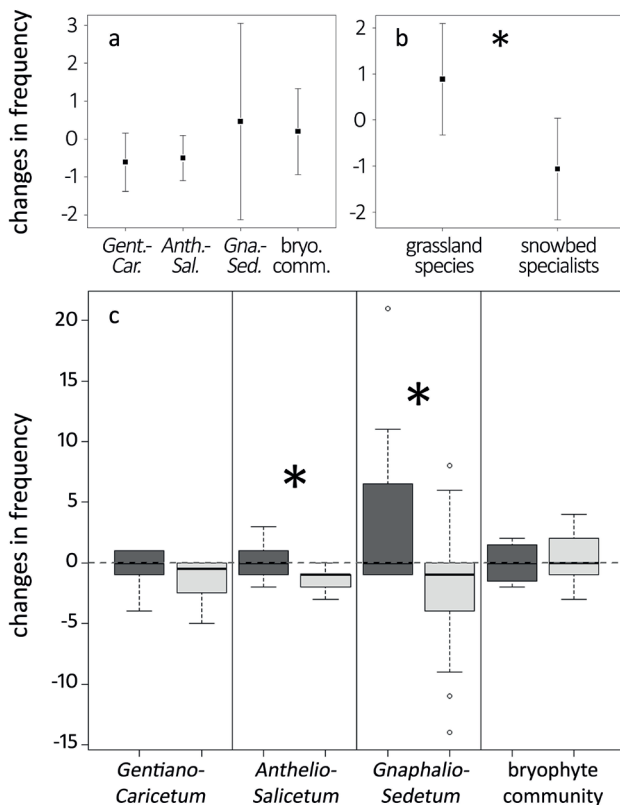


Fig. 5. Changes in the frequencies of species present in the transect depending on the vegetation groups (or communities) found along the transect, and on the sets of species considering their habitat specificity (i.e. grassland species and snowbed specialists): **a**, mean and 95% confidence interval of changes in frequency between communities; **b**, mean and 95% confidence interval of changes between sets of species; **c**, changes of frequency between the sets of species depending on the community (dark grey, grassland species; light grey, snowbed specialists). Asterisks in a plot mean significant differences ($p < 0.05$)

and it was almost the same in 2012 (38 taxa). The new species found in 2012 were generalists (*Festuca eskia*, *Murbeckiella pinnatifida* and *Vaccinium uliginosum* subsp. *microphyllum*) and occurred only in one subsample. On the other hand, *Campanula scheuchzeri*, which in 2003 appeared only in one subsample, was not detected in 2012.

Analyses of changes in the frequency of species showed contrasted results. On one hand, vegetation groups (or communities) did not show significant differences between them ($F_{3,85} = 1.16$, $p = 0.329$; Fig. 5a), whereas when grouping species depending on their habitat specificity, we found significant differences ($F_{1,85} = 5.77$, $p = 0.0185$), with grassland species showing an increase of frequency along the transect and snowbed specialists a decrease (Fig. 5b). The analyses of the sets of grassland and snowbed species for each vegetation group separately showed the same trends than the general test, i.e. an increase in the frequency of grassland species and a decrease of snowbed specialists (Fig. 5c). We found significant differences between these two sets of species in the communities situated in the central part of the snowbed, concretely *Anthelio-Salicetum* ($F_{1,22} = 6.891$, $p = 0.0155$) and *Gnaphalio-Sedetum* ($F_{1,26} = 4.956$, $p = 0.0349$). Although

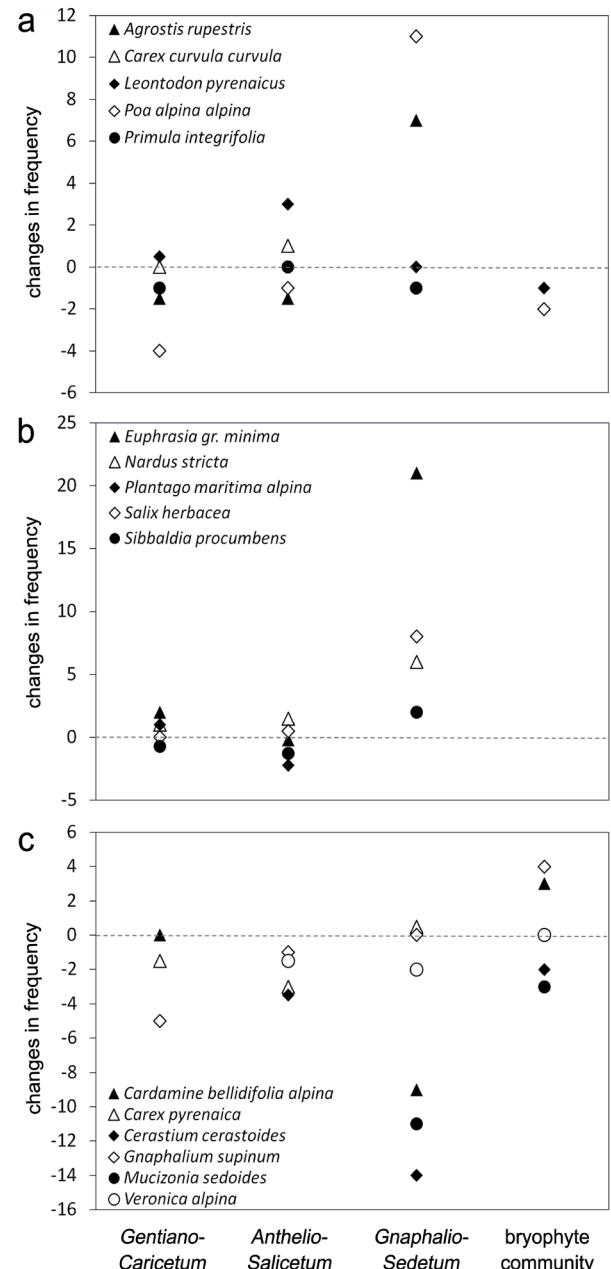


Fig. 6. Changes in the frequency of the most representative faithful species in the four communities present along the transect: **a**, *Gentiano-Caricetum* faithful species; **b**, *Anthelio-Salicetum* faithful species; **c**, *Gnaphalio-Sedetum* faithful species.

in the *Gentiano-Caricetum* grassland community we also observed a decrease of snowbed specialists, differences with grassland species were not significant. On the other hand, at the snowiest end of the transect, snowbed specialists showed a non-significant trend towards an increased frequency.

At species level, the distribution and abundance of most species along the transect remained more or less constant after 9 years (Appendix 1), although some of them showed clear trends. Species that were faithful to *Gentiano-Caricetum* did not show any trend in their group, but *Agrostis rupestris* and *Poa alpina* experienced a considerable increase in their frequency in *Gnaphalio-Sedetum* (Fig. 6a, Appendix 1). *Euphrasia gr. minima*, *Nardus stricta* and *Salix herbacea*,

all of them faithful to *Anthelio-Salicetum*, also experienced a considerable increase in *Gnaphalio-Sedetum* (Fig. 6b). Finally, snowbed specialists with high fidelity values for *Gnaphalio-Sedetum*, not only decreased in frequency in *Gentiano-Caricetum* and *Anthelio-Salicetum* when present, but also experienced an enormous decrease in their own group, mainly *Cardamine bellidifolia* subsp. *alpina*, *Cerastium cerastoides* and *Mucizonia sedoides*. However, the frequency of *Cardamine bellidifolia* subsp. *alpina* and *Gnaphalium supinum* showed a slight tendency to increase in the bryophyte community, at the snowiest end of the transect (Fig. 6c).

IV. Discussion

After nine years, the snowbed studied had the same vegetation communities along the snowmelt gradient, and the species were mostly the same. However, there were changes in the distribution and frequency of these species. On one hand we found a generalised decrease of chionophilous plants (or snowbed specialists) except in the snowiest part of the snowbed, where they seemed to experience a slight increase. On the other hand, grassland species colonised the internal sectors of the transect and became more frequent in the different snowbed groups except in the bryophyte community. Thus, our findings confirm the predictions of some authors about the vulnerability of chionophilous species face to the neighbouring grassland species (HEEGAARD & VANDVIK 2004, BJÖRK & MOLAU 2007, SCHÖB *et al.* 2008).

Climatic variability, mainly a decrease in summer precipitation, has been observed during the last ten years in a meteorological station near our study site. In addition, a three-year monitoring-period of environmental conditions in this site showed a high irregularity on the date of snowmelt (LUENT 2007), and the monitoring of other snowbeds in the Pyrenees confirms this situation (LUENT 2007, ILLA *et al.* 2011). Regarding snowfall, although LÓPEZ-MORENO (2005) observed a reduction of snow depth due to a reduction in winter precipitation during the second half of the 20th century in the Pyrenees, in the study area winter precipitation has remained similar than the reference values during the 2003-2012 period (data not shown).

The high reduction of summer rainfall could be one of the main factors explaining the observed decrease in the frequency of snowbed specialists along the transect, as they need a fair water supply, which comes from the melting snow in early-to mid-summer, and from summer rainfall.

Species with high moisture requirements such as *Cerastium cerastoides* or *Epilobium anagallidifolium* (MATTHEWS 1992, BOLÒS *et al.* 2005) could have suffered from summer drought, exemplified by a reduction of their frequency in the snowbed communities of the central part of the transect, only remaining more or less constant in the snowiest end of the snowmelt gradient.

Other climate-related events can also have negative effects on snowbed vegetation. A reduction of snowpack persistence can expose snowbed species to frost events, and differences in the growing season length affect the phenological cycle of some snowbed species (LUENT *et al.* 2013) and thus, their reproductive success. Not only the negative effects of frost

damage or summer drought on snowbed species, but also their low competitive ability, can allow grassland species to colonize gaps within snowbed plants, especially when the total cover of the vegetation is low. In our study site, *Gnaphalio-Sedetum* illustrates this situation. Small hemicryptophytes dominate in this community, where vegetation cover is not as high as in the neighbouring *Anthelio-Salicetum* (where the creeping subshrub *Salix herbacea* largely covers the surface), and bare ground is abundant. Certainly, this community experienced the largest changes in the frequency of both snowbed and grassland species, with the latter becoming relatively abundant. Grassland species colonising snowbed patches were mainly graminoids, which in alpine meadows were found to increase with increasing growing season (OSTLER *et al.* 1982). Their higher frequency in 2012 could then suggest a trend towards an earlier snowmelt date or towards an increased amount of energy during the growing season in the snowbed studied.

A relevant aspect when assessing changes in vegetation is the ability of species to colonize new favourable areas. As mentioned above, snowbed vegetation is subjected to a short growing season (KÖRNER 2003, ILLA *et al.* 2011), but also to a certain development of soil (BRAUN-BLANQUET 1948). Usually, the snowiest end of a snowbed has a rocky, very immature soil, so the retreat of snowbed communities to this area may be unfeasible. In addition, permanent or almost permanent snowfields are usually rocky places which do not hold any vegetation, or just typical species from rocky habitats. Then, even if snow melts earlier, these topographic situations are not suitable places for the establishment of snowbed vegetation, which in a near future may experience a clear retreat in their southern distribution limit due to climate change.

V. Conclusions

Despite its limited scope, as the monitoring period is short and only one gradient was studied, we believe that this study can contribute to the understanding of the relationship between climate and snowbed vegetation. Indeed, the period between 2003 and 2012 was long enough to evidence some changes in snowbed vegetation, that could be related to strong inter-annual irregularity of meteorological data, with a tendency to reduced summer precipitation. Although the shifts found in snowbed vegetation were small, they drew a rather clear directionality, concretely a retraction of the area occupied by chionophilous species, and an increase of the area occupied by grassland species, mainly grasses. In the current context of climate change, more snowbed sites may be surveyed in order to predict the future of snowbed communities and species, especially in their southernmost distribution limit.

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BIBLIOGRAFIA

- BENISTON, M., F. KELLER, B. KOFFI & S. GOYETTE. 2003. – Estimates of snow accumulation and volume in the Swiss Alps under changing climatic conditions. *Theoretical and Applied Climatology*, 76: 125-140.
- BEZDEK, J.C. 1987. – Some non-standard clustering algorithms. *Developments in Numerical Ecology*, 14: 225-287.
- BJÖRK, R.G. & U. MOLAU. 2007. – Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic and Alpine Research*, 39: 34-43.
- BOLÒS, O., J. VIGO, R.M. MASALLES & J.M. NINOT. 2005. – *Flora Manual dels Països Catalans*, 2nd edn Pòrtic, Barcelona, 1310 pp.
- BOUXIN, G. 2005. – Ginkgo, a multivariate analysis package. *Journal of Vegetation Science*, 16 : 355-359.
- BOWMAN, W.D. 1992. – Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic, Antarctic, and Alpine Research*, 24: 211-215.
- BRAUN-BLANQUET, J. 1948. – *La végétation alpine des Pyrénées orientales*. Monografia de la Estación de Estudios Pirenaicos y del Instituto Español de Edafología, Ecología y Fisiología Vegetal, Barcelona, 306 pp.
- CÁCERES, M. DE. 2005. – *La Classificació numèrica de la vegetació basada en la composició florística*. Thesis Universitat de Barcelona, 367 pp.
- CHYTRÝ, M., L. TICHÝ, J. HOLT & Z. BOTTA-DUKÁ. 2002. – Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13: 79-90.
- DUNN, J.C. 1976. – Indices of partition fuzziness and detection of clusters in large data sets. In: *Gupta M (ed.) Fuzzy automata and decision processes*. Elsevier, New York, pp. 271-283.
- ENGLER, R., C.F. RANDIN, W. THUILLER, S. DULLINGER, N.E. ZIMMERMANN, M.B. ARAÚJO, P.B. PEARMAN, G. LE LAY, C. PIEDALLU, C.H. ALBERT, P. CHOLER, G. COLDEA, X. DE LAMO, T. DIRNBÖCK, J.C. GÉGOUT, D. GÓMEZ-GARCÍA, J.A. GRYTNES, E. HEEGAARD, F. HOISTAD, D. NOGUÉS-BRAVO, S. NORMAND, M. PUSCAS, M.T. SEBASTIÀ, A. STANISCI, J.P. THEURILLAT, M.R. TRIVEDI, P. VITTOZ & A. GUISAN. 2011. – 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17: 2330-2341.
- GALEN, C. & M.L. STANTON. 1995. – Responses of snowbed plant species to changes in growing-season length. *Ecology*, 76: 1546-1557.
- HAEBERLI, W. & M. BENISTON. 1998. – Climate change and its impacts on glaciers and permafrost in the Alps. *Ambio*, 27: 258-265.
- HEEGAARD, E. & V. VANDVIK. 2004. – Climate change affects the outcome of competitive interactions - an application of principal response curves. *Oecologia*, 139: 459-466.
- ILLA, E., A. LLUENT & E. CARRILLO. 2011. – Gradient tèrmic i canvis de vegetació en congegteres pirenaïques. In: *Actes del IX Colloqui Internacional de Botànica Pirenaico-cantàbrica*. IEA (Institut d'Estudis Andorrans), Ordino. Andorra, pp. 209-216.
- JOHNSON, P.L. & W.D. BILLINGS. 1962. – The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecological Monographs*, 32:105-135.
- KÖRNER, C. 2003. – *Alpine plant life: functional plant ecology of high mountain ecosystems*, 2nd edn Springer, Berlin, XI + 349 pp.
- LLUENT, A. 2007. – *Estudi de l'estructura i funcionament de les comunitats quionòfiles en relació a la variació dels factors ambientals*. Universitat de Barcelona, 243 pp.
- LLUENT, A., A. ANADON-ROSELL, J.M. NINOT, O. GRAU & E. CARRILLO. 2013. – Phenology and seed setting success of snowbed plant species in contrasting snowmelt regimes in the Central Pyrenees. *Flora*, 208: 220-231.
- LLUENT, A., E. ILLA & E. CARRILLO. 2006. – Establiment d'una xarxa d'estacions per al seguiment de la vegetació de les congegteres del Parc Nacional. In: *VII Jornades sobre Recerca al Parc Nacional d'Aiguestortes i Estany de Sant Maurici*, pp. 161-176.
- LÓPEZ-MORENO, J.I. 2005. – Recent variations of snowpack depth in the central Spanish Pyrenees. *Arctic, Antarctic, and Alpine Research*, 37: 253-260.
- LÓPEZ-MORENO, J.I., S. GOYETTE & M. BENISTON. 2009. – Impact of climate change on snowpack in the Pyrenees: Horizontal spatial variability and vertical gradients. *Journal of Hydrology*, 374: 384-396.
- MATTHEWS, J.A. 1992. – *The ecology of recently-deglaciated terrain*. Cambridge University Press, Cambridge, XVII + 390 pp.
- OSTLER, W.K., K.T. HARPER, K.B. MCKNIGHT & D.C. ANDERSON. 1982. – The effects of increasing snowpack on a subalpine meadow in the Uinta Mountains, Utah, U.S.A. *Arctic, Antarctic, and Alpine Research*, 14: 203-214.
- R Development Core Team. 2016. – R: A language and environment for statistical computing.
- RAO, C.R. 1995. – A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Qüestió*, 19 (2): 3-63.
- SCHÖB, C., P.M. KAMMER, Z. KIKVIDZE, P. CHOLER & H. VEIT. 2008. – Changes in species composition in alpine snowbeds with climate change inferred from small-scale spatial patterns. *Web Ecology*, 8: 142-159.
- STANTON, M.L., M. REJMANEK & C. GALEN. 1994. – Changes in vegetation and soil fertility along a predictable snowmelt gradient in the mosquito range, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 26 : 365-374.

	<i>Gentiano- Caricetum</i>	<i>Anthelio- Salicetum</i>	<i>Gnaphalio- Sedetum</i>	bryophyte community
grassland species				
<i>Agrostis rupestris</i>	-1	-1	7	
<i>Armeria maritima alpina</i>	1		0	2
<i>Campanula</i> gr. <i>scheuchzeri</i>			-1	
<i>Carex curvula curvula</i>	0	1		
<i>Euphrasia</i> gr. <i>minima</i>	1	0	21	
<i>Festuca eskia</i>				
<i>Gentiana acaulis alpina</i>	-1	-1		
<i>Leontodon pyrenaicus pyrenaicus</i>	0	3	0	-1
<i>Luzula spicata monsignatica</i>	1			
<i>Murbeckiella pinnatifida</i>				1
<i>Nardus stricta</i>	1	1	6	
<i>Pedicularis kernerii</i>	1	-1	-1	
<i>Phyteuma hemisphaericum</i>	1	2		
<i>Plantago maritima alpina</i>	1	-2		
<i>Poa alpina alpina</i>	-4	-1	11	-2
<i>Polytrichum alpinum</i>	0			
<i>Polytrichum piliferum</i>	-3			
<i>Primula integrifolia</i>	-1	0	-1	
<i>Ranunculus pyrenaicus pyrenaicus</i>		0	0	
<i>Selinum pyrenaicum</i>		-1	-1	
<i>Vaccinium uliginosum microphyllum</i>		1		
snowbed species				
<i>Anthelia juratzkana</i>	-4	-1	6	
<i>Arenaria biflora</i>	0		-2	
<i>Brachythecium glaciale</i>				-1
<i>Cardamine bellidifolia alpina</i>	0		-9	3
<i>Carex pyrenaica</i>	-1	-3	0	
<i>Cerastium cerastoides</i>		-3	-14	-2
<i>Epilobium anagallidifolium</i>			-4	0
<i>Gnaphalium supinum</i>	-5	-1	0	4
<i>Luzula alpinopilosa</i>			0	
<i>Mucizonia sedoides</i>			-11	-3
<i>Oreochloa disticha blanka</i>		-2	0	
<i>Polytrichum sexangulare</i>		0	-1	
<i>Sagina saginoides</i>		-1	4	2
<i>Salix herbacea</i>	0	0	8	
<i>Sedum alpestre</i>	-1			-1
<i>Sibbaldia procumbens</i>	0	-1	2	
<i>Taraxacum alpinum</i>			-1	2
<i>Veronica alpina</i>		-1	-2	0

Appendix 1. Changes in the frequency of all species present along the transect in the different vegetation groups where they are present