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Patterns of plant traits in Pyrenean alpine vegetation ☆

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Abstract

Here we studied the adaptation of plant communities to environment in the alpine belt of the Catalan Pyrenees through comparative analysis of plant traits. The starting point consisted of about 800 phytocoenological relevés from the Banc de Dades de Biodiversitat de Catalunya, which corresponded to 47 communities (associations and subassociations) and included 683 taxa. Eleven attributes were examined in each community. Some of these traits are directly referred to the community level (averages of cover, species richness or diversity of life forms) and others to species level, but expressed as the relative cover in the communities (percentages of life forms, succulence, evergreeness, woodiness, lateral spread ability, dissemination type). Alpine landscape is mainly made up of hemicryptophytes, of which graminoids dominate in terms of cover and non-graminoids in species number. Strong persistence via plurennial stocks or dense turfs, entire above-ground renewal over winter, lateral spreading over short distances and generalistic diaspore dissemination complete the main attributes of the High Pyrenees and most alpine floras. Nevertheless, considerable percentages of particular plant types (like therophytes, various kinds of chamaephytes, succulents, evergreens and berry-producers) give a highly diversified alpine belt.

On the basis of the attributes, we performed a fuzzy multivariate classification of plant communities, which gave seven main vegetation groups, and five subgroups in the largest category (pastures). Most of the groups coincided with high-level syntaxa (classes, orders) and corresponded to the main habitats of the alpine belt, defined in terms of topography and related soil and microclimate descriptors. With respect to the spectrum of attributes of the whole alpine flora, the most differentiated groups of communities corresponded to several main habitats, all of which associated with stress conditions (scarcity of soil, unfertile or waterlogged substrata). These plant communities tend to be species-poor and show relatively high percentages of particular types. Groups less differentiated from the global spectrum included mainly richer communities with more shared dominances, and correspond to more balanced environments.

Keywords: Functional attributes; Habitats; Plant communities; Ordination; High mountain

Introduction

Plants are subjected to several limiting constraints in alpine habitats: shortness of vegetation period, scarcity of soil, low levels of nutrients, strong daily thermal

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☆*Nomenclature*: Names of higher plants follow De Bolòs et al. (2005), and names of syntaxa are those stated in the Banc de Dades de Biodiversitat de Catalunya (Font 2005).

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amplitudes and related processes (Billings and Mooney 1968; Braun-Blanquet 1948; Körner 1999; Onipchenko and Blinnikov 1994). These constraints determine the main feature of the alpine belt, i.e., the lack of forest development. Hence, alpine potentiality corresponds to pastures, which are diversified into various communities depending on microclimate and soil conditions. However, alpine landscapes include notable surfaces that offer extreme conditions for plant life, such as short growth period in snow beds, extreme winter temperatures in ridges and steep slopes, or waterlogging and infertility in the bottom of valleys. In these conditions, as well as on surfaces occupied by scree or rock, pastures are replaced by particular plant communities (Braun-Blanquet 1948; Carreras et al. 1993; Carrillo and Ninot 1992; Vigo 1996). Consequently, alpine vegetation is diversified into dense mosaics following heterogeneous ecological conditions. The boundaries between neighbouring communities are often sharp, and discriminate not only between distinct species sets but also between contrasting plant forms and functions (Körner 1999; Onipchenko 1994; Shaver et al. 1997).

Moreover, the alpine belt has not escaped human influence, although the effects of human activities are weaker than at lower altitudes. Pastures have been grazed for centuries by domestic livestock and have been extended downwards by means of clearing subalpine pinewoods. This process has strongly modified the transition zone above the timberline (De Bolòs et al. 2004; Pignatti et al. 1988), where scrubs and open krummholz formations previously prevailed and have since been replaced by pastures, which hold woody units only on rocky or abrupt surfaces. In addition, the structure and composition of the best alpine pastures are conditioned by increased grazing pressure of domestic cattle and sheep.

Like in other landscapes, alpine plant communities are dynamic assemblages, where changing events may produce considerable changes in species composition and structure. A notable part of the alpine landscape is subjected to non-equilibrium situations, species replacements may therefore involve substantial shifts in coarse vegetation structure and ecosystem function. Several examples of these shifts, caused by Quaternary climatic changes, have been documented from soil and lacustrine sediments over the last millenia (Blinnikov 1994; Carcaillet and Brun 2000; Montserrat 1992; Tinner and Theurillat 2003). The present coupling of climatic change and pasture abandonment is expected to contribute to further strong shifts.

In this context, and to increase our knowledge of vegetation dynamics, a comprehensive analysis of the alpine vegetation in terms of structure and function is crucial. Although several studies have addressed phytocoenological aspects in the Pyrenees, few functional studies have been performed. Therefore, a broad morpho-functional analysis of alpine vegetation is required, supported by phytocoenological data and by trait assessment of the species included. In this regard, the reductive analyses of flora and vegetation, such as the spectra of life forms (Raunkiaer 1934), growth forms (Barkman 1988), plant strategies (Grime 2001; Frey and Hensen 1995) and plant functional types (Box 1996; Chapin et al. 1996; Gitay and Noble 1997) contribute to our understanding of the ecological constraints of plants and their communities from scaling abstraction levels. These analyses involve accurate selection and evaluation of attributes, with a compromise between ecological significance and the possibility to assess the whole alpine flora. The community level has been identified as the most adequate for the study of specific adaptive responses to particular environments (Körner 1999, p. 2).

Here, we analyse plant adaptation to environmental conditions in the alpine belt, considering plants structured into communities, and evaluating them through their main morpho-functional traits or attributes. This study is a basic step, useful both per se as a standardised compilation of functional knowledge, and providing a starting point for further studies. In addition, the results can be applied for the conservation management of communities and landscapes.

Material and methods

Study area

The study was performed in the alpine belt of the Catalan Pyrenees, i.e., the high mountain areas where subalpine *Pinus uncinata* forests do not develop because of climatic constraints. The deforested higher part of the subalpine belt was not included, although at present it hosts plant communities that are very similar to those found in the alpine belt. According to Carreras et al. (1996), the alpine belt occurs from 2400 m a.s.l. upwards on south-facing slopes and from 2200 m a.s.l. upwards on north-facing exposures, flats or concavities. These altitudinal boundaries run about 100 m lower in the eastern part of the range and in the Aran valley, both areas subject to more maritime climates.

Although bioclimatic conditions are extremely variable over the alpine belt, there is a general trend, i.e., the length of the plant growth period decreases regularly in parallel with increasing altitude, from 88 days at 2300 m a.s.l. to 42 days at 2700 m a.s.l., and to 0–3 days at 3100 m a.s.l. (Gómez et al. 1997).

The study area, made up of alpine surfaces in Catalonia and Andorra (Fig. 1), is split into irregular units, corresponding to the higher slopes and summits of various ranges. The Pre-Pyrenean ranges appear as

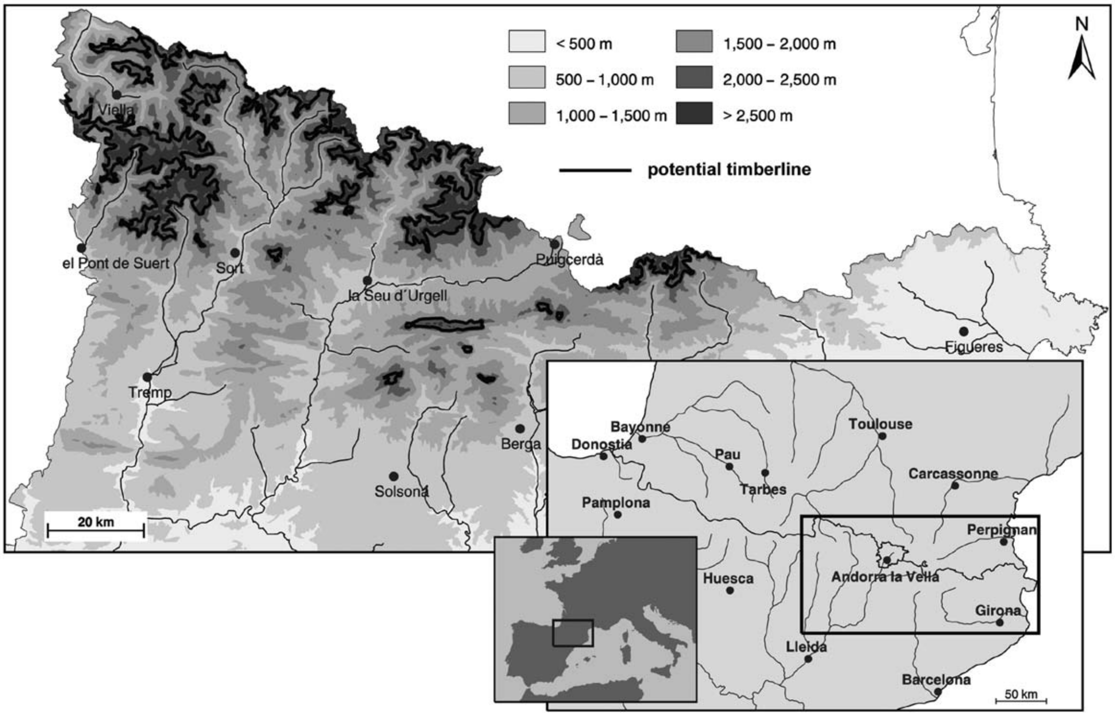

Fig. 1. Delimitation of the alpine belt in the Catalan Pyrenees.

small to medium-sized islands detached southwards from the main range, peaking between 2400 and 2600 m; their alpine vegetation is dominated by calcicolous taxa and includes several Mediterranean orophytes. From Puigcerdà eastwards, the eastern part of the main range also forms a unit, reaching altitudes of 2600–2800 (2909) m, and bearing floristic particularities and a maritime climate. In contrast, in the north-western corner, around Viella, is the Aran valley, with higher altitudes, also ranging from 2600 to 2800 (3014) m, and showing Atlantic influence from climatic to landscape aspects, as it is part of the north face of the main range. The rest comprises complex mountains and massifs (including a number of summits over 3000 m, and considerable surfaces above 2800 m), mainly acidic, abrupt, and under continental climatic influence.

The total surface projection of the study area is 735 km^2, of which the Pre-Pyrenees account for 37 km^2, the eastern Pyrenees 83 km^2 and the Aran valley 129 km^2 (Carreras et al. 1996). The area shows a clear dominance of acidic pastures, extensive rocky surfaces and scarcity of fens and scrubs (De Bolòs et al. 2004) (Table 1).

Table 1. Surface projection of the main habitats in the Catalan alpine belt

Habitats	Surface (km^2)	Percentage
Rhododendron scrub	15.0	2.0
Acidophilous pastures	432.6	58.9
Calcicolous pastures	53.6	7.3
Acidic rocks and screes	187.3	25.5
Calcareous rocks and screes	38.3	5.2
Fens	2.1	0.3
Lakes	5.7	0.8

Vegetation data

For this study, we used the relevés available for the alpine belt of the Catalan Pyrenees. Using a comprehensive list of the alpine plant communities known from there, we searched all the corresponding relevés which fulfil the "alpine" condition (as described in the previous section) in the data bank "Banc de Dades de Biodiversitat de Catalunya" (Font 2005). To ensure the significance of data, communities with less than five relevés were rejected. Therefore, a few specific associations were not studied, such as Cratoneuretum commutati or Gnaphalio-Sedetum hoppeani. We next retained 798 relevés, classified into 47 communities (43 associations, two of them split into subassociations; see Appendix A).

The compilation of the relevés and the following calculations were done using the "Quercus" processor, part of the "VegAna" package (De Cáceres et al. 2003). We changed the dominance/abundance indexes given in the original relevés to the mean cover values defined by Braun-Blanquet (1979) and we averaged the covers for each community and taxon in order to build a synthetic table. After some nomenclature unification and simplification of low-level taxonomy, the table included 683 taxa (× 47 columns), 560 of which were higher plants and 123 terricolous mosses, lichens or liverworts.

Statement of attributes

After a review of the literature on plant attributes (Barkman 1988; Box 1996; Gitay and Noble 1997; Grime et al. 1988; etc.) and taking into account the volume and nature of the data to be handled, we selected 11 easily measured traits which have been identified as potentially useful predictors of ecosystem functioning. These can be ordered into general community attributes and functional plant attributes. Community attributes are as follows:

(a) *Global cover* of the vegetation, i.e., the average of the covers given to the relevés of each community.
(b) *Cumulate cover*, i.e., the sum of the cover means of the taxa included in each community. This measure evaluates general cover and structure; values higher than 100 express above-ground overlapping or stratification.
(c) Mean of higher plant taxa included in the relevés as an evaluation of *species richness* of each community.
(d) Total *number of families* in the whole community, assuming this to be a rough evaluation of diversity, complementary to species richness.

The plant attributes selected were:

(e) Raunkiaer (1934) *life forms*, subdivided into narrower types following other sources (Halloy 1990; Körner 1999). The main cryptogam groups settling on soil were also considered. Thus, we obtained 11 types: nanophanerophytes, suffruticose chamaephytes (like *Vaccinium myrtillus*), diffuse chamaephytes (*Sideritis hyssopifolia*), pulviniform chamaephytes (or small cushions, like *Silene acaulis*), creeping chamaephytes (*Thymus nervosus*), graminoid hemicryptophytes, non-graminoid hemicryptophytes, geophytes, therophytes, bryophytes and lichens.
(f) *Diversity of life forms*, calculated through the Shannon–Weaver index, as follows:

$$\mathrm{SHDI} = -\Sigma(p_i \ln p_i),$$

where p is the partial cover of each life form over 1, and i is each life form. Higher values are expected for the communities with more life forms included, and these more evenly distributed.

(g) *Succulence* considers three levels: non-succulent, semi-succulent (some Liliaceae, Orchidaceae or Saxifragaceae) or succulent (Crassulaceae).
(h) *Evergreeness* considers fully evergreen taxa, partially evergreen taxa (like *Vaccinium myrtillus*) or plants that lack green parts in winter.
(i) *Woodiness*, expressed also as a three degree characteristic; semi-woody taxa correspond to some chamaephytes, mainly herbaceous but with a conspicuous woody basis.
(j) Capacity for *lateral spread* and clonal multiplication, evaluated as four possible states: lack of lateral expansion, spreading to short distance (few tillers closer than 2.5 cm to the mother plant), spreading to long distance (tillers farther than 2.5 cm caused by long rhizomes, or creeping, rooting twigs in some woody plants) or forming dense turfs.
(k) *Dissemination* type, or distance reached by diaspores, considering five states: very long distance (species with dust-like seeds or spores), long distance (as in Asteraceae with hairy or plumose achenes), short distance (species setting winged or membranous diaspores, like *Peucedanum ostruthium* or *Festuca* spp.), no apparent mechanism (*Rhododendron ferrugineum* or *Silene acaulis*) and endozoochory (a few dwarf shrubs with fleshy fruits). Finally, for analytical purposes, we merged categories one and two because they give similar results at the landscape scale.

The attributes that directly referred to plant communities (*a, b, c, d* and also *f*) were expressed as numerical values. Attributes *g*, *h* and *i*, each categorised into three states, were also expressed as a single value each per community, calculated as the relative cover of plants presenting the fully developed attribute plus half of the relative cover of plants partially bearing the attribute. Regarding the other attributes (*e, j* and *k*), the relative cover of the group of taxa bearing each attribute in each state was taken as a community descriptor (such as relative covers of nanophanerophytes, or of taxa with long-distance dissemination). In most of the proposed systems of plant attributes, characters of diverse type are combined and organised into a hierarchy (Barkman 1988; Box 1996; Halloy 1990, etc.); however, we considered all attributes at the same level, since there is not enough basis on which to give more relevance to particular ones (Orshan 1986; Semenova and Van der Maarel 2000). The combination of plant attributes into specific life histories results in plant strategies, which define the capacity of each taxon to persist and expand, disseminate and colonise, and also modify its environment. When combined at community level, these attributes define community functions and relationships with the environment, including responses of ecosystems to changing conditions (Lavorel and Garnier 2002).

Classification of communities and analysis of the vegetation groups

To study the segregation of attributes across alpine habitats, the classification of communities into groups should be done on the basis of these functional characters. However, community classification generates the transitional position of certain units between distinct groups, which reflects some of the progressive transitions of nature. Therefore, here we chose a fuzzy classification of communities. The main feature of this classification system is that one element's membership can be shared between two or more groups. Here we used Fuzzy C-means (Bezdek 1981), a classification method available in the statistical module "Ginkgo", part of the "VegAna" package (De Cáceres et al. 2003). One drawback of this method is that it requires the specification of the number of groups to be found. As a criterion to facilitate this decision, we used a non-parametric statistic of cluster isolation called "Silhouettes" (Rousseuw 1987).

Using the standardised data on community attributes, we built a similarity matrix, which was the reference matrix used for classification. The resulting fuzzy groups and subgroups of communities were considered units in the comparative analysis of attributes with respect to the main habitats in which they are found.

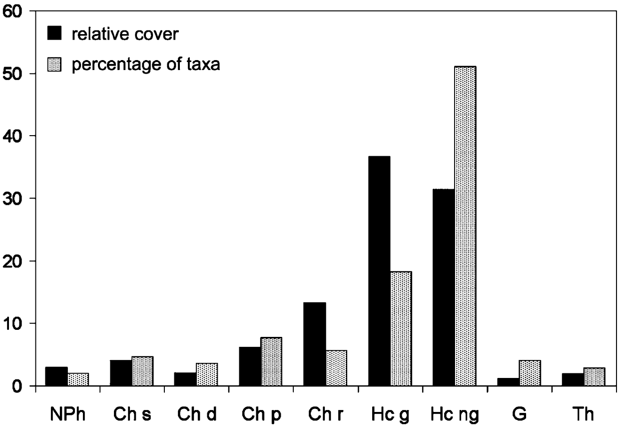

Fig. 2. Percentages of life forms of higher plants in the alpine vegetation of the Catalan Pyrenees, taken as the mean values across the communities recorded. NPh, nanophanerophytes; Ch s, suffruticose chamaephytes; Ch d, diffuse chamaephytes; Ch p, pulviniform chamaephytes; Ch r, creeping chamaephytes; Hc g, graminoid hemicryptophytes; Hc ng, non-graminoid hemicryptophytes; G, geophytes; Th, therophytes.

Results and discussion

General trends in the attributes of alpine vegetation

A first general characterisation of alpine vegetation may be attempted from the data summarised in the general table of Appendix B, which provides an average of the values of each attribute in the 47 communities studied.

The main structural aspect corresponds to the spectrum of life forms (Fig. 2), which showed a strongly uneven distribution, both in terms of number of taxa and plant cover. Two groups were dominant: graminoid and non-graminoid hemicryptophytes. These two groups showed opposite patterns. While graminoids accounted for more than one-third of mean cover across the alpine communities (36.6%), and a moderate 18.3% of the alpine taxa, forb hemicryptophytes exhibited a slightly lower mean cover (31.6%) but much more diversity (51.1% of total taxa). Similar patterns have been described in other alpine landscapes and in the arctic (Körner 1995; Komárková and McKendrick 1988). Together, these two groups reflected the strong prevalence of hemicryptophytes in the alpine belt (68.2% of mean cover, 69.4% of taxa), where plants are subjected to a clearly seasonal regime, in which the growing period, although rather short, is favourable (at least concerning light, temperature and water) and predictable.

All the subgroups of chamaephytes presented low percentages, but together accounted for 25.7% of mean cover and 21.7% of taxa. This significant presence is related to various stress conditions – mainly derived from infertile soils – and to low perturbation regimes, which enable plants to persist for many years with small above-ground perennial structures, which are frequently lignified (Gerdol et al. 2000a; Shaver et al. 1997). This situation is exemplified by the two main subgroups, creepers (13.3% of mean cover, 5.7% of taxa) and pulvinules (6.2%, 7.7%), both frequently found in rocky sites. Pulvinules are especially adapted to summits and other high mountain habitats. According to Körner (1999, p. 39), their fitness is related to thermal functioning caused by a compact form, which would not be functional in warmer lowland habitats, and to substrate improvement through retention of litter, water and soil fertility.

Therophytes, geophytes and nanophanerophytes are minor groups in alpine flora (Bliss 1971; Gómez et al. 1997; Körner 1999). In our study, the two former types presented lower cover percentages than species diversity, and were sparse in the whole belt. In contrast, nanophanerophytes showed greater cover than diversity and were restricted to the lower part of the belt.

Evergreeness, woodiness and succulence seem inadequate attributes under alpine conditions. Plants with each of these traits accounted, nevertheless, for about 7% of the taxa (Table 2). While evergreeness and woodiness are clearly more relevant at lower altitudes, succulence is more frequent in the alpine belt (Carrillo and Ninot 1992; Vigo 1996); according to Körner et al. (1989), this succulence pattern is a general feature in high mountain areas in temperate regions.

Table 2. Means of cover and occurrence percentages of taxa with the functional attributes considered in the whole Catalan alpine vegetation

	Cover (%)	Taxa (%)
Vegetative particularities		
Succulent taxa	6.8	7.2
Woody taxa	13.9	7.0
Evergreen taxa	10.9	6.8
Lateral spread		
Taxa without lateral spreading	3.6	4.3
Taxa spreading to < 2.5 cm	26.3	39.5
Taxa spreading to > 2.5 cm	29.6	30.3
Taxa forming dense turfs	40.5	25.9
Diaspore dissemination		
Taxa with dust-like diaspores	3.0	4.9
Taxa with hairy or plumose diaspores	13.7	13.0
Taxa with winged or membranous diaspores	34.4	24.7
Taxa with seeds lacking special mechanisms	44.2	54.3
Taxa with fleshy fruits (endozoochory)	4.7	3.1

Our data corroborate lateral spread and eventual clonal multiplication as useful attributes in alpine environments, as only 4.3% of taxa did not show lateral expansion (Table 2), which is consistent with the findings of other studies performed in alpine and arctic areas (Billings and Mooney 1968; Körner 1995). The development of these strategies may be attributed to generalised difficulties in completing life cycles under harsh arctic and alpine conditions (Bliss 1971). Vegetative expansion is the mechanism by which alpine plants achieve crown expansion and eventual dominance, and community structure is maintained (Forbis 2003). The same capacity is shown by arctic vegetation and has been related to the space and time heterogeneity encountered by plants (Carlsson et al. 1990). In our study, the most efficient expansion mechanism seems to combine persistence in microsites with slow expansion through nearby offspring, as most of the alpine flora (65.4%) expanded a short distance from the mother plant (Table 2). This is achieved through dense turfs, mainly in dominant graminoids, or by means of few sprouts, in less dominant plants.

Temporal and spatial colonisation is achieved through diaspores, which, in addition, accomplish sexual reproduction. These ecosystem functions are uneven and even hazardous under alpine conditions because of climatic constraints. Thus, the supply of diaspores aimed to regeneration of populations and colonisation of new habitats must be accomplished in the few years with good seed production (Molau and Larsson 2000). Our observations indicate that only a few plants are related to zoochory: no species showed clear adaptations to ectozoochory, and only 3.1% were endozoochorous (some Ericaceae and *Juniperus communis* ssp. *alpina*). Even in this case, the production of fleshy fruit is more related to phylogeny than to function, as this dissemination mechanism in *Vaccinium* species shows low efficiency (Vander Kloet and Hill 1994). More than half the taxa do not show apparent mechanisms for dispersing diaspores, which are generally small and isometric, a typical feature of plants that have the capacity to persist in soil seed banks (Thompson et al. 1993). Thus, most of these taxa would be able to recover their populations in situ after perturbations, such as vegetation dieback and soil erosion, or the opening of small gaps. Long-distance dissemination was observed in almost 18% of taxa with plumose or dusty diaspores, which may dominate the colonisation of newly open habitats, like moraines uncovered by ice, snow beds or stream banks (Ozinga et al. 2004). Moreover, in spite of the low percentages of specialised modes of dispersal, frequent and long-distant diaspore dissemination is common in arctic and alpine landscapes (Tollesfrud et al. 1998). This may become significant in case of climatic change, as main governing factor of changes in composition and structure of varying communities (Molau and Larsson 2000).

Grouping alpine communities in function of plant attributes

The ordination of the communities on the basis of attributes is shown in Fig. 3 using the first two axes. In this ordering, we took the fuzzy partition into seven groups, since it yielded the highest value of silhouette average within the range from four to 11 groups. This classification is also meaningful with respect to vegetation physiognomy and functioning:

1. Evergreen scrubs: from dwarf, creeping *Loiseleuria* carpets to medium-sized heaths (numbers 43–46 of Appendix A).
2. Deciduous scrubs: woody snow bed communities and similar dwarf scrubs (39, 41, 42).
3. Hygrophilous communities: herbaceous carpets developing in and around rivulets and springs (1, 2, 11).
4. Rock communities: disperse fissuricolous communities (6–10, 15) and one open, transitional pasture (33).
5. Therophytic scree communities: sparse communities formed by annuals and perennials, settling on small- to medium-textured scree (14, 16, 17) or on gravel- and sand-rich snow beds (40).
6. Perennial scree communities: sparse communities of perennials, settling on medium- to coarse-textured scree (12, 13, 18, 19).
7. Pastures, in broad sense.

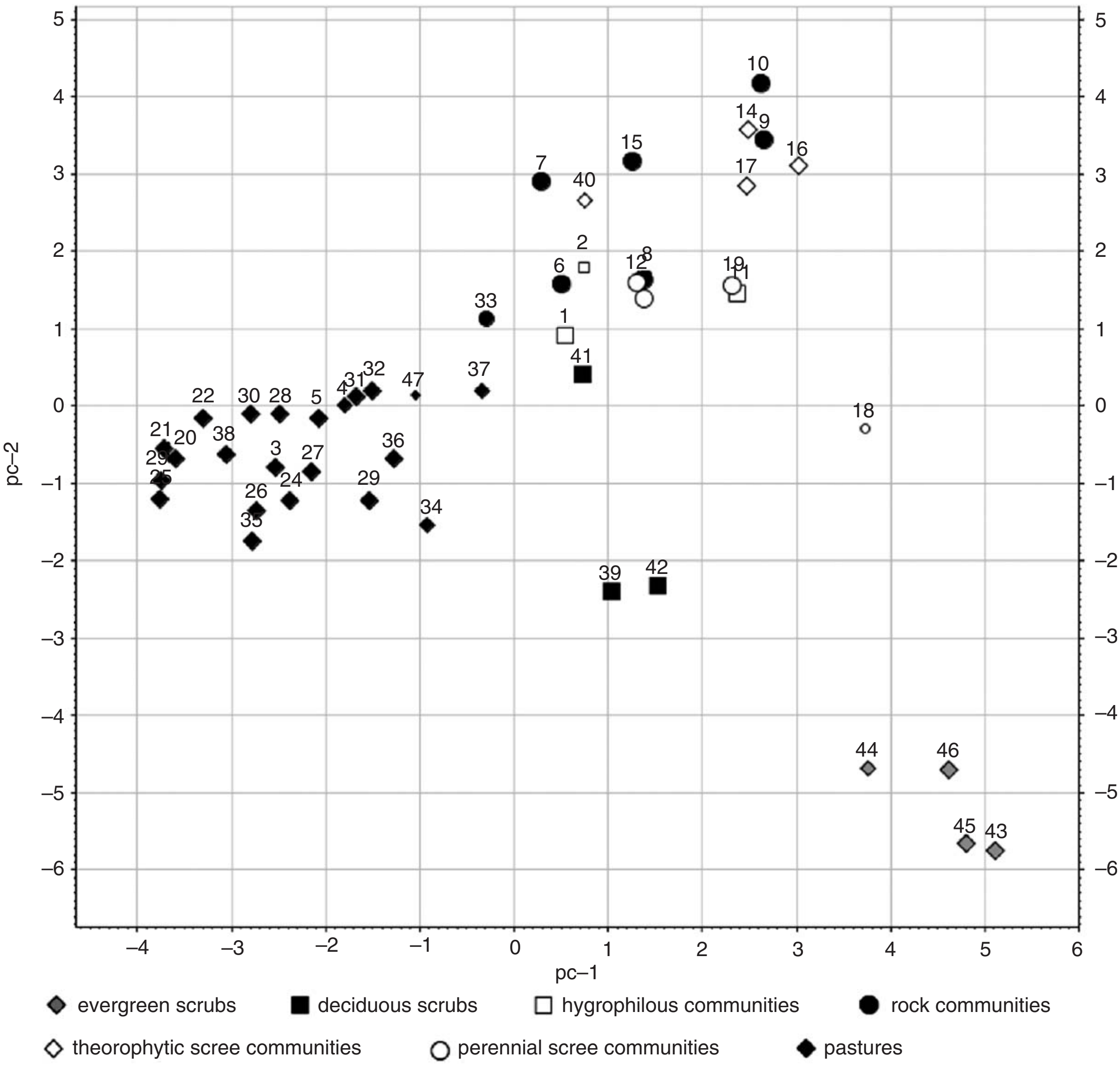

Fig. 3. Fuzzy C-means ordination of the communities studied on the space defined by the two first axes (23.96% and 19.42% of variance). The size of the symbols indicates the membership degree of each community to the corresponding group. Numbering of communities is given in Appendix A.

As expected, the group of pastures was much larger (22 communities) than the other categories. Thus, we performed a second analysis restricted to pastures and took the cut-off level of five subgroups, as this was the most meaningful from a physiognomic and functional viewpoint (Fig. 4):

7a. Dense pastures (numbers 20–23, 25, 30, 38).
7b. Summit open pastures (26–29, 31, 34).
7c. Sloping open pastures (24, 32, 35–37).
7d. Fens (3–5).
7e. Tall-herb community (47).

Most of these groups and subgroups coincided with high-level syntaxa (classes, orders), in some cases with small differences, such as the inclusion of Saxifrago-Minuartietum (33) in rock communities, or Gnaphalio-Sedetum (40) in communities on fine scree, which is related to strong functional particularities of both associations within their phytocoenological classes. The attribute-based classification did not reflect differentiation between calcicolous or calcifuge communities, which results in distinct orders or classes in the floristic-based, phytocoenological system. However, it assembles in the same group functionally related communities, such as sloping pastures, or dense pastures. The attribute-based ordination and classification reflect the main habitats of the alpine belt, defined in terms of topography and related soil and microclimate descriptors (Fig. 5). As a general rule, the vegetation groups most coincident with syntaxa (1, Vaccinio-Piceetea; 3, Montio-Cardaminetea; 4, Asplenietea; 7d, Scheuchzerio-Caricetea; 7e, Betulo-Adenostyletea) are more associated with certain

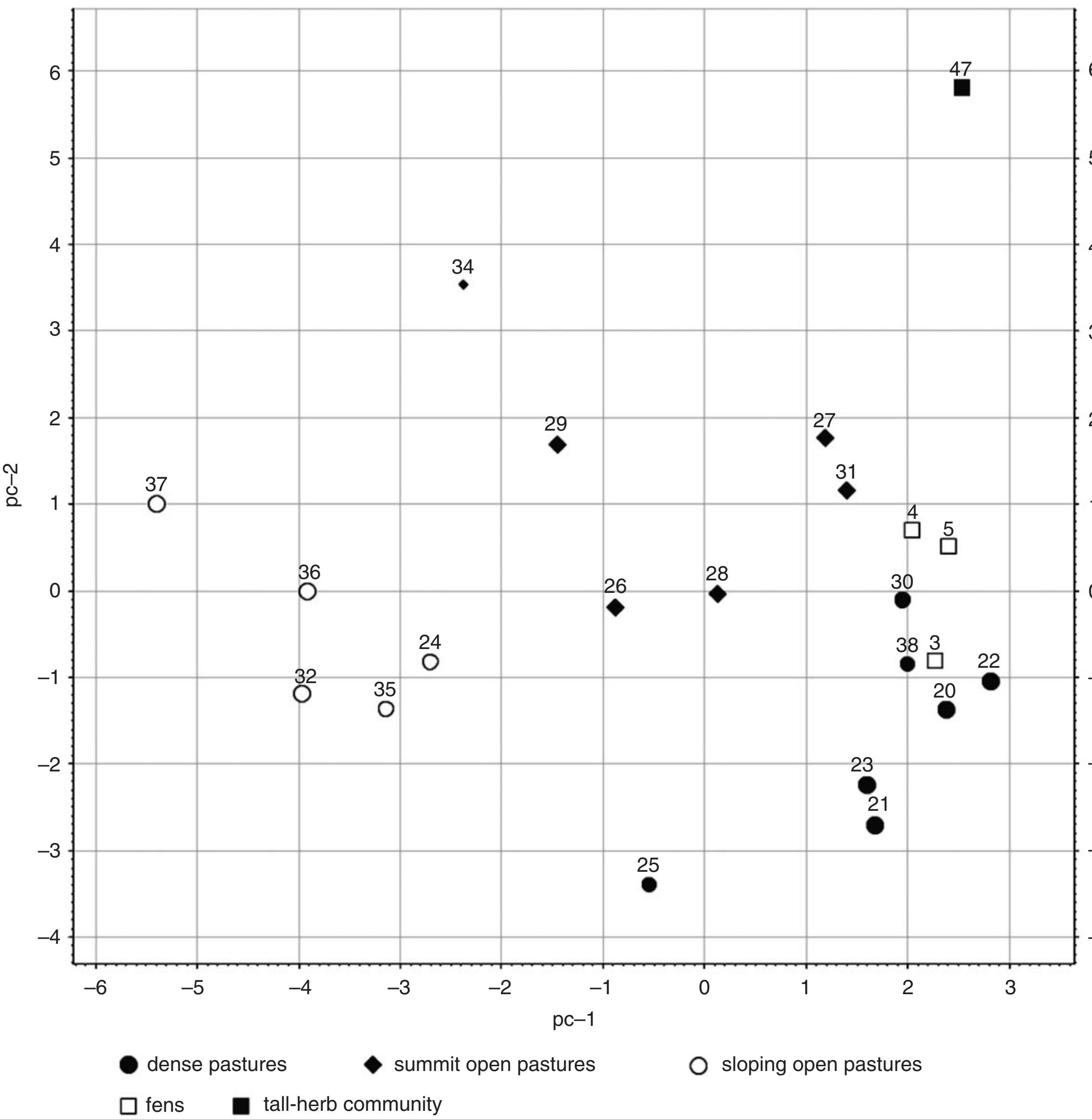

Fig. 4. Fuzzy C-means ordination of the pasture communities on the space defined by the two first axes (26.26% and 16.64% of variance). The size of the symbols indicates the membership degree of each community to the corresponding group. Numbering of the communities is given in Appendix A.

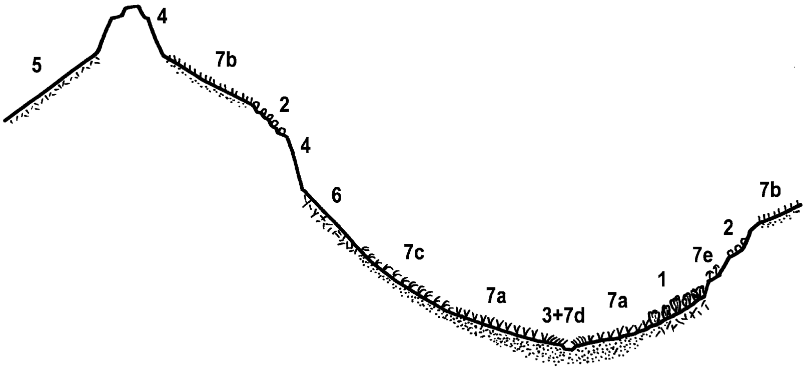

Fig. 5. Catenal situation of vegetation groups in main habitats of the alpine belt. (1) evergreen scrubs, (2) deciduous scrubs, (3) hygrophilous communities, (4) rock communities, (5) therophytic scree communities, (6) perennial scree communities, (7a) dense pastures, (7b) summit open pastures, (7c) sloping open pastures, (7d) fens, (7e) tall-herb community.

conditions, which implies particular environment stress, such as waterlogging, soil scarcity or low fertility (Braun-Blanquet 1948; Carreras et al. 1993; Carrillo and Ninot 1992). Therefore, the corresponding communities are mainly species-poor, and clearly dominated by one or a few species, thereby strongly influencing the spectra of that particular community.

Defining traits of alpine vegetation groups

It has been widely reported that the spectra of plant life forms are good descriptors of functional morphology. They may express the strong determinism of differentiated microclimates and soils within small surfaces typical of alpine and arctic landscapes. This space heterogeneity is related to strong variations in several ecosystem descriptors, like primary production, total biomass or soil organic matter (Shaver et al. 1997). In our study, strong spectra differentiation occurred between the seven main vegetation groups (Fig. 6); even pastures were noticeably differentiated at this level (Fig. 7). The average values of the other attributes (functional attributes: Tables 3 and 5; community attributes: Tables 4 and 6) also define the characteristics of each vegetation group, and hence indicate preference for particular environmental conditions. However, elsewhere, group averages masked considerable differences between communities in the same group when referring to a single attribute, which is reflected in the tables as high scores of standard error (Tables 5 and 6).

Woody vegetation (groups 1 and 2)

Scrubs included the most apparent woody plants, which attained distinct coverage in the two groups: woodiness reached 64.3% in evergreen scrubs and 27.8% in deciduous scrubs. In the former, this strong woody dominance was shared mainly by nanophanerophytes (22.5%) and suffruticose (13.6%) and creeping (33.0%) chamaephytes. This codominance is related to the varied physiognomy of the communities included, which may be erect (*Rhododendron ferrugineum* scrub), diffuse (*Arctostaphylos uva-ursi* carpets) or creeping (*Loiseleuria procumbens* dwarf carpets). Other characteristics of evergreen scrubs were the lowest cover percentage of non-graminoid hemicryptophytes (11.3%), and the highest cover reached by terricolous lichens (5.7%). These cryptogams are absent in the *Rhododendron* and in the *Juniperus communis* subsp. *nana* scrubs (0.9% and 0.3%, respectively), but cover noticeable surfaces in the *Loiseleuria* and in the *Empetrum nigrum* subsp. *hermaphroditum* carpets (15.0% and 6.7%).

Evergreeness is the most characteristic attribute of evergreen scrubs, which was due to several taxa (*Rhododendron, Loiseleuria, Empetrum, Juniperus*) that have adapted to cold environments and poor soils (Bliss 1971). Evergreen shrubs are the only plants that can build complex epigeous structures. They must face the energetic costs involved in the maintenance of evergreeness under alpine conditions, probably because whole foliage sprouting is not viable in plants of this size, in spite of their mycorrhizae symbioses and considerable stem and root stocks (Lamaze et al. 2003).

In deciduous scrubs, creeping, semi-woody chamaephytes were dominant (*Salix* spp., *Dryas octopetala*; 46.7%), and the two types of hemicryptophytes accounted for 40.2% of the cover, which indicates the transitional position of these communities between scrubs and pastures. It is interesting to note that while evergreen scrubs are restricted mainly to the lower part of the alpine belt, deciduous ones were spread across the belt, and were especially abundant in the places with most snow (Braun-Blanquet 1948; Carrillo and Ninot 1992). According to Tieszen et al. (in Komárková and McKendrick 1988), the higher efficiency of deciduous arctic chamaephytes in winter storage compared with evergreen shrubs allows them to sprout faster at the beginning of summer and to escape from winter desiccation caused by leaf transpiration when the soil is frozen. The strategy of deciduous chamaephytes involves greater resource dynamics, related to habitat quality and to higher herbivorous interaction, while evergreen scrubs occupy and maintain poorer substrata (Chapin et al. 1996; Gerdol 2005; Gerdol et al. 2000b).

These two scrub types showed high percentages of long-distance vegetative expansion from the mother plant. Most dominant shrubs and subshrubs show layering via lateral rooting branches, which may result in phalanx colonisation and clonal spreading over sizable surfaces (Albert et al. 2005; Pornon et al.1997). Regarding diaspore dissemination, endozoochory is exclusive to evergreen scrubs, where berry-producers account for more than half the cover. In contrast, deciduous scrubs showed by far the highest percentage (78.9%) of long-distance dispersion, which is attributed to the dominance of subshrubs that bear plumose diaspores (*Salix* spp., *Dryas octopetala*).

Communities of particular habitats (groups 3, 4, 5 and 6)

Rock and scree surfaces strongly limit plant colonisation because of the scarcity and space dispersion of soil, which, in addition, implies lower water and nutrient reserves. Low vegetation cover is a clear expression of these constraints (Burga et al. 2004). Rock communities

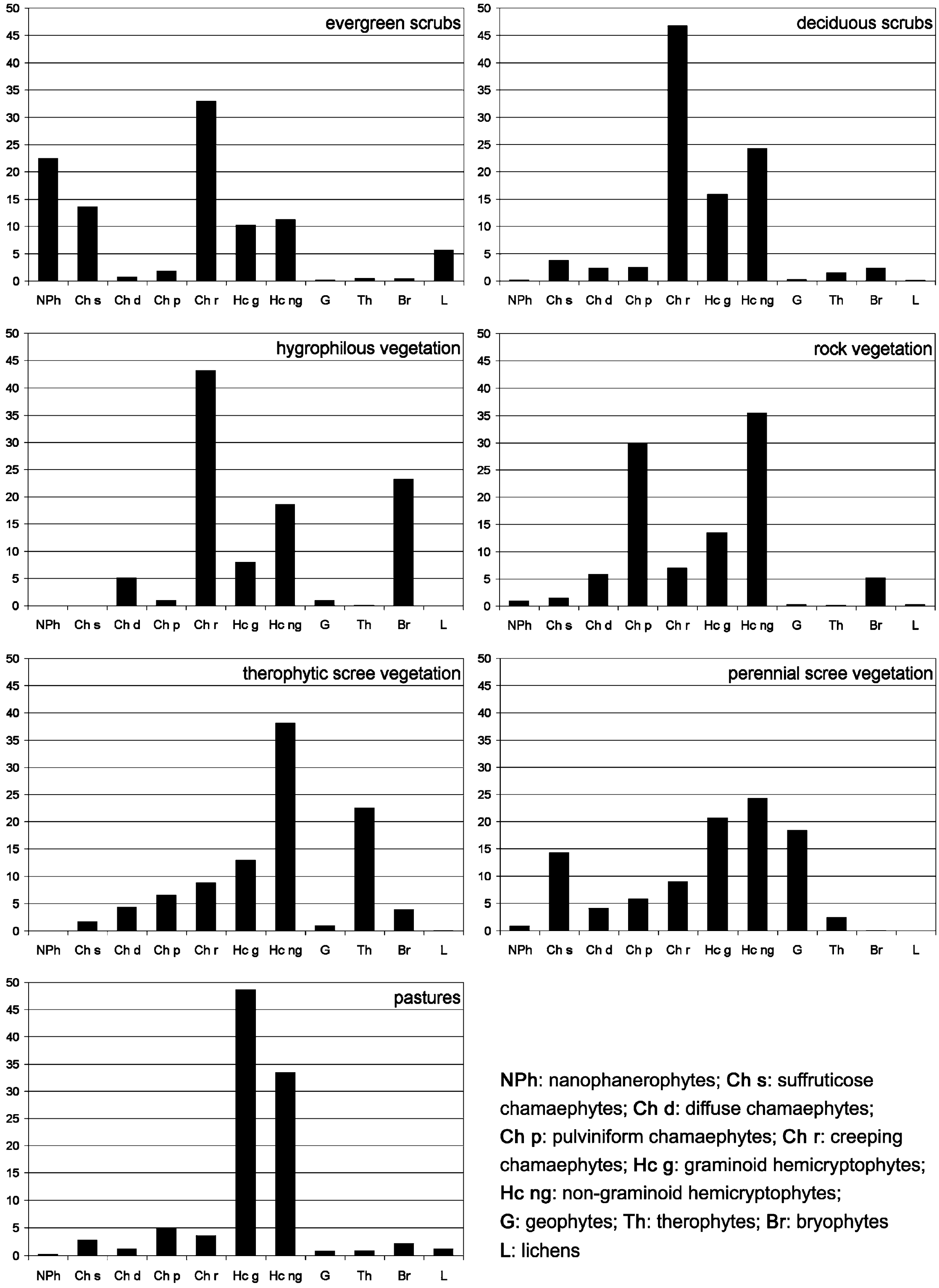

Fig. 6. Relative cover values of life forms in the vegetation groups. The bars correspond to the mean covers of each life form across the communities included in each group.

were characterised by a very high percentage of pulvinules (29.9%, much higher than in the other groups), which codominated with non-graminoid hemicryptophytes (35.5%). The relative cover of pulvinules, other chamaephytes (14.3%) and bryophytes (5.2%), together with evergreeness (17.9% of cover, 27.9% of

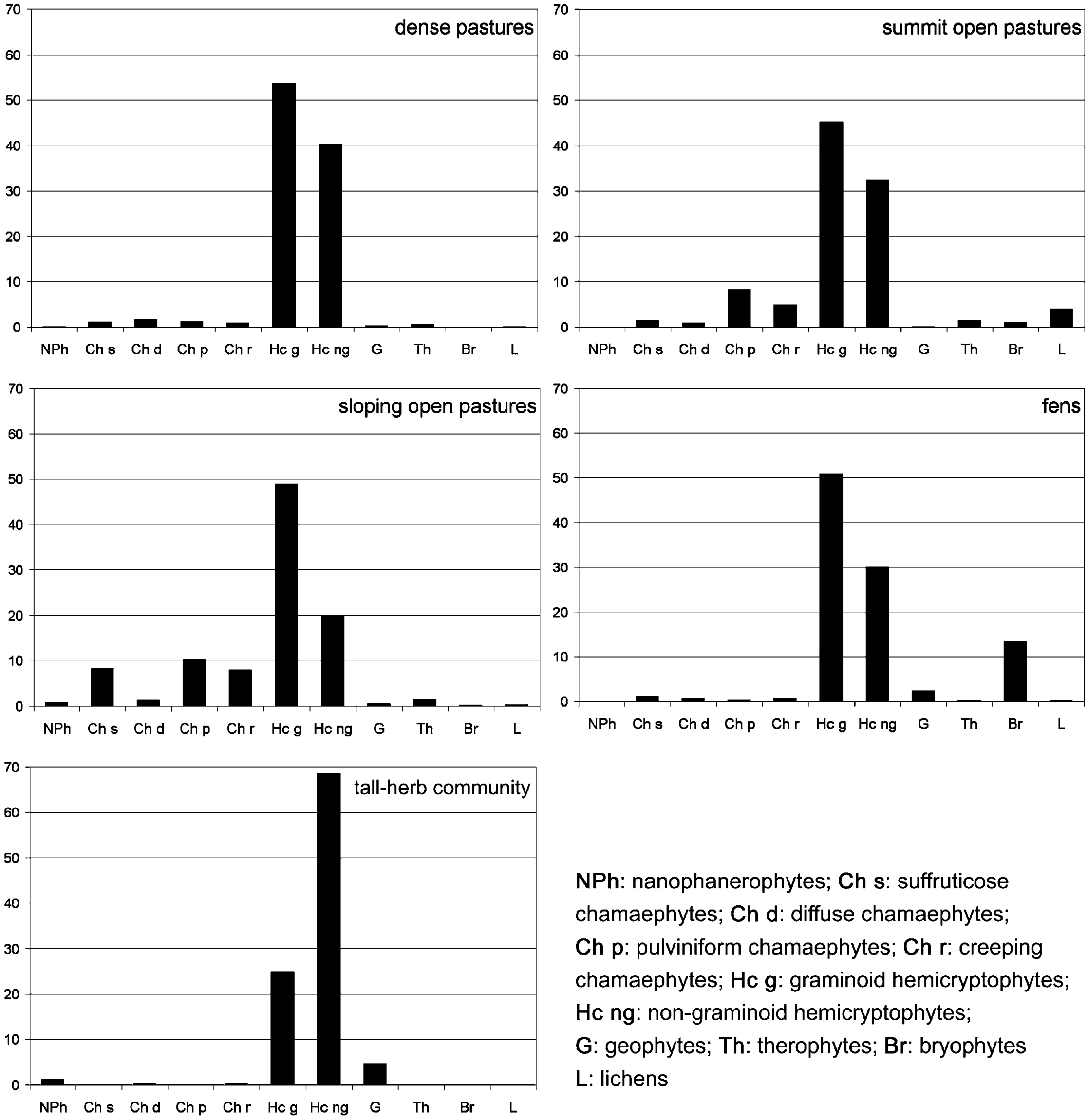

Fig. 7. Relative cover values of life forms in each subgroup of pasture communities.

taxa) and succulence (8.8%, 11.8%) indicates environmental stress conditions, which lead to slow growth and low turnover (Bliss 1971).

Perennial glareicolous communities are mainly related to scree of medium-sized to large pieces, even to huge blocks. Slope sliding is there a minor constraint compared to the scarcity of soil. This is frequently reduced to small, remote interstices among rock material, in the form of soil pockets conserved by the dense root systems of specialised plants, which can thus survive land movements (Somson 1984). These scree surfaces are good niches for a number of geophytes (several mountain ferns and forbs: *Cryptogramma crispa* – cf. also Tomaselli et al. (2005), *Crepis pygmaea*), which accounted for 18.4% of the relative cover. Together with these, hemicryptophytes (graminoid and non-graminoid, 20.7% and 24.3%, respectively) comprise the bulk of the communities. A high percentage of long-distance lateral expansion (67.7%) is related to the irregularity of the substrate, which leads plants to produce long rhizomes or to resprout after being covered by rock debris.

The significant presence of annuals was the most distinctive trait of the therophytic communities that settle on scree and in some acidic snow beds. Their relative cover (22.6%), which was much higher than their average cover in alpine vegetation (2.0%), indicates that these substrata provide an adequate habitat for such short-lived plants (*Galeopsis pyrenaica* var. *nana, Iberis spathulata, Mucizonia sedoides*). These substrata comprise generally small to medium-sized rock pieces, which periodically slide. However, beneath these gravel, there are less conspicuous matrixes of fine earth (Somson 1984), which may harbour considerable seed banks. In this regard, these scree communities also

Table 3. Cover percentages (and ±SE) of taxa with the functional attributes considered in the vegetation groups

	Evergreen scrubs	Deciduous scrubs	Hygroph. veg.	Rock veg.	Theroph. scree	Perenn. scree	Pastures
Vegetative particularities							
Succulence	0.2±0.1	1.2±0.5	28.0±6.4	8.7±2.0	7.2±5.3	2.4±1.0	1.6±0.2
Evergreeness	50.7±4.5	1.4±0.2	0.9±0.3	17.9±3.7	1.7±0.7	11.5±5.8	1.8±0.3
Woodiness	64.3±3.6	27.8±2.4	0.0±0.0	3.6±1.8	0.7±0.1	1.3±0.8	2.9±0.6
Lateral spread							
Absent	0.0±0	0.0±0.0	0.0±0.0	0.8±0.8	33.8±3.7	1.2±1.2	1.1±0.8
<2.5 cm	2.4±1.4	40.3±29.9	31.2±16.3	47.8±8.0	21.9±13.4	6.6±3.7	25.0±3.1
>2.5 cm	95.4±1.8	56.1±28.1	35.1±20.2	9.6±2.5	33.0±16.2	67.7±12.3	10.5±3.1
Dense turf	2.2±2.2	3.6±1.8	33.6±26.7	41.8±8.6	11.3±4.3	24.5±8.9	63.4±2.8
Diaspore dissemination							
Long distance	0.0±0.0	78.9±5.9	5.8±3.8	11.5±4.5	22.2±11.5	52.2±16.1	6.9±2.1
Short distance	2.2±2.2	8.2±8.2	9.2±4.5	16.9±3.8	9.3±3.6	19.0±9.7	63.0±5.6
No dissemin.	45.6±13.0	12.9±3.0	85.0±8.1	71.5±5.2	68.5±13.4	28.8±6.6	30.2±4.7
Endozoochory	52.2±12.2	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0

Table 4. Mean values (and ±SE) of community attributes in the vegetation groups

	Evergreen scrubs	Deciduous scrubs	Hygroph. veg.	Rock veg.	Theroph. scree	Perenn. scree	Pastures
Global cover	93.4±1.3	91.7±2.0	84.6±3.6	14.0±8.1	30.6±12.0	19.1±5.5	81.6±3.9
Cumulate cover	154.3±10.0	139.9±8.7	120.1±7.8	57.2±16.2	65.1±15.9	45.2±4.7	155.4±6.4
Species richness	14.4±0.9	17.6±1.5	9.7±1.6	12.1±1.2	9.7±0.9	9.9±1.4	18.0±1.0
Number of families	24.5±1.8	29.0±2.9	17.7±1.2	18.1±2.3	18.5±2.5	17.0±2.6	25.4±1.2
Shannon diversity index	1.6±0.1	1.4±0.0	1.2±0.1	1.4±0.1	1.6±0.1	1.6±0.1	1.2±0.1

Table 5. Cover percentages (and ±SE) of taxa with the functional attributes considered in the subgroups of pastures

	Dense pastures	Summit pastures	Sloped pastures	Fens	Tall-herb com.
Vegetative particularities					
Succulence	1.3±0.4	2.1±0.4	1.0±0.4	2.4±0.0	0.5
Evergreeness	0.6±0.1	3.0±0.4	2.9±0.6	0.9±0.3	1.1
Woodyness	0.9±0.3	3.7±1.5	6.0±0.6	1.5±0.8	1.3
Lateral spread					
No spreading	0.0±0.0	0.0±0.0	4.8±3.0	0.0±0.0	0.0
<2.5 cm	34.1±5.0	29.4±5.8	10.1±3.1	24.6±3.9	11.2
>2.5 cm	0.7±0.7	9.3±5.9	15.8±1.8	11.0±6.9	58.0
Dense turf	66.3±5.2	61.3±2.9	69.3±5.6	64.3±5.8	30.8
Diaspore dissemination					
Long distance	3.6±1.4	13.9±3.6	0.0±0.0	1.9±1.9	37.3
Short distance	83.4±3.6	43.3±9.6	74.9±6.2	46.3±18.9	27.8
No dissemination	13.0±3.1	42.7±8.4	25.2±6.2	51.9±20.2	35.0

showed high cover percentages of plants that lack lateral expansion (33.8%) mainly annuals. Nevertheless, this scree type was dominated by non-graminoid hemicryptophytes (38.1%, the highest relative cover of this type), which produce long rhizomes that can resprout after being covered by debris, moved or even fragmented (*Viola lapeyrousiana, Veronica nummularia, Galium cometerrhizon*; Somson 1984).

The communities related to running waters showed the highest bryophyte cover (23.3%) and the lowest presence of graminoid hemicryptophytes (8.0%). The dominance corresponded to creeping herbaceous

Table 6. Mean values (and ±SE) of community attributes in the subgroups of pastures

	Dense pastures	Summit pastures	Sloped pastures	Fens	Tall-herb com.
Global cover	93.6±3.0	85.0±1.9	52.4±6.3	91.6±2.8	94.0
Cumulate cover	161.0±7.0	170.7±7.7	117.5±15.4	178.7±3.1	144.5
Species richness	17.2±1.3	21.7±1.4	18.9±2.8	12.8±1.4	12.2
Number of families	25.6±1.8	24.7±2.9	27.6±2.5	25.7±3.8	17.0
Shannon diversity index	0.9±0.1	1.4±0.0	1.5±0.1	1.2±0.1	0.8

chamaephytes (43.2%), generally one of these species per relevé (*Saxifraga aquatica, S. stellaris, Epilobium alsinifolium*). Curiously, these communities showed the highest values for succulence (28% of cover, 14% of taxa). Hygrophylous communities include some succulent (*Sedum villosum, Saxifraga aizoides*) and also semi-succulent plants (*Saxifraga* spp., *Dactylorhiza* spp.), a few of which may be abundant. Since succulence indicates particular resource niches, and not necessarily water scarcity (Shmida and Burgess 1988), in our study this trait may be related to various stress factors, namely low water and nutrient supply in rocky habitats and nutrient deficiency in waterlogged soils. Alternatively, succulence may partially reflect phylogenetic links expressed by taxa excluded from better habitats.

In general, communities related to rocks, scree and running waters showed low diversity, at least when expressed as number of species and number of families. This trend reflects that the constraints of these habitats exclude most of the alpine flora and, at the same time, favour a number of taxonomic groups (families, genera) in each case. The density of endemics and other particular taxa (Braun-Blanquet 1948; Küpfer 1974) show that these stressful habitats have been a suitable arena both for persistence of paleoendemics and for geographic and ecologic selection at the species level.

Pastures (group 7)

Although this group is the most diversified into associations, its coarse physiognomy is quite uniform and gives the main feature of the alpine belt. This group showed the highest percentage of one life form, namely grasses and related plants, which accounted for almost half the cover (48.6%). The presence of non-graminoid hemicryptophytes was also high (33.4%), while all the other types presented much lower percentages (<5%). This observation indicates that, excluding extreme substrata (scree, rock, water-saturated soils, etc.), hemicryptophyte form and function is the most efficient type in alpine vegetation. The combination of persistence, ensured through strong below-ground structures, and dynamics, performed by seasonal leaves and shoots, suits contrasting alpine seasonality.

Given the generalised dominance of hemicryptophytes, the subgroups of pastures showed only small particularities (Fig. 6). Only the tall-herb community differed clearly; the prevalence of forb hemicryptophytes with respect to graminoids (68.5 vs. 25.0%) is related to particular conditions (i.e., fertile soils with good water supply, in the lower alpine belt) that enhance rapid growth and crown competition for light. Fens stand out at this level because of the high cover of bryophytes (13.5%). The characteristics of the environment these communities occupy (waterlogged soil) were hardly reflected by the percentages of life forms observed, as the general graminoid dominance was maintained through sedges instead of grasses. Among the typical pastures, hemicryptophytes reached the highest percentage in the subgroup of dense communities, which settle on flats or gentle slopes with relatively good soil (deep, stable, neither flooded nor drying out), mainly in the lower alpine belt (Carreras et al. 1993; Carrillo and Ninot 1992). Other life forms find there low possibilities, as reflected by the very low cover recorded. In the two subgroups of open pastures, chamaephytes (creeping, suffruticose, pulvinules) reached significant values (most between 5–10%), mainly at the expense of non-graminoid hemicryptophytes, which, in sloped pastures, had the lowest abundance within the group (19.9%). Summit pastures were characterised by the relatively high presence of terricolous macrolichens (4%). According to Onipchenko (1994), in typical alpine pastures, lichens benefit from the smaller lateral extension shown by main grasses and dwarf shrubs above ground than in the root system. At the community level, the presence of these cryptogams together with that of pulvinules and creepers indicate hard conditions (stoniness, dryness, erosion) and a certain degree of community stability.

The dominant grasses and sedges also define the regenerative strategies of the group of pastures. The type of dense turfs reaches its maximum resulting into slow, massive lateral expansion of most plants, typical of habitats with limited fertility. The dissemination type of these main graminoids is to short distances, through flattened or membranous diaspores. According to Semenova and Onipchenko (1994), most of the dominant plants of well-established alpine communities do not make permanent seed banks, as their persistence is ensured by perennial roots and bases. On the contrary, non-dominant species in these communities, and most plants in communities of unfavourable habitats (scree, rock, water), are more dependent on permanent seed banks, as their persistence is more related to disturbance and opening of gaps ("explorative" taxa, sensu Onipchenko et al. 1998).

Synthesis of main trends and conclusions

In the Catalan alpine landscape, hemicryptophytes are dominant, both at the species level (69.4%) and as mean of cover percentages (68.2%), which reflects the appropriateness of this life form for general alpine conditions. Other very dominant features of plants in this vegetation belt include the lack of green parts in winter, the capacity for lateral spreading to short distances and the absence of disseminating mechanisms. Nevertheless, the general spectrum of attributes includes diversity of types which, although showing low general percentages, are significant in particular environments. Hence, the communities most differentiated from the general alpine spectrum settle on a variety of unbalanced habitats, mainly associated with stress conditions (scarcity of soil, nutrient-poor or waterlogged substrata). These communities tend to be species-poor and with relatively high percentages of particular types. Groups less differentiated from the global spectra, i.e., with great dominance of hemicryptophytes, included richer communities, with more shared dominances, and correspond to more balanced environments. Like in other landscapes, richer alpine communities become classified into richly hierarchised syntaxa (Elyno-Seslerietea, Juncetea trifidi), and show gradual transitions among them and towards other peripheral syntaxa (Thlaspietea, Scheuchzerio-Caricetea), a scheme similar to that shown at physiognomic and functional levels.

Communities of several harsh habitats show mainly low diversity at species and family levels, together with high taxonomic specialisation. The lowest values are found in scree and water communities (less than 10 species per relevé) and also fens (12.3 taxa/relevé). Limiting conditions are also reflected by plant cover, most strikingly in rock and scree communities, but also in hygrophilous communities and in extreme pastures on rocky areas or sliding slopes. In contrast, scrubs and pastures have the highest covers (global and cumulative) and number of species per relevé. Although there is a strong dominance of one or few species in most of these communities, the poor above-ground plant stratification and the microtopographic irregularities favour the settlement of many subordinate species. Therefore, in alpine communities, a general positive correlation is observed between species richness and cover values. However, the lowest structural diversities are found in dense pastures and fens, while scree and rock communities exhibit the highest heterogeneity (i.e., high number of life forms, evenly distributed). Hence, this sparse vegetation would be less sensitive to environmental changes at the community level.

The capacity of plants to spread laterally, mainly over small distances, is very general in alpine flora. Moderate foraging and displacement is combined in most species with strong persistence of plurennial bases. This strategy is most evident in dominating turfs of pastures and fens, and also in small cushions. In addition, more loose chamaephytes and nanophanerophytes follow the same strategy, but on a larger scale. Concerning dissemination, snow bed carpets and perennial scree communities include high percentages of long-distance types. In other stressful habitats, such as rocks, waters and fine screes, most plants show no apparent dissemination mechanism. These trends, together with dominant short distance dissemination in pastures and zoochory in scrubs indicates that the coarse dissemination types observed here may be more related to phylogeny than to function. In alpine landscapes, selection pressure on dispersal mechanisms is low or random because of various ecological features, mainly generalised difficulties in setting seeds, low chance of seedling or juvenile establishment and intense slope dynamics. Therefore, the major plant strategy consists of strong persistence and moderate regeneration, which is for the most part short distance offspring, and eventually the setting diaspores over space or via the soil bank.

The typical alpine geomorphology produces highly heterogenous landscapes in terms of microclimates and substrata, thereby leading to dense, contrasting land mosaics. Thus, while alpine pastures depend principally on general bioclimates and become finely diversified at the floristic level, neighbouring plant communities bear strong differentiation and are tightly related to a wide scope of specific environments. In particular, the morphology and functioning of these plant communities show adaptive persistence of various plant sources at the cost of coupling with various stress conditions. Therefore, while vegetation dynamics is not a significant cause of diversity in alpine landscapes, the abundance of particular species richness at these altitudes is the result of a broad spectrum of habitats that are stressful, extended and conservative.

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Appendix A. Syntaxonomic scheme of the communities treated

Montio-Cardaminetea Br.-Bl. et Tüxen ex Klika et Hadac 1944
Montio-Cardaminetalia Pawl. 1928
Cardamino-Montion Br.-Bl. 1926

1. **Saxifragetum aquaticae** Br.-Bl. 1948
2. **Montio-Bryetum schleicheri** Br.-Bl. 1925

Scheuchzerio-Caricetea fuscae Tüxen 1937
Caricetalia fuscae Koch 1926
Caricion fuscae Koch 1926

3. **Caricetum fuscae** Br.-Bl. 1915
4. **Narthecio-Trichophoretum** Br.-Bl. 1948 **primuletosum integrifoliae** Ninot et al. 2000

Caricetalia davallianae Br.-Bl. 1949
Caricion davallianae Klika 1934

5. **Swertio-Caricetum nigrae** Vigo 1984

Asplenietea trichomanis (Br.-Bl.) Oberd. 1977
Potentilletalia caulescentis Br.-Bl. 1926
Saxifragion mediae Br.-Bl. 1934

6. **Saxifragetum mediae** Br.-Bl. 1934 1948
7. **Sileno borderei-Potentilletum nivalis** (G. Monts.) Ninot et Soriano 1996

Androsacetalia vandellii Br.-Bl. 1934
Androsacion vandellii Br.-Bl.1926

8. **Saxifrago-Androsacetum vandellii** Carrillo et Ninot 1986
9. **Saxifragetum iratianae** Nègre 1969
10. **Saxifragetum pubescentis** Br.-Bl. (1934) 1948

Thlaspietea rotundifolii Br.-Bl. 1948
Thlaspietalia rotundifolii Br.-Bl. 1926
Iberidion spathulatae Br.-Bl. 1948

11. **Saxifragetum praetermissae** Br.-Bl. 1948
12. **Festucetum glaciali-pyrenaicae** Rivas-Mart. 1977
13. **Crepidetum pygmaeae** Br.-Bl. 1946
14. **Iberidetum spathulatae** Br.-Bl. 1948

Androsacetalia alpinae Br.-Bl. 1926
Androsacion alpinae Br.-Bl 1926

15. **Oxyrio-Doronicetum viscosae** (Chouard) Gruber 1978

Senecion leucophylli Br.-Bl. 1948

16. **Violetum diversifoliae** Fern. Casas 1970
17. **Galeopsio-Poetum fontqueri** Br.-Bl. 1948
18. **Senecietum leucophylli** Br.-Bl. 1948

Dryopteridion oreadis Rivas-Mart. 1977

19. **Cryptogrammo-Dryopteridetum abbreviatae** Rivas-Mart. 1970

Juncetea trifidi Hadac 1944
Caricetalia curvulae Br.-Bl. 1926
Nardion strictae Br.-Bl. 1926

20. **Alchemillo-Nardetum strictae** Gruber 1975 **nardetosum strictae** Carrillo et Ninot 1990
21. **Selino-Nardetum** Br.-Bl. 1948
22. **Trifolio-Phleetum gerardi** Br.-Bl. 1948
23. **Selino-Festucetum eskiae** Nègre 1968 (= Ranunculo-Festucetum eskiae Nègre 1974)

Festucion eskiae Br.-Bl. 1948

24. **Festucetum eskiae** Br.-Bl. 1948
25. **Carici-Festucetum eskiae** Rivas-Mart. 1974

Festucion supinae Br.-Bl. 1948

26. **Hieracio-Festucetum supinae** Br.-Bl. 1948 **typicum**
27. **Hieracio-Festucetum supinae juncetosum trifidi** Br.-Bl. 1948
28. **Hieracio-Festucetum supinae caricetosum curvulae** Baudière et Serve 1975
29. **HieracioFestucetum supinae kobresietosum myosuroidis** Carrillo et Vigo 1993
30. **Gentiano-Caricetum curvulae** Nègre 1969
31. **Leontodonto-Caricetum curvulae** Br.-Bl. 1948
32. **Arenario-Festucetum yvesii** Baudière et Serve 1975
33. **Saxifrago-Minuartietum sedoidis** Carrillo et Ninot 1989

Elyno-Seslerietea Br.-Bl. 1948
Elynetalia Oberd. 1957
Oxytropido-Elynion Br.-Bl. 1949

34. **Elyno-Oxytropidetum hallerii** Br.-Bl. 1948

Seslerietalia caeruleae Br.-Bl. 1926
Festucion scopariae Br.Bl. 1948

35. **Festucetum scopariae** Br.-Bl. 1948
36. **Oxytropido-Caricetum humilis** Carrillo et I. Soriano 1997 **typicum**
37. **Oxytropido-Caricetum humilis helictotrichetosum sedenensis** (Carreras et Carrillo) Carrillo et al. 2000

Primulion intricatae Br.-Bl. ex Bolòs 1970

38. **Festuco-Trifolietum thalii** Br.-Bl. 1948
39. **Dryado octopetalae-Salicetum pyrenaicae** Vanden Berghen 1970 (incl. Alchemillo-Dryadetum I. Soriano 2001)

Salicetea herbaceae Br.-Bl 1948
Salicetalia herbaceae Br.-Bl. 1926
Salicion herbaceae Br.-Bl 1926

40. **Gnaphalio-Sedetum candollei** Br.-Bl 1948
41. **Salici-Anthelietum juratzkanae** Br.-Bl 1948

Arabidion coeruleae Br.-Bl. 1926

42. **Carici parviflorae-Salicetum retusae** (Br.-Bl.) Rivas Mart. 1969

Vaccinio-Piceetea Br.-Bl. 1939
Piceetalia Pawl. 1928
Juniperion nanae Br.-Bl. et al.1939

43. **Genisto-Arctostaphyletum** Br.-Bl. (1939) 1948

Loiseleurio-Vaccinion Br.-Bl. 1926

44. **Cetrario-Loiseleurietum** Br.-Bl. 1926

Rhododendro-Vaccinion G. et J. Br.-Bl. 1931

45. **Saxifrago-Rhododendretum** Br.-Bl 1939 **typicum**
46. **Empetro hermaphroditi-Vaccinietum uliginosi** Br.-Bl. 1926

Betulo-Adenostyletea Br.-Bl. et Tüxen ex Br.-Bl. 1948
Adenostyletalia G. et J. Br.-Bl. 1930
Adenostylion alliariae Br.-Bl 1926

47. **Peucedano-Luzuletum desvauxii** Br.-Bl. 1948

Appendix B. Values of attributes of the communites treated

	Alchemillo-Nardetum	Arenario-Festucetum	Caricetum fuscae	Carici-Festucetum	Carici-Salicetum	Cetr.-Loiseleurietum	Crepidetum pygmaeae	Crypt.-Dryopteridetum	Dryado-Salicetum	Elyno-Oxytropidetum	Empetro-Vaccinietum	Ferstucetum eskiae	Festucetum gl.-pyren.	Festucetum scopariae	Festuco-Trifolietum	Galeopsio-Poetum	Gen.Arctostaphyletum	Gentiano-Caricetum	Gnaphalio-Sedetum	Hier.-Festuc. caricet.	Hier.-Festuc. juncet.	Hier.-Festuc. kobresiet.	Hier.-Festuc. typicum
Global cover	98.4	35.2	95.0	78.8	87.8	92.8	11.2	10.6	92.5	82.2	90.0	67.5	20.5	60.8	100	30.0	95.0	90.1	64.8	82.0	88.3	93.0	82.0
Cumulate cover	174.6	79.0	184.8	154.2	126.5	152.1	44.9	32.3	156.2	161.1	138.3	128.6	54.2	166.3	196.0	73.4	143.7	150.3	106.1	169.5	196.6	188.2	163.5
Mean of higher plant taxa	19.6	12.6	11.4	18.7	19.8	14.8	13.2	7.3	18.3	21.6	15.5	17.0	11.2	28.5	22.9	9.5	11.8	16.6	11.1	20.3	26.5	22.8	23.0
Total number of families	25	25	29	25	34	29	23	11	29	37	24	32	15	35	28	15	20	25	25	20	21	20	30
Nanophanerophytes	0.0	0.1	0.1	0.3	0.1	0.6	0.0	3.5	0.6	0.1	7.5	2.5	0.0	0.4	0.0	0.0	38.1	0.1	0.0	0.0	0.0	0.0	0.1
Suffruticose chamaephytes	0.0	0.8	0.3	3.7	3.4	0.6	3.4	1.8	7.9	2.8	24.0	9.7	0.0	6.6	0.7	1.9	10.9	0.1	0.1	0.1	0.2	4.2	1.6
Diffuse chamaephytes	1.7	1.7	0.4	0.6	1.3	0.5	6.0	0.0	0.1	1.8	2.0	0.7	4.4	3.3	7.0	1.4	0.3	0.7	3.9	0.6	1.4	0.0	0.8
Pulviniform chamaephytes	0.4	15.3	0.5	0.4	1.7	2.5	10.8	0.0	4.3	5.6	1.1	2.0	8.7	9.9	2.8	1.0	1.7	4.1	0.4	11.2	9.7	7.1	8.2
Creeping chamaephytes	1.7	9.5	1.3	1.0	51.6	57.6	12.8	0.0	43.7	17.0	38.8	2.6	18.3	9.6	0.8	6.5	23.0	2.0	3.7	1.8	1.6	4.8	3.4
Graminoid hemicryptophytes	49.5	56.6	51.7	67.3	12.5	11.7	21.6	14.2	22.9	40.4	7.5	49.2	31.1	46.1	45.5	8.7	13.4	45.8	18.1	48.9	43.7	51.0	46.1
Non graminoid hemicrypt.	46.3	13.6	18.6	24.9	24.6	10.8	24.5	39.8	18.2	27.4	11.0	30.9	20.4	22.8	41.5	45.5	11.1	45.8	41.6	34.2	35.2	25.0	33.6
Geophytes	0.4	0.1	5.0	0.7	0.2	0.0	18.8	40.7	0.4	0.4	0.0	0.7	12.3	0.4	0.3	2.6	0.7	0.0	0.0	0.0	0.0	0.0	0.1
Therophytes	0.0	2.1	0.2	1.1	0.6	0.9	2.1	0.0	1.8	1.4	0.6	0.7	4.8	1.0	1.0	32.5	0.6	0.8	16.3	2.7	0.8	1.7	1.8
Bryophytes	0.0	0.0	21.9	0.0	3.8	0.0	0.0	0.0	0.0	0.7	0.7	1.0	0.0	0.0	0.1	0.0	0.0	0.1	15.7	0.3	0.9	0.0	0.5
Lichens	0.1	0.1	0.0	0.0	0.4	14.9	0.0	0.0	0.0	2.4	6.7	0.0	0.0	0.0	0.1	0.0	0.3	0.5	0.2	0.1	6.4	6.3	3.8
Diversity of life forms	0.9	1.3	1.3	0.9	1.4	1.3	1.9	1.2	1.5	1.6	1.7	1.4	1.8	1.5	1.2	1.4	1.6	1.0	1.6	1.2	1.4	1.4	1.4
Succulence	0.5	1.0	3.0	0.3	1.9	1.7	4.3	0.0	0.6	1.8	1.7	2.2	1.8	1.3	1.5	2.8	0.0	5.6	23.6	4.2	4.0	1.8	2.4
Evergreeness	0.1	3.8	0.5	1.0	1.0	48.9	3.0	10.2	1.4	1.7	39.7	4.6	4.5	2.5	0.3	0.3	61.0	1.2	2.7	3.0	2.6	4.6	3.1
Woodiness	0.8	4.5	0.5	2.5	49.8	58.8	0.3	3.5	33.8	9.7	57.4	5.8	0.5	5.5	0.8	1.1	71.0	1.2	0.6	1.0	0.9	6.9	3.4
No lateral spread	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0	42.5	0.0	0.0	29.2	0.0	0.0	0.0	0.0
Lateral spread < 2.5 cm	39.8	13.5	18.5	8.6	13.2	5.5	6.0	3.5	7.7	9.4	4.0	6.3	17.1	0.0	39.4	0.0	0.0	47.1	54.6	39.7	40.4	21.0	20.8
Lateral spread > 2.5 cm	0.0	12.7	9.5	0.0	81.4	94.5	50.3	81.2	87.0	37.0	96.0	15.4	43.9	17.4	4.7	57.5	91.2	0.0	0.0	0.0	0.0	7.6	11.2
Dense turf	60.2	73.8	72.0	91.4	5.4	0.0	43.7	15.3	5.3	53.6	0.0	78.2	34.3	82.6	55.9	0.0	8.8	52.9	16.3	60.3	59.6	71.5	68.0
Long distance dissemination	0.0	0.0	5.6	0.0	87.3	0.0	33.8	82.7	67.6	28.8	0.0	0.0	16.6	0.0	4.7	45.7	0.0	9.0	38.2	10.5	21.0	7.1	8.5
Short distance dissemination	82.7	73.8	72.0	92.0	0.0	0.0	33.4	0.0	24.7	20.0	0.0	84.6	37.7	91.2	74.2	7.2	8.8	69.1	16.3	60.2	33.7	20.2	79.2
No space dissemination	17.3	26.2	22.4	8.0	12.7	73.1	32.8	17.3	7.7	51.2	51.0	15.4	45.7	8.8	21.1	47.1	27.4	21.9	45.5	29.3	45.4	72.8	12.2
Endozoochory	0.0	0.0	0.0	0.0	0.0	26.9	0.0	0.0	0.0	0.0	49.0	0.0	0.0	0.0	0.0	0.0	63.8	0.0	0.0	0.0	0.0	0.0	0.0

	Iberidetum spathulatae	Leontodo-Caricetum	Montio-Bryetum	Narth.-Trichophoretum	Oxyrio-Doronicetum	Oxytr.-Caricetum helict.	Oxytr.-Caricetum typ.	Peucedano-Luzuletum	Salici-Anthelietum	Saxifragetum aquaticae	Saxifragetum iratianae	Saxifragetum mediae	Saxifragetum praeter.	Saxifragetum pubesc.	Saxifr. –Androsacetum	Saxifr. –Minuartietum	Saxif.–Rhododendretum	Selino-Festucetum	Selino-Nardetum	Senecietum leucophylli	Sileno-Potentilletum	Swertio-Caricetum	Triolio-Phleetum	Violetum diversifoliae
Global cover	15.2	82.2	89.0	86.1	7.2	40.0	58.3	94.0	94.6	87.3	1.0	7.8	77.5	4.0	7.0	62.1	96.0	89.1	99.2	34.0	9.0	93.8	99.5	12.3
Cumulate cover	45.6	145.2	132.5	175.7	53.7	90.4	123.3	144.5	137.2	105.8	32.3	52.9	122.1	27.0	37.4	151.7	183.1	160.8	142.7	49.3	45.2	175.5	147.9	35.3
Mean of higher plant taxa	10.9	15.9	7.9	11.4	13.3	15.0	21.2	12.2	14.8	8.3	8.2	13.3	13.0	9.3	12.6	17.9	15.4	14.5	14.0	8.2	9.9	15.6	13.9	7.3
Total number of families	20	20	17	30	21	22	24	17	24	20	11	29	16	13	18	21	25	34	18	19	14	18	24	14
Nanophanerophytes	0.0	0.0	0.0	0.1	0.0	0.6	0.5	1.2	0.0	0.0	0.0	1.4	0.0	2.5	3.2	0.0	43.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Suffruticose chamaephytes	5.1	0.0	0.0	2.4	0.0	10.3	14.1	0.0	0.0	0.0	0.0	1.1	0.0	4.3	3.2	0.0	18.9	2.6	0.5	51.9	1.5	0.7	0.1	0.0
Diffuse chamaephytes	9.1	1.1	2.1	0.5	13.2	0.7	0.0	0.3	5.6	0.3	6.5	0.4	13.0	13.0	3.2	2.8	0.0	0.3	0.5	6.1	2.0	1.0	0.8	3.1
Pulviniform chamaephytes	11.1	8.0	1.5	0.0	18.3	18.4	5.8	0.0	1.5	0.7	43.0	26.8	0.7	29.6	25.7	39.5	2.1	0.4	0.0	3.7	26.0	0.2	0.5	13.5
Creeping chamaephytes	8.9	1.1	8.2	0.7	7.0	13.2	5.1	0.3	44.9	69.2	9.6	10.8	52.2	0.0	13.9	4.4	12.4	0.5	0.0	4.8	2.9	0.2	0.5	16.0
Graminoid hemicryptophytes	14.3	41.0	7.3	55.9	16.6	44.2	49.1	25.0	12.4	11.2	8.7	8.5	5.4	4.9	19.3	25.2	8.2	54.2	64.9	15.9	11.5	45.0	49.0	10.7
Non graminoid hemicrypt.	28.0	39.5	18.4	33.3	34.5	10.2	22.0	68.5	30.0	13.6	7.4	50.7	23.6	45.7	30.5	23.5	12.3	41.1	33.4	12.3	56.0	38.5	48.9	37.4
Geophytes	1.2	0.0	0.1	2.2	0.6	0.8	0.8	4.7	0.2	0.2	0.0	0.2	2.5	0.0	1.1	0.0	0.2	0.6	0.2	1.9	0.0	0.0	0.1	0.0
Therophytes	22.3	0.5	0.1	0.0	0.0	1.6	1.5	0.0	2.3	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.1	0.2	0.6	3.0	0.0	0.5	0.2	19.2
Bryophytes	0.0	3.9	62.2	4.5	9.8	0.0	0.0	0.0	3.2	4.8	24.8	0.0	2.7	0.0	0.0	1.8	1.2	0.0	0.0	0.3	0.0	14.0	0.0	0.0
Lichens	0.0	5.0	0.0	0.4	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diversity of life forms	1.9	1.3	1.2	1.1	1.6	1.5	1.7	0.8	1.4	1.0	1.5	1.3	1.3	1.4	1.7	1.5	1.6	0.9	0.7	1.5	1.2	1.1	0.8	1.6
Succulence	1.9	4.1	18.3	10.1	8.4	0.2	0.3	0.5	3.2	40.0	6.8	7.3	26.8	17.3	7.2	15.7	0.2	0.7	1.0	3.7	0.5	5.2	4.2	0.9
Evergreeness	3.2	2.8	1.4	1.4	10.1	2.2	1.3	1.1	1.0	0.4	27.8	17.1	0.3	30.6	24.6	9.9	53.3	0.3	0.1	28.1	5.5	0.5	0.2	0.6
Woodiness	0.4	0.8	0.0	3.0	0.1	6.2	8.1	1.2	23.1	0.0	0.0	6.8	0.0	5.2	13.6	0.5	70.1	0.7	0.2	0.8	0.7	0.9	0.2	0.6
No lateral spread	37.4	0.0	0.0	0.0	0.0	10.3	13.8	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.2
Lateral spread < 2.5 cm	32.9	45.3	63.1	32.0	72.4	12.6	17.9	11.2	100	9.2	52.6	38.6	21.4	77.8	28.7	22.2	0.0	35.5	25.0	0.0	42.5	23.4	43.2	0.0
Lateral spread > 2.5 cm	10.6	0.0	28.6	0.0	11.5	21.9	11.6	58.0	0.0	3.9	16.0	18.1	73.0	4.0	12.3	5.1	100	0.0	0.0	95.3	0.0	23.6	0.0	64.0
Dense turf	19.2	54.7	8.4	68.0	16.1	55.2	56.7	30.8	0.0	86.9	31.4	43.3	5.6	12.7	59.0	72.6	0.0	64.5	75.0	4.7	57.5	53.0	56.8	9.8
Long distance dissemination	5.1	7.6	13.0	0.0	0.0	0.0	0.0	37.3	81.8	4.4	0.0	28.8	0.0	17.5	11.5	0.0	0.0	0.0	7.1	75.9	23.0	0.0	4.4	0.0
Short distance dissemination	13.7	46.8	18.2	9.3	26.4	55.6	69.1	27.8	0.0	3.9	11.3	21.9	5.6	0.0	28.7	19.8	0.0	93.0	92.9	4.7	10.4	57.5	80.3	0.0
No space dissemination	81.3	45.6	68.8	90.7	73.6	44.4	30.9	35.0	18.2	91.8	88.7	49.3	94.4	82.5	59.8	80.2	62.3	7.0	0.0	19.4	66.6	42.5	15.3	100
Endozoochory	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0

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