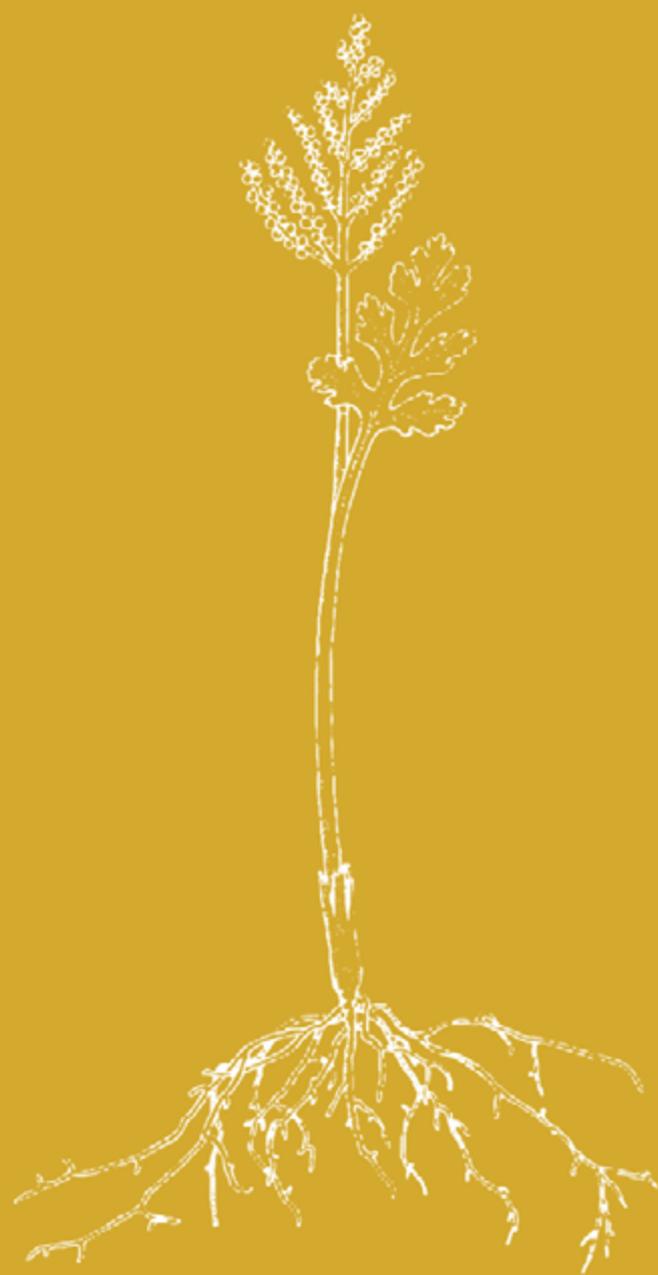


Actes del XII Col·loqui Internacional de Botànica Pirenaica - Cantàbrica



Actes del XII Col·loqui Internacional de Botànica Pirenaica - Cantàbrica

Girona - 3, 4 i 5 de juliol - 2019

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How alpine landscapes enhance contrasting vegetation mosaics and flora in the Pyrenees

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Abstract

Alpine landscapes include strong abiotic gradients, which promote the coexistence along short distances of varying plant communities. Here, we analyse the vegetation of the alpine belt of the Catalan and Andorran Pyrenees through functional plant traits, to better understand plant diversity as coupled with the varying alpine landscapes. For this purpose, we used 800 phytosociological relevés to characterize the associations in terms of plant traits, and to relate them to species diversity and functional properties.

Most of the community-types assessed reflect the distinct stressing conditions found in alpine environments, and are species-poor at the plot level. This is more evident in particularly limiting environments, such as scree, rocky areas or snowbeds which, however, host many singular species in the biogeographic and functional aspects. Most grassland vegetation reflects better ecological conditions; community-types are species-richer, and include great regional and ecological variation. Alpine heaths respond to the local fitness of a few woody species able to exert dominance through persistence. There is still a lack of knowledge on the actual effect of grazing on the relative role played in contemporary landscapes by alpine heaths and grasslands.

Resumen

Los paisajes alpinos incluyen notables gradientes ambientales, que conllevan la coexistencia de variadas comunidades vegetales en áreas relativamente reducidas. En este trabajo analizamos la vegetación del piso alpino de los Pirineos catalanes y andorranos a través de rasgos funcionales de plantas, con el fin de comprender mejor la interrelación entre diversidad vegetal y la variabilidad del paisaje alpino. Para ello, partimos de 800 inventarios fitosociológicos para caracterizar las asociaciones en base a rasgos funcionales, y para relacionarlas con diversidad específica y aspectos funcionales.

La mayoría de las comunidades reflejan algún tipo de condiciones de estrés, comunes en ambientes alpinos, y resultan pobres en especies a escala de parcela. Esto se hace más evidente en los ambientes más limitantes, como son roquedos, pedrizas o neveros, donde en cambio habitan muchas especies singulares tanto en el aspecto biogeográfico como en el funcional. Los pastos densos traducen en general condiciones más favorables; incluyen asociaciones más ricas en especies, que muestran una gran variabilidad regional y ecológica. Los matorrales alpinos reflejan adaptaciones locales de unas pocas especies leñosas, capaces de ejercer dominancia por el hecho de ser persistentes. Un aspecto todavía poco conocido es hasta qué punto los efectos del pastoreo han condicionado la extensión y el rol que pastos y landas juegan actualmente en los paisajes alpinos.

Introduction

One of the most apparent properties of the alpine landscapes is the contrasting array of plant communities that they include. Although most of these plant communities show moderate species richness, the contrast from one to another in terms of physiognomy, plant composition and ecologic function gives to these landscapes a high overall diversity (Körner, 2003; Onipchenko 2004; Fig. 1). Moreover, they include a number of plant species of biogeographical interest (Braun-Blanquet, 1948; Gómez *et al.*, 2017).

The flora found in the Pyrenean alpine belt reflects the main constraints imposed by high elevation environments through its life-form spectrum, where strong seasonality involving a pleasant growth period favours dominance of hemicryptophytes (Illa *et al.*, 2006). They respond to seasonality renewing all or almost all aboveground structures yearly, a strategy coupled with varying herbivory by farm or wild fauna (Grime, 2001). Other life-forms are mainly found in contrasting habitats, from which those implying particular plant limitations (such as dryness, soil scarcity or shortened growing season) are particularly place for a wide array of chamaephytes (Illa *et al.*, 2006).

Most of the Pyrenean alpine flora is shared with other great mountains of central and southern Europe as a result of repeated interchange throughout Pleistocene cold periods. Other orophytes are restricted to the Pyrenees, mainly secluded in rocky habitats and secondly in grasslands; overall, Pyrenean endemics account for roughly 12% in the alpine belt. Other important chorotypes in the alpine belt are Boreo-Alpine disjuncts, and medio-European (= Euro-Siberian) taxa (Gómez *et al.*, 2017).

The study of the Pyrenean alpine vegetation started in the mid twentieth century, and mainly by Braun-Blanquet (1948). Following the phytosociological method, he established the most common plant associations in the eastern Pyrenees and the regional syntaxonomical scheme. Some decades later, a good deal of particular papers enlarged and deepened this knowledge, mostly referred to the central and eastern sectors (Gruber, 1978; Rivas-Martínez *et al.*, 1991; Carrillo & Ninot, 1992; Carreras *et al.*, 1993; Vigo, 1996; etc.). This has led to a good knowledge of the alpine plant communities in this area, and has facilitated regional syntheses of the Pyrenean vegetation (Ninot *et al.*, 2007 and 2017b).

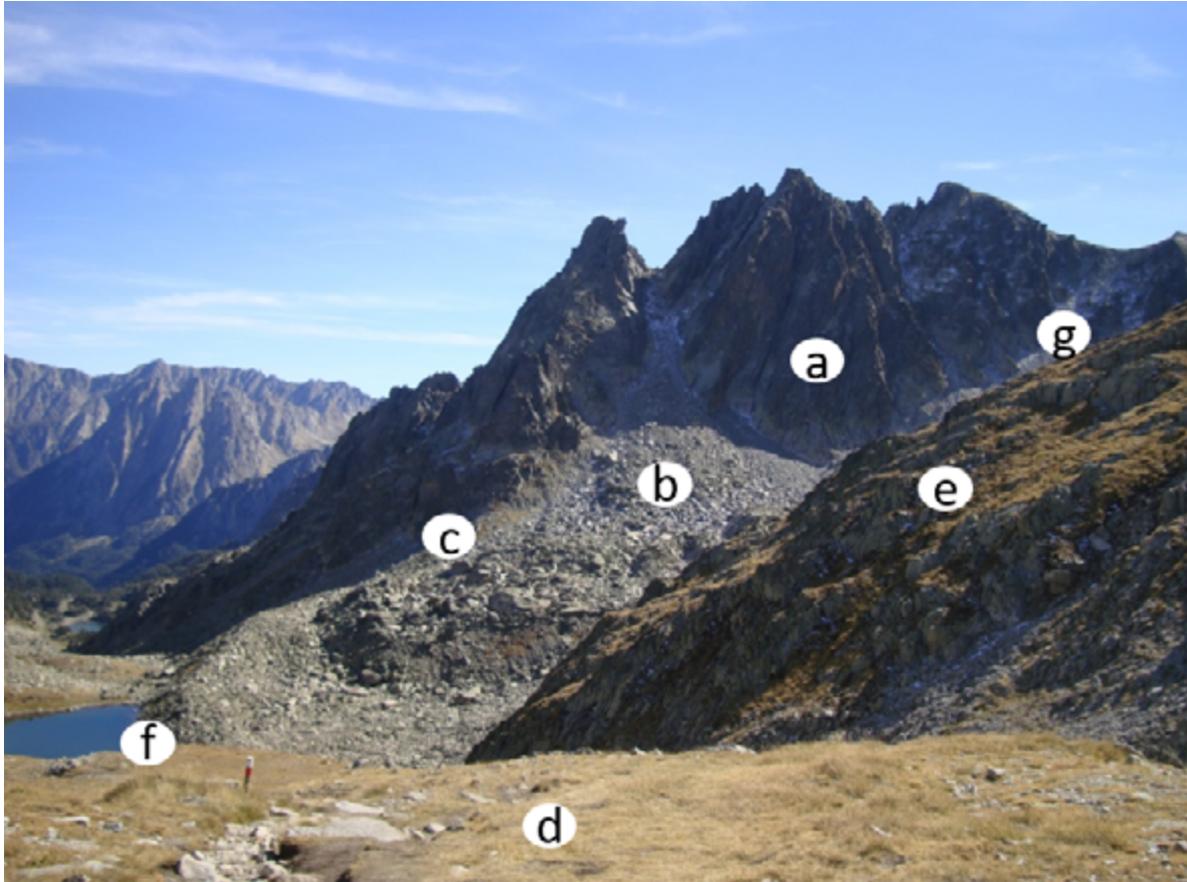


Figure 1. Example of an alpine landscape at the Espot valley, central Pyrenees, where contrasting habitats and plant communities may be found within short distances. Rocky areas (a) and scree (b) cover most of the steeper relieves, together with staircase grasslands (c) and heaths (e); even grassland (d) settle on gentle areas; and water-related ecosystems (f) and snowbeds (g) occur restricted to particular environments.

At the same time, the cumulative knowledge on plant traits grew into a useful tool to address comparative plant ecology (Grime *et al.*, 1988) and led to acknowledge the role played by plant species in structuring vegetation through contrasting plant strategies fitting to distinct environments, and then co-occurring in recurrent plant assemblages (Grime, 2001). Moreover, behind focusing on plant competence as the mechanism structuring vegetation, positive interactions between plants took more relevance as alternative explanatory processes (Pugnaire, 2010). Particularly in stressing environments (e.g., alpine tundra, fellfields) facilitation effects would shape plant communities. Interestingly, this enriched view of vegetation structure incorporates the temporal dimension, since plant-plant interactions change along the ontogeny of individuals. Therefore, plant species play a relevant role in structuring vegetation by means of their functional traits, which are not only response to environment gradients, but also drive vegetation and ecosystem processes (Lavorel & Garnier, 2002; Grime & Pierce, 2012).

In this paper we use the example of the alpine vegetation of the Catalan and Andorran Pyrenees to illustrate how phytosociology, behind a classification tool, is a strong framework for analysing the relationship between plant cover and environment, and thus for understanding plant diversity through the varying alpine landscapes.

Materials and method

For this purpose, we used 800 phytosociological relevés gathered in a vegetation databank (Banc de Dades de Biodiversitat de Catalunya; Font, 2009) which have been classified into 46 community-types (associations). Then we have characterized the associations assessing the most frequent plant species by means of a wide scope of traits, summarized at the relevé level, and then at the association level.

Then we selected nine plant traits covering different aspects of plant life, thus making a good approach to a complete plant strategy, and feasible to be assessed for a high number of species. Each trait was split into a number of discrete states or categories:

- Life-form (i.e., nanophanerophytes, suffruticose chamaephytes, diffuse chamaephytes, prostrate chamaephytes, reptant chamaephytes, graminoid hemicryptophytes, non-graminoid hemicryptophytes, geophytes, therophytes)
- Succulence (not at all, semisucculent, succulent)
- Evergreenness (not at all, semievergreen, evergreen)
- Woodiness (not at all, semiwoody, woody)
- Lateral expansion (not at all, few nearby resprouts, few far resprouts, caespitose)
- Dissemination mode (four categories, from closer to farther from the mother plant)
- Seed weight (<0.01 mg, 0.01-0.05 mg, 0.05-0.5 mg, 0.5-5 mg, >5 mg)

These traits were mainly assessed or inferred from standard floras and herbarium material, but seed weight was mainly obtained from own material. Then we built a main table where the 46 community-types were characterized by means of the relative cover achieved by the group of plant species involving any trait state (thus, a table with 46 × 31 cells).

We evaluated the relationships between plant associations on the basis of their adaptive traits through Principal Component Analyses, one for the whole vegetation, and other for the main core group of associations (for more details, see Ninot *et al.*, 2018).

Complementarily, we characterized the plant associations in terms of a few descriptors related to plant structure and function (plant cover, diversity of plant forms), and to plant diversity (species richness, number of endemics), as mean values of the corresponding relevés, thus at plot level.

Results

Vegetation groups based on functional traits

The multivariate ordinations evidenced a few vegetation groups defined by the dominant plant strategies, which could be related with distinct alpine environments. Thus, the first ordination performed showed three vegetation groups; from which one formed a dense cloud contrasting with respect to two more disperse clouds (Fig. 2). One of these corresponded to seven associations of dwarf to taller heaths and other layering communities, whereas the other is formed by ten associations settling on rocky areas, surface waters or snowbeds. The first axis is strongly correlated with woodiness towards its negative part, whereas the second axis express a wide array of functionally unrelated traits (such as graminoids, semisucculents or diffuse chamaephytes; data not shown).

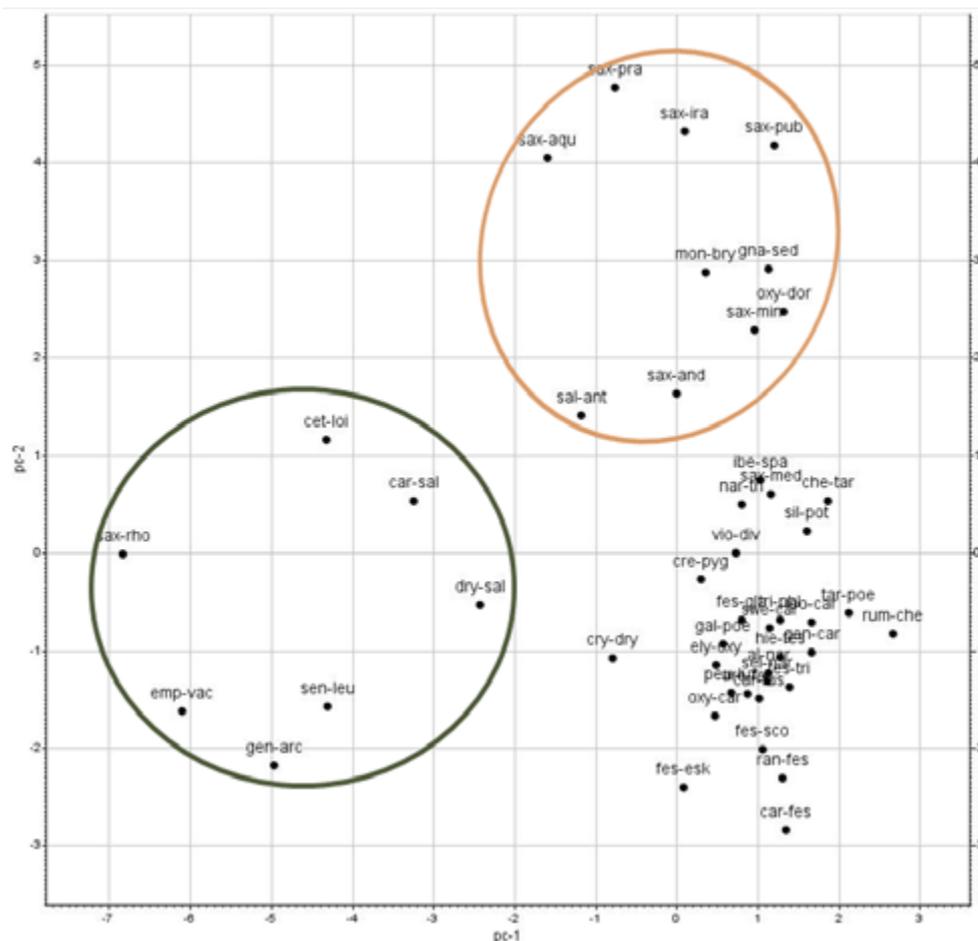


Figure 2. Ordination of the 46 associations (black dots with abbreviated association names) on the two first axes of the first PCA (accounting for 0.209 and 0.162 of total variance, respectively), according to the weight performed by the distinct plant traits. Two vegetation groups appeared detached from a dense cloud of other associations.

The second analysis done within the denser cloud allowed distinguishing four ecological groups (Fig. 3), from which three more peripheral. These peripheral groups correspond to ruderal communities, sparse plant communities settling on gliding scree, and discontinuous grassland adopting a staircase appearance. Finally, the larger group includes a scope of even grassland, from medium-sized dense swards to short open pasture. The first axis is related to plant structure, with graminoid habit in the negative part and creeping chameaphytes and long-distance expansion in the positive part. The second axis expands the difference between dense-turfed graminoids versus other hemicryptophytes (data not shown).

Emergent characteristics of vegetation groups

The vegetation groups above presented showed suggesting trends concerning functional structure and plant diversity at the association level, as shown in Figs. 4 and 5. To better

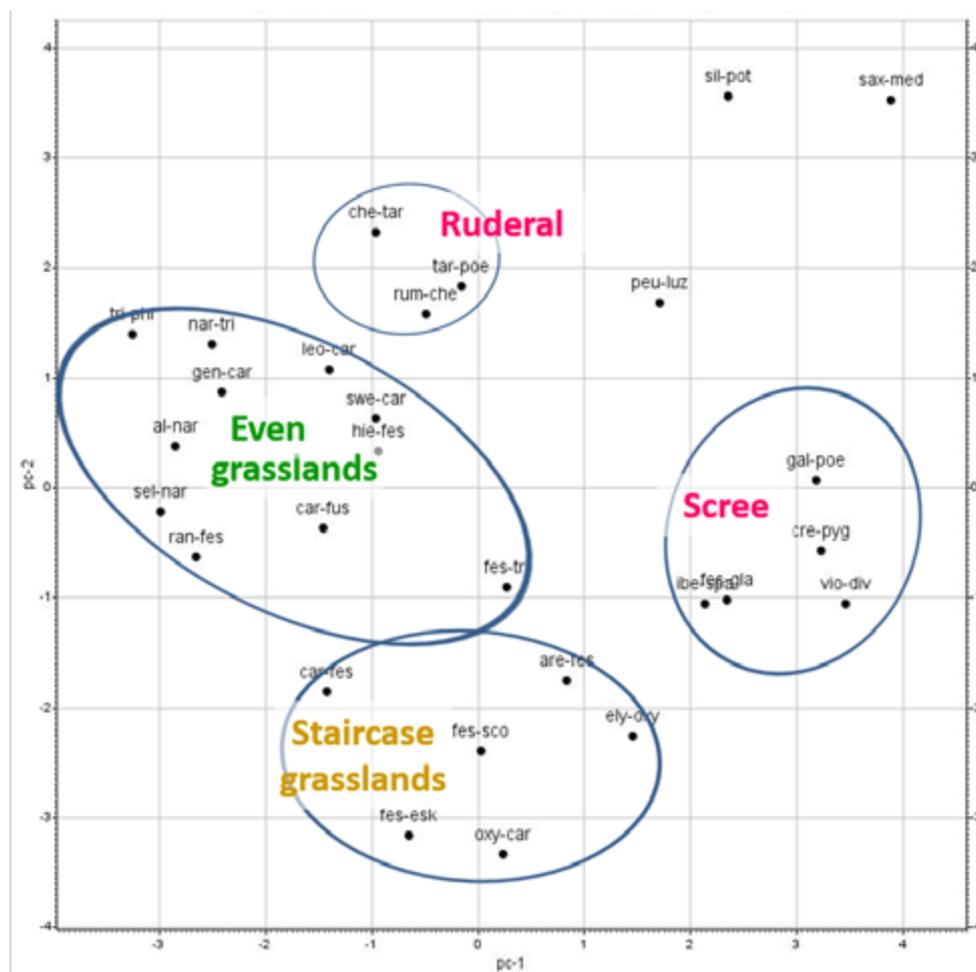


Figure 3. Ordination of the 29 associations from the denser cloud in Fig. 2, on the two first axes of the second PCA (accounting for 0.221 and 0.157 of total variance, respectively), according to the weight performed by the distinct plant traits. Most of them may be distributed into four vegetation groups.

illustrate these trends, we have split some of the vegetation groups evidenced after plant traits into smaller groups, following phytosociological criteria, namely according to the floristic contents of the plant associations.

In the case of structural descriptors (Fig. 4), some vegetation groups reflected the stress conditions where they occur through low plant cover (rupicolous, scree, riverine). The other groups achieved clearly higher values, with minor differences between groups exhibiting distinct physiognomy (e.g., heaths, staircase grasslands, even grasslands). The co-occurrence of different plant forms is a general trend in the alpine associations, given the high values of the Shannon index at plot level. Only the ruderal vegetation and the dense grasslands showed clearly lower values in this index.

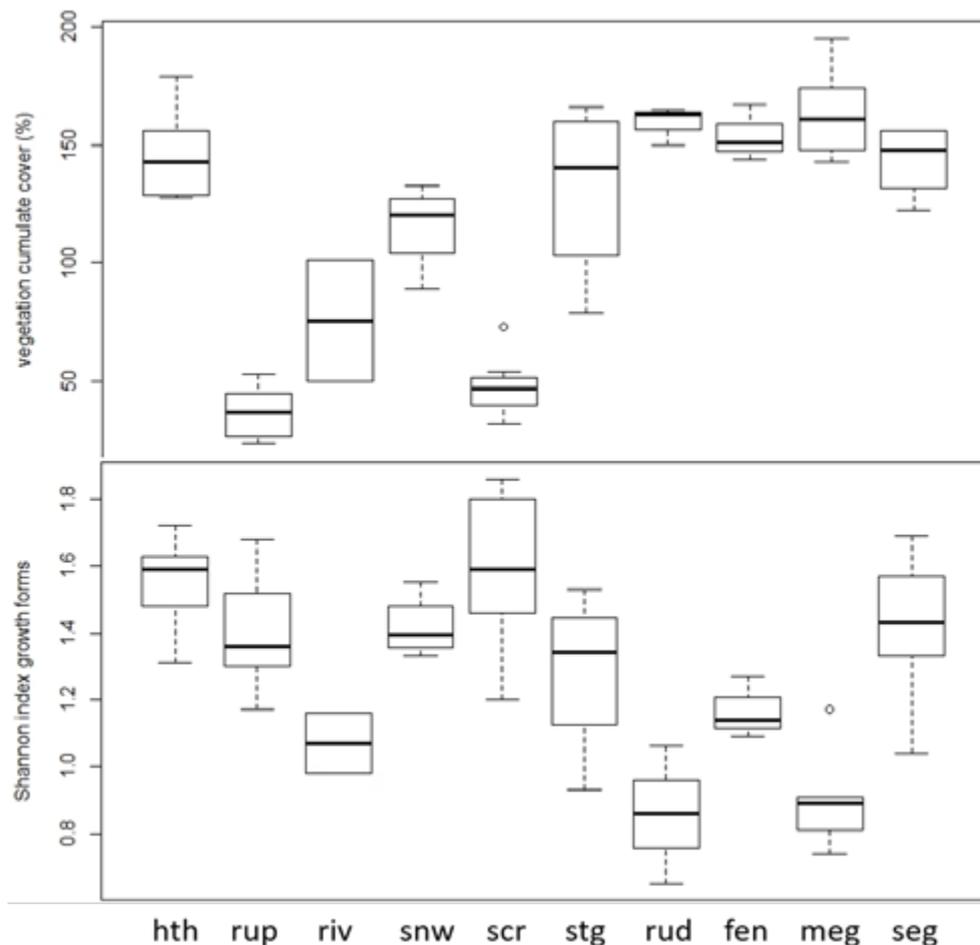


Figure 4. Comparison of vegetation groups in terms of two structural descriptors, cumulative plant cover (top) and diversity of growth forms (bottom) at plot level. These groups correspond partly to those evidenced in figures 2 and 3, and partly to subgroups delimited after phytosociological criteria. The boxplots reflect the distribution of the values for the associations within each group: hth, heaths (5 associations); rup, rupicolous (5); riv, riverine (2); snw, snowbeds (4); scr, scree (8); stg, staircase grasslands (4); rud, ruderal (3); fen, fens (3); meg, dense medium-sized even grasslands (5); seg, open short even grasslands (6).

Species richness and singularity (evaluated as percentage of endemic species) partly followed parallel trends through the vegetation groups, namely richer plant associations include more endemics (Fig. 5). This trend is not so in scree vegetation, where species-poor communities include fair number of endemics; nor in ruderal vegetation, where moderately rich communities are very poor in endemics.

Discussion

The vegetation groups built through general plant traits give support to a number of phytosociological groups, mainly at class level. This works where particular environments drive singular plant traits, thus plant assemblages (e.g., scree, ruderal or heath groups),

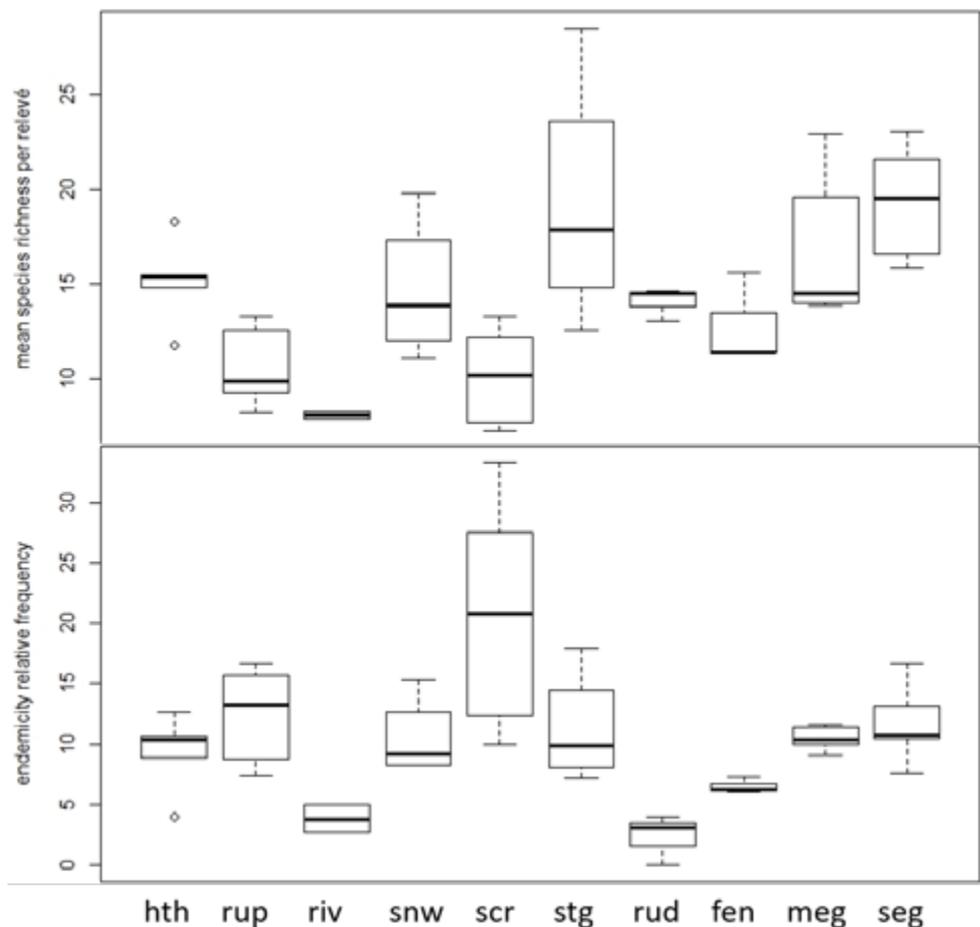


Figure 5. Comparison of vegetation groups in terms of two descriptors of plant diversity, species richness (top) and relevance of endemic species (bottom) at plot level. These groups correspond partly to those evidenced in figures 2 and 3, and partly to subgroups delimited after phytosociological criteria. The boxplots reflect the distribution of the values for the associations within each group: hth, heaths (5 associations); rup, rupicolous (5); riv, riverine (2); snw, snowbeds (4); scr, scree (8); stg, staircase grasslands (4); rud, ruderal (3); fen, fens (3); meg, dense medium-sized even grasslands (5); seg, open short even grasslands (6).

involving physical particularities such as slope dynamics, rock dominance, stronger grazing pressure, or enhanced development for woody habit. However, contrasting stress types such as those found in rocky areas and in semi-submerged vegetation give similar plant assemblages in terms of basic plant forms and traits.

Other main habitat characteristics, particularly those referring to soil richness in carbonate, do not drive particularities in the plant traits assemblages. Thus, contrasting with strong differentiation between calcicole and calciphuge associations, the underlying environmental gradient does not translate into changes in basic plant traits. This is also the case of fens, where particular flora adapted to hydromorphic soils does not bear apparent functional distinction.

According to these findings, the alpine vegetation may be ordered following main stress gradients in the way that Keddy (2005) named 'Centrifugal model of dominant plants according diverging stress factors'. In our alpine case (Fig. 6), the core habitats (i.e., the milder habitats) give advantage to a few potentially dominant species (e.g. *Festuca airoides*, *F. eskia* or *Nardus stricta*) able to structure rather stable plant communities under moderate grazing pressure. These occur on flat or gently sloping areas, coupled with general alpine bioclimate and, typically, neither subjected to singular stress conditions nor to particular disturbance regimes. The dominant graminoids show higher competitive ability and persistence through dense caespitose habit, which is coupled with generalized turnover of above-ground structures. The community strategy here is the response to moderate stress conditions and moderate disturbance by grazing, which results into fair species-rich assemblages from plot to region levels (Gómez *et al.*, 2003; Illa *et al.*, 2006). Some of these associations are taken as climax vegetation (Braun-Blanquet, 1948; Vigo, 1996).

Farther towards different stressing conditions, distinct plant communities hold in the whole high plant diversity and, particularly, plant singularity, as the result of hosting stress-tolerant species, which generally show low competitive ability. These are singular species (endemics, disjuncts) and functional types (pulvinules, semelparous) coupled to one or another stress category, forming species-poor communities at the plot level (Gómez *et al.*, 2003). This is clear for distinct stress categories (such as drought, hydromorphy or shortness of growing season), but also for disturbance (typically, slope dynamics in scree, but also recurrent grazing and manuring in selected pasture areas). The occurrence of woody species (from dwarf to low shrubs) able to form dense stable carpets may be understood as a form of biotic stress for the rest of the plant community, and thus these are similar to plant communities placed in other stressing positions.

The case of woodiness is certainly particular. Although this would not be a functionally relevant plant trait in the alpine belt, it enhances dominance at community level, mainly for plants able to clonal growth. This gives an ecological opportunity for a few dwarf shrubs, either evergreen or deciduous. Taller shrubs (such as *Rhododendron ferrugineum* or *Juniperus communis* subsp. *nana*) seem doomed to evergreenness, a plant trait that involves more investment in persistent leaves (Illa *et al.*, 2017) but that is, together with taller

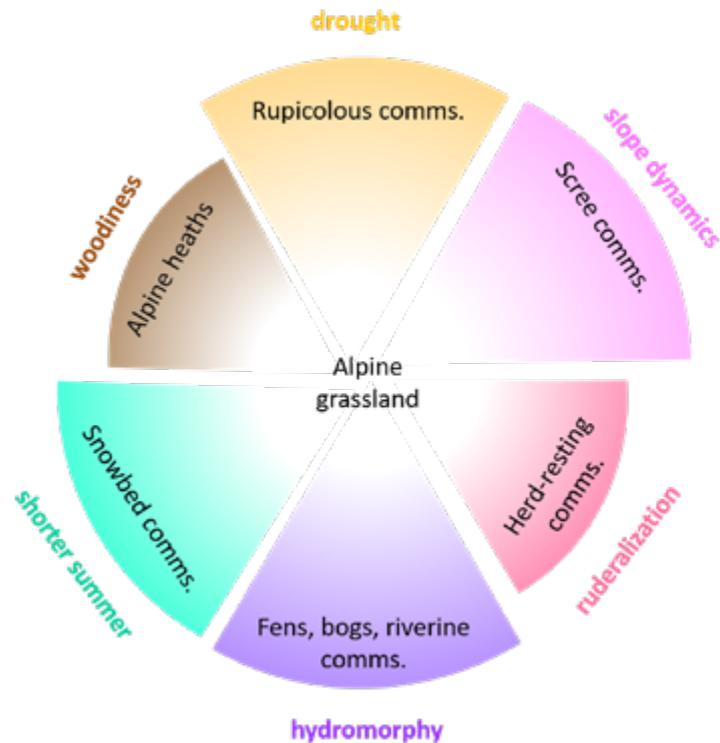


Figure 6. An explanatory model for alpine vegetation according to relevant stress gradients, or disturbance regimes, represented as centrifugal shadowing going from a balanced community-type (i.e., climatic alpine grassland) to diverging environments limiting plant life. The shorter sectors of woodiness and ruderalization reflect limited development of these trends in the alpine belt.

canopies, the basis for higher competitive ability. Other evergreens (*Arctostaphylos uva-ursi*, *Loiseleuria procumbens*) clearly thrive under stressing conditions found in ridges and rocky snowless slopes, grace to their xeromorphous leaves. Deciduous heaths, contrarily, have their opportunity in snowy spots, where shorter growing season is compensated by better soils (Braun-Blanquet, 1948).

In fact, heath vegetation is the only vegetation category within the alpine belt where a few species (taller woody plants) clearly exert a competitive advantage over a wide species pool, and thus may drive plant succession to more steady vegetation. The contemporary prevalence of alpine grassland over heath could be related to very ancient equilibriums driven by grazing pressure (Gassiot *et al.*, 2017). Pre-humanized herbivores and anthropic herds might have extended grassland over alpine heath. The contemporary occurrence of heaths, mainly secluded in more or less rocky areas, could reflect the lower ability of woody species to recover from grazing disturbance. Present encroachment seems to proceed very slowly (or irregularly) in the true alpine belt (Montané *et al.*, 2007; Ninot *et al.*, 2017a) —contrasting with the Arctic tundra (Myers-Smith *et al.*, 2011, Björkman *et al.*, 2018). In spite of the slowness of clonal shrubs to expand, however, cumulative encroachment could mean a deterministic recovery of an ancient ‘shrubby lower alpine belt’.

In some of the stress categories (i.e., slope dynamics, hydromorphy) there is a trend to occur higher number of plant community-types towards growing stress intensity, namely there is a number of associations settling on scree (according to distinct chemical and physical properties of the scree), and fewer grassland types covering sliding slopes or in the core habitat. This may be understood as more determinism in stressing conditions (where abiotic properties drive species-poor communities), and higher prevalence of vegetation structure on the ecosystem under milder conditions.

The strategic scheme of the alpine vegetation shown in Fig. 6 could help at previewing vegetation trends related to the on-going global change, although clear responses are difficult to forecast. On the one hand, rising temperatures and increase in rainfall irregularities (López-Moreno *et al.*, 2009) could affect plant communities presently located in drier environments (rock crevices, shelves) and reduce the occupancy of mesic grassland and heath. However, there is no evidence pointing to a real effect of drought on plant distribution in the alpine. It could really affect the hygrophilous vegetation, by reducing water amounts and dynamics, and more precisely those depending on direct rainfall (i.e., ombrotrophic bogs). More clearly, reduced snowfall and warmer summers endanger snowbed vegetation, as is already recorded in permanent plots of these sensitive plant communities (Illa, 2016). On the other hand, changes in land use through decreasing extensive herding and allowing the expansion of spontaneous or introduced herbivores may drive the alpine landscape to not previewed situations.

Conclusions

The vegetation knowledge acquired through the phytosociology method and gathered in data banks is a very appropriate foundation to functional attempts, since it consists in a species-specific evaluation of plant assemblages, related to distinct environments. The system used relies on the evaluation of relevés (i.e., plot communities) through their species composition, not by their phytosociological adscription. This illustrates how two distinct scientific approximations to plant life add particular, valuable knowledge each, and thus may be used synergistically to improve actual plant knowledge.

High mountain environments involve distinct particular life conditions and processes, which drive particular biological plants and plant assemblages. Processes such as slope dynamics, snowpack accumulation in appropriate spots (i.e., snowbeds) or the maintenance of initial stages of primary succession (i.e., bare rock) generate place for plant species particular in the functional aspects and in their biogeographical status.

Steady alpine habitats, namely gentle slopes neither affected by noticeable slope dynamics nor by other environmental particularities, are mostly place for grassland apparently well-coupled with alpine macroenvironment (i.e., moderately short growing season, moderate grazing pressure), taken as climax vegetation. However, there is still a lack of knowledge on the actual effect of grazing on the spatial distribution of main vegetation types; heath could be actually recovering part of these habitats, mostly in the lower alpine belt.

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