Sensors of change: riparian ecosystem sensitivity to local and large scale gradients in high elevation lakes

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ABSTRACT

Riparian ecotones are aquatic-terrestrial interfaces integrating climate and nutrient fluxes across the landscape' physical elements. Despite experiencing severe nutrient and climate constrains, high elevation lakes have unequally productive riparian ecosystems. With climate change rapidly encroaching in the alpine biome, it becomes increasingly vital to understand how their natural ecosystem balance is sustained through multi-scale interactions of lake and catchment processes, before major deleterious effects are experienced.

A total of 189 glacial origin lakes and ponds in the Central Pyrenees were surveyed to test how lake, catchment, and geographical-scale factors interact at different scales to drive riparian vegetation composition. Secondly, we aimed to evaluate how underlying catchment factors influence the formation of riparian plant communities and their potential sensitivity to environmental change. At each lake plant taxonomic composition was assessed, and samples of water and sediment were analysed for major and trace element composition. Ecosystem-relevant local and catchment-scale factors were estimated together with geolocation, and their influence on vegetation was modelled using the logic of Fuzzy Set Ordination.

Catchment hydrology-hydrodynamics was the main driver of riparian vegetation structure, followed by topography formation and geomorphology. Although the study area extended over a relatively small range, the lake riparian surface was able to capture the transitional gradient between large pan European climatic zones. Lake sediment Mg and Pb and water Mn and Fe are safe indicators of riparian vegetation composition, likely reflecting bedrock geology, and hydrology-driven redox fluctuations in the riparian zone. Community analysis identified four riparian groups, characteristic to: (a) damp environment, (b) snow beds-silicate bedrock, (c) wet heath, and (d) limestone bedrock. Their sensitivity to geographic and ecotopic gradients are further evaluated.

With climate change threatening major shifts in the alpine biome, the findings provide critical information on how natural riparian ecosystem balance is maintained by multi-scale interactions inside and outside the catchment, and provide invaluable baseline data for better predicting future responses to environmental changes.

Keywords: High Altitude Lakes, Riparian Vegetation, Natural Drivers, Catchment heterogeneity, Ecotope, (Multidimensional) Fuzzy Set Ordination, PGMA Clustering, Indicator Species Analysis, Pyrenees.

1. INTRODUCTION

Although they occupy 24% of the Earth's land surface, mountains directly and indirectly provide resources for more than half of its humanity, as well as releasing nutrients into the wider biosphere (Price, 2004). This is primarily due to their elevated topography and exposed geology that creates conditions for water precipitation and accumulation, and nutrient release through continued weathering and denudation. Most of the low resolution land forms of the present mountain landscape, including the vast majority of mountain lakes are generally the legacy of the last Pleistocene glaciation (Thornbury, 1969). There are more than 50,000 remote mountain lakes estimated only in Europe (Kernan et al., 2009), and > 4000 in the Pyrenees, with >797 km shore line (Castillo-Jurado, 1992). Together with harsh climate and hydrology, high altitude geomorphic surfaces provide physical and chemical support to unique ecosystems. In no other circumstance is clearer the strong connection between bedrock weathering and overlying ecosystem than when this balance is disturbed by changes in atmospheric chemistry (Storkey et al. 2015) and climate (Williamson et al., 2009).

At the interface between terrestrial and aquatic environments, riparian ecotones mediate most the water, nutrients and carbon fluxes between the lake and its catchment, and host a disproportionately high diversity of life forms compared to the surrounding landscape (Gregory et al., 1991). Cross scale interactions between surface morphology, geochemistry and climate are responsible for the development of unique plant and animal communities, giving them a high ecological value (Kernan et al., 2009). Likewise, geographical relationships between catchment physical elements and vegetation can result in species/community distribution patterns along large continuum gradients (Austin and Smith, 1989; Hengeveld, 1990). Baroni-Urbani et al. (1978) introduced the term "chorotype" to define a pool of species with significantly similar distribution patterns, which are different from those of other associations. A chorotype has two components: the area occupied by a community, and the biotic element, i.e. the species association within that distribution. Moreover, when association membership of species cannot be established, they are assumed to follow continuum distributions (Báez et al., 2005).

The rough topography of the elevated terrain and the severity of its environment (low temperature, abrasion by snow/ice, high UV radiation and water-level fluctuations) are expected to drive population fragmentation, and the emergence of insular communities that are tightly connected to local resources. Species composition and gene flow in these communities are expected to be restricted by the low connectivity between waterbodies. Climatological variations such as the type and intensity of precipitation, daily temperature variation, frequency of 0ºC temperatures and the duration of freezing (Keller et al., 2005), as well as variation in these factors with slope orientation and altitude, have been shown to affect the distribution of plant cover over localized areas (Baker, 1989). Effects of climate change, including changes in precipitation, air temperature/ freezing line and snow cover (Zaharescu et al., 2015a), catchment hydrology and lake temperature and mixing (Thompson et al., 2005) are expected to greatly influence the thermodynamics and geochemistry of high altitude catchments, and consequently their lake and riparian communities. Evidence has shown considerable climate change related upward shift in mountain biome, with visible consequences on catchment hydrology, climate and geochemistry (Parker et al., 2008, Thompson et al., 2005). With ecosystems in mountain regions likely to reach tipping points (Kreyling et al., 2014; Khamis et al., 2014), it has become critically important to better understand the natural multi-scale interactions between catchment physical template (ecotope) and riparian ecosystem over relevant areas, before climate change major effects are predicted.

Research on how a riparian ecosystem connects to its ecotope and catchment surface properties 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).

The motivation for this study was therefore to address two important scientific issues missing in the literature, which are key to understanding the impact of climate change on high altitude freshwater resources: (i) achieve a mechanistic understanding of cross-scale interactions of catchment surface properties and how they drive lake riparian ecosystem composition, using vegetation data; (ii) identify indicator communities potentially sensitive to environmental changes; and (iii) provide a baseline dataset that can be used to address further questions pertaining to the integrated (ecosystem-physical environment) understanding of the consequences of climate change on the alpine biome. We hypothesized that due the oligotrophic nature of high altitude catchments, riparian zone will respond more strongly to local catchment than to large gradients, which in turn will create local indicator communities susceptible to environmental change.

Pyrenees location at the intersection of four large biogeographical regions in Europe (Atlantic, Continental, Mediterranean, and Alpine) makes it richer in biodiversity than other similar areas such as the Alpins,and is home to a relatively high proportion (± 11.8%) of endemic alpine plant species (Gómez et al., 2003). This makes the region particularly suitable for this study, as any climate change is expected to induce major effects on riparian ecosystem, their 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's floors and valleys. The lakes, in different stages of evolution, are more abundant on the steeper French side, which generally receives more precipitation.

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 a S-to-N direction. A great number of the lakes are drained by temporary

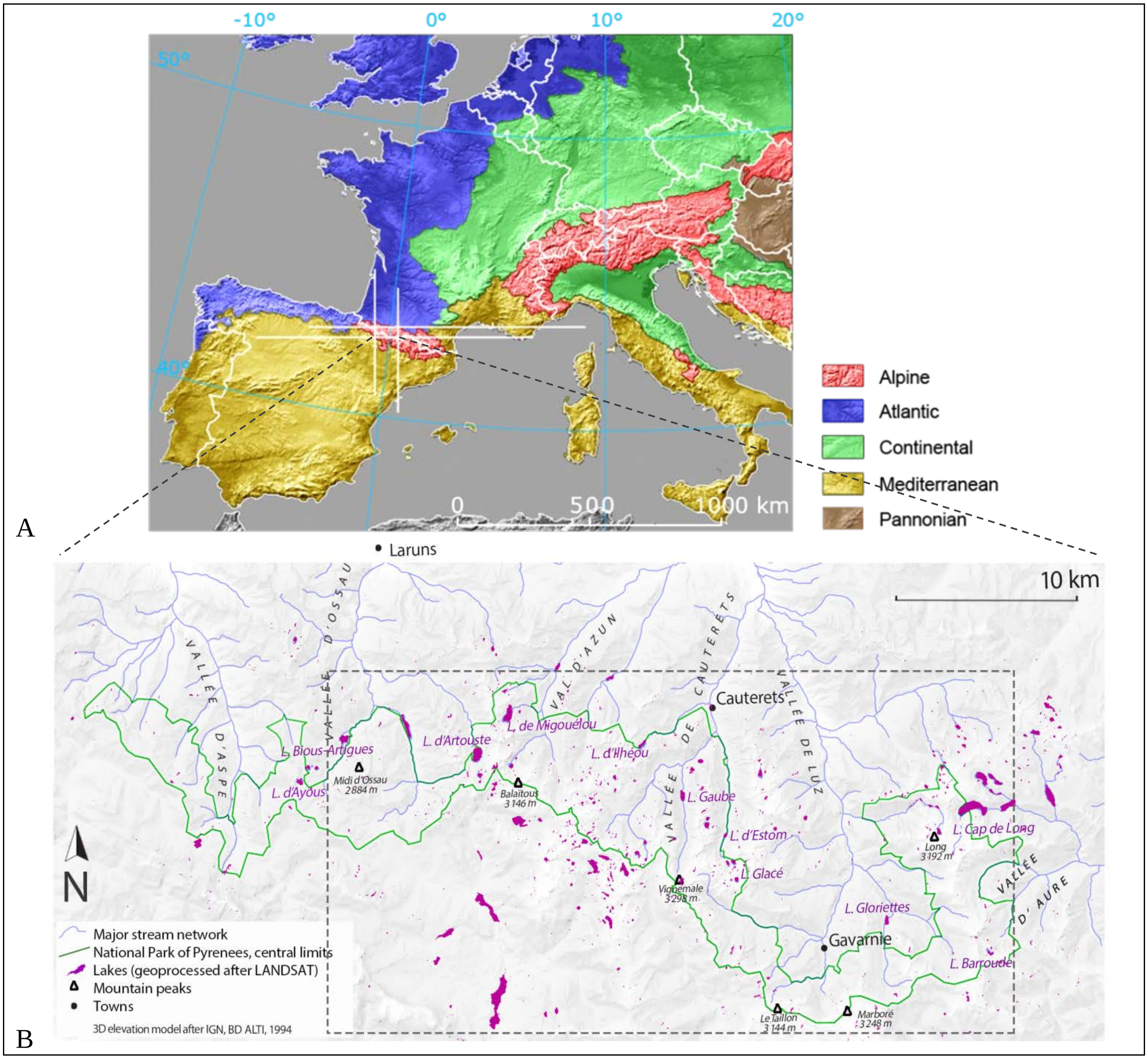

Figure 1 Biogeorgaphical regions of W Europe (A, after EEA, 2001), with location study area (B) in the axial part of Pyrenees National Park, France. Only lakes within the boundaries of the park and enclosed by dash-line box were surveyed.

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 number of 189 altitude lakes and ponds, ranging from 1161 to 2747m a.s.l. were visited during the month of July 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 present 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 portable herbarium to the laboratory for complete identification. They were thereupon identified using Flora Europea (available online at: http://rbg-web2.rbge.org.uk/FE/fe .html).

At each location a number of 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. 2015b). 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 (Zaharescu et al. 2009). The sediments comprised fragmented rocks, coarse sands and fine materials. As the chemical composition of the finer 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 2 days and sieved through a 0.1mm sieve. Trace and major element contents were characterised by X-ray fluorescence spectrometry (XRF). A portion of 5g 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 variability (%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 analyses followed standard procedures and QA/QC protocols.

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

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.

ecotope processes being investigated (Table 1). This was performed by summarising the variables into regression factor scores of the principal components (Varimax rotation) which were used as explanatory composite factors in further analysis. The analysis was performed in PASW (former SPSS) statistical package, and exhaustively detailed in Zaharescu et al. (2015b).

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 traditional 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 strong 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 a 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 eliminate distortions in the ordination space (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 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 cluster procedure (Pair-Group Method using the Arithmetic Averages (PGMA) using flexible linkage parameter, parameter= 0.6) 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 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 Summarising 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).

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 ought to be summarised as PC regression factor scores, in order to use them as predictors of vegetation composition in further analysis.

3.2 Riparian vegetation: lake, catchment and geographical 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 contents (major redox indicators of water fluctuations in the riparian zone), Mg in sediment, horizontal

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			

gradients latitude and longitude, and catchment-scale variables (topography formation and hydrodynamics). To remove potential covariance between factors and better quantify the effect 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 confidently 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 individual relationship with vegetation variability (Fig. 2a), its effect seemed to be a covariant in the multivariate solution (Table 3).

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 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.

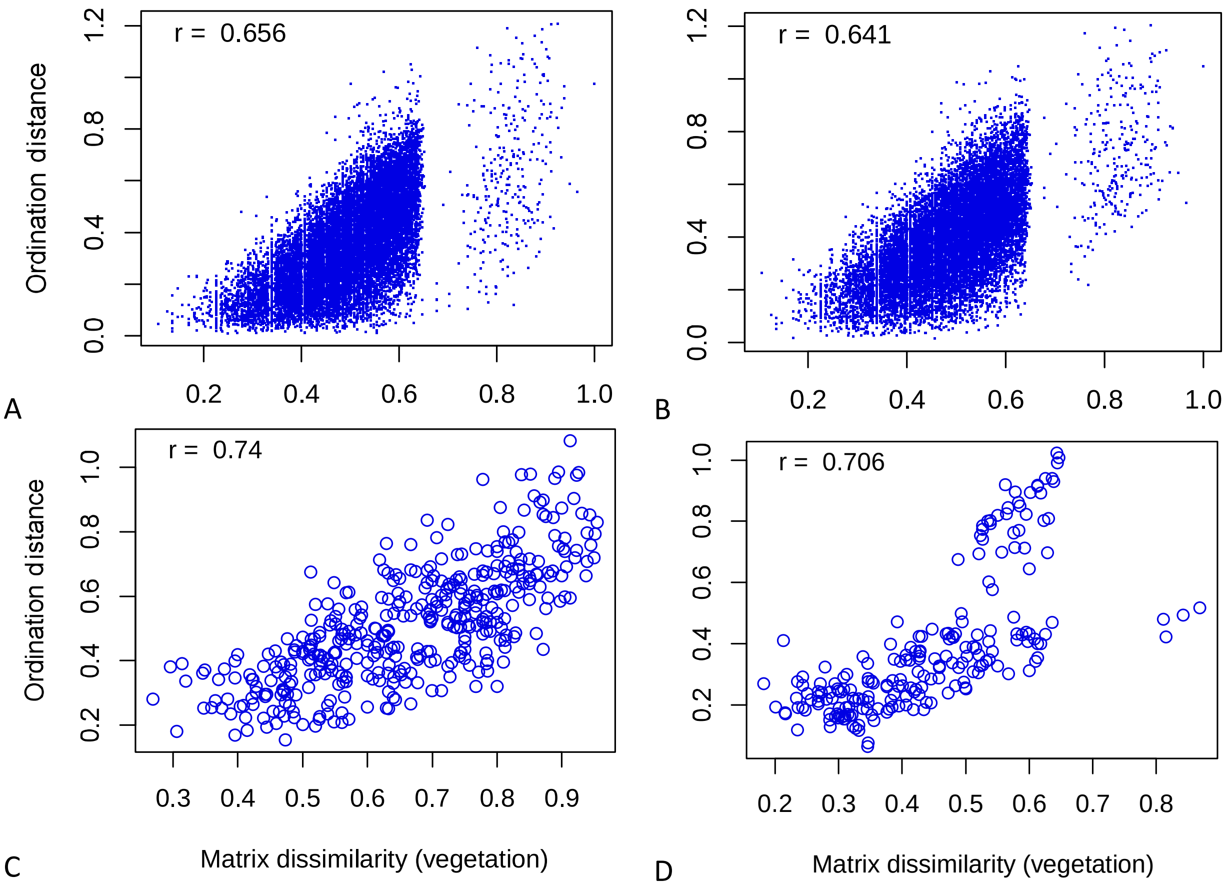

Figure 2 Multidimensional Fuzzy Set Ordination (FSO) depicting the effect of **(A)** large geographical gradient, i.e. altitude (m a.s.l.), latitude (UTM) and longitude (UTM), **(B)** catchment factors, i.e. hydrodynamics (PC1), geo-morphology (PC2) and topography (PC3; Table 1), **(C)** sediment chemistry, 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.

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 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. head of glacial valley, U and V shape valleys, mountain pass and slopes; Zaharescu et al. 2015b)-

legacies of the last glaciations that shaped the landscape at 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 form 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/metasedimentary materials. Granitic geomorphology, which is more resistant to weathering, is associated to steeply and unstable terrain, of low vegetation coverage and less developed riparian zone (lower fractal order; Table 1), and contributes less 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) of 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. 2015b), 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 2015a). 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, 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 colonization 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. Or their statistical importance being similar among the plant species, they have not been picked up by MFSO. 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 riparian zone by lake water is common in high altitude waterbodies, 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).

3.3 Plant 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 represented the 189 lakes into 4 well-defined groups (Fig. 3). Of the total of 168 plant species (List S2), 79 associated into 4 communities (chorotypes) representing the 4 lake types. Table 4 shows the species with 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. 3).

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 to these were also a limited number of plants of drier/stony habitats, including cosmopolites (*Bellis),* nitrogen fixing legumes *(Trifolium)* and endemic (*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. 3 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

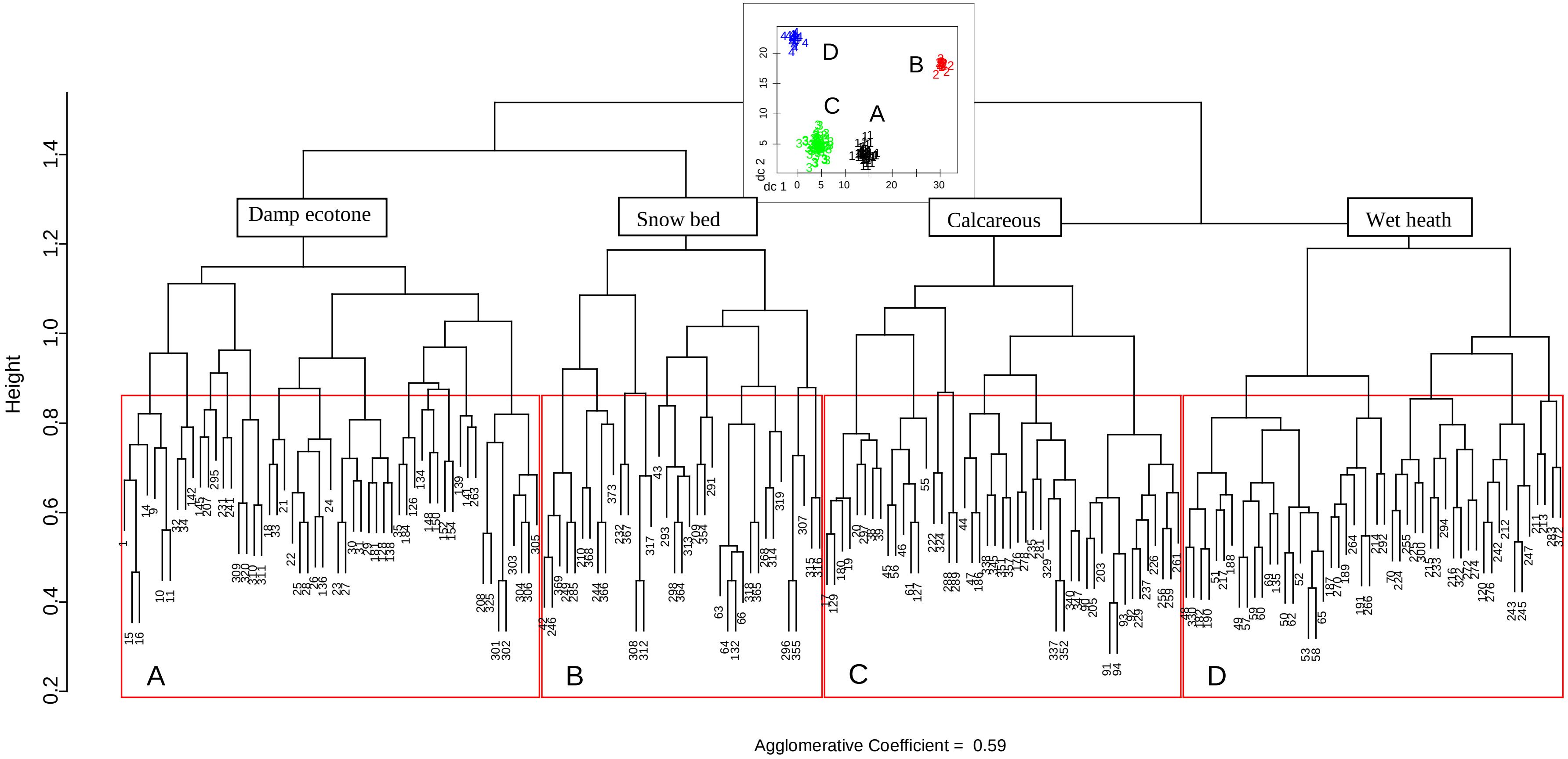

Figure 3 Dendrogram showing lake ecosystem types based on their riparian vegetation communities (shared species). This is a PGMA hierarchical cluster analysis (flexible linkage, parameter=0.6) on Sørensen similarity matrix of incidence plant data. A plot of cluster solutions in discriminating space (inset) shows an effective clustering. Ecosystem properties are approximated from Indicator Species Analysis (Table 4). N =189 lakes and 166 plant species. Lakes are identified in List S1.

Phyteuma), and legumes (*Trifolium*). This community tolerates both, siliceous and calcareous substrates.

Table 4: Riparian plant groups and their fidelity to lake types (Fig. 3), 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, $p<0.05$		Cluster D, $p<0.05$	
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, $p<0.05$		Cluster C, $p<0.25$	
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.

There is also a weak possibility for a number of plants to associate with lake cluster C (Fig. 3) 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 reside 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.

3.4 Community sensitivity to geographic and catchment gradients

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. 4). 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 altitudinal span, was

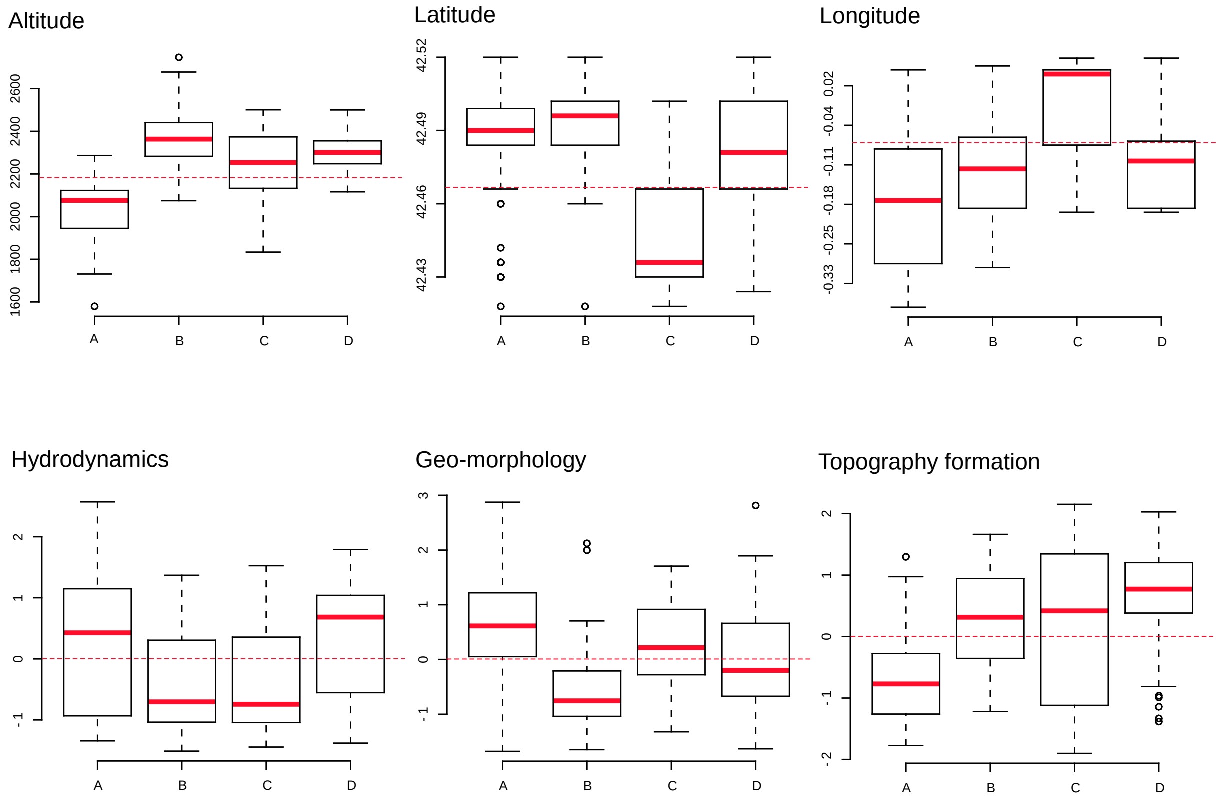

Figure 4 Boxplots showing the distribution of indicator plant communities along geographical (altitude, m a.s.l.; latitude, degrees N; and longitude, degrees E/W, +/-) and composite catchment gradients. Hydrodynamics range from (-) small waterbodies to (+) large lakes (and their associated variables, Table 1); geo-morphology from (-) granite and schist, to (+) limestone and conglomerate; topography formation from (-) valley floor and plain, to (+)valley head. Boxplots show the median value, first (25%) and third (75%) quartiles, with whiskers extending to the 5th and 95th percentiles. Plot horizontal dash line is set at group average.

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. 4).

These results reinforce community analysis findings, 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., 2015a).

4. CONCLUSIONS

Results of FSO and MFSO show that high altitude lake riparian ecosystem is controlled by large geographical, catchment and local scale physical gradients.

As the results suggest, topographical formations left behind by the last glaciers retreat of the Pyrenees, with their main effect on snow coverage and lake connectivity, are dominant catchment-scale determinants of riparian vegetation development and diversity. Hydrodynamics, with nested contribution from lake size and nature and size of input/output, was the second most important factor, which linked lake size to riparian vegetation composition. This supports the theory that high altitude lakes are biodiversity islands in an equilibrium state, which makes them sensitive to changes in the surrounding environment. Geo-morphology, associating geology, sloping, vegetation coverage and riparian fractal development covaried greatly with the first 2 factors in its influence of riparian ecosystem, and reflected major geomorphological units of the central Pyrenees, extending across igneous, metasedimentary and sedimentary materials.

Locally, sediment Mg and Pb, and water Mn and Fe contents, indicated major ecosystem restriction from bedrock geochemistry and moisture fluctuations in riparian soils. Overlapping catchment and local drivers, riparian ecosystem composition changed across large altitudinal and geoclimatic (latitudinal) gradient, capturing the transition between major biogeographic regions in Europe in the otherwise a narrow study area.

High altitude riparian ecotones, connecting complex topography, geology and water regimes, assembled species from both wet and dry environments, which can withstand regular flooding. Community analysis identified four such eurytopic communities (damp ecotone, snow bed-silicates, calcareous and wet heath), of relatively large niche breadth that characterized four lake/ecosystem types. These communities were sensitive to a range of horizontal and vertical gradients in geography, catchment and lake (climate, physical and chemical) factors. It remains to be seen how the composition of these water-sensitive ecosystems, particularly their communities, change as climate change continues to affect their underlying ecotopic drivers through its manifold of variables and scales. Such information could, for example help with prediction models on how environmental change affects ecosystem-catchment interactions in the complex high altitude topography.

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Supplementary Information

Sensors of change: riparian ecosystem sensitivity to local and large scale gradients in high elevation lakes

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List S1. Taxonomical composition of riparian vegetation in the 380 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
Carex riparia
Carex rostrata
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
Kobresia simpliciuscula
Leontodon autumnalis
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.
Ranunculus alpestris
Ranunculus aquatilis
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
Veronica beccabunga
Veronica fruticans

Carex sempervirens
Carum carvi
Chara foetida
Chenopodium bonus-henricus
Cochlearia officinalis
Leontopodium alpinum
Leucanthemopsis alpina
Linaria alpina
Lotus alpinus
Luzula alpinopilosa
Ranunculus pyrenaeus
Ranunculus repens
Ranunculus reptans
Rhamnus pumilus
Veronica nummularia
Veronica officinalis
Viola biflora
Viola palustris

N(number of species)=168.