Vegetation and hydrogeology along the distribution of *Centaurium somedanum*, a narrow endemic of mountain calcareous springs

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Abstract

Calcareous springs support bryophyte-dominated habitats relevant to biodiversity and conservation, but little is known about the ecology of vascular plants restricted to these environments. Here we investigate vegetation and hydrogeological patterns within the distribution of *Centaurium somedanum,* a threatened vascular plant that is restricted to mountain calcareous springs in Spain. We studied the hydrogeological characteristics of the spring systems where the species occurs and identified three types (a) springs with active travertine deposition in small valleys, (b) springs in rock fall avalanches and (c) springs fed by calcareous water close to geological faults. Vascular plants and bryophytes co-occurring with the study species were sampled in 1 m^2 plots to identify major vegetation types and to assess the relationships between species composition and topography. The presence of *C. somedanum* was associated with vegetation of calcareous spring fens (*Caricion davallianae*) in geological faults; tufa concretions (*Adiantion*) in active travertines; and other vegetation type of calcareous flushes (*Pinguiculion*) that was found in all the spring types. *C. somedanum* shows a wider ecological range than other vascular plants of calcareous springs, occupying micro-habitats with similar cover of bryophytes but differences in the cover of vascular plants. Although plant communities are primarily dependent on the hydrology of springs, the variation on species composition is correlated to the slope and solar radiation at the micro-scale. Our study demonstrates how a vascular plant with a calciphile character may occur in a wide range of habitats along the spring-flush-fen gradient, as a possible adaptation to tufa-forming niches occurring at different altitudes and geohydrological conditions.

Keywords: Fen; Gradient; Species composition; Travertine; Wetland

Introduction

In temperate mountains, calcareous springs occur naturally on limestone and other carbonate-rich bedrocks, when groundwater intersects the topographic surface and produce characteristic calcium deposits named as tufa (Pentecost, 2005; Jones and Renaut, 2010). Because of their uniqueness and widespread distribution, calcareous springs and related habitats are rare ecosystems that support an important rate of threatened vascular plants, mosses, algae or invertebrates (Cantonati et al. 2006; Virtanen et al. 2009). Besides their natural rarity, these habitats have suffered a strong historical decline because of hydrological changes such as dranaige (Grootjans et al. 2006; Mälson et al. 2008). In consequence, calcareous springs and associated species are considered as conservation priorities in most of the temperate zones of the world (Kooijman et al. 1994; Grootjans et al. 2005) and therefore it is necessary to adequately assess the environmental constrains of their biodiversity.

Most species found in calcareous springs and related habitats are adapted to the special ecological conditions provided by tufa precipitation and calcareous groundwater flows, such as nutrient-deficiency and high mineralization (Cantonati et al. 2006). Among these species, bryophytes of the families *Amblystegiaceae* or *Calliergonaceae* are dominant and represent an important structural part of spring communities in Europe and North America (Miller et al. 2005; Virtanen et al. 2009). In contrast, vascular plants seem to be restricted to very few species, many of them being associated with the accumulation of precipitated tufa and the existence of sub-halophyte conditions (Amon et al. 2002). In Europe, typical examples of vascular plants closely related to calcareous springs are *Arabis soyeri* Reut. and Huet., *Saxifraga aizoides* L. or *Cochlearia pyrenaica* DC., although there are other species more or less dependent on these habitats (Zechmeister and Mucina, 1998, Tomaselli et al. 2011). However, the ecological preferences of these species are in many cases poorly understood, and the co-occurrence of different vegetation types in the spring systems makes difficult the interpretation of their habitat (Devillers et al. 2001; Pentecost, 2005).

Solar radiation, altitude, pH and nutrient content have been identified as the main predictors of the floristic composition in spring habitats (Tomaselli et al. 2011; Sekulová et al. 2012). In calcareous springs, these factors are mainly influenced by the hydrological characteristics of the spring systems and the micro-topography of stands supporting plant species (Pentecost, 2005). The variation on micro-niches along spring-related habitats was described by Wheeler and Proctor (2000) as the “spring-flush-fen” gradient, resulting in different conditions from the spring heads to the surrounding habitats. This results in a complexity of ecological conditions that determine the distribution of vascular plants and bryophytes to micro-scale observation (Cantonati et al. 2006), which distribution is expected to be the result of their adaptation to the hydrogeological characteristics of each spring (the abiotic component) and the interaction with other species (the biotic component). Because of their better adaptation to tufa accumulation, bryophytes dominate the microhabitats directly related to the spring heads (Pentecost and Zhaohui, 2002) while vascular plants are expected to occupy outer positions along the spring-flush-fen gradient. However, there are few examples investigating the habitat differentiation of plant species in calcareous springs. Species-based approaches dealing with the distribution and vegetation ecology of vascular plants dependent on these habitats may provide useful information for their management and conservation.

In this paper, we investigate how hydrogeological and topographical factors influence the distribution and vegetation ecology of *Centaurium somedanum* M Laínz, a threatened vascular plant species closely related to calcareous springs in Spain. This species seems to find its proper ecological niche in the tufa deposits found in the surrounding of calcareous springs along a wide environmental range, from forested to sub-alpine landscapes (Aldasoro, 1996; Jiménez-Alfaro et al. 2005). To assess the main factors influencing the habitat occupied by *C. somedanum* and the potential implications for developing conservation efforts, we study the whole distribution of the species to address the following research questions: (1) What is the range of vegetation types in which *C. somedanum* occurs and what are their relationships with hydrogeological conditions? (2) How are companying species of vascular plants and bryophytes affected by topographical factors on a micro-scale?

Materials and Methods

Study species and study area

Centaurium somedanum is a perennial plant of the *C. littorale* group, a special section of the genus including perennial and sub-halophytic species from Central and Northern Europe (Mansion et al. 2005). The species is endemic to the Cantabrian Range (Spain) and globally categorized as Vulnerable according to the IUCN criteria, with only 16 populations currently known (Jiménez-Alfaro et al. 2010). Because of its rarity, *C. somedanum* is protected by local and national Spanish governments; it is a Priority species in Europe (92/43 EU Directive) and a flagship species for conservation in the UNESCO-MAB Biosphere Reserves of Somiedo and Babia (Spain). Our study covers the whole distribution of *C. somedanum* (Figure 1). The study area is part of the Atlantic Biogeographic Region of Europe (Roekaerts, 2002) and is characterized by temperate bioclimatic conditions with a strong Mediterranean influence. Mean annual temperature of the study area ranges from 6.4 to 10.2 ºC, while the total amount of annual Precipitation varies from 1170 to 1500 mm (data from climatic models developed from meteorological stations, Ninyerola 2001). The area is geologically dominated by mixed limestone and siliceous formations, with a rough topography and a wide range of altitudes (between 600 and 2400 meters) in relatively short distances (< 20 kilometres). The abundance of limestone and the hydrogeological settings of the region provide an adequate framework for the occurrence of calcareous springs, although they are relatively rare and have a scatter distribution.

Characterization of spring systems

We visited the main 10 sites where *C. somedanum* is known, covering the total altitudinal range of the species (Table 1) but excluding nearby micro-populations influenced by the same spring systems. The geological map of the study area (Instituto Geológico y Minero de España IGME, 1:25.000) and own field surveys were used to identify the hydrogeological settings of the springs. We defined three spring types which act as not confined aquifers recharging water by diffuse rainfall and superficial run off (Figure 2). The first type (Figure 2a) corresponds to active travertine formations occurring in Karstic environments, where tufa formation needs a continuous and slow calcareous water flow. In these areas, the water flows slowly in open caves and sinkholes through the vadose zone until the water table. The open caves act as local base level and supersaturated groundwater drains into the gorge wall as springs, promoting the travertine formation (Ford and Williams, 1989). The second type (Figure 2b) consists on rock fall avalanches in old glacier valleys forming deposits that act as discontinuous aquifers and springs with tufa deposits. These aquifers have slow discharge flows under seasonal control and have a chaotic framework based on piled rock fragments that develop confined open spaces disconnected of the regional water table. In these semi-confined spaces the groundwater flows in turbulent regime following very sinuous paths ways (Wassmer et al. 2004). The third type (Figure 2c) corresponds to bedrock water fluxes from the saturated zone. These springs take place associated to geo-structural features as faults promoting the formation of perched aquifers. Other hydrogeological settings associated to this water system take place when a very permeable layer of rock is above the main water table aquifer but below the topographical surface (Frezze and Cherry, 1979). Under very wet conditions, confined water bodies can discharge water via springs along geological faults which act as deep water collectors from aquifer to the surface (Hinds et al. 1999).

The springs associated to geological faults were the most frequent type found along the distribution of *C. somedanum,* followed by the travertine type and the springs in rock avalanches (Table 1). The ecological variation of the three spring types was assessed by measuring surface water pH and conductivity with a field sensor (Crison NM40) over 10 points randomly selected along the water flow of the springs. Springs with active travertine deposition provided higher water temperature ($P = 0.005$; Kruskall-Wallis test; $N = 3$) and higher conductivity ($P < 0.001$; Kruskall-Wallis test; $N = 3$) than the other two types, while rock fall avalanches showed lower pH values ($P < 0.010$; Kruskall-Wallis test; $N = 3$).

Vegetation data

The occupancy area of *C. somedanum* in each site was estimated using a submetric GPS receptor (Trimble Geo-Explorer) to locate the individuals at 1 m resolution. The species co-occurring with *C. somedanum* were sampled in 53 micro-plots of 1 m^2 regularly distributed along the area of occupancy of the species. The cover of vascular plants and bryophytes by plot was estimated using an ordinal system based on the Braun-Blanquet cover-abundance scale (Van der Maarel, 1979). The number of plots by site varied proportionally to the area occupied by the species in each spring system, from 2 in the smaller systems (sites 6 and 10) to 19 (site 1), using a minimal distance of 5 metres between plots. Altitude (in meters) and micro-slope (in degrees) per plot were measured using a barometric receptor and a five-degree scale (from 0 to 90) respectively. Solar radiation (Wm^2) by plot was estimated from exposure and solar trajectory using a Digital Terrain Model (5 m x 5 m resolution), the mean annual solar radiation and intermediate (0.5) values of light transmittance according to the Solar

Analyst utility for ArcGIS (Fu & Rich 2000). We followed Castroviejo et al. (1986) for the nomenclature of vascular plants, Hill et al. (2006) for bryophytes and Casas et al. (2009) for hepatics.

Data analysis

Vegetation and environmental data were stored in a database using TURBOVEG software (Hennekens and Schaminee, 2001) and analyzed with JUICE 7.0 (Tichy, 2002), CANOCO 4.5 software (Biometris, Wageningen, NL) and R version 2.14.0 (R Development Core Team, 2011). Plots were classified using the modified TWINSPAN algorithm (Rolececk et al. 2009) and three pseudo-species cut levels (0, 5 and 25). To identify an optimal number of clusters, we used the crispness of classification (Botta-Dukát et al. 2005) implemented in JUICE. For the calculation of crispness, we randomly selected a total number of 10 species with more than 10 occurrences from the whole data set. Vegetation types were then interpreted according to the diagnostic species as defined by the Phi coefficient standardized to equal group size (Tichý and Chytrý, 2006) and the syntaxonomic description of vegetation types of the Iberian Peninsula (Rivas-Martínez et al. 2002). To assess possible differences on the cover of vascular plants and bryophytes in the vegetation types, we compared mean estimates of all species corresponding to both groups using transformation standards for each plot as implemented in JUICE. Cover estimates among groups were compared with the non-parametric Kruskal-Wallis test.

Since TWINSPAN runs as a divisive method, their diagnostic species can be compared with ordination methods (Dale, 1995) for the interpretation of gradients (Leps & Smilauer 2003). Here we analyzed the variation on species composition using Detrended Correspondence Analysis (DCA) with previous square-root transformation of cover values and down-weighting of rare species. DCA was computed to (i) interpret major gradients of species composition, (ii) assess the distribution of samples and vegetation types in the ordination space and (iii) calculate the relationship between species composition and topographical variables. We used the Kendall´s tau to detect correlations between the ordination scores of the plots and the altitude, slope and solar radiation.

Results

A total number of 101 species were identified as companion species of *C. somedanum*, from which 74 were vascular plants and 27 bryophytes (see Appendix S1 for a full list of species). The vascular plants with a higher frequency of co-occurrence with *C. somedanum* were *Pinguicula grandiflora* (81% of the total number of plots) and *Carex lepidocarpa* (64%), while *Palustriella commutata* (64%) and *Aneura pinguis* (41%) where the most frequent bryophytes.

Based on the TWINSPAN analysis, we distinguished three vegetation types (Table 2). A first division of TWINSPAN separated one distinct group that was interpreted as calcareous fens (alliance *Caricion davallianae*) in which *Pinguicula grandiflora* (91%) and *Carex lepidocarpa* (78%) were the most frequent species. A second division from the remaining samples split the data into a second group identified as spring communities from calcareous flows (alliance *Pinguiculion*) where the most frequent species were *Pinguicula grandiflora* (100% of the plots) and *Carex lepidocarpa* (100%); and a third group with termophilous communities of tufa concretions (alliance *Adiantion*) where the most frequent species were *Adiantum capillum-veneris* (75%) and *Pinguicula grandiflora* (60%). Samples assigned to the three vegetation types showed significant differences in the cover of vascular plants ($P < 0.001$; Kruskal-Wallis; $N = 3$) with higher values for *Caricion davallianae* (Mean cover ± Standard Deviation; 52.4% ± 17.2) than *Pinguiculion* (37.9% ± 10.0) and *Adiantion* (25.0% ± 10.2). On the other hand, the cover of bryophytes showed only marginal significant differences ($P < 0.075$; Kruskal-Wallis; N = 3) with a relatively lower cover (20.1% ± 11.7) in *Pinguiculion* than *Adiantion* (29.9% ± 20.9) and *Caricion davallianae* (36.1% ± 20.2).

The three vegetation types were distinctly associated with the hydrology of springs. Group 1 (*Caricion davallianae*) was completely (100% of plots) restricted to the springs of geological faults, while group 3 (*Adiantion*) was predominantly found (85%) in active travertines but also in geological faults (15%). Group 2 (*Pinguiculion*) was present along the three springs types, with a higher frequency in geological faults (52%) than rock avalanches (30%) and active travertines (18%). The correlation of topographical variables with species composition reflected by the DCA (Figure 3) showed a main gradient (length of first axis = 4.317; eigenvalue = 0.659) positively correlated with the micro-slope (Kendall´s tau = 0.77; $p < 0.01$) and negatively with the altitude (Kendall´s tau = -0.63; $p < 0.01$). The second axis still explained part of the variation on species composition (length = 2.994; eigenvalue = 0.307) and was correlated to solar radiation (Kendall´s tau = -0.33; $p < 0.01$) and the altitude (Kendall´s tau = 0.27; $p < 0.01$). The third (eigenvalue = 0.211) and fourth axes (eigenvalue = 0.161) were scarcely or not significantly correlated with these variables.

Discussion

Our study demonstrates how a vascular plant restricted to calcareous springs occurs in a wide range of habitats influenced by different hydrogeological settings and vegetation types. The variety of habitats along the distribution of *C. somedanum* partially corresponds with the spring-flush-fen gradient described by Wheeler and Proctor (2000) to explain physiognomic rather than floristic variation within spring fens. In our study case, the spring-flush-fen gradient may be recognized as a complex of micro-habitats with different species composition, influenced by landscape hydrogeological conditions and spring topography. Although there are many studies focused on vegetation of pure springs (Molina, 2001;

Tomaselli et al. 2011) spring fens (Boyer and Wheeler, 1989; Hajek et al. 2002) and fen meadows (Jansen et al. 2000) less attention has been paid to the species that potentially live in all these habitats. The patterns observed in our study species have been suggested for other species living in tufa habitats of temperate regions (Amon et al. 2002) and therefore it is expected that other species of calcareous springs could show similar habitat differentiation.

Vegetation types and hydrogeology

From the three vegetation types occupied by *C. somedanum*, calcareous fens (*Caricion davallianae*) are commonly identified as alkaline fens (Šefferová Stanová, 2008) or small-sedge fens (Ellenberg, 1998), but hydrogeological studies have been mainly focused on lowland regions (e.g. Grootjans et al. 2006). Our plant communities are closely related to the tufa-forming fens described by Hájek et al. (2006) with high calcium concentrations and extremely nutrient-deficiency conditions. In Central Europe, tufa-forming fens are also refuge for the rare halophytic *Centaurium uliginosum*, a species with a phylogenetic relationship with *C. somedanum* (Mansion et al. 2005) that may indicate genetic-based adaptations to these environments. Furthermore, calcareous fens with tufa-forming indicators (e.g. *Palustriella commutata*) have been identified as rare ecosystems in the Alps (Bergamini et al. 2006), the Carphatians (Hájek et al. 2002) or the Cantabro-Pyrenean range (Jiménez-Alfaro et al. 2012) supporting their conservation value in mountain regions.

Plant communities identified as tufa concretions (*Adiantion*) and calcareous flushes (*Pinguiculion*) correspond explicitly to the spring plant communities recognized in Europe (Zechmeister and Mucina, 1994). Vegetation of the *Adiantion* alliance is characterized by thermophile species (e.g. *Adiantum capillus-veneris*, *Hymenostylium recurvirostrum*) occurring at low-altitude springs of the European mountains (Tomaselli et al. 2011). In the study area, these communities occur in foothill springs with active travertine formation, where cold groundwater that is saturated in calcium carbonate triggers the tufa precipitation when emerge to air conditions with much higher temperatures. The high conductivity of travertines in comparison with the other spring systems is in accordance with the high amount of tufa deposition that characterizes this habitat (Pentecost, 2005; Brusa and Cerabolini, 2009). Accumulation of tufa also produces an additional effect on the morphology of these systems, where the steep slopes determine shady and wet conditions dominated by bryophytes but limiting the presence of vascular plants.

Calcareous flushes with *Pinguiculion* spring communities show similar floristic composition than the tufa concretions of *Adiantion*, but they can be found in different hydrogeological conditions. Within the distribution of *C. somedanum*, *Pinguiculion* communities are dominant in the rock fall springs, but they are well represented in the three spring types identified in this study. This may be explained by the presence of micro-habitat interspaces with high water flow and tufa formation in the context of the spring types, i.e. intermediate slope positions along the spring-flush-gradient (Wheeler & Proctor 2000). These stands seem to be less dependent of the hydrogeological settings of the springs, forming tufa-forming niches occupied by very few species. In the Iberian Peninsula, this vegetation type is restricted to calcareous springs of temperate and Mediterranean mountains harbouring a high number of endemic species of *Pinguicula* (Blanca et al. 1999). Similar communities have been also characterized in the context of calcareous flushes of the British Isles (Rodwell, 1991) and the European habitats (Hill et al. 2004) but they have been scarcely studied.

Companion species and the habitat of C. somedanum

The three vegetation types identified along the gradient of species composition showed significant differences in the cover of vascular plants, in agreement with the expectation that travertines are bryophyte-dominated habitats (Pentecost and Zhaohui, 2002) and calcareous fens are similarly dominated by sedges and mosses (Hajek et al. 2006). The most frequent species occurring with *C. somedanum* (*Pinguicula grandiflora* and *Palustriella commutata*) are commonly referred as indicators of low nutrient availability and tufa formation (Legendre, 2000; Pentecost, 2005) suggesting a similar ecological requirement for the studied species. Thus, *C. somedanum* may be considered a calciphile species (Amon et al. 2002) which distribution primarily depends on the availability of tufa-forming springs independently of their altitudinal range and the dominance of vascular plants or bryophytes at the micro-scale.

The occurrence of calciphile species along different hydrological conditions has been suggested in the vegetation of Central-European and coastal rich fens (Grootjans et al. 2006) and also in bryophyte species (Pentecost and Zhaohui, 2002; Hedenäs and Kooijman, 2004), but very few studies have previously focused on the habitat of vascular plants exclusively related to spring habitats. The high adaptation of *C. somedanum* to spring environments might be explained by the capability of its long-dispersed seeds to germinate at cold temperatures that commonly occur in the bryophyte-dominated habitats (Fernández Pascual et al. 2012). Furthermore, the specialization of perennial *Centaurium* species to subhalophitic and calcareous-rich habitats could have permitted the species ancestor to find appropriate niches on the calcareous springs of the study region, as a possible result of long-term isolation and speciation processes related to geo-edaphic factors (Rajakaruna, 2004).

Implications for management and conservation

Our study shows how one vascular plant occurs in tufa-forming habitats ranging from low altitude to sub-alpine calcareous springs, a patter that is more commonly observed in moss spring species. This finding suggests a wider ecological range of *C. somedanum* than other vascular plants of calcareous springs such as *Cochlearia sp.pl.* or *Arabis sp.pl.*, which are more frequently restricted to pure spring communities (Kochjarová et al. 2006; Tomaselli et al. 2011). Thus, the conservation management of *C. somedanum* could be better approached considering the vegetation-habitat differences of their populations, and the understanding of the influence of hydrology may be essential for the restoration of spring habitats (Jansen et al. 2000; Grootjans et al. 2005). According to the European Classification of Habitats (Davies et al. 2004; EUNIS, 2011) the habitat ”C2.1 Petrifying springs with tufa or travertine formation” is considered of conservation concern (code 7220 in Habitat Directive 92/43/EEC) as well as the habitat “D4.1 Rich fens, including eutrophic tall-herbs and calcareous flushes and soaks” (code 7230). Although the description of both habitats suggests the possibility of mosaic-like vegetation types between each other, there is little information in the literature about such relationships. Our study therefore suggests that some vascular plants may be closely related to both habitats, and further biological patterns of these species (dispersal, genetic diversity, etc.) could depend on wider ecological ranges than could be initially expected.

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Table 1. Environmental characteristics of the 10 spring systems studied along the distribution of *Centaurium somedanum*. Site numbers correspond with Figure 1. AOO indicates the Area of Occupancy of *C. somedanum* in each site. Altitude refers to the medium value from each site. Mean values ± Standard Deviations of water pH, conductivity (Cond) and temperature (Temp) were measured in 10 points random along each one of the spring systems.

Site	**Spring Type**	**AOO (m^2)**	**Altitude (m)**	**pH**	**Cond (µS/cm)**	**Temp (ºC)**
1	Travertine	635	600	8.2 ±0.3	314 ±35	18.2 ±1.4
2	Travertine	480	780	8.3 ±0.2	328 ±63	14.4 ±2.4
3	Travertine	47	920	8.1 ±0.1	365 ±21	16.2 ±1.7
4	Rock avalanche	64	1050	7.9 ±0.2	277 ±20	13.1 ±1.8
5	Bedrock water	216	1250	8.2 ±0.1	237 ±12	10.4 ±0.8
6	Bedrock water	168	1350	8.3 ±0.2	249 ±27	17.8 ±0.7
7	Bedrock water	273	1400	7.8 ±0.2	267 ±32	13.3 ±4.2
8	Bedrock water	151	1350	8.5 ±0.1	277 ±14	15.9 ±2.2
9	Bedrock water	320	1600	7.7 ±0.3	339 ±77	16.3 ±1.6
10	Bedrock water	273	1720	8.1 ±0.3	226 ±21	13.3 ±2.0

Table 2. Synoptic table showing the percentage frequency (%) of diagnostic species in the three vegetation types identified by TWINSPAN. Species are ordered according to the Phi-coefficient (* > 0.40; **> 0.50). Only species with a probability of occurrence not differing from random (Fisher exact test; $p < 0.05$) are shown. (br) indicates bryophytes.

TWINSPAN group	1	2	3
Number of samples	22	20	11
Mean number of species per plot ± SD	17.5 ±5.6	11.9 ±4.4	9.8 ±2.8
1. Calcareous fens (*Caricion davallianae*)			
Parnassia palustris	**82****	.	.
Juncus articulatus	**64****	.	.
Philonotis calcarea (br)	**50****	.	.
Crepis paludosa	**45****	.	.
Palustriella falcata (br)	**55****	.	.
Bryum pseudotriquetum (br)	**41****	.	.
Carex flacca	**86****	.	.
Prunella vulgaris	**36****	.	.
Carex panicea	32*	.	.
Mentha longifolia	32*	.	.
Briza media	59*	.	.
Carex davalliana	27*	.	.
Plantago media	23*	.	.
Selaginella selaginoides	23*	.	.
Caltha palustris	23*	.	.
2. Calcareous flushes (*Pinguiculion*)			
Molinia caerulea	23	**73****	5
Globularia nudicaulis	9	**82****	40
Anagallis tenella	.	45*	.
Aneura pinguis (br)	32	82*	30
3. Tufa concretions (*Adiantion*)			
Adiantum capillus-veneris	.	.	**75****
Hymenostylium recurvirostrum (br)	.	18	**55****
Eupatorium cannabinum	.	.	30*
Eucladium verticillatum (br)	.	18	50*
Agrostis schleicheri	9	27	60*

Figure 1. Location of the study area in the Cantabrian Range of the Iberian Peninsula, and the 10 spring sites covering the distribution of *Centaurium somedanum* (see Table 1 for detailed information about the sites).

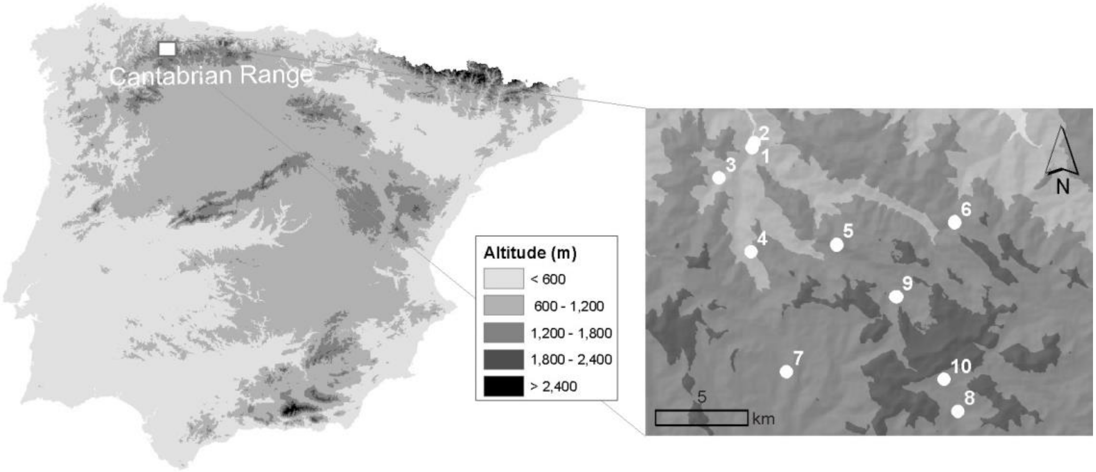

Figure 2. Hydrogeological representation of the three spring types identified along the distribution of *Centaurium somedanum*: (a) active travertines, (b) springs in rock avalanches and (c) springs of geological faults.

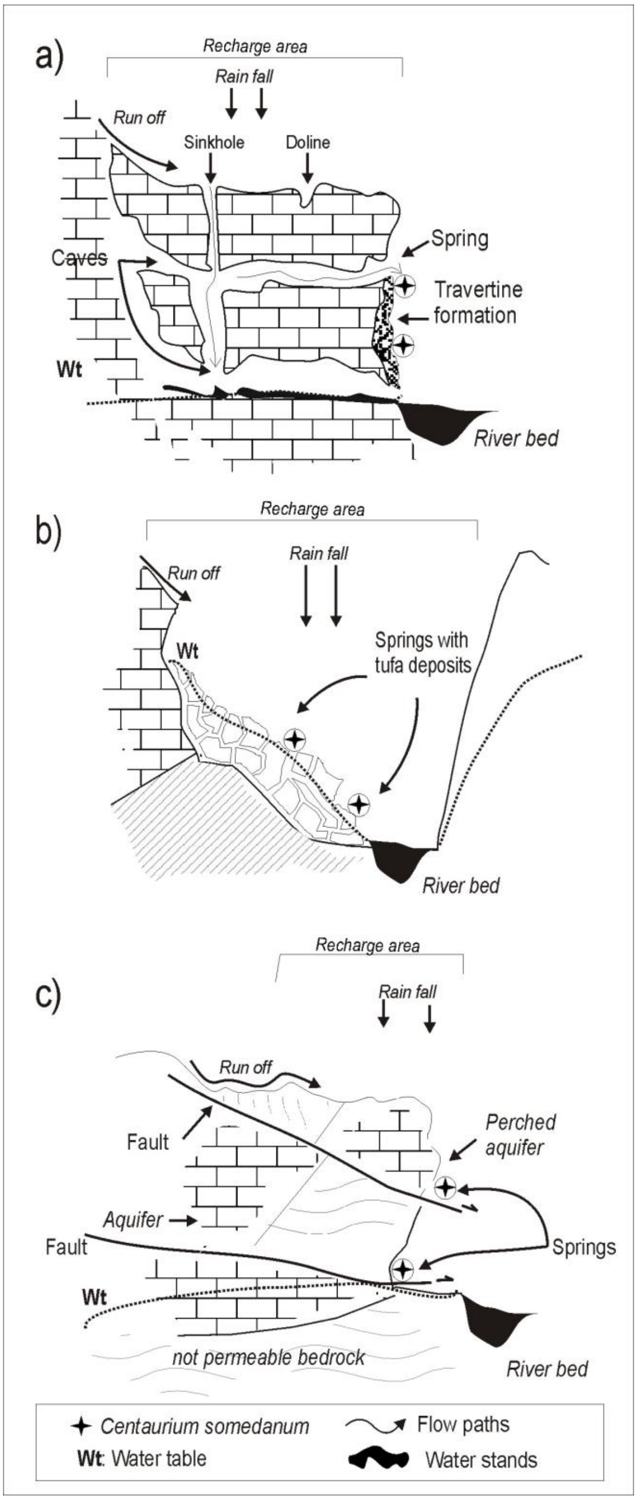

Figure 3. DCA plot (first and second axis) of the vegetation plots analysed in this study. Line envelopments group the three vegetation types identified by TWINSPAN. Environmental variables: altitude (ALT); solar radiation (RAD); micro-slope (SLO). A full list of the species scores along the gradient is presented in the Appendix S1.