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Nodes in the alpine connectome. Exploring the linkages between riparian ecosystem and geo-climatic elements across the mountain environment

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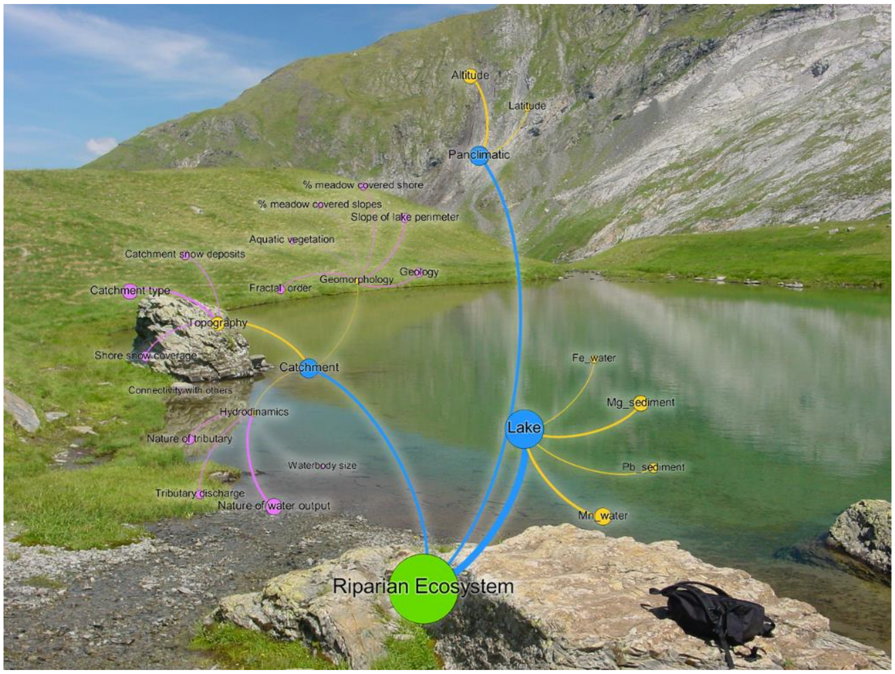

Running title: Riparian ecosystem in the alpine connectome

ABSTRACT

Riparian ecotones are aquatic-terrestrial interfaces integrating climate and nutrient fluxes across landscape physical elements. Despite experiencing severe nutrient and climate restrictions, high elevation lakes host a disproportionally diverse riparian ecosystem. With climate change rapidly encroaching in the alpine biome, it is vital to understand how the functional connectivity between lakes and their surrounding landscapes maintains a natural ecosystem diversity before they experience major deleterious effects.

A total of 189 glacial origin lakes in the Central Pyrenees were surveyed to test how key elements of lake and mountain surface connect at different scales to support riparian vegetation. Secondly, we evaluated how these underlying ecotope properties drive the formation of riparian communities and discuss their potential sensitivity to environmental change. At each lake plant taxonomic composition was assessed together with the elemental composition of water and sediment and ecosystem-relevant geographical factors. Their influence on vegetation was modelled using the Fuzzy Set Ordination and conceptually illustrated using network analysis.

Hydrology-hydrodynamics was the main catchment-scale factor connecting riparian vegetation with large water fluxes, followed by topography and geomorphology. At macroscale vegetation related to pan-climatic gradients altitude and latitude, which captured, in a relatively narrow geographic area the transition between large European climatic zones. Locally, sediment Mg and Pb and water Mn and Fe were reliable predictors of plant composition, reflecting connections with catchment nutrient availability, and water saturation in the soil. Community analysis identified four riparian groups, characteristic to (a) damp environments, (b) snow bed-silicate bedrock, (c) wet heath, and (d) limestone bedrock. Their distribution along geographic gradients is further explored. With climate change being a serious threat to the alpine biome, this study provides critical information on the linkages between the riparian ecotone and the extended environment, which could prove invaluable in assessing future responses to environmental change.

Keywords: Alpine Lakes; Riparian Vegetation; Catchment heterogeneity; Ecotope; Fuzzy Set Ordination; Indicator Species Analysis.

1. INTRODUCTION

Although they occupy < 24% of Earth's land surface mountains, directly and indirectly provide resources for more than half of its humanity, as well as they are responsible for > 50% of total nutrient release into the wider biosphere (Price, 2004; Larsen et al. 2014). This is primarily due to an elevated and steep topography, and exposed geology that creates conditions for water precipitation and accumulation, and nutrient release through accelerated weathering and denudation (Larsen et al. 2014). At high elevations, the harsh climate, abundant hydrological energy, and exposed geology provide a combination of physical and chemical factors that sustain uniquely adapted ecosystems. In no other circumstance is the connection between bedrock and overlying ecosystem clearer than in mountain regions, and this is obvious during small changes in external factors such as atmospheric chemistry (Storkey et al. 2015) and climate (Williamson et al., 2009).

Most of the low-lying landforms of the present mountain landscape, including the vast majority of mountain lakes, are the legacy of Pleistocene glaciation (Thornbury, 1969). There are more than 50,000 remote mountain lakes estimated in Europe alone (Kernan et al., 2009), and > 4000 in the Pyrenees (Castillo-Jurado, 1992). At the interface between terrestrial and aquatic environments, riparian surfaces mediate the fluxes of water, nutrients and carbon between lakes and their catchments, and host a disproportionately high diversity of life forms compared to the surrounding landscapes (Gregory et al., 1991, Kernan et al., 2009). There is > 797 km of shoreline only in the Pyrenees (Castillo-Jurado, 1992).

Cross-scale interactions between vegetation, surface properties (including morphology and geochemistry) and climate can determine species distribution in patterns which are developed along environmental gradients (Austin and Smith, 1989; Hengeveld, 1990). Baroni-Urbani et al. (1978) introduced the term *chorotype* to define a pool of species with overlapping distributions. Fattorini (2015) revisited the concept and further classified the chorotype into global (for worldwide spatial responses) and regional. A regional chorotype is assumed to occupy a small geographic area, regularly a study area within a biome, and it can be more or less uninterrupted. Cluster analysis is generally used to groups species according to their distribution

(Fattorini 2015). When association membership of species cannot be established statistically, they are assumed to follow continuum distributions (Báez et al., 2005).

The rough topography and the severity of the environment- characteristic to the alpine biome, including low temperature, abrasion by snow and ice, high UV radiation and water-level fluctuations, are expected to drive considerable fragmentation in riparian populations and determine the emergence of insular communities around lakes, which are tightly connected to local resources. Species composition and gene flow in such communities are therefore likely to be restricted by the high environmental stress and the low connectivity between waterbodies. Such restrictive influences on plant cover have been shown over localized areas, due to climate factors such as the type and intensity of precipitation, daily temperature, frequency of freezing temperatures and their duration (Keller et al., 2005), as well as variation in these factors with slope orientation and altitude (Baker, 1989).

Climate change correlates, including precipitation, air temperature, freezing line and snow cover can greatly influence the thermodynamics and geochemistry of high altitude catchments (D. G. Zaharescu et al. 2016a, Parker et al., 2008, Thompson et al., 2005), and consequently their riparian communities. With populations of many mountain ecosystems nearing their tipping points (Kreyling et al., 2014; Khamis et al., 2014), it has become critically important to better define the breadth and strength of natural linkages between riparian ecosystem and its supporting physicochemical template (ecotope) in both, lake and the broader landscape, before they can be irreversibly severed. We use term connectome (first introduced by Sporns, 2006, and Hagmann, 2005 in neurosciences) to represent the functional connectivity between a lake ecosystem and the wider environment, as it offers a natural way to understand ecosystem interactions in natural sciences.

Research exploring the connectivity between riparian ecosystem and its supporting physical template in the conceptual framework of ecotope is rare, and it has largely been conducted at low altitudes, focusing on local scale alterations in hydrological and habitat disturbance affecting riparian communities (Merritt et al., 2010). Related work in high altitude watersheds has recently quantified the relative contribution of geomorphic characteristics at different scales to predicting riparian plant community types and species abundances

(Engelhardt et al., 2015). More recently, a conceptual model of ecotope development in the study area has been advanced by Zaharescu et al. (2016b), and its influence on the benthic ecosystem explored in Zaharescu et al., 2016(c).

The motivation behind this study lies in addressing three important issues missing in the literature, which can be key to attain a mechanistic understanding of ecosystem function and the impact of climate change on high-altitude environments: (i) define the cross-scale linkages between catchment surface properties, lake, and riparian ecosystem composition, and their strength, using vegetation data; (ii) identify keystone communities and lakes that can potentially be sensors of environmental change, and (iii) study their distribution with respect to large-scale pan-climatic gradients. These questions pertain to the integrated ecosystem-physical environment understanding of the consequences of climate change on the alpine biome. We hypothesized that due to the geoclimatic setting, high altitude riparian zones will be connected more strongly to local variables than to large gradients, which in turn will create local indicator communities that can be highly susceptible to environmental change.

The location of the Pyrenees at the intersection of four large biogeographical regions in Europe (Atlantic, Continental, Mediterranean, and Alpine), imprints the region a richer biodiversity compared to similar areas such as the Alps, and a relatively high proportion (± 11.8%) of endemic plant species (Gómez et al., 2003). This means that any climate change is expected to greatly disturb riparian ecosystem in such areas, its connection to the physical support, and ultimately the services they provide.

2. METHODS

2.1 The area

The Pyrenees are a relatively young mountain chain in SW Europe and form a natural barrier between Spain and France. Their topography was sculptured mostly during the last glaciation 11,000 years ago, which left an abundance of high altitude lakes and ponds in cirque floors and valleys. The lakes, in different stages of evolution, are more abundant on the steeper, more northerly French side, which generally receives more precipitation.

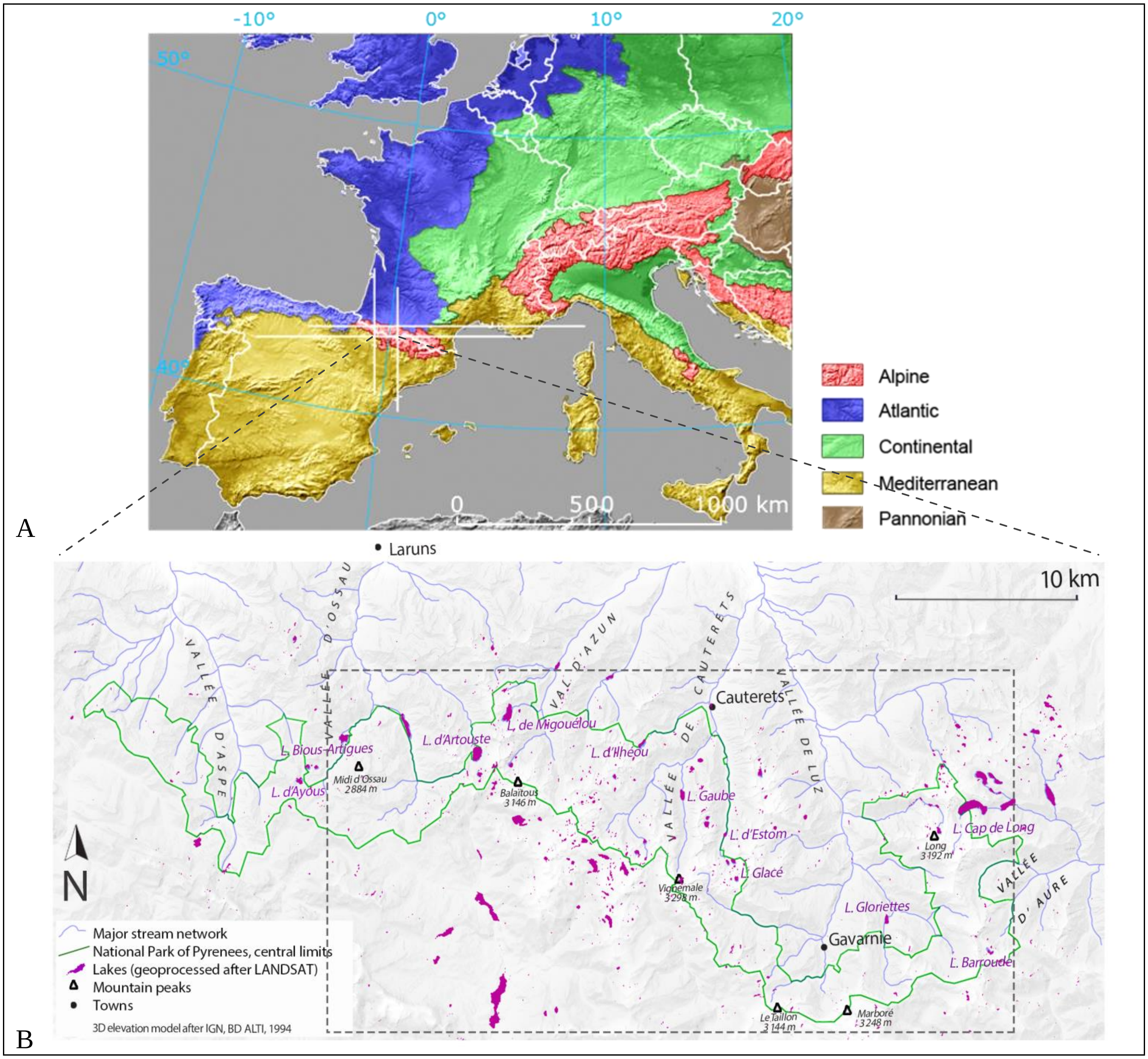

Figure 1 Biogeographical regions of W Europe (A, after EEA, 2001), with location study area (B) in the axial part of Pyrenees National Park, France. Only lakes within the boundaries of the park and enclosed by dash-line box were surveyed.

The study area extended from -0˚37'35" to 0˚08'19" E and 42˚43'25" to 42˚49'55" N in the axial region of the Pyrenees National Park (Fig. 1). The geology is dominated by granitic batholiths, surrounded by old metamorphic and sedimentary materials, including slates, schist, and limestone. The hydrology is broadly shaped by Atlantic influences, which feed >400 lakes and ponds in the national park. The physiography is represented by patterns of relief that generally follow an S-to-N direction. A great number of the lakes are drained by temporary torrents and permanent streams, which converge into major valleys, though isolated waterbodies and karstic systems are not rare. Some of the big lakes at lower altitudes were transformed into reservoirs and are used for hydropower and as freshwater reserves of high quality.

2.2 Sampling strategy

A total of 189 high-altitude lakes and ponds, ranging from 1161 to 2747m a.s.l. was visited during the month of July in 2000, 2001 and 2002. The sampling strategy was designed to cover the great majority of waterbodies in the region in a minimum period, so as to capture a snapshot of their ecosystem phenology in the summer season.

Each lake was characterised according to riparian vegetation composition and a range of catchment physical and chemical attributes. Information on the type of species around each waterbody was collected in the field using Grey-Wilson and Blamey (1979), Fitter et al. (1984) and García-Rollán (1985) keys. Certain species needed to be collected and transported in a vasculum to the laboratory for identification. They were thereupon identified using Flora Europea (available online at http://rbg-web2.rbge.org.uk/FE/fe .html).

At each location hydrological (tributary discharge, nature and size of water input/output), geomorphological (bedrock geology, % slope of lake perimeter, fractal order, % shore/slopes covered by meadow and aquatic vegetation) and topographical (catchment type, catchment/shore snow coverage and connectivity with other lake/s) attributes were visually inspected and scored according to dominant units. Their detailed description is given in (Zaharescu et al. 2016b). Geolocation, i.e. altitude, latitude, and longitude was recorded at each lake using a portable GPS device.

To test for relationships between lake chemistry and riparian vegetation composition, < 2cm depth littoral sediments and water ± 5m off the littoral (for small waterbodies, the distance was less) were sampled using standard protocols employed in Zaharescu et al. (2009). The sediments comprised fragmented rocks, coarse sands, and fine materials. As the chemical composition of the fine sediment fraction is the most likely to relate to riparian vegetation, sampling deliberately targeted this fraction. To assure sample homogeneity each sample comprised ~ 5 randomly selected subsamples. All sediment and water samples were kept at < 4˚C until laboratory analysis.

Water pH and conductivity were recorded on site, at the surface and bottom of the lake from samples taken with a Teflon bottom water sampler. Portable pH/conductivity probes were used in this case.

2.3 Sample preparation for major and trace element analysis

The sediment samples were dried at 40 °C for two days and sieved through a 0.1mm sieve. Trace and major element contents were characterised by X-ray fluorescence spectrometry (XRF). A 5g portion of the sample was prepared as lithium tetraborate melt for the determination of trace (As, Ba, Co, Cr, Cu, Ni, Pb, Mn, Rb, Sr, Zn and V) and major (Al, Ca, Cl, Fe, K, Mg, Na, P, S, Si and Ti) elements. Results are expressed in mg kg^{-1} and % mass-mass, respectively for trace and major elements. Fusions were performed in Pt–Au crucibles. Calibration and quality control analyses were carried out using replicated certified reference materials from National Research Council of Canada, NRCC (SO-3, SO-4, HISS-1, MESS-3 and PACS-2, soils and sediments) and from South Africa Bureau of Standards, SACCRM (SARM 52, stream sediment). Additionally, a given sample was analysed several times during the analysis run. The analysis was highly reliable, with the recovery figures for the reference materials being within an acceptable range for all major elements (±10%). Percent coefficient of variation (%CV) between replicates was <5% and % relative standard deviation, RSD (1σ) between measurements of the same sample <2%.

Total C and N contents were simultaneously determined by flash combusting 5 mg dried sediments in a Carlo Erba 1108 elemental analyser following standard operating procedure (Verardo et al., 1990).

Water samples were prepared for analysis by filtering through 0.45 μm cellulose nitrate membrane followed by acidification to 2% with ultrapure Merck nitric acid. The acidified samples were analysed for Cu, Li, Mn, Ni, Pb, Rb, Se and Sr by inductively coupled (argon) plasma – mass spectrometry (ICP-MS), and for Al, B, Ba, Ca, Fe, Ga, K, Mg and Na by inductively coupled plasma - optical emission spectrometer (ICP-OES) using standard ICP-MS/OES operating conditions. The analysis, following standard procedures and QA/QC protocols, were performed at the University of Vigo's Centre for Scientific and Technological Support (CACTI).

2.4 Statistical procedures

2.4.1 Principal component analysis to summarise ecotope factors

Principal component analysis (PCA) was used to reduce the multiple catchment-scale variables to a limited number of composite factors (principal components, PCs) that represent the major ecotope processes being investigated (Table 1). This was done by summarising the variables into regression factor scores of the principal components (*Varimax* rotation), which were then used as explanatory composite factors in the further analysis. Data analysis was performed in PASW (former SPSS) statistical package and exhaustively detailed in Zaharescu et al. (2016b).

2.4.2 (Multidimensional) Fuzzy Set Ordination to quantify riparian drivers

To understand the potential effects of catchment gradients on vegetation composition/incidence we used Fuzzy Set Ordination (FSO) followed by a forward stepwise multidimensional FSO (MFSO), both run on a distance matrix of species incidence data.

Introduced by Roberts (1986), FSO is a better alternative to constrained ordination methods, e.g. CCA and RDA. Unlike classical theory (linear algebra), where cases are either in or out of a given set (0 or 1), in FSO cases are assigned partial membership (fuzzy) values ranging from 0 to 1 that denote their membership in a set (Roberts, 2008). Likewise, species responses to environmental factors are generally not limited to a certain function; they can be, for example, nonlinear or discontinuous. FSO, therefore, is a generalized technique (Roberts, 1986) that overcomes this problem and includes the types of ordination that ecologists are more familiar with, such as direct gradient analysis (Whittaker, 1967) and environmental scalars ordination (Loucks, 1962). Thus, in fuzzy logic applications, the results **can facilitate the expression of rules and processes**.

First, a distance matrix of species incidence was calculated. For the binary data considered herein, we used Sørensen similarity index, as suggested by Boyce and Ellison (2001). This gave a measure of similarity between sites based solely on biota composition. This was followed by one-dimensional FSO, taking distance matrices as response variables and the environmental variables as explanatory variables. FSO also requires that the environmental variables be as much uncorrelated as possible (Boyce, 2008). A number of landscape variables showed a strong

Table 1 Association of lake catchment variables into three composite factors. Variables are displayed in the order of correlation with the principal components (PC). Highest correlation of a variable with any of the components is in bold. PC1 was interpreted as hydrodynamics; PC2, geo-morphology, and PC3, topography formation.

	Principal component		
	PC 1	PC 2	PC 3
Tributary discharge	**0.92**	0.04	0.02
Nature of tributary	**0.90**	0.02	0.01
Nature of water output	**0.87**	-0.17	0.07
Waterbody size	**0.52**	-0.38	0.05
% meadow covered slopes	-0.07	**0.72**	-0.37
% meadow covered shore	0.21	**0.68**	-0.24
Slope of lake perimeter	0.30	**-0.67**	-0.03
Geology	-0.23	**0.60**	0.07
Aquatic vegetation	-0.16	**0.58**	-0.22
Fractal order	0.07	**0.50**	0.08
Catchment snow deposits	0.09	-0.10	**0.86**
Catchment type	0.05	0.07	**0.79**
Shore snow coverage	-0.11	-0.11	**0.75**
Connectivity with others	0.39	-0.36	**0.52**
Total Eigenvalue (rotated)	3.07	2.69	2.46
% of variance explained	21.96	19.24	17.59
Cumulative %	21.96	41.20	**58.79**

Rotation method: Varimax with Kaiser normalization.

correlation. Their summarised version, i.e. the PC regression factor scores from prior PCA (Table 1), were therefore used as explanatory variables in FSO. By default, the principal components of PCA computed with Varimax rotation are uncorrelated, therefore, suitable for this approach.

A multidimensional FSO (MFSO) was run on the best subset of variables (highest correlation with the distance matrix at $p < 0.05$ significance level) selected from the individual FSO and allowed multidimensional interpretability of the results. Statistically, MFSO first performs an FSO on the variable that accounts for most of the variation. Then, the residuals from that fuzzy ordination are used with the next most important variable, and the process is repeated until no more variables are left. Therefore, unlike classical ordination methods used in ecology, e.g. Canonical Correspondence Analysis (CCA) and distance-based redundancy analysis (DB-RDA), in MFSO each variable selected by the model can be considered as an independent axis, and only the fraction of axis membership values which is uncorrelated with previous axes is included into the model (Roberts, 2009a). Moreover, MFSO is expected to perform better than the other methods on more complex datasets, and it is insensitive to rare species and noise in environmental factors (Roberts, 2009a).

The effect magnitude of each variable on species composition is assessed visually by the relative scatter attributable to that variable, and can be numerically assessed by the increment in correlation attributable to that variable (Roberts, 2009a). In FSO/MFSO, if an axis is influential in determining the distribution of vegetation, then one should be able to estimate the values of that variable based on species composition (Roberts, 2009b). Following MFSO, a "step-across" function was used to improve the ordination with high beta diversity, when there are many sites with no species in common (Boyce and Ellison, 2001).

The significance of the matrix correlation coefficient between environmental variables and species composition was established by permuting the rows and columns of one of the matrices 1000 times in both, FSO and MFSO, recalculating the correlation coefficient and comparing the observed matrix correlation coefficient with the distribution of values obtained *via* permutation.

FSO and MFSO were computed with FSO (Roberts, 2007a) and LabDSV (Roberts, 2007b) packages, while the step-across function was computed with VEGAN package (Oksanen et al., 2009), R statistical language and environment.

2.4.3 Network diagram

A conceptual diagram summarizing the connections between landscape elements and riparian vegetation composition and their magnitude of influence was assembled in the open-source visualization tool Gephi 0.9.1 (https://gephi.org; Bastian et. el. 2009) using Yifan Hu layout. Gephi is a highly interactive visualization platform capable of displaying the relationships between nodes of a semantic network based on object abundances or objects weight. It allows users to intuitively discover patterns, isolate network structures and singularities, and derive hypotheses in social and biological networks analyses. We used the independent (increment) *r* values derived by MFSO as variable weights. Likewise, multiple regression with Akaike Information Criterion model selection (Automatic Linear Modelling option in SPSS) provided the magnitude of influence landscape variables have on the composite landscape factors (previously summarized by PCA).

2.4.4 Indicator community analysis

The riparian vegetation composition (species incidence) was analysed for species association into chorotypes, i.e. species with significant co-occurrence patterns. First, the lakes were grouped on the basis of shared species. For this, a clustering procedure (Pair-Group Method using the Arithmetic Averages (PGMA) using flexible linkage (beta) parameter, with beta = -0.2) was computed on the Sørensen distance matrix of species incidence. This allowed selecting the most appropriate clustering for dendrogram nodes cut.

The selected clusters were subsequently assigned code numbers into a new categorical variable. This variable was used as a grouping variable in Indicator Species Analysis (Dufrene and Legendre, 1997) to determine plant species with significant affinity to the lake categories, i.e. species of similar ecological preferences. An indicator community comprises species that are most characteristic in the riparian zone of lakes of that type. The higher the indicator value is the greater is the species affinity to a lake type. Furthermore, ecotope/environment selectivity of the resulting vegetation communities was tested by box-plotting them against environmental gradients. Sørensen similarity matrix was computed with ADE4 (*dist.binary* function; Thioulouse et al., 1997), cluster and boxplot analyses with CLUSTER (*agnes* and *boxplot* functions, respectively; Kaufman and Rousseeuw, 1990), Discriminant Analysis with FPC (*plotcluster* function; Hennig, 2005) and Indicator Species Analysis with LabDSV (*indval* function; Dufrene and Legendre, 1997) packages for R statistical language (R Core Development Team, 2005); available online at http://cran.r-project.org/.

3. RESULTS AND DISCUSSION

3.1 Summarizing catchment scale variables

Riparian ecosystem structure of high elevation lakes is generally controlled *via* complex interactions in the catchment, and large geographical gradients, which together can characterize major driving forces. To better understand this complexity, we reduced the catchment-scale variables to main drivers by principal component analysis (PCA). The first three extracted components accounted for more than 58% of the total variance in lake characteristics (Table1).

Table 2 One-dimensional fuzzy relationships between riparian vegetation species composition and environmental factors in the central Pyrenees lakes. Factor superscripts: (a) geoposition, (b) landscape (Table 3.1), (c) sediment chemistry, and (d) water chemistry. Correlations between factors and apparent factors predicted by vegetation are listed in descending order. Factors with correlations >0.3 (in bold) were retained for further MFSO analysis. *P* represents the probability after 1000 permutations

Variable	*r* (Pearson)	*P*	Variable *(continued)*	*r* (Pearson)	*P*
^{a}Altitude	**0.855**	0.001	^{c}Sr	-0.005	0.545
^{a}Latitude	**0.695**	0.001	^{c}Na	-0.020	0.439
^{a}Longitude	**0.636**	0.001	^{c}Ti	-0.107	0.540
^{b}Topography (PC3)	**0.644**	0.001	^{c}Rb	-0.164	0.624
^{b}Geo-morphology (PC2)	**0.603**	0.001	^{c}Al	-0.443	0.900
^{b}Hydrodynamics (PC1)	**0.442**	0.001	^{d}Mn	**0.751**	0.001
^{c}Mg	**0.712**	0.001	^{d}Fe	**0.730**	0.001
^{c}Pb	**0.515**	0.003	^{d}Conductivity (surface)	**0.584**	0.001
^{c}Ca	**0.510**	0.004	^{d}Conductivity (bottom)	0.545	0.001
^{c}Cu	**0.501**	0.007	^{d}Al	**0.531**	0.014
^{c}Co	**0.497**	0.006	^{d}Cu	**0.465**	0.009
^{c}Ba	**0.484**	0.007	^{d}pH (bottom)	**0.307**	0.002
^{c}Ni	**0.432**	0.018	^{d}pH(surface)	0.257	0.002
^{c}Mn	**0.405**	0.024	^{d}K	0.254	0.108
^{c}Fe	**0.362**	0.037	^{d}Na	0.204	0.170
^{c}Zn	**0.361**	0.033	^{d}B	0.177	0.089
^{c}C	**0.351**	0.032	^{d}Pb	0.130	0.272
^{c}Si	**0.337**	0.046	^{d}Ba	0.108	0.248
^{c}N	**0.324**	0.036	^{d}Sr	0.088	0.293
^{c}Cr	**0.309**	0.069	^{d}Se	0.057	0.340
^{c}V	0.210	0.130	^{d}Ni	-0.010	0.482
^{c}C/N	0.114	0.145	^{d}Ga	-0.020	0.445
^{c}S	0.112	0.249	^{d}Li	-0.030	0.462
^{c}As	0.110	0.298	^{d}Mg	-0.101	0.590
^{c}K	0.029	0.342	^{d}Ca	-0.234	0.746
^{c}P	0.013	0.394	^{d}Rb	-0.350	0.841
^{c}Cl	-0.001	0.418			

The first principal component (PC1) was interpreted as hydrodynamics and accounted for tributary nature and discharge, water output and waterbody size (Table1). The second component (PC2) characterizes the main bedrock geo-morphology, i.e. geology, shore sloping, % of slope/shore covered by meadow, fractal order/riparian development and the presence of aquatic vegetation. The third PC represents topography, i.e. catchment type, visible connectivity with other lakes, and catchment and shore snow deposits. The three composite factors were therefore regarded as major drivers of the lake ecotope and ecosystem development. They were summarized as PC regression factor scores, in order to use them as predictors of vegetation composition in further analysis.

Table 3 Independent effect of each factor from ^{a} geoposition, ^{b} catchment, ^{c} sediment and ^{d} water chemistry datasets on riparian vegetation composition, as given by MFSO. Figures for geoposition, catchment and water characteristics result from MFSO improvement by step-across function. γ (gamma)= a vector of the independent variance fraction of a factor/axis. Factors with the highest influence in the model, in bold, are listed in order of their weight in the model.

Axis	Cumulative *r*	Increment *r*	*P*-value	γ
^{a}Altitude	0.46	**0.46**	0.002	1.00
^{a}Latitude	0.65	**0.19**	0.001	0.97
^{a}Longitude	0.66	0.01	0.740	0.06
^{b}Topography (PC3)	0.43	**0.43**	0.026	1.00
^{b}Geo-morphology (PC2)	0.52	**0.09**	0.325	0.54
^{b}Hydrodynamics (PC1)	0.64	**0.12**	0.001	0.97
^{c}Mg	0.49	**0.49**	0.270	1.00
^{c}Pb	0.74	**0.25**	0.044	0.49
^{c}Ca	0.74	0.01	0.057	0.09
^{c}Cu	0.75	0.01	0.035	0.05
^{c}Co	0.76	0.01	0.025	0.05
^{c}Ba	0.75	-0.01	0.142	0.06
^{c}Ni	0.75	-0.004	0.157	0.02
^{c}Mn	0.75	-0.001	0.135	0.02
^{c}Fe	0.75	0.002	0.096	0.02
^{c}Zn	0.75	-0.001	0.118	0.01
^{c}C	0.74	-0.01	0.334	0.09
^{c}Si	0.74	0.00	0.180	0.004
^{c}N	0.74	0.00	0.164	0.01
^{d}Mn	0.56	**0.56**	0.281	1.00
^{d}Fe	0.73	**0.17**	0.384	0.22
^{d}Conductivity	0.71	-0.03	0.406	0.06
^{d}Al	0.71	0.002	0.177	0.03
^{d}Cu	0.71	0.003	0.182	0.09
^{d}pH (bottom)	0.71	-0.01	0.297	0.13

Due to the high-dimensional variability of the dissimilarity matrix, the correlation probability for the one-dimensional solution sometimes has low significance, but it is still valid.

3.2 Riparian vegetation: lake, catchment, and pan-climatic drivers

As an initial step in the evaluation of environmental control on vegetation composition all environmental factors, i.e. geoposition, landscape, and lake sediment and water chemistry were screened independently in a single-dimensional FSO (Table 2). Clearly, altitude exerted the largest influence on riparian vegetation composition, followed by water Mn and Fe concentration (major redox indicators of water fluctuations in the riparian zone), Mg in sediment, horizontal gradients latitude and longitude, and catchment-scale variables (topography formation and hydrodynamics). To remove potential covariance between factors and better quantify the effect

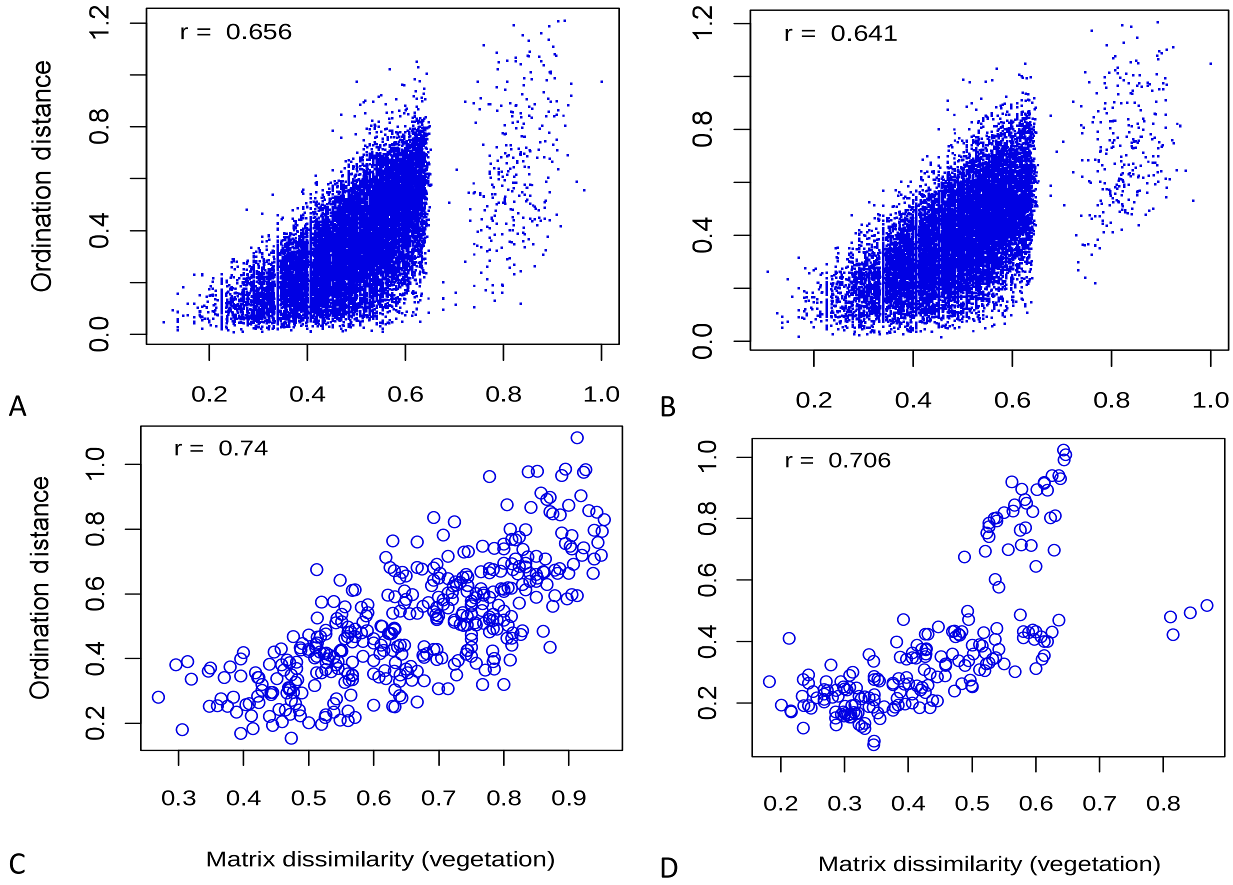

Figure 2 Multidimensional Fuzzy Set Ordination (FSO) depicting the effect of **(A)** large geographical gradient, i.e. altitude (m a.s.l.), latitude (UTM) and longitude (UTM), **(B)** catchment factors, i.e. hydrodynamics (PC1), geo-morphology (PC2) and topography (PC3; Table 1), **(C)** sediment chemistry, and **(D)** water chemistry, on riparian plant composition (Sørensen similarity of species incidence data). MFSO in A and B were improved by using a step-across function. Variables are input in the model in the order of decreasing Pearson fuzzy correlation with plant dissimilarity matrix (Table 3). Number of permutations = 1000.

size of each selected factor on riparian vegetation, MFSO was run on factors with correlation > 0.3. The analysis further supported FSO results (Table 3) and is detailed below.

3.2.1 Large vertical and horizontal gradients

Table 3 and Fig. 2a show the significant factors/axes in order of their independent correlation with the *apparent factors* predicted by vegetation composition. MFSO gave a two-dimensional solution, with altitude and latitude reliably predicting riparian plant composition at 0.65

cumulative *r*. Altitude, the most influential, is a classical large-scale constraint of ecosystem composition along the alpine climate gradient. While the study area covered a relatively narrow latitudinal span, it receives four biogeographical influences: Atlantic and Continental from the N and NW, Mediterranean from SE, overlapping local alpine gradient (Fig. 1). This implies that the area under study was sufficiently large to capture macroregional transition in its riparian ecosystem. Though longitude showed an individual relationship with vegetation variability (Fig. 2a), its effect seemed to be a covariant in the multivariate solution (Table 3).

3.2.2 Catchment geomorphological and hydrological elements

MFSO on composite landscape-scale variables gave a three-dimensional solution, with topography formation (PC3) largely dominating over hydrodynamics (PC1) and geo-morphology (PC2), (cumulative r =0.64; Table 3 and Fig. 2b) in its influence on vegetation species structure. Since this factor is a composite (Table 1), it means that collectively catchment type, with local effects from snow cover and lake connectivity, is the major catchment-scale driver of riparian vegetation community variability. It also means that glaciological formations (e.g. glacial valley head, U, and V-shaped valleys, mountain pass and slopes; Zaharescu et al. 2016b)- legacies of the last glaciations that shaped the landscape at the macroscale, are topographical factors that form different microclimates and shaped the vegetation settlement and community formation. For instance, at the head of glacial valleys, snow would generally last longer around the lakes, create longer wet conditions from thaw water than on mountain slopes or mountain passes, where the soil would be drier, and experience earlier sun exposure These contrasting conditions would allow the colonisation of different sets of species. Water connectivity can also shape the structure of riparian communities *via* its important role in propagule dispersion and colonisation. Previous research has shown that topography can control terrestrial vegetation in alpine regions through its effect on snow coverage (Keller et al., 2005), which is a visible consequence of topography interaction with climatic variables like radiation, precipitation, and wind (Körner, 1999).

Hydrodynamics added to the influence of the previous axis (Table 3 and Fig. 2b), through the nature and discharge of the tributaries, and associated effects from waterbody size and nature of output (Table 1). These variables control nutrient and sediment fluxes from the drainage basin, and nutrient transfer from the lake area to riparian zone - all these influencing riparian ecosystem composition. Therefore, it implies that stream-fed medium-to-large lakes (Table 1) hold significantly different vegetation communities than the shallower direct precipitation-fed ponds.

Although its separate influence was high (Table 2), bedrock geology (with associated effects from shore slope, vegetation coverage and shore development, PC2), represented the smallest independent (catchment-scale) driver of riparian vegetation, likely due to its covariation with the first two factors (Table 3 and Fig. 2b). Geology has been reported to influence the establishment of vegetation, especially through its role in habitat/soil chemistry and niche formation (Kovalchik and Chitwood, 1990). The bedrock of the study region is marked by two contrasting units: an igneous core (granite) in its central part, which is flanked by sedimentary and metasedimentary materials. Granitic geomorphology, which is more resistant to weathering, is associated with steeply sloping and unstable terrain, with low vegetation coverage and less developed riparian zones (lower fractal order; Table 1), and contributes fewer nutrients to the lake. Conversely, more reactive bedrock such as limestone produces a more chemically rich environment, better development of riparian zones (higher fractal order), a more stable terrain (less slope) with more vegetation coverage (Table 1). Together with topographical and hydrological differences these two geological substrates sustain different riparian plant assemblages.

The strong role of the three catchment-scale factors in riparian ecosystem variability also supports the conceptual work outlined previously (Zaharescu et al. 2016b), which detailed how catchment physical elements aggregate into major lake ecotope units and predict lake ecosystem dynamics.

3.2.3 Sediment chemistry. Indicator elements

Lake and riparian sediments at high elevations are generally dominated by catchment bedrock denudation products, and autochthonous organic matter fixation (Zaharescu et al., 2009 and 2016a). Results of the MFSO of riparian vegetation composition against sediment nutrients, major and trace elements contents resulted in a bi-dimensional solution, with Mg and Pb able to reliably predict the vegetation composition (cumulative r =0.74; Table 3 and Fig. 2c). Catchment lithology, i.e. the geological structure, the proportion of rock types, their mineralogy, chemistry and weathering resistance, is tightly related to the chemistry (e.g. nutrients, major and trace elements) of high altitude water bodies (Lewin and Macklin, 1987; Zaharescu et al, 2009), through cross-ecosystem fluxes of sediment and water. Magnesium, as part of chlorophyll, is an essential macronutrient for the photosynthesis in green plants, and it is also essential in activating many enzymes needed for growth. Soils developed on basic bedrock such as limestone generally contain higher Mg levels (~ 0.3-2.9%) than on granite or sandstone (~ 0.01-0.3%) (Beeson, 1959). Results show that in the nutrient-poor high elevation environment plant response and competition for bedrock-derived Mg can determine their community composition.

The influence of Pb in a natural landscape is not totally clear. One possible explanation is that our results reflect the distribution of plants using mycorrhizae, e.g. the legumes, since mycorrhizal colonisation has been related with Pb plant uptake under low soil metal concentrations (Wong et al., 2007). Or, plant's naturally high sensitivity to Pb (Kabata-Pendias and Pendias, 2001) could also have determined changes in vegetation composition along a natural Pb stress gradient, particularly in metamorphic areas where Pb is at higher bedrock concentrations, as reported for the central Pyrenees (Catalan et al., 2006; Zaharescu et al., 2009).

The low independent effect of other essential elements is likely due to their co-variability with the independent Mg and Pb factors, as part of natural geochemistry. Nonetheless, these interesting findings merit further mechanistic examination into why Mg and Pb are indicators of riparian vegetation in high altitude lakes, and not other elements.

3.2.4 Water chemistry. Indicator elements

Water chemistry in exposed high elevation topography is dominated by weathering solutes and is expected to drive major ecosystem processes in the catchment. The MFSO of riparian vegetation composition and selected water chemistry variables, also resulted in a bi-dimensional solution, with Mn and Fe as the major influential axes (cumulative r =0.73) (Table 3 and Fig. 2d). Iron and Mn are major redox players in soils/ sediments, and varying water table/level can modify their solubility and uptake by plants (Alam, 1999). For instance, in water-saturated soil biotic respiration drives reduction chemistry, and this can affect plant performance not only by preventing macro and micronutrient (e.g. Mg, Ca and Fe) uptake but also by restricting root development (Couto et al., 1983). Differential response of plant species to the build-up of soluble Fe and Mn have been suggested as the potential factors in species ecology and habitat distribution (Alam, 1999), and it has been reported for a variety of species including grasses, legumes (Couto et al., 1983) and trees (Good and Patrick, 1987).

Variable moisture level and flooding of the riparian zone by lake water are common in high altitude water bodies, being regulated by thawing of snow deposits in the catchment, and by the frequency and volume of summer storms. The plant compositional change along Mn and Fe gradients seen in this study may, therefore, have been shaped by riparian flooding (a secondary effect of topography; Table 1), with higher moisture in lakes at the head of glacial valleys and drier conditions in those on the slopes/mountain passes. Unsurprisingly, water pH, conductivity and a number of elements appeared to co-vary with Fe and Mn in the multivariate solution (Tables 2 and 3).

A conceptual network diagram incorporating the riparian ecosystem of a hypothetical lake and its linkages to elements of lake, catchment and pan-climatic gradients is illustrated in Fig. 3. Important dependence connections have been established between riparian vegetation composition and lake-scale sediment nutrient content (reflecting catchment nutrient transport and availability) and water redox condition, as well as with nature of lake source and draining, shore line development, catchment type and geology, and large-scale altitudinal gradient. These are main elements of the surrounding landscape operating at different scales that influence the riparian vegetation composition.

3.3 Community analysis

Due to the restrictive environmental condition in high altitude lakes, riparian ecosystems may form species pools (associations) that are dependent on local habitat resources, and whose distributions are dictated by the connectivity between lakes. Results of the PGMA cluster analysis revealed a relatively good grouping (agglomerative coefficient = 59%), which classified the 189 lakes into four well-defined groups (Fig. 4). Of the total of 168 plant species (List S2), 79 formed four communities (chorotypes) representing the four lake types. Table 4 shows the species with

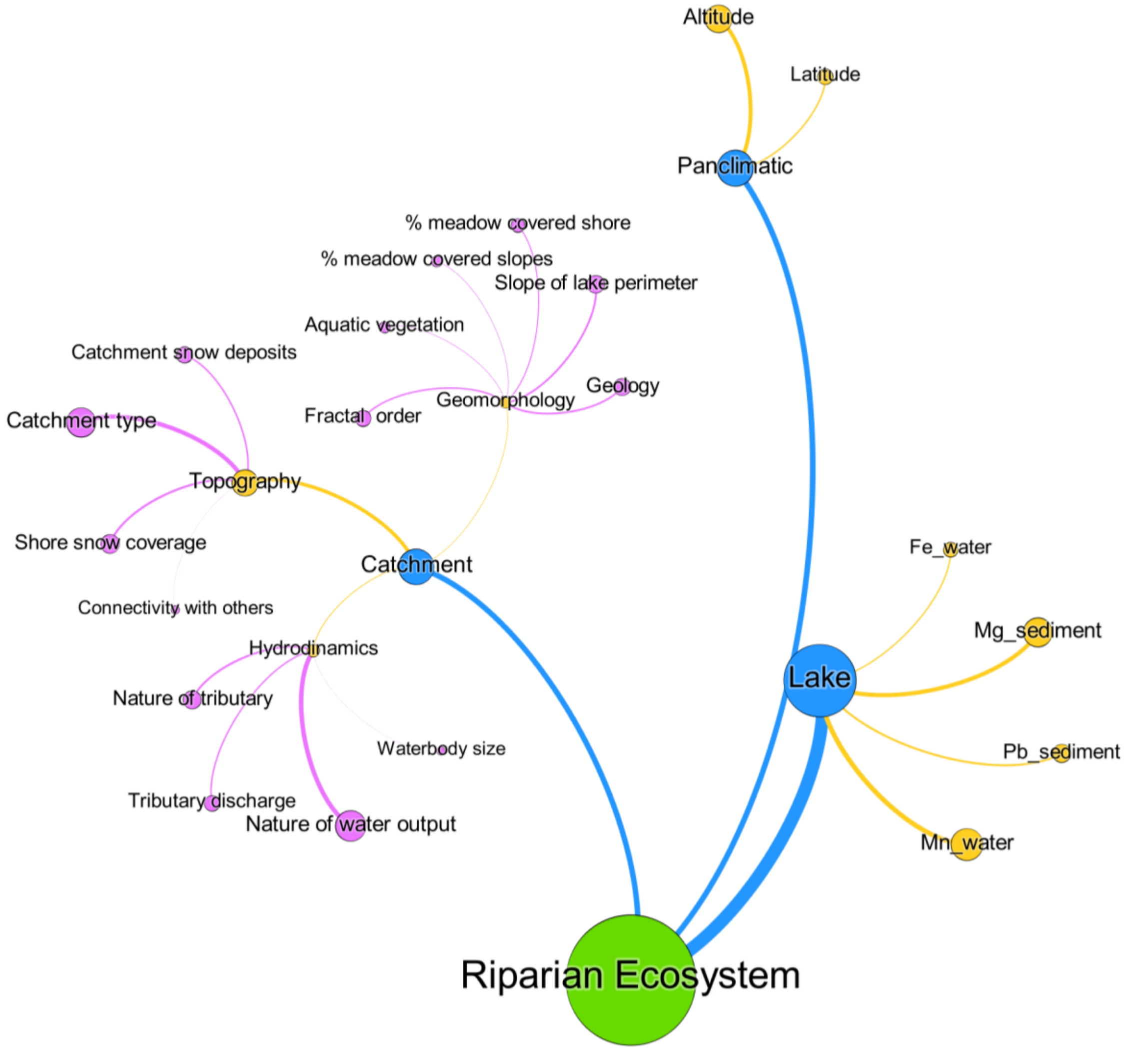

Figure 3 Conceptual network diagram showing the connections between riparian ecosystem of a typical lake and its influencing elements of the lake, its catchment, and larger panclimatic gradients. Nodes and label sizes, as well as connections thickness, are proportional to the magnitude of their influence on target nodes. Connections borrow the colors of source nodes, representing different layers of organization in the model.

significant co-preference for the lake sets and their probability of group membership. Plant communities A, B, and D yielded a high degree of confidence (Fig. 4). The species characteristic of lake type A mostly comprised hygrophilous species of damp ecotones such as bog-associated species with *Sparganium, Ranunculus, Chara, Sphagnum* moss, *Selaginell*a fern, sedges (*Carex)* and rushes *(Juncus)*, and other small plants of damp soil (Table 4). Associated with these was also

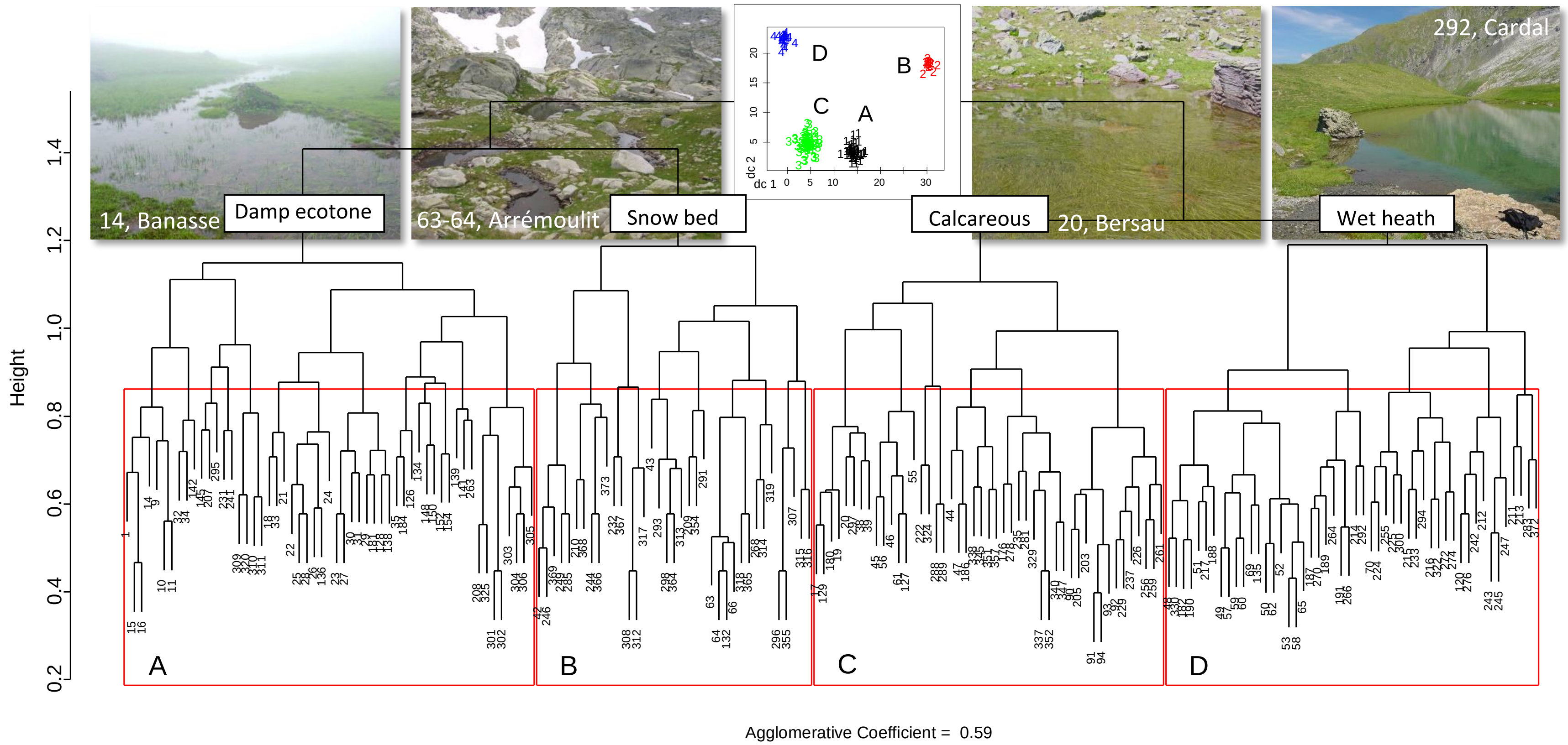

Figure 4 Dendrogram showing lake ecosystem types based on their riparian vegetation communities (shared species), together with representative examples. A PGMA hierarchical cluster analysis (flexible linkage = 0.6) on Sørensen similarity matrix of incidence plant data was used. A plot of cluster solutions in discriminating space (inset) shows an effective clustering. Plant groups and ecosystem types are derived from Indicator Species Analysis (Table 4). N =189 lakes and 166 plant species. Plants are listed in List S1, while lakes in Zaharescu et al., 2016b (supplementary Information).

Table 4: Riparian plant groups and their fidelity to lake types (Fig. 4), as given by Indicator Species Analysis. A species was classified into a group for which its group indicator value was highest and significant. Cluster C had lower significance. Species that were not associated to any of lake clusters followed relatively continuum distributions.

Cluster A, damp ecotone, $p<0.05$		Cluster D, calcareous, $p<0.05$	
Species	Indicator value	Species	Indicator value
Potentilla erecta	0.47	*Pinguicula vulgaris*	0.42
Caltha palustris	0.42	*Gentiana acaulis*	0.40
Parnassia palustris	0.36	*Rhododendron ferrugineum*	0.35
Thymus serpyllum	0.25	*Primula integrifolia*	0.30
Trifolium repens	0.23	*Vaccinium uliginosum*	0.30
Hieracium pilosella	0.20	*Trichophorum cespitosum*	0.29
Campanula rotundifolia	0.19	*Calluna vulgaris*	0.26
Sphagnum sp.	0.19	*Silene acaulis*	0.26
Bellis perennis	0.18	*Trifolium alpinum*	0.25
Alchemilla vulgaris s.l.	0.17	*Homogyne alpina*	0.25
Sparganium angustifolium	0.15	*Soldanella alpina*	0.22
Carex echinata	0.14	*Geum montanum*	0.21
Juncus filiformis	0.13	*Vaccinium myrtillus*	0.21
Anthoxanthum odoratum	0.13	*Hutchinsia alpina*	0.20
Carex nigra	0.13	*Armeria maritima alpina*	0.19
Cardamine raphanifolia	0.11	*Phyteuma orbiculare*	0.18
Merendera pyrenaica	0.11	*Bartsia alpina*	0.17
Prunella vulgaris	0.11	*Viola palustris*	0.17
Juncus articulatus	0.11	*Geranium cinereum*	0.14
Leontodon autumnalis	0.10	*Luzula alpinopilosa*	0.12
Ranunculus aquatilis	0.10	*Lotus alpinus*	0.11
Selaginella selaginoides	0.09	*Pedicularis mixta etc*	0.10
Polygala alpina	0.09	*Thalictrum alpinum*	0.10
Carex flava	0.09	*Saxifraga aizoides*	0.09
Polygonum viviparum	0.08	*Gentiana lutea*	0.06
Carum carvi	0.07		
Galium verum	0.07		
Luzula desvauxii	0.07		
Ranunculus reptans	0.07		
Sanguisorba officinalis	0.07		
Deschampsia cespitosa	0.06		
Chara foetida	0.05		

Cluster B, snow bed, $p<0.05$		Cluster C, wet heath, $p<0.25$	
Species	Indicator value	Species	Indicator value
Gnaphalium supinum	0.51	*Rumex crispus*	0.04
Cryptogramma crispa	0.47	*Carex flacca*	0.03
Leucanthemopsis alpina	0.34	*Cochlearia officinalis*	0.03
Epilobium alsinifolium etc	0.28	*Leontopodium alpinum*	0.03
Sibbaldia procumbens	0.25	*Oxytropis campestris*	0.03
Kobresia myosuroides	0.23	*Veronica officinalis*	0.03
Veronica alpina	0.22	*Callitriche palustris*	0.02
Jasione montana	0.21		
Galium pyrenaicum	0.19		
Poa annua etc	0.17		
Doronicum austriacum	0.16		
Saxifraga stellaris	0.14		
Festuca eskia	0.12		
Meum athamanticum	0.10		
Salix herbacea	0.10		

N =166 riparian plant species from 189 water bodies.

a limited number of plants of drier/stony habitats, including cosmopolites (*Bellis),* nitrogen-fixing legumes *(Trifolium)* and endemics (*Merendera pyrenaica)*. The association tolerates a wide bedrock chemistry, including acidic (*Sphagnum),* neutral (*Trifoliums*) and basic (*Polygala*). This heterogeneous association seems, therefore, to inhabit a combination of habitat types along lake shores, reflecting an uneven catchment composition.

The second association (type B, Fig. 4 and Table 4), comprises a high proportion of species with affinity to snow bed and a short growing season (*Saxifraga, Veronica, Sibbaldia*), herbaceous shrubs (*Salix*), and ferns (*Cryptogramma*). Most of these species are silicophilous, tolerate low nutrient substrate of different textures, including scree/rocky, grassland, and damp soil. Endemic grass *Festuca eskia* plotted with the same group.

Riparian community D comprises wet heath species of Ericaceae shrubs (*Vaccinium* and *Calluna*), accompanied by snow bed plants (*Primula, Soldanella,* and *Bartsia*), sedges (*Trichophorum*), rushes (*Luzula*), together with species growing in moist substratum (*Pinguicula* and *Homogyne*). In small number are species of drier habitat (*Gentiana, Hutchinsia,* and *Phyteuma*), and legumes (*Trifolium*). This community tolerates both, siliceous and calcareous substrates.

There is also a weak possibility for a number of plants to associate with lake cluster C (Fig. 4) but their membership was less significant ($p < 0.25$; Table 4). These species prefer moist-to-dry calcareous banks. It is, however, safe to assume that this association was not very common. Since the rest of the species had no group association, they largely follow continuous or gradient distributions (Báez et al., 2005).

While the identified communities incorporated species from major terrestrial groups (Gruber, 1992; Grey-Wilson and Blamey, 1995; Minot et. al, 2007), it is clear from our results that they tolerate the wet condition of the riparian zone. However, their broad habitat range means they are eurytopic, i.e. complex communities with large niche breadth, present in a variety of habitats. This condition presumably allowed them to colonise the harsh and diverse environments bordering high altitude lakes. This may also explain the relatively low (but significant) indicator values (< 0.5) obtained for the plant associations (Table 4). However, the ecological importance of these communities resides in that they indicate natural ecological conditions of the riparian zone. Further study is, therefore, necessary to understand how these communities and their underlying ecotopes respond to climate changes.

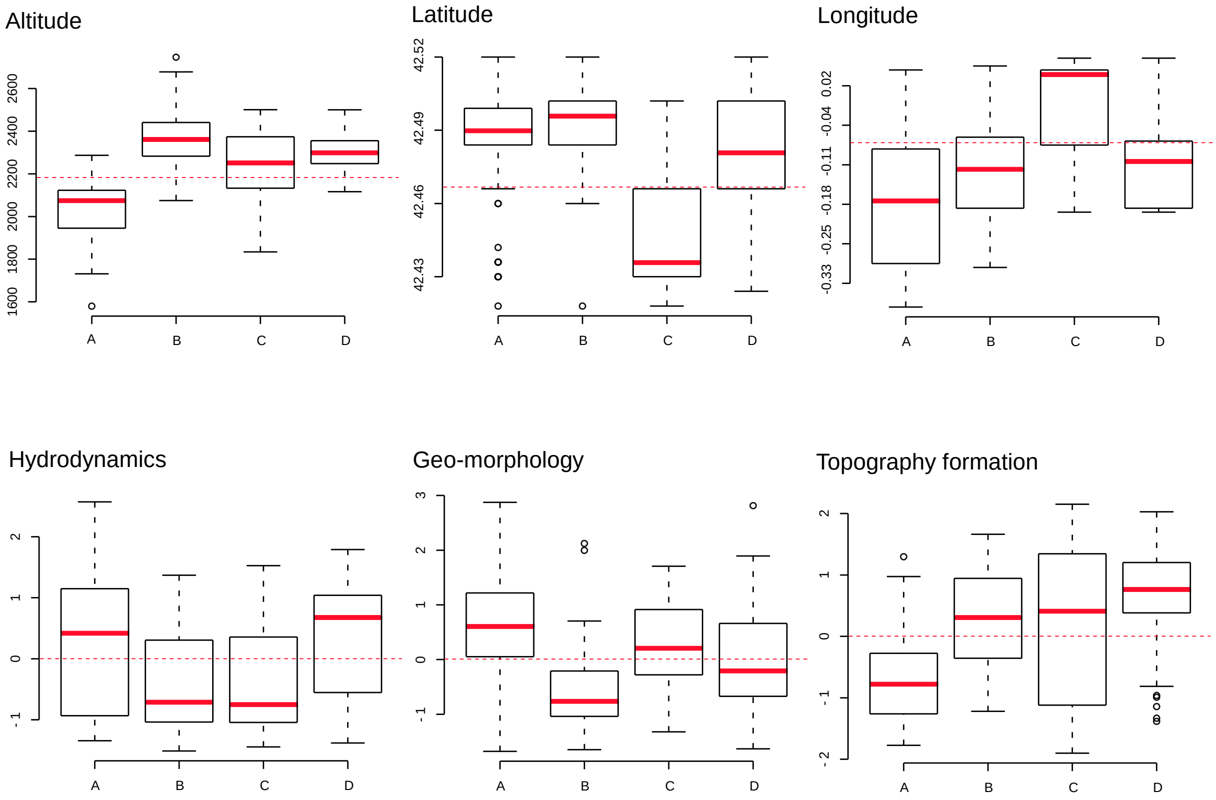

Figure 5 Boxplots showing the distribution of indicator plant communities along geographical (altitude, m a.s.l.; latitude, degrees N; and longitude, degrees E/W, +/-) and composite catchment gradients. Hydrodynamics factor ranges from (-) small waterbodies to (+) large lakes (and their associated variables, Table 1); geo-morphology from (-)igneous and metamorphic, to (+) sedimentary materials; topography formation from (-) valley floor and flat topography, to (+) valley head. Boxplots represent median, first (25%) and third (75%) quartiles, with whiskers extending to the 5th and 95th percentiles. Horizontal red dash line in each plot is set at group average.

3.3.1 Environmental preferences

To better understand the sensitivity of identified associations to environmental factors, their distribution was plotted against geoposition and composite catchment gradients.

Overall, plant communities responded to large horizontal and vertical gradients, as well as to catchment variables (Fig. 5). Community A was distributed on damp riparian areas around larger lakes on the floor/slope of (meta)sedimentary glacial valleys with less summer snow, at comparatively low altitudes (median ~ 2100 m a.s.l.), that had higher shore fractal development. Community B- with a high proportion of snow bed species, grew around smaller waterbodies on high granitic topography (e.g. head of glacial valleys and mountain passes, ~ 2400 m a.s.l.), of steep slopes and low fractal(riparian) development, persistent summer snow and lower water turnover (i.e. fed mainly by precipitation). Less resilient association C spanned a wide altitudinal range and topographical formation (from valley floors to valley heads), establishing around small lakes/ponds of low input/output. Community D, had the narrowest altitude span, was found across a wide range of hydrological conditions but had some preference to areas with persistent summer snow around larger lakes at catchments heads, of high water turnover, as shown by group medians (Fig. 5).

These results reinforce findings from community analysis and clearly show that none of the evaluated ecotope factors were the sole drivers of community establishment in the intricate topography. Rather, a complex pool of microclimatic and geomorphologic conditions worked together to sustain riparian communities. Since these communities/species can reflect environmental gradients that sustain their formation, their long-term monitoring is necessary, as climate change can affect their distribution through effects on their physical drivers, including precipitation, freezing line, hydrology and weathering fluxes (Zaharescu et al., 2016a).

4. CONCLUSIONS

Fuzzy Set Ordination results showed that alpine lake riparian ecosystems are connected to local, catchment, and large-scale surface elements of the landscape in a variety of ways. Topographical formation left behind during the last glacial retreat, with contemporary effects of snow coverage and lake connectivity, form the dominant catchment-scale elements that influence riparian plant development and diversity. Hydrodynamics, with nested contribution from lake size and nature and size of input/output, was the second most important catchment element affecting riparian vegetation composition mostly through lake size. The two factors support the idea that alpine lakes are not isolated islands in the landscape, but rather interconnected biodiversity nodes controlled by catchment's physical properties. Geo-morphology, associating geology, shore slope, and vegetation coverage, and riparian fractal development greatly covaried with the first two factors in its influence on the riparian ecosystem, and reflected major geomorphological units in the central Pyrenees, extending from igneous, metasedimentary and sedimentary materials.

Locally, vegetation relationship with sediment (Mg and Pb) and water (Mn and Fe) chemical elements, indicated major linkages with catchment nutrient availability and moisture fluctuations in riparian soils. Superimposed on catchment and local drivers, large pan-climatic gradients altitude and latitude captured the transition between major biogeographic regions of Europe in the plant composition of an otherwise a narrow study area.

The alpine riparian ecotone, connecting complex topography, geology and water regimes, assembled species from both wet and dry environments, which are subjected to regular flooding. Community analysis identified four such eurytopic communities, i.e. damp ecotone, snow bed-silicates, calcareous and wet heath, of significant niche breadth that characterized four lake groups. These communities responded to a range of horizontal and vertical gradients in climate, physical and chemical factors. It, therefore, remains to be seen how the composition of these water-sensitive ecosystems changes as climate change continues to affect their functional connectivity with the supporting ecotope through its manifold of elements and scales.

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AUTHOR CONTRIBUTION

Design of field research, A. Palanca-Soler; data collection, R.N. Lester, C. Tanase, A. Palanca-Soler and D.G. Zaharescu; study design and manuscript preparation D.G. Zaharescu, P.S. Hooda and C.I. Burghelea. The authors assert no competing interests.

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Supplementary Information

Nodes in the alpine connectome. Exploring the linkages between riparian ecosystem and geo-climatic elements across the mountain environment

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List S1. Taxonomical composition of riparian vegetation in the 189 central Pyrenean lakes and ponds surveyed for this study.

Aconitum spp.
Adenostyles alliariae
Agrostis capillaris
Alchemilla alpina
Alchemilla vulgaris
Allium schoenoprasum
Androsace carnea
Antennaria dioica
Anthoxanthum odoratum
Anthyllis vulneraria
Armeria alliacea
Armeria maritima alpina
Arnica montana
Bartsia alpina
Bellis perennis
Betula pendula
Botrychium lunaria
Callitriche palustris
Calluna vulgaris
Caltha palustris
Campanula rotundifolia
Cardamine raphanifolia
Carduus carlinoides
Carex atrata
Carex brachystachys
Carex caryophyllea
Carex curvula
Carex demissa
Carex echinata
Carex flacca
Carex flava
Carex frigida
Carex hallerana
Carex macrostylon
Carex nigra
Carex pulicaris
Cryptogramma crispa
Deschampsia cespitosa
Dethawia tenuifolia
Doronicum austriacum
Draba aizoides
Empetrum nigrum
Epilobium alsinifolium etc
Equisetum variegatum
Erica sp.
Eriophorum latifolium
Euphrasia sp.
Festuca eskia
Fontinalis antipyretica
Galium pyrenaicum
Galium verum
Gentiana acaulis
Gentiana lutea
Gentiana verna
Geranium cinereum
Geranium sylvaticum
Geum montanum
Globularia repens
Glyceria fluitans
Gnaphalium supinum
Gnaphalium sylvaticum
Hieracium pilosella
Homogyne alpina
Huperzia selago
Hutchinsia alpina
Hypericum montanum
Jasione montana
Juncus articulatus
Juncus filiformis
Juncus inflexus
Juniperus communis ssp. nana
Kobresia myosuroides
Luzula desvauxii
Luzula luzuloides
Luzula nutans
Luzula sudetica
Lychnis alpina
Menyanthes trifoliata
Merendera pyrenaica
Meum athamanticum
Minuartia sedoides
Molinia caerulea
Myosotis alpina
Myosotis scorpioides
Nardus stricta
Nigritella nigra
Oxyria digyna
Oxytropis campestris
Oxytropis pyrenaica
Parnassia palustris
Pedicularis mixta
Phleum alpinum
Phyteuma orbiculare
Pinguicula grandiflora
Pinguicula vulgaris
Plantago alpina
Plantago lanceolata
Plantago media
Poa annua
Polygala alpina
Polygonum viviparum
Potentilla anserina
Potentilla erecta
Primula farinosa
Primula integrifolia
Primula viscosa
Prunella vulgaris
Pulsatilla sp.
Rhinanthus minor
Rhododendron ferrugineum
Rumex alpinus
Rumex crispus
Rumex scutatus
Sagina procumbens
Salix herbacea
Salix reticulata
Sanguisorba officinalis
Saxifraga aizoides
Saxifraga oppositifolia
Saxifraga stellaris
Sedum album
Selaginella selaginoides
Sempervivum arachnoideum
Sempervivum montanum
Sesamoides pygmaea
Sibbaldia procumbens
Silene acaulis
Soldanella alpina
Sorbus aucuparia
Sparganium angustifolium
Sphagnum sp.
Succisa pratensis
Swertia perennis
Taraxacum sp.
Thalictrum alpinum
Thesium alpinum
Thymus serpyllum
Trichophorum cespitosum
Trifolium alpinum
Trifolium repens
Vaccinium myrtillus
Vaccinium uliginosum
Veratrum album
Veronica alpina

Carex riparia
Carex rostrata
Carex sempervirens
Carum carvi
Chara foetida
Chenopodium bonus-henricus
Cochlearia officinalis
Kobresia simpliciuscula
Leontodon autumnalis
Leontopodium alpinum
Leucanthemopsis alpina
Linaria alpina
Lotus alpinus
Luzula alpinopilosa
Ranunculus alpestris
Ranunculus aquatilis
Ranunculus pyrenaeus
Ranunculus repens
Ranunculus reptans
Rhamnus pumilus
Veronica beccabunga
Veronica fruticans
Veronica nummularia
Veronica officinalis
Viola biflora
Viola palustris

N (number of species) = 168.