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Functional Plant Traits and Species Assemblage in Pyrenean Snowbeds

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Abstract In mid-latitude mountains, snowbeds often consist of small, scattered alpine belt units that host many plants of high biogeographic interest. Because most snowbed species are weak competitors, it is important to study the dissemination and persistence of their seeds to better understand their population dynamics. This study analyzed the snowbed flora of the Central Pyrenees using 11 morpho-functional traits, mostly related to seed function. The seeds of most plants found in snowbeds are small or very small, they have ovoid to elliptical shapes, and have no attributes related to dispersal. When only snowbed specialists (i.e., with a phytosociological optimum in snowbed habitats) are considered, three strategy groups become apparent: *i*) annuals or pauciennials producing abundant small seeds prone to accumulate in the soil; *ii*) chamaephytes or hemicryptophytes that produce anemochorous seeds; and *iii*) other perennials – mainly hemicryptophytes – with no specific seed traits. In the first two groups, the extant populations are maintained either by permanent soil seed banks or by means of vegetative persistence and dispersal. The lack of specific traits in the third group suggests that these plants could be more sensitive to direct competitive exclusion from non-chionophilous species under a changing climatic scenario in which snowbeds tend to disappear.

Keywords Alpine vegetation · Dispersal · Plant strategies · Salicetea herbaceae · Soil seed bank

Plant nomenclature Bolòs et al. (2005)

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Introduction

High-altitude mountains, typically the alpine belt, are a suitable environment to investigate the relationships between environmental constraints, species pools and adaptive plant traits (Körner 2003: 2). Snowbeds are a particularly interesting habitat in the alpine belt, because long-lasting snow cover adds specific constraints over the general restrictions associated with altitude. Snowbeds are mainly characterized by a very short growing period. Plants living there undergo marked physical disturbance as a consequence of snow accumulation (on the plant carpet and soil) and intense soil leaching during the long snowmelt period (Komárková 1993; Körner 2003: 47–62). Notwithstanding, plants settling on snowbeds benefit from efficient thermal insulation during winter and spring, and from an abundant water supply during the growing season (Björk and Molau 2007; Lluent 2007).

Several plant communities in the snowbeds of alpine mountains have been described in relation to the environmental constraints of these habitats (e.g., Braun-Blanquet 1948; Onipchenko 2004; Choler 2005). Such communities are clearly different in terms of species composition and their functional structure and dynamics from those in neighbouring grasslands. Moreover, different snowbed communities can be found within a short transect (just a few meters) from an alpine grassland to the almost bare ground in the center of the snowbed, because the length of the growing season causes a steep gradient that affects snowbed communities. The substrate type (e.g., lime rich *vs* siliceous, soil texture) is also a determinant of the plant communities' composition.

The most common plants growing in snowbeds correspond to Arctic-Alpine taxa, which occur in rather isolated localities across the Pyrenees, where most of them have their southernmost populations in Europe (Bolòs et al. 2005). Most snowbed specialists are poor competitors (Kudo et al. 1999; Onipchenko and Semenova 2004; Schöb et al. 2010). They may occur in small gaps in alpine grasslands with abundant snow cover in winter, but they only develop optimally where long-lasting snow cover (i.e., snowbeds) hampers the establishment of grassland species. Also, a number of grassland plants settle on snowbeds from neighbouring mother-plants, and form scattered populations (Galen and Stanton 1995; Volkova et al. 2005).

The seed phase is important in a plant's life cycle because colonizing new sites and regenerating extant populations promotes gene flux. In relation to seed morphology, production and functioning in the particular snowbed environment, we hypothesize that seed dispersal across the landscape and persistence in the soil seed bank could have shaped to some extent the composition of snowbed communities. According to this, some snowbed species have been identified as opportunistic in other alpine ecosystems because of their regenerative strategies (Scherff et al. 1994; Semenova 2004), mostly in relation to their seed traits that ensure long persistence in the soil (Thompson 1993b; Cerabolini et al. 2003). However, other plant traits related to life history could also be responsible for the particular plant assemblage occurring in snowbeds.

Our aim is to assess the extent to which the species pool found in Pyrenean snowbeds supports this hypothesis. Thus, we analyze these species in terms of morpho-functional traits, mostly related to the seed function in this particular environment; we also highlight and discuss the main trends found in snowbed specialists – plants with their optimum in snowbed communities – compared to the remaining taxa – plants more frequent in pastures and rocky places, but also found in snowbeds. This comparison may help to explain the present and future fate of both groups, in the context of present interannual snow-cover variation and of future hypothetical reduction and disappearance of most Pyrenean snowbeds.

Material and Methods

Study Area and Vegetation

The study was performed in the Aigüestortes i Estany de Sant Maurici National Park, in the Central Pyrenees, in Catalonia (NE Iberian Peninsula). The alpine landscape of the area is highly representative of the Central Pyrenean high mountains. It consists of varied plant formations covering from exposed rocky surfaces to gentle slopes and valley bottoms with fens and lakes. The core of the study area is formed by a massive granodiorite batholith, although a few calcareous and slate outcrops are also found surrounding it.

Snowbed vegetation is widespread in the alpine belt, from (2,000)2,300 m a.s.l. to 2,700(2,900) m a.s.l., and includes most of the Pyrenean plant communities of the class Salicetea herbaceae (Carrillo and Ninot 1992). The abrupt relief given by granodiorite and lime leads to the formation of snowbeds mainly on footslopes of cliffs and other glacial geoforms. As such, chionophilous vegetation is restricted to small, irregular patches where concavities or gentle landforms favor some soil formation. In the most developed examples, distinct plant communities make clear graded catenas; these are modulated by substrate characteristics and by the length of the snowmelt period, which varies from the edges to the center of the snowbeds.

On siliceous soils the vegetation gradient goes from bryophyte carpets in the center of the snowbed, where snow lasts until mid-July and summer radiation is at its minimum, to Gnaphalio-Sedetum and *Salix herbacea* formations at the edges, which give way to grasslands with moderate snow cover and higher radiation (Trifolio-Phleetum gerardii Br.-Bl. 1948, Selino-Festucetum eskiae Nègre 1969). In calcareous areas, snowbeds are usually found at lower altitudes in the alpine belt, coinciding with particular, rocky north-facing slopes. In most cases, chionophilous vegetation consists of a dwarf-shrub community of *Salix reticulata* and *S. retusa*, which covers skeletal soils with protruding bedrock. The calcicole Potentillo-Gnaphalietum hoppeani and a moderately calcifugue *Salix herbacea* formation (Salici-Anthelietum thalictretosum) are found only where fine-textured soil covers gentle slopes. Outside the snowbed, this chionophilous vegetation contacts with the calcicole grasslands – Festuco-Trifolietum thalii Br.-Bl. 1948 in slight-snowpack zones, and Oxytropido-Elynetum myosuroidis Chouard 1943 in early-melting areas. More precise information on the snowbed vegetation is given in Table **S1** in Electronic Supplementary Material and in Carrillo and Ninot (1992).

Given the small area covered by snowbeds in most cases and the marked changes in topography and snow conditions of these surfaces, the whole set of snowbed plant communities may occur within a few meters. In addition, snowbed communities frequently include species more characteristic of neighbouring grasslands and of rocky places. Also, these grasslands offer good conditions for some plants typical of snowbeds (*Gnaphalium supinum*, *Sagina saginoides*, *Sibbaldia procumbens*), which frequently settle in small gaps. Moreover, interannual variability of snow cover causes small changes in the location and nature of the boundaries between plant communities (Lluent et al. 2006; Lluent 2007).

Analyses

We investigated the Spermatophyta occurring in the snowbeds of the Aigüestortes i Estany de Sant Maurici National Park, namely the species or subspecies found in at least 5 % of 233 phytosociological relevés of Salicetea herbacea taken in the area, for a particular monitoring program (reported in Lluent et al. 2006). Then, we added to this list a few other taxa considered characteristic of this vegetation class that were less frequent or were not sampled due to their local or regional rarity. This provided a list of 81 taxa, including species or subspecies that were strictly chionophilous, or typical of alpine habitats other than snowbeds, or even ubiquitous. The nomenclature used follows that given in Bolòs et al. (2005).

We selected a set of seed traits corresponding to morpho-functional aspects, five referring to seed characteristics (following the proposal of Thompson 1993a), and two measuring seed production and size of the soil seed bank (Table **1**). Seed is here understood as the diaspore unit or dispersule, i.e., including the walls of indehiscent fruits and the appendages (awns, pappi) or bracts attached to it during dispersal. Only in the case of seed mass do we refer to the germinule (i.e., excluding bracts, pappi or other attachments), because this trait is examined with the aim of evaluating the chance of emerging and settling on a new site.

The seed traits were analyzed from a specific collection of seeds and fruits sampled in the study area from 2006 to 2010, and kept in the Herbarium of the University of Barcelona (BCN). Morphological aspects were observed under a stereoscopic microscope at 10–40-fold magnification. The measurements correspond to the mean of ten seeds, and seed mass was calculated from five samples of at least 50 air-dried seeds each, weighed to the nearest mg. Exceptionally, for the few taxa that were not well documented from this collection, data were obtained or complemented from a few sources (particularly Bojňanský and Fargašová 2007; Castroviejo et al. 1986–2009; and Liu et al. 2008), under the assumption that these morphological data are relatively constant among populations of the same species living in different areas.

We evaluated the dispersal mode from seed morphology, assuming barochory for the seeds with no apparent dispersal attributes, short-distance anemochory (or zoochory) for seeds with awns or small wings (or small elaiosomes), and long-distance anemochory for seeds with pappi. Seed production was estimated after multiplying mean values of the number of seeds per fruit, and then fruits per infructescence, and infructescences per ramet, which were assessed from a minimum of ten cases during the specific sampling mentioned above.

The estimation of the seed-bank size was based on greenhouse germination experiments of soil samples obtained from the study area. The data on seed germination were recorded from more than 100 samples of different snowbed communities, and synthesized as the average densities for surface area from the samples where each

Table 1 Plant traits considered and data structure

Traits	Data structure	Units or categories
Seed length, width and breadth (including appendages)	quantitative	mm
Weight of germinule	quantitative	mg
Number of seeds per ramet	quantitative	–
Seed surface	categorized	1, smooth
		2, rugose, muricate
		3, striate
		4, hairy
Seed appendices	categorized	1, absent
		2, beak or hook
		3, wing(s)
		4, (hygroscopic) awn
		5, elaiosome
		6, persistent pappus
Seed morphology	categorized	1, sphaerical
		2, ovoid, rhomboidal
		3, tigonous, triquetrous
		4, lenticular, reniform, elliptical, subulate
		5, cylindrical, fusiform, ligulate
		6, conical, clavate
Density of seeds in the soil bank	categorized	1, <3 per m^2
		2, from 3 to 29 per m^2
		3, from 30 to 299 per m^2
		4, >300 per m^2
Lateral expansion	categorized	none
		few tillers, to short distance (<2.5 cm)
		many tillers, to short distance (dense turf)
		few tillers, to long distance (>2.5 cm)
Life form	categorized	therophyte
		non-gaminoid hemicryptophyte
		gramidoid hemicryptophyte
		diffuse chamaephyte
		pulvinular chamaephyte (small cushions)
		creeping chamaephyte

species occurred in the standing vegetation (methodology and results reported in Lluent 2007). Only in the few cases in which we could not collect enough reliable data from our experiments did we take density data from literature specific for snowbeds or alpine vegetation (Cerabolini et al. 2003; Semenova 2004; Welling et al. 2004; Marcante et al. 2009).

The seed analysis was complemented with the evaluation of two traits related to plant performance, namely lateral expansion and life-form (Table **1**). We sorted the taxa into six life-forms and into four categories of lateral expansion, as stated in Illa et al. (2006).

To define the distinct ecological groups and classify the plants analyzed, we synthesized the information about species ecological preferences assessed in the phytosociological studies by Carrillo and Ninot (1992) and in Bolòs et al. (2005) and created three distinct categories, i.e., three main habitats, in relation to the duration of snow cover: *i*) snowbeds (species characteristic of Salicetea herbaceae and included syntaxa, or typical of grasslands of late-melting sites); *ii*) grasslands (taxa from sites with medium snow duration, mainly typical of the alpine grassland classes Juncetea trifidi or Elyno-Seslerietea); and *iii*) rocky sites (plants from rock crevices, screes or fellfields, mainly thriving on early-melting surfaces). In the case of the first group, we distinguished the snowbed specialists by taking into account the phytosociological information from the BDBC data bank (Font 2009); from a pool of 1,600 relevés taken in the alpine belt of the Catalan Pyrenees, we considered to be snowbed specialists those taxa with at least 30 % of their occurrence in relevés of the class Salicetea herbaceae (i.e., more than 28 occurrences over 96 relevés). Although this threshold may seem a bit low, it allowed us to define a broader ecological group, which included locally rare snowbed species and also weakly chionophylous species. Among the non-specialist taxa, we defined the grassland species by using the same threshold (at least 30 % of occurrence in relevés of Caricetea curvulae or Elyno-Seslerietea). The inclusion of species into the third group, i.e., ecological preference for rocky sites, was based only on literature sources (Carrillo and Ninot 1992; Bolòs et al. 2005), given that most of them have a narrow ecological niche (e.g., humid crevices, lime-rich scree) although making a rather diverse group.

The data were organized in a rectangular table (81 species × 11 traits) to summarize the general spectra of the species found in the Pyrenean snowbeds. From this table we categorized the distribution of seed measurements or trait categories in the species pool investigated, and drew comparative analyses between the three ecological groups defined, based on species percentages of each trait category.

A general assessment of the functional diversification of the seeds was derived from a multivariate ordination of the species according to the traits stated in Table **1**. Data were analyzed in a Principal Component Analysis (PCA) using R.2.8.0 (R Development Core Team 2011). In the qualitative traits the categories were arranged in order of their functional significance and scored accordingly as qualitative traits (as ordered in Table **1**). The quantitative data were transformed logarithmically to normalize the distribution of the observations. Then, all variables were standardized so as to facilitate the comparison of different scales and units. To test the significance of the multivariate statistics, we ran a multivariate-ANOVA with 999 permutations (PERMANOVA test, Anderson 2001), using the 'vegan' package in R (Oksanen 2009).

Results

Trait Spectra in the Species Pool

Seeds of snowbed species are mostly very small: in 25 % of species the germinule weighs less than 0.1 mg, and in 75 % less than 0.6 mg (Table **2**; Fig. **S1**a in Electronic Supplementary Material). The number of seeds produced per ramet is in general moderate or low. For instance, in 36 % of species this value is lower than 40, and in 60 % it is lower than 80 (Fig. **S1**b in Electronic Supplementary Material). However, because most of the plants considered are small and have ramets that occupy an area of a few cm^2, these seed yields are relatively high at population or community levels.

As for the soil seed bank, the obtained values of viable seed density also gave a power distribution among species (more detailed data in Lluent 2007), with a few species (*Sagina saginoides*, *Murbeckiella pinnatifida*, *Cardamine bellidifolia*) concentrating the vast majority of viable seeds. 57 % of the species were apparently absent or almost absent in the soil seed bank, whereas the rest of the species were evenly distributed among the other density categories established (Table **2**).

68 % of the species had slightly longer than wide seeds, i.e., varying from ovoid to elliptical (Fig. **S1**c in Electronic Supplementary Material), with a smooth surface (78 %) and without appendages (58 %). However, 14 % of the species had pappi (Asteraceae, Salicaceae) that are more or less efficient in wind dispersion; and 17 % had awns – mostly short – or narrow wings, which may play some role in seed dispersal. No species had clear adaptations to zoochory (i.e., fleshy fruits, hooked dispersule, etc.), except for the small elaiosomes present in three *Luzula* species.

Of the life-forms considered, the most commonly observed in the snowbeds were hemicryptophytes (72 %), most of which were non-graminoid (Fig. **S1**d in Electronic Supplementary Material), as is generally the case in alpine vegetation (Illa et al. 2006). Chamaephytes made up the second group (22 %), including three woody creeping species of *Salix*. Therophytes were rare and geophytes were absent. In terms of ecological preference, we included 23 species in the group of snowbed specialists, and distributed the remaining species into the groups of grasslands (45 taxa) and rocky sites (13 taxa), as described in the methods section.

Relationships between Seed Traits and Species

The first PCA based on the seed traits revealed strong correlation between width, breadth, length and weight, and between these traits and the type of appendix. To avoid an over-biased ordination, we performed a second analysis rejecting some of the most correlated traits (seed breadth, mostly correlated with seed width, and seed shape, also dependent on the three seed dimensions). Among the remaining traits, correlation within pairs in absolute values ranged from almost zero (weight and surface) to about 0.71 (length and width) as shown in Table **3**.

The species ordination shown in Fig. **1a** highlights the trade-off between seed mass and seed production, i.e., from taxa producing a few big seeds (in the upper central part: e.g., *Trifolium alpinum*, *Androsace carnea*, *Arenaria purpurascens* or *Galium pyrenaicum*) to those bearing large numbers of tiny seeds (in the lower right corner: e.g., *Gentiana nivalis*, *Saxifraga moschata*, *S. aizoides* or *Veronica alpina*). Most of

Table 2 Characterization of the taxa analyzed according to nine traits (see Table 1) and to habitat preference: Longitude and Width of the dispersule (mm), Weight of the germinule (mg), Number of seeds per ramet, Surface type (1–4, from smooth to hairy), Appendices of the dispersule (1–6, from none to pappus), Seed Bank density in the soil (1–4, from <3 to >300 of seeds * m^{-2}), Lateral Expansion (1 – none; 2 – few tillers to short distance; 3 – many to short distance; 4 – few to long distance), Life Form (Th – therophyte; Hng – non-graminoid hemicryptophyte; Hg – graminoid hemicryptophyte; Chd – difuse chamaephyte; Chp – pulvinular chamaephyte; Chr – creeping chamaephyte), and Habitat preference relating snow duration (Sb – snowbeds; Gld – grasslands, Rk – rocky places)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Agrostis alpina	6.4	0.5	0.070	30	3	4	1	3	Hg	Gld
Agrostis rupestris	3.6	0.6	0.080	40	3	4	3	3	Hg	Gld
Alchemilla fissa	1.5	0.9	0.400	18	1	1	1	4	Hng	Sb
Alchemilla pentaphyllea	1.3	0.8	0.336	6	1	1	1	4	Hng	Sb
Alopecurus alpinus	5.2	0.8	0.260	60	4	4	1	3	Hg	Sb
Androsace carnea	2.5	1.5	1.532	10	2	1	1	2	Hng	Gld
Antennaria carpatica	4.5	2.0	0.080	100	1	6	1	2	Hng	Gld
Arenaria biflora	0.8	0.7	0.133	144	2	1	3	4	Chr	Sb
Arenaria purpurascens	1.7	1.2	1.056	12	1	1	1	3	Chp	Gld
Armeria alpina	5.5	1.2	0.928	15	3	4	1	3	Hng	Gld
Astrantia minor	4.0	1.6	0.796	120	3	3	1	2	Hng	Rk
Campanula scheuchzeri	0.8	0.4	0.043	75	1	1	1	2	Hng	Gld
Cardamine bellidifolia subsp. *alpina*	1.3	1.0	0.198	40	1	1	4	2	Hng	Sb
Cardamine resedifolia	1.3	1.0	0.200	184	1	3	1	2	Hng	Rk
Carex atrata subsp. *nigra*	3.3	1.6	0.490	96	1	2	3	3	Hg	Gld
Carex curvula subsp. *curvula*	4.8	1.6	1.304	20	1	2	3	3	Hg	Gld
Carex pyrenaica	3.8	0.9	0.336	16	1	2	3	3	Hg	Sb
Cerastium cerastoides	1.1	0.9	0.166	26	2	1	4	2	Chr	Sb
Epilobium anagallidifolium	8.2	3.5	0.075	130	1	6	3	2	Hng	Sb
Euphrasia minima	1.3	0.5	0.110	70	1	1	1	1	Th	Gld
Festuca eskia	7.4	1.4	1.292	140	3	4	1	3	Hg	Gld
Festuca glacialis	5.0	0.8	0.510	18	3	4	1	3	Hg	Rk
Festuca nigrescens	7.0	1.0	0.980	80	3	4	3	3	Hg	Gld
Galium pyrenaicum	1.5	1.2	1.400	12	1	1	1	3	Chp	Rk
Gentiana alpina	0.9	0.3	0.200	50	2	1	1	2	Hng	Gld
Gentiana nivalis	0.9	0.5	0.078	1250	2	1	1	1	Th	Gld
Gentiana verna	0.9	0.5	0.090	625	2	1	1	2	Hng	Gld
Gnaphalium hoppeanum	4.9	2.5	0.090	96	4	6	2	2	Hng	Sb
Gnaphalium supinum	5.0	2.7	0.107	96	4	6	4	2	Hng	Sb
Helictotrichon sedenense	18.0	1.3	1.800	56	1	4	3	4	Hg	Gld
Hieracium lactucella	4.8	1.7	0.093	25	3	6	1	2	Hng	Gld
Kobresia myosuroides	2.5	1.0	0.690	14	1	1	3	3	Hg	Gld
Leontodon pyrenaicus	9.0	1.0	0.768	30	1	6	2	2	Hg	Gld
Leucanthemopsis alpina	3.0	1.0	0.400	30	3	3	1	2	Hng	Gld
Linaria alpina	1.8	1.6	0.160	140	1	1	1	2	Chr	Rk
Lotus corniculatus subsp. *alpinus*	1.9	3.1	1.608	60	1	1	1	2	Hng	Gld

Table 2 (continued)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Luzula alpinopilosa	1.2	0.6	0.210	108	1	5	1	2	Hg	Sb
Luzula lutea	1.4	0.7	0.360	108	1	5	2	2	Hg	Gld
Luzula spicata	1.1	0.7	0.356	57	1	5	2	2	Hg	Gld
Minuartia sedoides	0.9	0.8	0.260	75	2	1	1	3	Chp	Rk
Minuartia verna	1.2	1.0	0.312	85	2	1	1	2	Chp	Gld
Mucizonia sedoides	0.5	0.2	0.030	40	1	1	3	1	Th	Sb
Murbeckiella pinnatifida	1.1	0.5	0.122	280	1	3	4	2	Hng	Rk
Myosotis alpestris	1.8	1.1	0.540	192	1	1	1	2	Hng	Gld
Nardus stricta	10.4	0.9	0.380	15	3	4	3	3	Hg	Gld
Oreochloa disticha subsp. *blanka*	3.9	1.3	0.340	11	4	1	1	3	Hg	Gld
Oxytropis pyrenaica	2.2	1.7	2.000	48	1	1	3	2	Hng	Gld
Pedicularis kerneri	2.2	1.0	0.202	120	3	1	1	2	Hng	Gld
Phyteuma hemisphaericum	1.1	0.4	0.150	500	1	1	1	2	Hng	Gld
Plantago alpina	2.1	0.9	0.544	75	1	1	2	2	Hng	Gld
Plantago monosperma	3.3	1.6	2.990	15	2	1	3	2	Hng	Gld
Poa alpina	3.2	0.8	0.350	100	3	1	3	3	Hg	Gld
Polygonum viviparum	2.6	1.5	2.500	20	2	1	3	2	Hng	Gld
Potentilla brauneana	1.1	0.9	0,320	12	1	1	1	2	Hng	Sb
Primula elatior subsp. *intricata*	1.6	1.1	0.850	288	2	1	1	2	Hng	Gld
Primula integrifolia	1.5	1.0	0.200	159	1	1	2	2	Hng	Gld
Pritzelago alpina	1.7	0.7	0.236	30	3	3	4	2	Chd	Rk
Ranunculus alpestris	2.2	0.9	0.408	40	1	2	4	2	Hng	Sb
Ranunculus pyrenaeus	2.7	1.5	1.040	25	1	2	1	2	Hng	Gld
Sagina saginoides	0.4	0.3	0.020	450	1	1	4	2	Chd	Sb
Salix herbacea	4.0	3.0	0.510	20	1	6	1	2	Chr	Sb
Salix reticulata	3.2	2.7	0.050	96	1	6	1	4	Chr	Sb
Salix retusa	5.5	2.7	0.050	70	1	6	1	4	Chr	Sb
Saxifraga aizoides	0.7	0.4	0.050	600	2	1	2	2	Chd	Rk
Saxifraga androsacea	0.6	0.3	0.050	80	1	1	3	2	Hng	Sb
Saxifraga moschata	0.6	0.3	0.030	432	2	1	3	3	Chp	Rk
Saxifraga oppositifolia	1.1	0.5	0.110	258	3	1	2	4	Chr	Rk
Sedum alpestre	0.7	0.3	0.030	225	1	1	3	2	Chd	Sb
Sedum atratum	0.8	0.3	0.040	50	3	1	1	1	Th	Rk
Selinum pyrenaeum	4.5	3.0	1.580	300	3	3	1	2	Hng	Gld
Sibbaldia procumbens	1.2	0.9	0.470	48	1	1	3	2	Hng	Sb
Silene acaulis	1.2	1.0	0.316	21	2	1	1	3	Chp	Rk
Soldanella alpina	1.0	0.8	0.228	60	1	1	1	2	Hng	Gld
Taraxacum alpinum	11.0	4.0	0.450	30	3	6	1	2	Hng	Gld
Taraxacum dissectum	10.3	4.0	0.416	30	3	6	1	2	Hng	Gld
Thalictrum alpinum	3.1	1.1	0.432	30	3	1	1	2	Hng	Gld
Thymus nervosus	0.7	0.5	0.130	48	1	1	1	4	Chr	Gld

Table 2 (continued)

	Long	Width	Weight	Nmb	Srf	App	S-B	L-E	L-F	Hab
Trifolium alpinum	2.7	2.3	5.300	8	1	1	1	2	Hng	Gld
Trifolium thalii	1.4	1.2	0.840	30	1	1	1	2	Hng	Gld
Veronica alpina	0.9	0.6	0.040	170	1	1	4	2	Hng	Sb
Veronica aphylla	1.1	0.9	0.090	63	1	1	1	2	Hng	Sb

the species studied are spread along the area between these two extremes, with those with more rounded, unappendaged, smoother seeds located near the upper right edge. In contrast, dispersules with more conspicuous appendages and higher dimensions appear from the central part of the field to the lower left corner. This extreme consists of Asteraceae, Salicaceae and analogous types (e.g., *Gnaphalium supinum*, *G. hoppeanum*, *Salix retusa*, *S. reticulata*, *Taraxacum alpinum* or *Epilobium anagallidifolium*).

Species Groups

Life-forms show no obvious pattern in relation to seed traits. The most abundant type, hemicryptophytes, occupies almost all the area defined by the PCA (Fig. 1a). Among these, while non-graminoids are widespread, graminoids remain mostly reduced to the central-left part of the cloud. Therophytes and short-lived chamaephytes tend to be found at the lower right part, and pulvinules are mainly placed in the upper central part.

The ecological groups also overlap in the area defined by the PCA, although snowbed specialists are mostly concentrated in peripheral parts of the species cloud (Fig. 1b). The PERMANOVA test gives statistical support (P-value 0.018) to separate the two ecological groups shown in the figure (snowbed specialists *vs* non-specialists). Besides, two sub-groups of snowbed specialists may be observed in rather extreme positions (right and lower left), whereas the others are spread within the main core (upper central part).

Table 3 Pearson’s product moment correlations between the variables measured: Numb – number of seeds per ramet; Width & Long – dimensions of the dispersule; Weight – weight of the germinule; Append – appendage type of the dispersule; Soil – density of seeds in the soil bank; Surf – surface type of the dispersule. * – statistically significant at $P<0.05$

	Numb	Width	Long	Weight	Append	Soil
Width	−0.3082*					
Long	−0.3442*	0.7071*				
Weight	−0.4961*	0.5247*	0.455*			
Append	−0.0497	0.4919*	0.6766*	−0.0492		
Soil	0.0918	−0.1812	−0.0689	−0.1503	−0.0484	
Surf	−0.0255	0.1342	0.4067*	0.0086	0.2699*	−0.0861

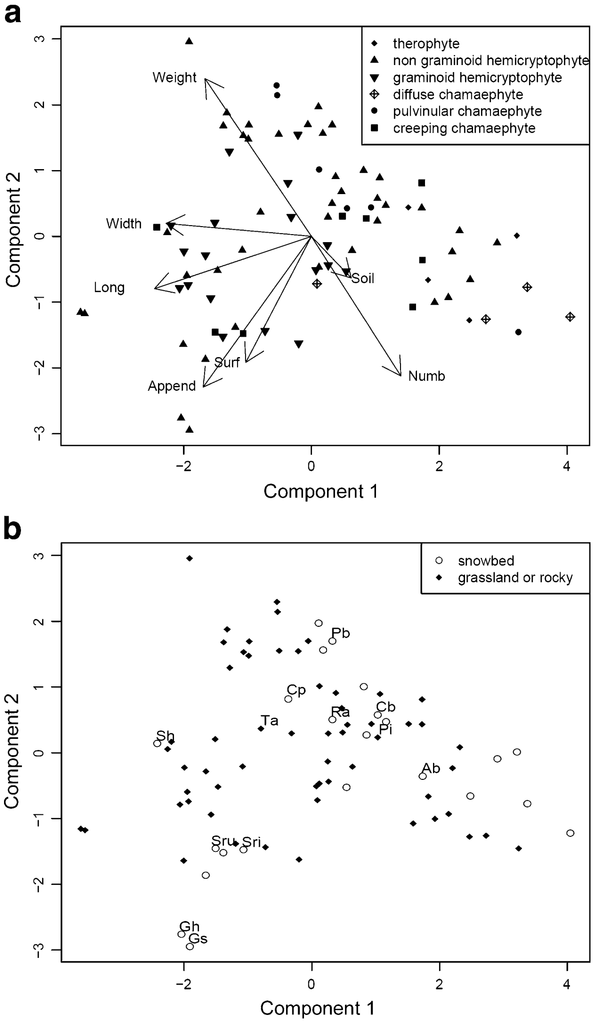

Fig. 1 Ordering of the taxa on the first two components (variance: 40.21 % and 20.15 %, respectively) given by the PCA, with the continuous variables transformed to $\log_{10}$: **a** Direction and relative weight of the traits in the analysis (abbreviated as in Table 3) indicated by the direction and size of the arrows, and life-form of the taxa; **b** Position of the snowbed specialists within the total pool considered, with the main species (Table S1 in Electronic Supplementary Material) abbreviated as follows: Ab – *Arenaria biflora*; Cb – *Cardamine bellidifolia*; Cp – *Carex pyrenaica*; Gh – *Gnaphalium hoppeanum*; Gs – *Gnaphalium supinum*; Ms – *Mucizonia sedoides*; Pb – *Potentilla brauneana*; Ra – *Ranunculus alpestris*; Sb – *Salix herbacea*; Sru – *Salix retusa*; Sri – *Salix reticulata*; Sp – *Sibbaldia procumbens*; Ss – *Sagina saginoides*

The distinct distribution of traits in each ecological group is illustrated in Fig. 2, which refers to three crucial aspects of plant life: vegetative expansion, soil seed bank, and dispersal. The group of snowbed specialists is similar to the grassland group in terms of general spectra, but is differentiated by the noticeable presence of species forming dense soil seed banks, by fewer turf-forming species and by more stoloniferous or long-rhizomatous plants. The snowbed group includes most of the long-distance disseminators; short-distance anemochory is less frequent than in grasslands, whereas barochory is more common, although clearly less so than in rocky places.

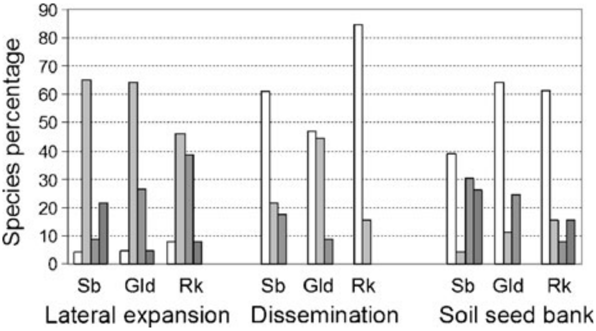

Fig. 2 Species percentages for three crucial traits in the three ecological groups considered (Sb – Snowbed specialists; Gld – Grasslands; Rk – Rocky places). The categories in each trait are indicated as growing grey intensities, in the following order: *i*) Lateral expansion: none, few tillers to short distance, dense turf, few tillers to long distance; *ii*) Dispersal mode: barochory, anemochory to short distance, anemochory to long distance; and *iii*) Density in the soil seed bank: from absent or very low to very high

Discussion

The Effect of Snowbed Constraints on the Flora

Snowbeds are particular habitats within alpine landscapes, in which plants are limited by various environmental constraints. Our results, together with other studies (Cherednichenko 2004; Choler 2005; Illa et al. 2006) show that snowbeds harbor less diversity of plant traits than do less restrictive habitats, and that they promote greater frequency of specific types or traits, such as deciduous woody chamaephytes, long stolons or rhizomes, or higher N content in leaves (Choler 2005). The snowbed species pool studied here includes no zoochorous species (producing fleshy fruits, or hooked or adherent seeds) nor geophytes. The seeds are mostly reduced to low-weight values and to ovoid or elliptical shapes (Fig. **S1** in Electronic Supplementary Material). A similar distribution of mass values has been found in other alpine assemblages (Zhang et al. 2004; Navarro et al. 2009), whereas in temperate floras the modal seed weight is one order of magnitude higher (Cerabolini et al. 2003).

A few plant types acquire particular relevance in snowbeds, more in terms of dominance than of species numbers. This is the case of deciduous chamaephytes (i.e., *Salix* spp.), and of therophytes and pauciennials, which produce large numbers of persistent seeds (*Mucizonia sedoides, Sagina saginoides*). In fact, the density of seeds found in the soil has been identified as a good surrogate for seed persistence in some snowbed ecosystems (Cerabolini et al. 2003; Semenova 2004; Lluent 2007).

These weak tendencies become stronger if the 23 snowbed specialists are considered as a unit (Fig. 2). This is partly related to the particular taxonomical composition of this group, in which the richer families in the alpine flora (i.e., Asteraceae, Poaceae, Brassicaceae, Caryophyllaceae and Fabaceae; Körner 2003: 14) are poorly represented (Table **S2** in Electronic Supplementary Material). The rarity of Poaceae among snowbed specialists may be related to seed traits, because most grasses produce moderate numbers of seeds, which disseminate over a short distance and have low persistence in soil. Although these limitations are of minor importance in grasslands, they seem to become disadvantageous in snowbeds, where most species produce seeds that are persistent in the soil bank or are easily air-dispersed (Onipchenko and Semenova 2004). The relative decline of the other families mentioned above seems to be related to other biological features, because their seeds show no clear trends in relation to snowbed function. In fact, the relative increase of other taxa in the group of snowbed specialists (*Salix*, Crassulaceae) could explain the increase of co-occurring plant traits derived from their phylogenetic signal, which do not necessarily enhance their adaptation to snowbeds. Thus, the ecological filtering of plant traits in snowbeds seems to have shaped the chionophilous assemblage at the family level, because seed traits are rather dependent on these taxonomic entities (Šerá and Šerý 2004).

Diversification into Snowbed Microhabitats

It should be taken into account that snowbed specialists thrive in rather different microhabitats. Not only the duration of the period with snow cover, but also substrate properties affect them. Thus, chionophilous plants may be included in a few contrasting types and strategies, some of which involve specific seed traits. The morpho-functional analyses presented in this study (Fig. **1**) reveal three main strategy groups: *i*) annuals or short-lived perennials producing relatively small and abundant seeds, mostly without any dispersal aptitudes, which tend to accumulate in the soil bank up to high densities; *ii*) woody chamaephytes (ex. *Salix* spp.) or hemicryptophytes producing medium-to-high numbers of anemochorous seeds, thus ensuring vegetative persistence and wide wind dispersion; and *iii*) other perennials with no specific seed traits (medium production, low or no seed bank, barochory). In the first group, the maintenance of populations is based on the occupancy of patches with lower competition, which may generally develop in the late-melting parts of snowbeds or in small gaps of other snowbed parts or of neighbouring pastures (Semenova 2004; Welling et al. 2004; Lluent et al. 2006; Schöb et al. 2010). Favourable years would lead to a strong increase in the soil seed bank of these species in the areas where they normally or exceptionally thrive. In the second group, population maintenance is more ensured through perennial habit, mostly in the case of woody chamaephytes, and through annual seed rain facilitating occasional recolonization of favorable sites (Choler 2005; Lluent et al. 2006). Because the climatic conditions affecting snowbeds follow a very irregular pattern between years, species of the first two groups will presumably persist better if the decrease in areas occupied by snowbeds in the Pyrenees persists in the future (López-Moreno et al. 2009) under the expected warmer climate at regional scale (Esteban et al. 2010). Comparatively, the third group seems to face a more uncertain future; dispersal and persistence in soil are very limited (Scherff et al. 1994; Welling et al. 2004) and, in the cases of poorer tillering, vegetative performance may not ensure strong persistence.

Long-Term Persistence of Snowbed Plants

When estimating the nature of the soil seed bank in snowbeds, it should be taken into account that the persistence of viable seeds in natural conditions is only partially known. The few specific studies done on this subject (Molau and Larsson 2000; Semenova 2004) and our data neglect the presence of viable seeds of taxa with specific germination requirements, which cannot be reproduced in non-natural conditions. Most of the species pool investigated fulfils the morphological template proposed by Thompson (1993b; reviewed in Fenner and Thompson 2005: 82–86), which predicts that small seeds (<1 mg) with a fairly isometric shape (variance among dimensions <0.18) would persist easily in the soil (Fig. 3). This hypothesis has been supported by case studies on distinct species pools. However, these morphological traits do not ensure seed viability (Cerabolini et al. 2003). In our study, most of the species considered, and most of the snowbed specialists, fall in the graphic area (Fig. 3) that is characteristic of persistent seed banks. The only exceptions within these specialists are *Alopecurus alpinus* and *Carex pyrenaica*. However, a few non-chionophilous species with variance values higher than 0.18 were found in the soil bank (i.e., *Poa alpina*, *Helictotrichon sedenense*, *Nardus stricta*, *Kobresia myosuroides* and *Carex atrata* subsp. *nigra*). All these exceptions belong to Poaceae and Cyperaceae, whose bare fruits fulfil the shape conditions and may thus incorporate into the soil after losing the attached bracts or utricles. Moreover, the coarse soils found in snowbeds facilitate seed trapping, even for grasses and sedges, as experimentally found in sandy alpine soils (Chambers et al. 1991; Marcante et al. 2009).

Several snowbed specialists combine medium-to-high seed production with medium-to-high density of their soil seed bank, a trend also found in other snowbed ecosystems (Semenova 2004). Even some species producing only moderate seed numbers form large soil banks (*Sibbaldia procumbens*, *Sagina saginoides*, *Mucizonia sedoides*), which may progressively accumulate through time (Semenova 2004; Lluent 2007).

It has been hypothesized that snowbed specialists will be negatively affected under a scenario of rising temperatures because of the greater competitiveness of grassland species, which are favored by longer growing seasons (Schöb et al. 2009). More precisely, Björk and Molau (2007) envisage a stronger effect on chionophilous grasses and sedges than on chionophilous chamaephytes or forbs. In our case, only two species of these taxonomic groups are snowbed specialists, while others are weakly chionophilous. The seeds of these graminoids cannot ensure persistence in the

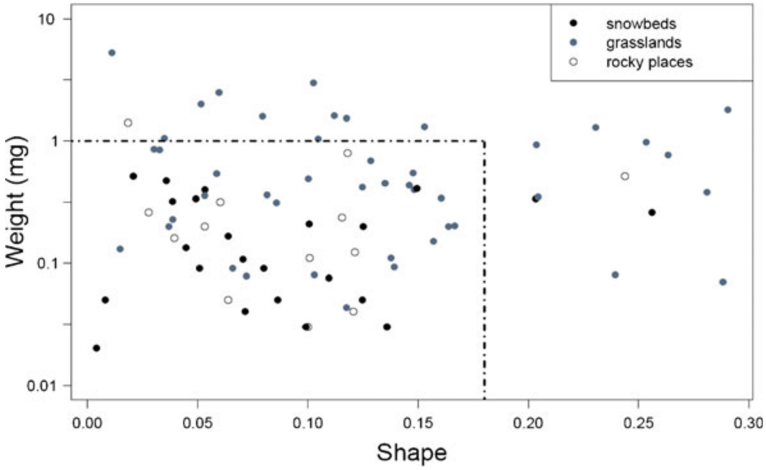

Fig. 3 Ordering of the taxa according to seed weight and seed shape coefficient (variance between dispersule length, width and breadth). The area hypothesized for species with persistent soil seed bank (seeds slighter than 1 mg, and with shape coefficient lower than 0.18) includes most of the snowbed specialists, and all the species well represented in the soil seed bank

soil or re-colonization from distant sites if they are displaced by more competitive alpine graminoids. More generally, snowbed specialists belonging to the third strategy group mentioned above seem to be prone to suffer more directly from competitive exclusion, in a scenario of a warmer climate (Esteban et al. 2010) and fluctuating or vanishing snowbeds. Their competitive disadvantage in respect to grassland species may not then be compensated by seed traits that favor their success in finding spatial or temporal ecological windows.

Concluding Remarks

As hypothesized, seed function seems to have played a noticeable role in the ecological selection of the extant snowbed plant assemblage in the Pyrenees. The group of snowbed specialists clearly shows some trait convergence in terms of seed types compared to the whole alpine flora. However, it still includes a few contrasting strategy sub-groups, whose persistence and regeneration in snowbeds depend on specific seed morphology and function combined with other plant traits.

The ecological filtering occurring in snowbeds has positively or negatively selected some taxonomic groups (families, genera) through the selection of some functional plant traits inherent to phylogeny (e.g., fruit type and vegetative tillering in grasses, or seed and habit in *Salix*).

The ongoing climate warming in the Pyrenees may reduce the chionophilous flora at regional scale, and we predict that it will have a stronger effect on those species that lack the specific morpho-functional traits associated with snowbeds.

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