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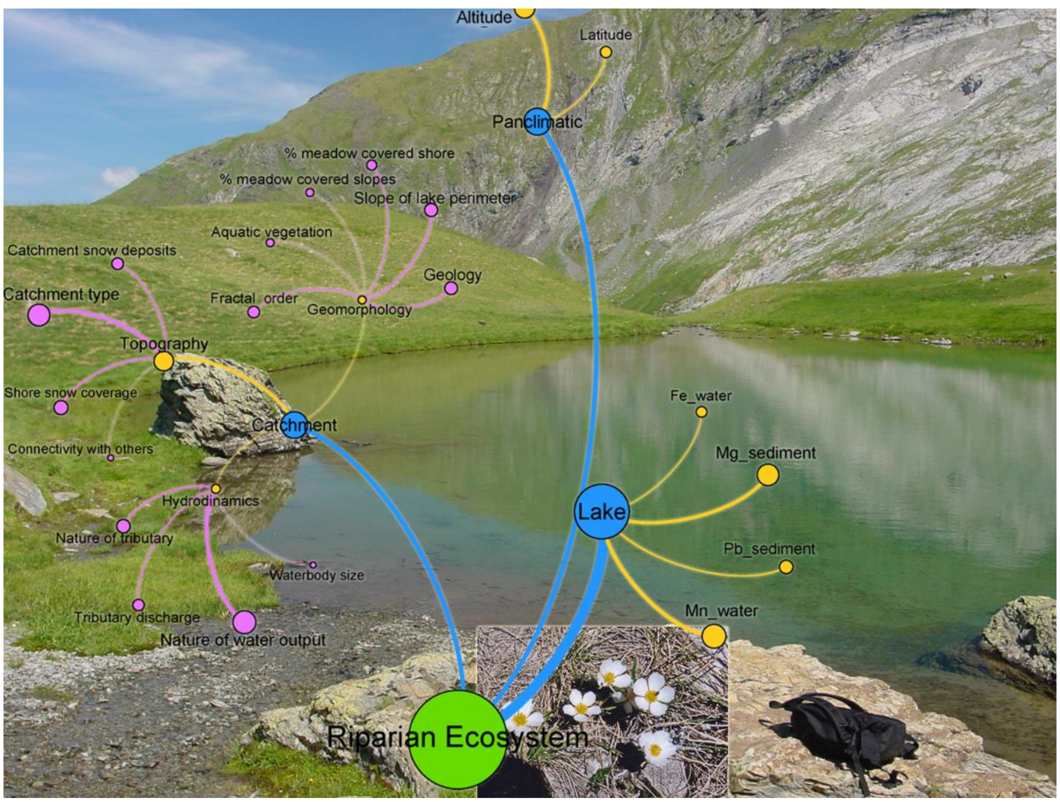
Riparian vegetation in the alpine connectome: Terrestrial-aquatic and terrestrial-terrestrial interactions

Dragos G. Zaharescu[a,b(*)], Antonio Palanca-Soler[b], Peter S. Hooda[c], Catalin Tanase[d], Carmen I. Burghelea[a,b], Richard N. Lester[e]

[a] Biosphere-2, University of Arizona, Tucson, Arizona, USA.
[b] Ecology and Animal Biology Department, University of Vigo, Vigo, Pontevedra, Spain
[c] School of Natural and Built Environments, Kingston University London, UK
[d] Faculty of Biology, Alexandru Ioan Cuza University, Iași, Romania
[e] Formerly at Birmingham University Botanic Gardens, Birmingham, UK
Passed away in April 2006 in Birmingham, UK

*Corresponding author: D.G. Zaharescu: zaha_dragos@yahoo.com
A. Palanca-Soler: apalanca@uvigo.es
P.S. Hooda: p.hooda@kingston.ac.uk
C. Tanase: tanase@uaic.ro
C.I. Burghelea: bcarmen@email.arizona.edu



Graphical abstract: Riparian ecosystem of Lake Cardal (0.3ha, 2224m a.s.l) in the Pyrenees National Park (France), with a network diagram connecting ecotope features at a wide scale range, and *Ranunculus pyrenaeus*. Photos by Antonio Palanca – Soler and Richard N. Lester.

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ABSTRACT

Alpine regions are under increased attention worldwide for their critical role in early biogeochemical cycles, their high sensitivity to environmental change, and as repositories of natural resources of high quality. Their riparian ecosystems, at the interface between aquatic and terrestrial environments, play important geochemical functions in the watershed and are biodiversity hotspots, despite a harsh climate and topographic setting. With climate change rapidly affecting the alpine biome, we still lack a comprehensive understanding of the extent of interactions between riparian surface, lake and catchment environments.

A total of 189 glacial - origin lakes were surveyed in the Central Pyrenees to test how key elements of the lake and terrestrial environments interact at different scales to shape riparian plant composition. Secondly, we evaluated how underlying ecotope features drive the formation of natural communities potentially sensitive to environmental change and assessed their habitat distribution.

At the macroscale, vegetation composition responded to pan-climatic gradients altitude and latitude, which captured in a narrow geographic area the transition between large European climatic zones. Hydrodynamics was the main catchment-scale factor connecting riparian vegetation with major water fluxes, followed by topography and geomorphology. Lake sediment Mg and Pb, and water Mn and Fe contents reflected local influences from mafic bedrock and soil water saturation. Community analysis identified four keystone ecosystems: (i) damp ecotone, (ii) snow bed-silicate bedrock, (iii) wet heath, and (iv) calcareous substrate. These communities and their connections with ecotope elements could be at risk from a number of environmental change factors including warmer seasons, snow line and lowland species advancement, increased nutrient/metal input and water level fluctuations. The results imply important natural terrestrial-aquatic linkages in the riparian environment at a wide range of scales, which could help better address further biomic impacts of environmental change.

Keywords: Alpine Lakes; Plant Composition; Ecotope; Catchment Heterogeneity; Fuzzy Set Ordination; Indicator Species Analysis.

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1 INTRODUCTION

Although they occupy < 24 % of Earth's land surface, mountains contribute > 50 % of total nutrients to the biosphere, as well as providing natural resources for more than half of the humanity (Price, 2004; Larsen et al. 2014). This is primarily due to an elevated and steep topography, and exposed geology, which create conditions for water precipitation and accumulation, and nutrient release through accelerated bedrock weathering (Larsen et al. 2014). The alpine biome, characterised by rough climate and topography, hosts ecosystems strongly connected to the underlying bedrock and is highly sensitive to small changes in external factors such as climate and atmospheric chemistry (Williamson et al., 2009; Storkey et el. 2015).

The vast majority of low-laying landforms in the present mountain landscape are the legacy of Pleistocene glaciation (Thornbury, 1969). This produced > 50,000 remote lakes in Europe alone (Kernan et al., 2009), and > 4000 in the Pyrenees (Castillo-Jurado, 1992). Their riparian surfaces, at the interface between terrestrial and aquatic environments, have a major role in modulating the fluxes of water and nutrients between catchment and lake ecosystems. These surfaces host a rich biodiversity compared to the surrounding landscapes (Gregory et al., 1991, Kernan et al., 2009), and are well extended (> 797 km of shoreline in the Pyrenees alone; Castillo-Jurado, 1992).

Interactions between vegetation, bedrock features, including morphology and geochemistry, and climate determine species distribution patterns in concert with 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 distribution) and regional. A regional chorotype is assumed to occupy a small geographic area, often used as study area in a biome, and it can present various degrees of continuity.

Stress related factors such as low temperature, snow and ice abrasion, high UV radiation and water-level fluctuations, overlapping to a variable geology and topography have the potential to increase fragmentation in alpine riparian populations and result in island communities tightly connected to their local environment. Waterbody isolation could also limit gene flow among such communities. Restrictive influence on plant distribution has been shown in localized areas, due to climate factors such as the type and intensity of precipitation, daily temperature, the frequency of freezing events and their duration (Keller et al., 2005), as well as slope orientation and altitude (Baker, 1989).

The influence of riparian vegetation on catchment chemistry can be diverse. On one hand, the production of organic acids and CO_2 by plant roots and microbial communities in the rhizosphere can modulate the fluxes of nutrients into a lake by enhancing bedrock weathering (Burghelea et al., 2015). On the other hand, litter degradation in the water-saturated environment can increment the export of dissolved organic carbon, which chelates major biogenic cations (Mg, Ca and Si), further mobilizing them (Zakharova et al., 2007). Metal-rich mafic and ultramafic deposits, as well as mining of metal-rich ores have been reported in this part of the Pyrenees, and tainting of stream water with Pb and Cr has also been described (Kilzi et al., 2016; Point et al., 2007). This mineralogy could imprint a strong effect on vegetation composition and its evolution through time, including by incrementing the endemism level (Galey et al., 2017). This then raises the question of whether the contrasting geology and the presence of mafic deposits in the Pyrenees can be reflected in the composition of its riparian ecosystems.

Anthropogenic climate change, particularly changes in precipitation, air temperature, freezing line, temporary and permanent snow cover, can greatly influence the thermodynamics and geochemistry of high altitude waterbodies (Thompson et al., 2005; Parker et al., 2008; Zaharescu et al. 2016a), and consequently their ecosystems (Khamis et al., 2014). With many mountain species already in dwindling numbers (Kreyling et al., 2014; Buma et al. 2016), it becomes critically important to better define the breadth and strength of their natural connectivity with the sustaining physicochemical template (ecotope) at both, local and the broader landscape scales, before this is irreversibly severed. We will use the term connectome (first introduced by Sporns, 2006, and Hagmann, 2005 in neurosciences) to denote the functional linkages between a riparian ecosystem and the wider environment, as it offers a more natural way to understand ecosystem interactions.

Research exploring the connection between riparian ecosystem and its physical template (ecotope) at different scales is rare. It has largely been conducted at low altitudes, e.g. by focusing on how local scale alterations in hydrological and habitat disturbance affect riparian communities (Merritt et al., 2010). Related work in mountain catchments has quantified the ability of bedrock geomorphology to predict the type of riparian plant communities and species abundances at different scales (Engelhardt et al., 2015). This study found that catchment-scale characteristics, including bedrock type, drainage area, and water discharge are the best predictors of riparian species composition in mountain streams. More recently, we proposed a conceptualized model of alpine lake ecotopes (Zaharescu et al., 2016b), and assessed their influence on zoobenthic communities (Zaharescu et al., 2016c). Catchment-scale hydrodynamics was the largest driver of a lake ecotope, while topography (controlling catchment type, snow coverage, and inter-lake connectivity) was the most influential in zoobenthic community formation. Locally, riparian plant assemblages also seemed to affect the zoobenthos composition, diversity and richness, likely through their nutrient and habitat support (Zaharescu et al., 2016b; Zaharescu et al., 2016c). Here we further explore how major ecotope structures interact to shape the riparian plant communities at several scales, using as a model an alpine region of limited human impact, i.e. Pyrenees National Park.

The motivation behind this study was to attain a mechanistic understanding of high-elevation riparian ecosystem development in relationship with its ecotope, and its potential response to environmental change. The objectives were: (i) to assess the cross-scale linkages between ecosystem, lake and catchment environments, and evaluate their strength; (ii) to identify keystone plant communities and lakes, which could be potential sensors of environmental change, and (iii) to evaluate their preference to landscape gradients. We postulate that the extreme geoclimatic setting of the alpine biome determines a strong riparian connection to local lake variables, and to a lesser extent to larger scale factors. This, in turn, creates local indicator communities, which may be highly susceptible to environmental change.

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The location of the Pyrenees at the intersection of four large biogeographical regions, i.e. Atlantic, Continental, Mediterranean and Alpine, makes them richer in biodiversity compared to similar areas, such as the Alps (± 11.8 % endemic plant species in the Pyrenees; Gómez et al., 2003), and highly susceptible to climate change. They are, therefore, an excellent candidate for this study.

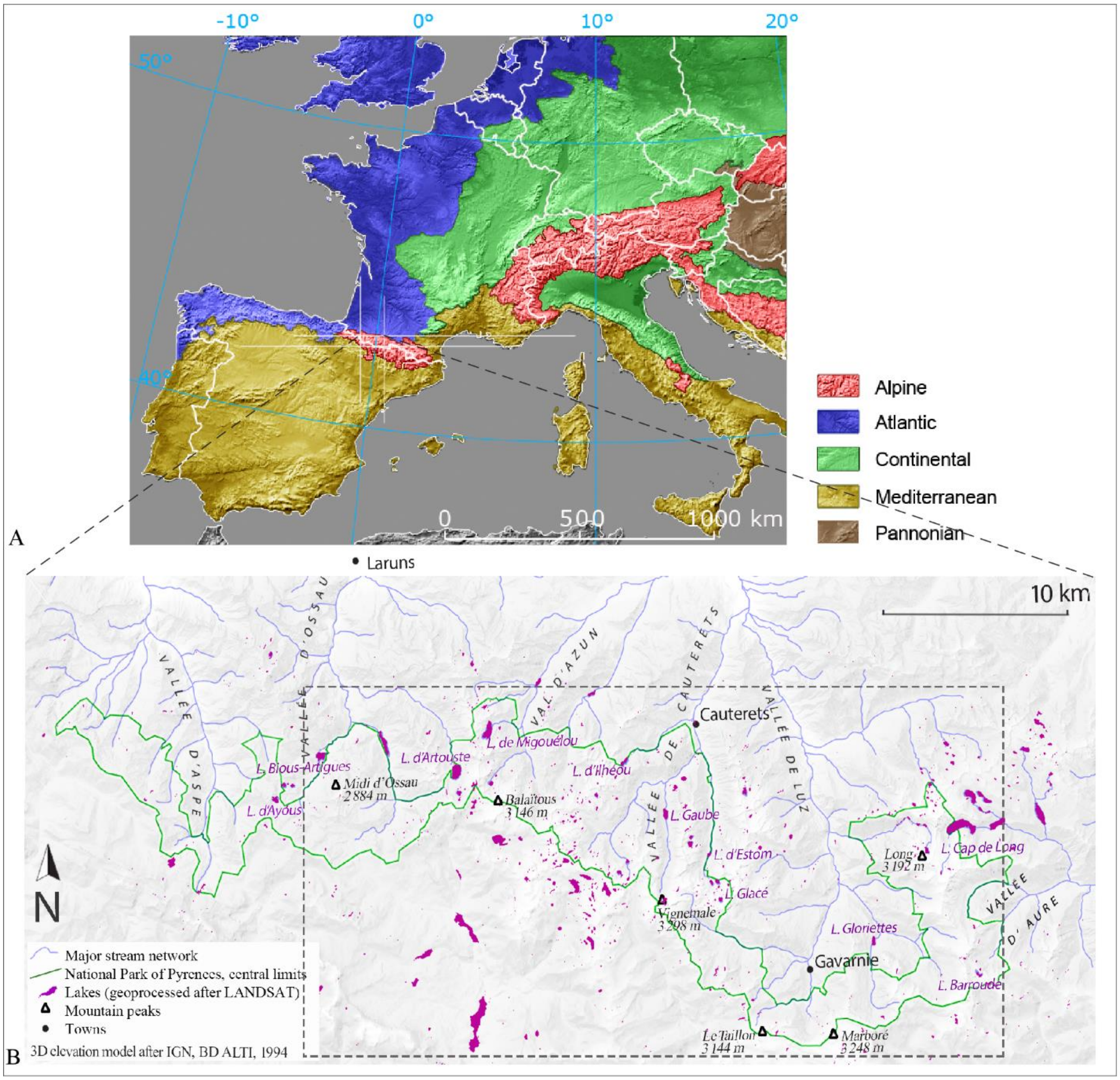

Figure 1 Biogeographical regions of W Europe (A, after EEA, 2001), with the location study area (B) in the axial part of Pyrenees National Park, France. Surveyed lakes, enclosed by a dash-line box, were within the park boundaries.

2 METHODS

2.1 The area

The Pyrenees are a relatively young mountain chain in SW Europe and a natural barrier between Spain and France. Their topography was carved mostly during the last glaciation 11,000 years ago, which left an abundance of lakes and ponds in cirques and valleys. The lakes, at different ecological succession stages, are more abundant on the steeper French side, which generally receives more precipitation.

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, France (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 park. A great number of lakes are drained by temporary torrents and permanent streams, which converge into major valleys, though isolated waterbodies and karstic systems are not rare. The valleys generally follow an S - N direction. 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

Three expeditions were conducted in July of 2000, 2001 and 2002 to sample the majority (n = 189) of lakes and ponds from the axial region of the park, from an altitudinal range of 1161 to 2747 m a.s.l. (Table S1). Due to the difficulty of sampling at high altitudes over extended periods (including > 6 winter months, extreme weather and steep topography), and to capture a comparable phenology, sampling was designed to cover the blooming summer phenology.

Each lake was characterised according to riparian vegetation composition and a range of catchment physical and chemical attributes (Table S2). Ocular identification of species in the perimeter of each waterbody was recorded in the field using Grey-Wilson and Blamey (1979), Fitter et al. (1984) and García-Rollán (1985) keys. Hard to identify plants were collected and transported in a vasculum to the laboratory for identification. They were thereupon identified using Flora Europaea (available online at http://rbg-web2.rbge.org.uk/FE/fe .html).

At each location, hydrological (tributary discharge, nature and size of tributary and output), geomorphological (bedrock geology, % slope of lake perimeter, fractal development level, % shore and near-catchment slope covered by meadow and aquatic vegetation) and topographical (catchment type, catchment and shore snow coverage and connectivity with other lakes) attributes were visually inspected and scored according to dominant features (Table S2). Geolocation, i.e. altitude, latitude, and longitude was recorded at each lake using a portable GPS device. Fractal shore development was estimated visually on a scale from 1(simple shoreline) to 2 (simple intrusions), 3 (branched intrusions) and 4 (2^{nd} order branched intrusions). It is assumed to roughly reflect shoreline development during a lake's ecological succession stages.

To test for relationships between lake chemistry and riparian vegetation composition, < 3 cm depth littoral sediments and water ± 5 m off the littoral (for small waterbodies, the distance was less) were sampled using a polyethylene trowel. The sediments comprised fragmented rocks, coarse sands, and fine silts. As the chemical composition of the fine sediment fraction is the most likely to relate to riparian vegetation, i.e. they are either source or sink of the bioavailable element fraction), sampling deliberately targeted this fraction. To assure sample homogeneity, at each lake the sample comprised roughly 5 randomly selected subsamples. All sediment and water samples were kept at < 4˚C until laboratory analysis.

Water pH and conductivity were measured on site, at the surface and bottom of the lake from samples taken with a Teflon bottom water sampler. Hach HQ40d portable pH and conductivity probes (IntelliCAL PHC201, accuracy ± 0.002 pH and IntelliCAL CDC401, accuracy ± 0.5 % from 1µS/cm - 200 mS/cm) were used.

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 100 µm sieve. Trace and major element contents were characterised by X-ray fluorescence spectrometry (XRF). A 5 g portion of the sample was prepared as lithium tetraborate melt for the determination of major (Na, Mg, Al, Si, P, S, Cl, K, Ca, Ti, and Fe) and trace (V, Cr, Mn, Co, Ni, Cu, Zn, As, Rb, Sr, Ba and Pb) elements. Results are expressed in % mass-mass and mg kg^{-1}, respectively for major and trace 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 analyzed 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 (1 σ) 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 analyzer 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 analyzed for Li, B, Na, Mg, Al, K, Ca, Mn, Fe, Ni, Cu, Ga, Se, Sr, Ba, Rb and Pb by inductively coupled plasma - optical emission spectrometer (ICP-OES) using standard ICP-MS/OES operating conditions. The results are expressed in mg L^{-1}. 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

A diagram of statistical analysis steps is presented in Fig. 2.

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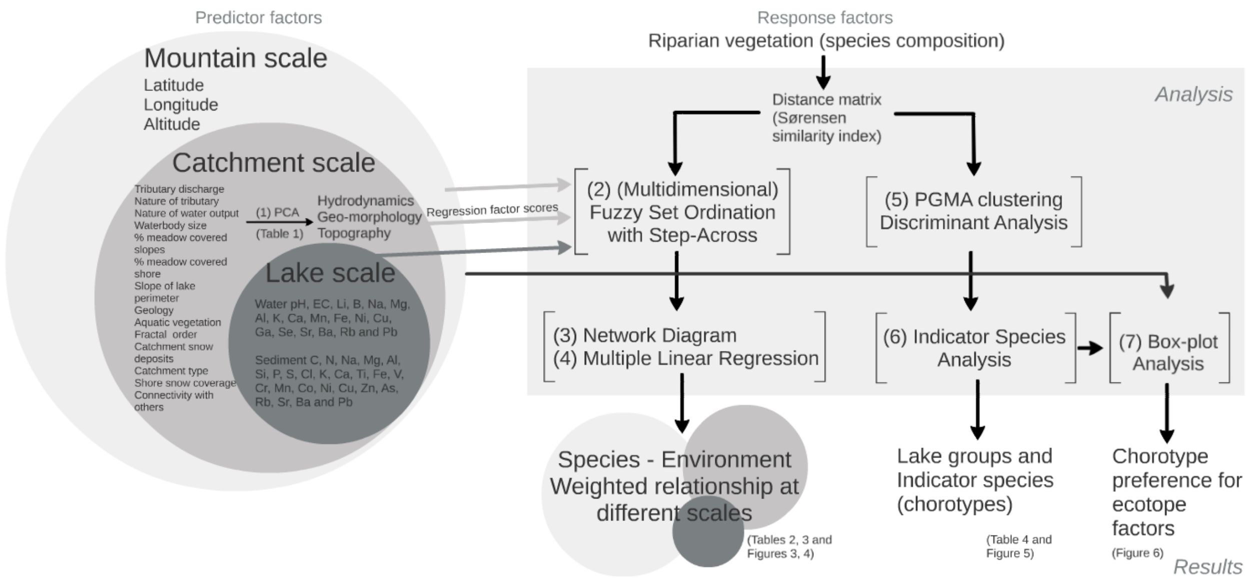

Figure 2 Data analysis flow chart displaying input variables collected at different scales (top and left), analysis steps (central box) and their outcomes (bottom).

Table 1 Association of lake catchment variables into three composite factors. Variables are listed in order of their 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. Variable values are in Table S2.

	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.

2.4.1 Principal component analysis to summarize 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), which represent major ecotope properties being investigated, according to the procedure developed in Zaharescu et al. 2016b (Table 1). The regression factor scores of the principal components (extracted after an orthogonal *Varimax* rotation) were then used as explanatory variables in the further analysis of vegetation data. This analysis was performed in PASW (currently IBM- SPSS) statistical package for Windows.

2.4.2 (Multidimensional) Fuzzy Set Ordination to quantify riparian drivers

To understand the potential effects of catchment gradients on vegetation species composition 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 more natural alternative to constrained ordination methods, e.g. CCA and RDA. Compared to the classical theory in 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 degree of 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), which overcomes this problem and includes the types of ordination that ecologists are more familiar with, such as gradient analysis (Whittaker, 1967) and environmental scalars ordination (Loucks, 1962). Thus, in fuzzy logic applications, the results can facilitate the expression of natural rules and processes.

First, a distance matrix of species incidence was calculated. For the binary data (presence-absence) 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 species composition. This was followed by one-dimensional FSO, taking distance matrices of species 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 correlation. Their summarized version, i.e. the PC regression factor scores from prior PCA (Table 1), were therefore used as

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explanatory variables in FSO. By default, the principal components of PCA computed with an orthogonal (e.g. Varimax) rotation are uncorrelated, therefore, suitable for this approach.

To remove potential covariance between factors and better quantify the effect size of each factor on riparian vegetation, a multidimensional FSO (MFSO) was run on factors with correlation coefficient with species distance matrix (r) > 0.3 ($p < 0.05$). This allowed a more accurate multidimensional interpretability of the results. Statistically, MFSO first performs an FSO on the variable accounting 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 the widespread ordination methods used in ecology, e.g. Principal Component Analysis (PCA), 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 other unconstrained ordination methods on more complex datasets, as it is less sensitive to rare species and noise in environmental factors (Roberts, 2009a) - therefore better reflecting the average community behavior.

The effect magnitude of each environment variable on plant species composition was assessed visually by the relative scatter attributable to that variable, and numerically by its increment in the correlation coefficient. Similar to regression modeling, if an axis is influential in determining the distribution of vegetation, then one should be able to predict the values of that variable based on species composition (Roberts, 2009b). A “step-across” function was used on MFSO results, to improve the ordination with high beta diversity, i.e. for 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 linkages between riparian vegetation and surrounding landscape elements, and their magnitude of influence was assembled in the open-source visualization tool Gephi 0.9.1 (https://gephi.org; Bastian et. al. 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 (incremental) *r* values derived by MFSO as variable weights. Likewise, a multiple regression with Akaike Information Criterion model selection (Automatic Linear Modelling option in IBM-SPSS) provided the magnitude of influence each landscape variable had in the composite landscape factors previously summarized by PCA.

2.4.4 Indicator community analysis

The riparian vegetation composition (incidence data) was analyzed for species association into chorotypes, i.e. species with significant co-occurrence patterns, using cluster analysis. First, the lakes were grouped on the basis of shared species. A Pair-Group clustering Method using the Arithmetic Averages (PGMA), flexible linkage parameter, beta = -0.2, was computed using 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. When clustering membership of species could not be established statistically, they were assumed to follow continuum distributions (Báez et al., 2005).

Furthermore, the selectivity of the resulting vegetation communities to different ecotope features 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 Major catchment-scale variates

Interactions between the lake, catchment, and larger geographical gradients create major environmental forces, which shape the development of ecosystems at the land-water interface. PCA extracted three principal components, together accounting for more than 58 % of the total variance in lake' catchment characteristics (Table 1).

The first component, PC1, is interpreted as hydrodynamics and is formed by tributary nature and discharge, type of water output and waterbody size (Table 1). The second component, PC2, characterises the major bedrock geo-morphology, i.e. geology, shore sloping, % of slope and shore covered by meadow, fractal order (riparian development) and the presence of aquatic vegetation. The third PC, PC3, represents topography influence, i.e. catchment type, visible connectivity with other lakes, and catchment and shore snow deposits. The three composite factors were, therefore regarded as major landscape drivers, and are expected to influence riparian the ecosystem development.

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3.2 Influence of lake, catchment, and pan-climatic drivers on vegetation composition

A single-dimensional FSO, used as an initial step in evaluating the linkages between large-scale, catchment-scale and lake scale variables, and vegetation composition (first objective in this study), clearly identified altitude to exert the largest influence (Table 2). This was followed by local-scale water Mn and Fe, and sediment Mg contents, large horizontal gradients latitude and longitude, and catchment-scale variables topography formation and hydrodynamics (Table 2). The effect size of each of the factors showing a correlation coefficient with vegetation composition *r* > 0.3 (p < 0.05), were introduced in an MFSO model (to remove potential covariation) and discussed in the following sections.

Table 2 One-dimensional fuzzy relationships between riparian vegetation species composition and environmental factors in the Pyrenees lakes. Factor superscripts: (a) macroscale, (b) catchment-scale (Table 1), (c) lake-scale sediment, and (d) lake-scale water variables. Correlations between factors and apparent factors predicted by vegetation are listed in descending order for each variable group (on different grey shades). 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			

3.2.1 Large vertical and horizontal gradients

Table 3 and Fig. 3a show the environmental factors in order of their independent correlation with the *apparent factors* predicted by vegetation composition. A two-axes solution resulted from MFSO, with altitude and latitude reliably predicting riparian plant composition (cumulative r = 0.65). Altitude, the most influential, is a classical vertical driver of ecosystem succession along the alpine climate gradient. The latitudinal variability in the study area (the secondly most important in the model) is relatively narrow. However, its location under four major biogeographical influences, namely Atlantic and Continental from the N and NW, Mediterranean

Table 3 Independent effect of [a] geoposition, [b] catchment, [c] sediment and [d] water chemistry factors on riparian vegetation composition, as given by MFSO. Figures for geoposition, catchment and water characteristics resulted from MFSO with step-across function. γ (gamma) = a vector of the independent variance fraction of a factor (MFSO axis). Factors with the highest independent influence in the model, in bold, are listed in order of their weight, for each variable group (highlighted by different grey shades).

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.

from SE, and the local alpine gradient (Fig. 1), implies that the study area was sufficiently large to capture macro-regional transitions in its riparian ecosystem. Longitude, while showing a separate relationship with vegetation (Table 2), played a covariate role in the multivariate model (Table 3).

3.2.2 Catchment geomorphological and hydrological elements

MFSO of catchment-scale variables produced a three-dimensional solution, with topography formation largely dominating hydrodynamics and geo-morphology, in its influence on vegetation

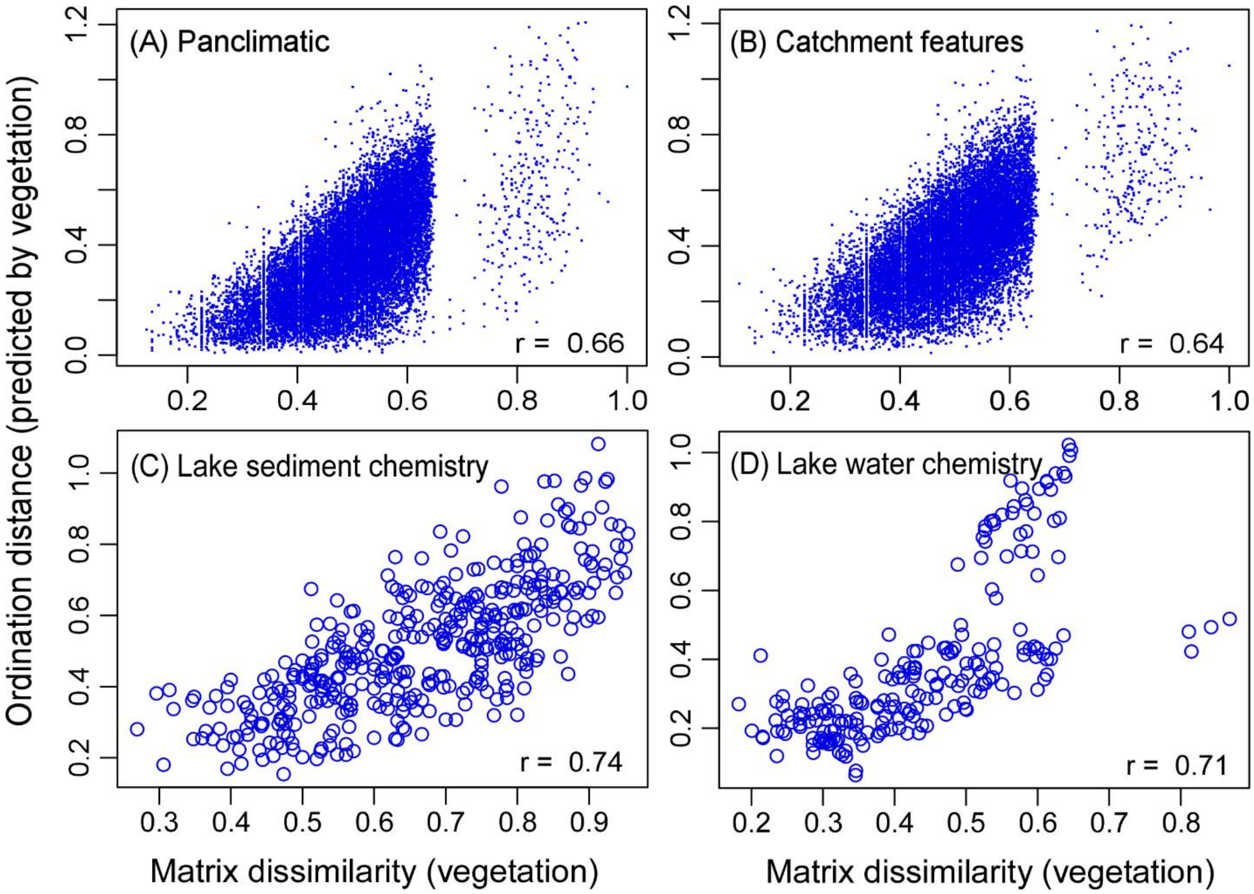

Figure 3 Multidimensional Fuzzy Set Ordination (FSO) depicting the effect of **(A)** large geographical gradients altitude, and latitude, **(B)** catchment factors topography (PC3), hydrodynamics (PC1), and geo-morphology (PC2), **(C)** sediment chemistry, and **(D)** water chemistry, on riparian plant composition. MFSO in A and B were improved by using a step-across function. Variables were introduced in the model in the order of decreasing Pearson fuzzy correlation (*r*; Table 3) with plant dissimilarity matrix. Number of permutations = 1000.

structure (cumulative *r* = 0.64; Table 3 and Fig. 3b). Since these factors are composite (Table 1), it means that catchment type - a legacy of the last glaciation, with local effects from snow cover and lake connectivity (important in propagule dispersion) create variable microclimates, which allow for colonization by different species. For instance, snow at valley head would last longer around lakes and create longer wet conditions than on mountain slopes or passes, which would experience earlier sun exposure. Previous research in alpine regions corroborates these findings and shown that topography and its effect on snow coverage can control terrestrial vegetation (Keller et al., 2005), a consequence of topography interaction with climate variables radiation, precipitation, and wind (Körner, 1999).

Hydrodynamics added to the influence of the previous axis (Table 3 and Fig. 3b), through the nature and discharge of 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 lake area to the riparian zone. It implies that stream - fed medium to large lakes (Table 1) host significantly different vegetation than the shallower, precipitation - fed ponds.

Although its separate influence was high (Table 2), bedrock geology (with nested effects of slope, vegetation coverage, and shore development, PC2), represented the smallest driver of riparian vegetation in the multivariate model, most likely due to its covariation with topography (Table 3 and Fig. 3b). Geology is known to influence the establishment of vegetation through its control on substrate chemistry and niche formation (Kovalchik and Chitwood, 1990). The bedrock of the area presents an igneous core (granitic) in its central part, flanked by sedimentary and metasedimentary materials. Granitic geomorphology, which is more resistant to weathering, is associated with steep slopes, low vegetation coverage, less developed riparian zones (lower fractal order; Table 1), and contributes fewer nutrients to the lake. Conversely, more reactive bedrock such as limestone sustains a more nutrient - rich environment, better developed riparian zones (higher fractal order), a more stable terrain with more vegetation coverage (Table 1). Together with topographic and hydrologic particularities, the two major geological units induce the development of different riparian assemblages.

3.2.3 Sediment chemistry. Indicator elements

At lake scale, results of the MFSO of riparian vegetation composition and sediment major and trace element contents resulted in a bi-dimensional solution, with Mg and Pb reliably predicting species composition (cumulative $r = 0.74$; Table 3 and Fig. 3c). Catchment lithology, namely the geological structure, the proportion of rock types, their mineralogy, chemistry, and weathering resistance, is tightly connected to the chemistry (major and trace elements and organic matter) of high altitude water bodies through cross-ecosystem fluxes of sediment and water (Lewin and Macklin, 1987; Zaharescu et al, 2009). Magnesium, a component of the photosynthesis molecule chlorophyll, and present in many growth enzymes, is an essential macronutrient in green plants. Soils developed on alkaline bedrock (limestone) generally contain more Mg (≈ 0.3

- 2.9 %) than those on more acidic substrates (granite or sandstone; ≈ 0.01 - 0.3 %; Beeson, 1959). The results show that differences in bedrock-derived Mg can modulate vegetation community composition at species scale, in the nutrient-poor environment.

The influence of Pb is rather surprising. One possible explanation is that it reflects the distribution of plants using mycorrhizae since mycorrhizal symbiosis has been related with increased Pb uptake (Wong et al., 2007). Or, more likely, plants' natural sensitivity to Pb (Kabata-Pendias and Pendias, 2001) could have also changed their composition along a natural Pb - stress gradient. It is known that in metamorphic areas of the central Pyrenees, Pb is an abundant mineral constituent, and has been detected in sediment and waters in significant levels (Catalan et al., 2006; Point et al., 2007; Zaharescu et al., 2009). Likewise, metal-rich (ferromagnesian) ultramafic rocks are common in this region of the Pyrenees (Kilzi et al., 2016), and they are known to influence vegetation composition and trigger high endemism levels in mountaintop ecosystems (Galey et al., 2017). It is therefore entirely plausible that the riparian ecosystem in our study has a strong response to elements of geology richer in heavy metals than in other nutrients.

The low effect of other essential elements in the multivariate model (although high independently; Table 2) is likely due to their mineral co-occurrence and co-leaching with Mg and Pb (Spearman correlation coefficient of Mg with Ca, Fe, Cr, Mn, Co, Ni, Cu, Zn, As and Ba $r >$ 0.38, and of Pb with Cu and Zn $r > 0.47$; $P < 0.05$). Nonetheless, plant relationship with Pb and Mg merit further mechanistic examination into why it is can be a dominant indicator of riparian vegetation composition.

3.2.4 Water chemistry. Indicator elements

The MFSO of riparian vegetation composition and selected water variables identified Mn and Fe as major influential axes (cumulative $r = 0.73$; Table 3 and Fig. 3d). Besides collecting weathering solutes, water in snow packs affects plant growing season, as well as controlling the temperature and oxygen reaching the ecosystem. Iron and Mn are major redox players in soil and sediment, and varying water table can modify their solubility and uptake by plants (Alam, 1999). For instance, in the water-saturated soil, biotic respiration drives reduction processes, which affects plant performance not only by preventing nutrient (Mg, Ca and Fe) uptake but also by restricting root development (Couto et al., 1983). Differential response of vegetation to the build-up of soluble Fe and Mn have been suggested in species ecology and habitat distribution (Alam, 1999), and it has been reported for grasses, legumes (Couto et al., 1983) and trees (Good and Patrick, 1987).

Variable moisture and flooding of the riparian ecosystem by lake water are common in alpine lakes, and they are regulated by snow thaw and frequency and volume of summer storms. The plant compositional change along Mn and Fe gradients are indicative of such process (a nested effect of topography; Table 1), with higher moisture near lakes at valley head and drier conditions on slopes and 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).

3.2.5 Conceptual network diagram

To illustrate the connection between riparian ecosystem and surrounding environmental features at the lake, catchment, and pan-climatic scales, a conceptual network diagram is presented in Fig. 4. The diagram shows important linkages being established between species presence, lake sediment chemistry and water redox condition, which reflects the flows of water and nutrients in the catchment. As well as with the nature of lake source and draining, shoreline development, catchment type and geology, and the large-scale altitudinal and latitudinal gradients. These landscape connections, of different strengths, and operating at different scales, are prone environmental change alteration. For instance, weak connections such as those with waterbody size, lakes connectivity, the extent of aquatic and terrestrial vegetation, and their large-scale distribution along latitude could suffer the most from deleterious effects of a changing climate. Long-range and local pollution, as well as climate change effect on weathering regimes, on the other hand, could alter the chemistry of nutrient and metal input. Increments in potentially toxic natural metal(oid) input (As and Ni) has been already reported in the Pyrenees, and it has been related to reductions in precipitation frequency, elevation of spring snow line, and increase in freezing days, particularly since the 1990s (Zaharescu et al., 2016a). Existing stronger connections, on the other hand, are expected

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to weaken under drastic environmental change, while new climate and geochemical relationships could be formed.

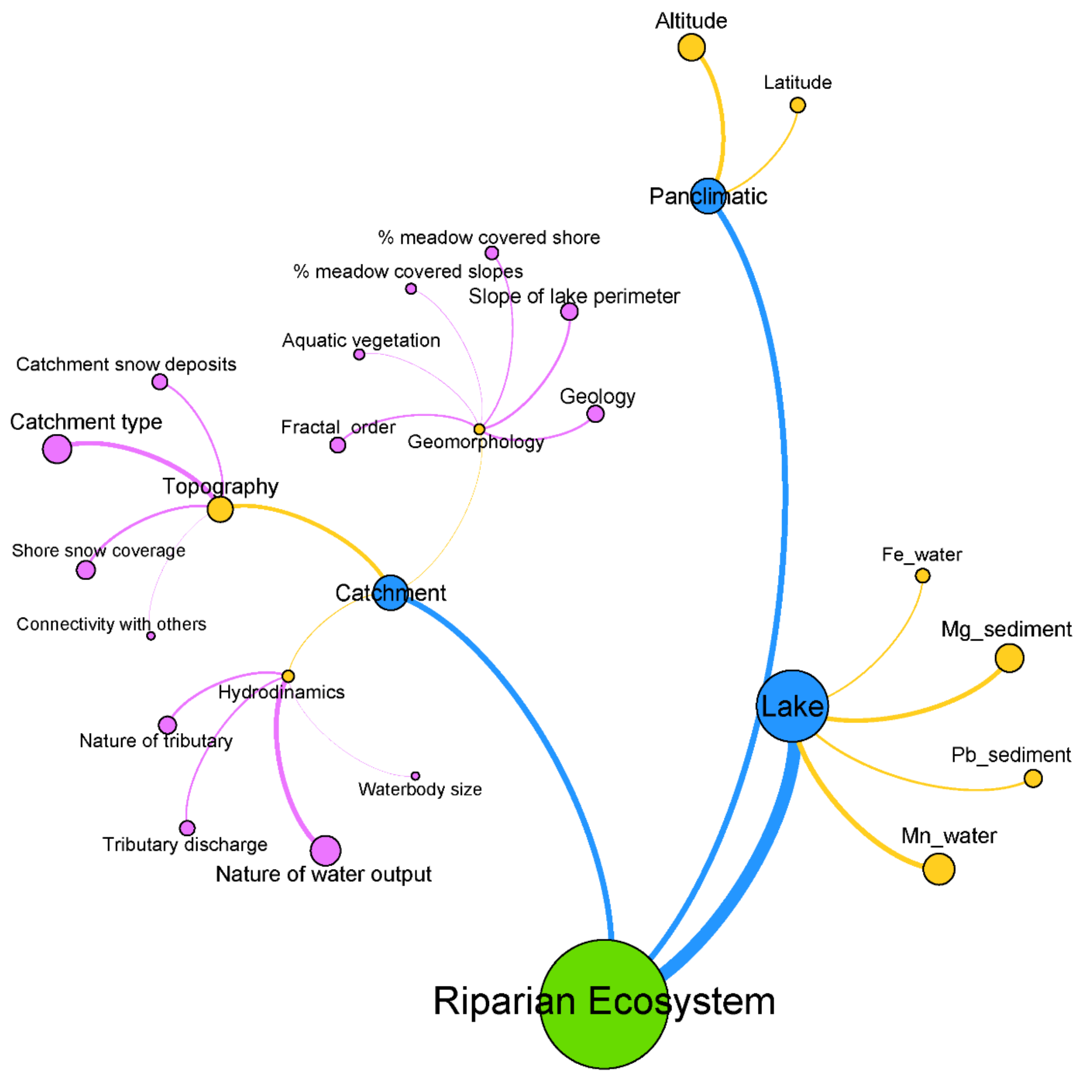

Figure 4 Conceptual network diagram showing the linkages between riparian ecosystem of a typical alpine lake and ecotopic features of the lake, catchment, and large pan-climatic gradients. Nodes and label sizes, as well as connections thickness, are proportional to the magnitude of their influence on target nodes. Connections borrow the colours of source nodes and represent different layers of organisation in the model.

3.3 Indicator communities and their environmental preference

3.3.1 Community analysis

To test whether the restrictive alpine environment harbors keystone plant communities (i.e. chorotypes; second objective), PGMA cluster analysis was used on species presence data. The

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results revealed a good grouping (agglomerative coefficient = 59 %), with the 189 lakes classified into four types (Fig. 5). Of the 168 total plant species (List S1), 79 formed four chorotypes, present

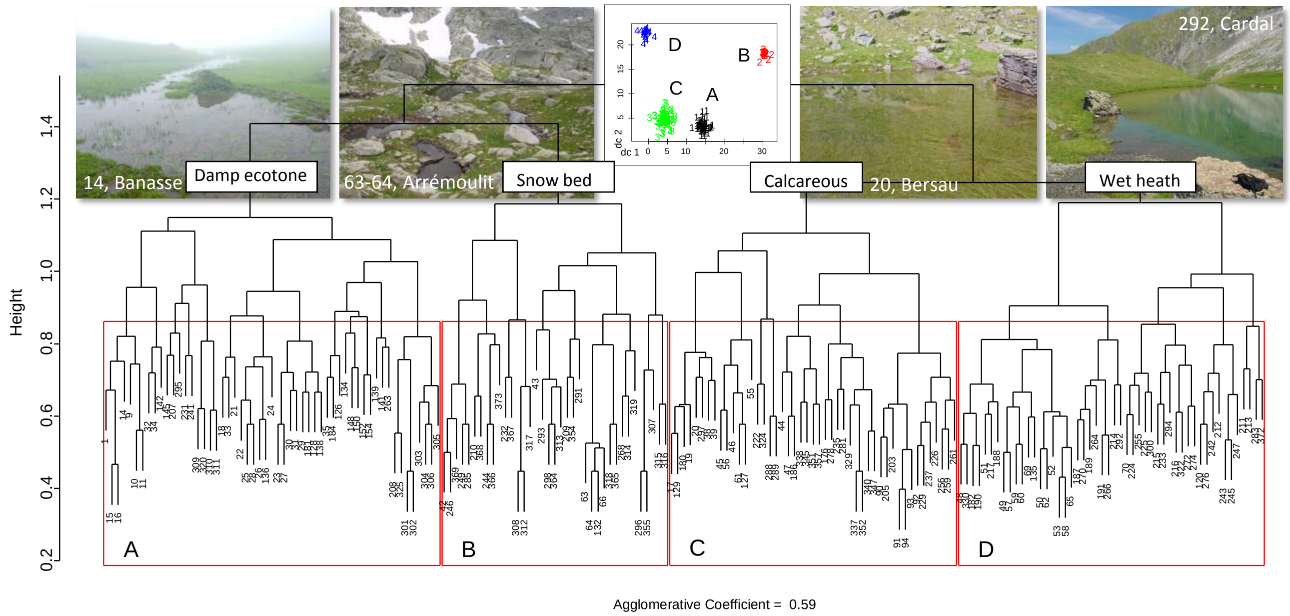

Figure 5 Dendrogram showing lake ecosystem types (clusters) based on similarity in riparian vegetation composition, together with representative examples. A plot of the clusters in discriminating space (inset) shows an effective clustering. Plant communities indicative of lake/ ecosystem types are in Table 4. N = 189 lakes and 166 plant species. Plants are listed in List S1, while lakes (at branches end) in Table S1 and Zaharescu et al., 2016b.

in the four lake environments. Table 4 shows the species with significant co-preference for each lake type and their probability of group membership. Plant communities A, B, and D yielded the highest degree of confidence (Fig. 5).

Type A lakes (Fig. 5 and Table 4) contain mostly species of damp ecotone. This includes bog-associated species with *Sparganium, Ranunculus, Chara, Sphagnum* moss, *Selaginell*a fern, sedges (*Carex)* and rushes *(Juncus)* (Table 4). Associated with these are 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 range of bedrock chemistry, including acidic (*Sphagnum),* neutral (*Trifoliums*) and basic (*Polygala*) substrates. This community seems to reflect an uneven physical template, common on the lake shores of the Central Pyrenees.

The second association (type B), smaller than type A, comprises a high proportion of species of short growing season with affinity to snow bed (*Saxifraga, Veronica, Sibbaldia*), herbaceous shrubs (*Salix*), and ferns (*Cryptogramma*). Most of them are silicophilous, adapted to low nutrient substrate of different textures, including scree/rocky, grassland, and damp soil.

Table 4: Riparian plant groups and their fidelity to lake ecosystems (Fig. 5), 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.

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.

Endemic grass *Festuca eskia* plotted in the same group.

Riparian community D is a large community comprising wet heath species of Ericaceae shrubs (*Vaccinium* and *Calluna*), accompanied by snow bed plants (*Primula, Soldanella,* and *Bartsia*), sedges (*Trichophorum*), rushes (*Luzula*), and species of wet substrate (*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.

Community C was the smallest and least common ($p < 0.25$; Table 4 and Fig. 5). Its members, including the water starwort, blue-green sedge, and edelweiss (a protected species in many European countries), prefer moist-to-dry calcareous banks. Since the rest of the species had no group association, they are assumed to follow continuum or gradient distributions (Báez et al., 2005).

The identified communities incorporate species from major terrestrial groups (Gruber, 1992; Grey-Wilson and Blamey, 1995; Minot et. al, 2007), but with a preference for the wet riparian environment. They are eurytopic associations of large niche breadths, present in a wide range of habitats. This characteristic is what must have allowed them to colonize the harsh and diverse environment surrounding high - elevation waterbodies. The ecological importance of these communities, however, is that they reflect a natural ecosystem condition. Their further study in connection with climate change models is, therefore, imperative to understand how these communities, and the underlying ecotopes, cope with a changing environment.

3.3.2 Environmental preference of indicator communities

To better define the distribution of identified associations along environmental gradients, and understand their habitats (third objective), they were plotted against geoposition and composite catchment variables (Fig. 6). As shown by the variability in their group medians, plant communities seemed to respond well to both, large horizontal and vertical gradients, and

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catchment - scale variables. Community A inhabited water - saturated areas surrounding the larger lakes, of large (riparian) fractal order, and limited summer snow cover. They were on the floors and slopes of (meta)sedimentary glacial valleys, at comparatively low altitudes (median ≈ 2100 m a.s.l.) in the NE of the study area (Fig. 6). Community B, with a high proportion of snow

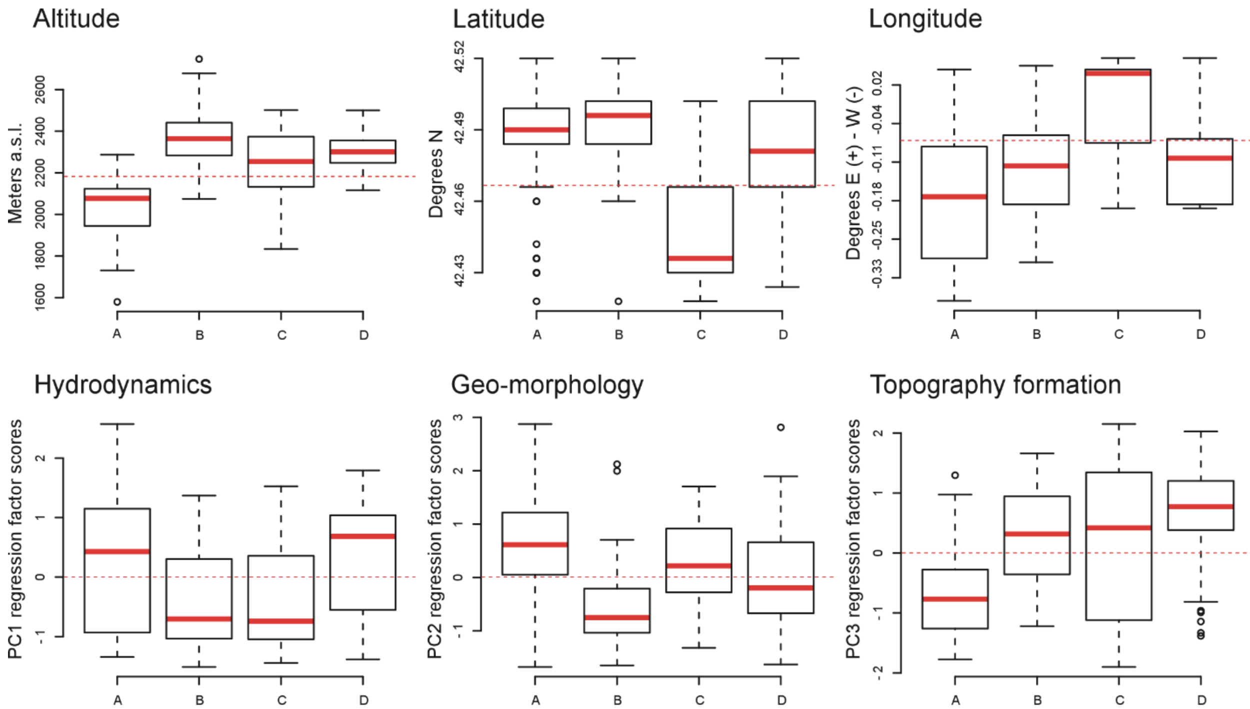

Figure 6 Boxplots showing the distribution of indicator plant communities along geoposition (altitude, latitude, and longitude) and composite catchment gradients. Hydrodynamics factor ranges from small water bodies (-) to large lakes (+), and their associated variables (Table 1); geo-morphology, from igneous and metamorphic (-), to sedimentary (+); topography formation from valley floor and flat topography (-), to valley head (+). Boxplots represent median (red), first (25 %) and third (75 %) quartiles, with whiskers extending to the 5th and 95th percentiles. Horizontal dashed red lines are set at plot averages.

bed species, grew in elevated granitic topography (e.g. glacial valleys head and mountain pass, ≈ 2400 m a.s.l., the central part of the region), of steep slopes and low fractal development. These habitats (mostly rain-fed lakes) had persistent summer snow cover and lower water turnover. Association type C established around small lakes of low input/output, in a wide range of altitude and topography, from valley floors to valley heads, in the SW of the study area (Fig. 6). Community D, of the narrowest altitude span, was mostly found inhabiting large catchment head lakes with persistent summer snow and high water turnover, in the central area.

These results support findings from community analysis and clearly show that none of the evaluated ecotope factors was the sole driver of community establishment in the intricate topography. Rather, a complex pool of microclimatic and geomorphologic conditions worked together to sustain the riparian communities. Since these communities reflect environmental gradients sustaining their formation, their long-term study is necessary, as climate change can affect their distribution through effects on the underlying physicochemical drivers.

3.3.3 Environmental change and protection approaches

Anthropogenic effects on climate, long-range atmospheric transport of pollutants (e.g. black carbon and heavy metals), and direct human encroachment (mining, farming, military activity and tourism/urbanization) can significantly affect pristine alpine environments, with potentially irremediable effects (Kohler et al., 2014; Huss et al., 2017). These can range from habitat loss due to species introduction, climate-enhanced diseases, altitudinal range shifts in species, waterbodies pollution, and loss of natural connectivity.

Climate change effects on precipitation, snow line, hydrology and weathering fluxes have been reported in the alpine and subalpine Pyrenees (Zaharescu et al., 2016a). This could affect riparian communities in various way. For instance, snow bed communities (B and D; in the central part of the study area; Fig. 6) could experience decreasing snow in their habitats, earlier springs, and dryer, longer summers. Since both communities also occupy the higher altitudes overall, competition from advancing low - altitude species could increase their fragmentation, species rearrangement in new communities and loss, particularly of endemic species. Changes in nutrient load from increased weathering, tourist-hosting industry, and aerial pollution can also preferentially affect community B, which is adapted to lower nutrient concentrations. Metal abundances in some catchments of the study area are high (Kilzi et al., 2016; Point et al., 2007), and they have been shown to increment under climate change, to potentially toxic levels in other regions of the Pyrenees (Zaharescu et al., 2016a). This can result in loss of less tolerant species, particularly those on metasedimentary materials (e.g. community A), in the lower, west front of the area Fig.6).

While this study explores natural linkages in a protected region, the sensitivity of riparian environments to both, aquatic and terrestrial stressors should bring them at the forefront of environmental protection strategies. Education approaches that promote the value of natural landscapes for current and future generations in a holistic way (biosphere, geosphere, hydrosphere and atmosphere coupling) should be prioritized, as well as long-term conservational approaches. Global scale collaborative efforts on long-term monitoring, e.g. Mountain Research Initiative (http://mri.scnatweb.ch/en/), Global Lake Ecological Observatory Network (http://gleon.org/) and Critical Zone Observatory Network (criticalzone.org/), setting up alpine research centres and botanical gardens, and citizen science (Zaharescu et al, 2006, 2007; Mix, 2014), could help improve the perception of mountain ecosystems as centres of biodiversity, providers of mental health benefits, and important players in the distribution of natural resources to the wider biosphere.

4 CONCLUSIONS

Results show that the connections between alpine riparian ecosystem and the surrounding aquatic and terrestrial environments extend over a wide range of scales. Topographical formations left behind by the last glaciation, with contemporary effects of snow cover and lake connectivity, are the dominant catchment-scale elements controlling ecosystem development and diversity. Hydrodynamics, with nested contribution from size and nature of the lake and its input and output, was the second to topography. The two suggest that these lake ecosystems are not isolated 'islands' in the landscape, but rather interconnected biodiversity nodes, controlled by the catchment physical elements. Geo-morphology, grouping geology, slope and complexity of shore line, and its vegetation cover, greatly covaried with the first two factors, and reflected major geomorphological units, extending from igneous, to metasedimentary and calcareous sedimentary materials. Geology also exerted local effects (through sediment Mg and Pb and water Mn and Fe) likely due to linkages with mafic and ultramafic materials. Superimposed to catchment and local drivers, the ecosystem captured the transition between major biogeographic regions of Europe, in an otherwise narrow study area.

The riparian ecotone, connecting complex topography, geology and water regimes, assembled species from both wet and dry environments, which withstand regular flooding. Community analysis identified four such eurytopic groups, i.e. damp ecotone, snow bedsilicates, calcareous, and wet heath. They have a broad niche breadth and characterise four ecosystem/lake types. The distribution and habitat preference of these communities are tell-tales of their sensitivity to a number of environmental change factors, including diminishing snow cover, modification in water level, increased nutrient and metal input from tourism industry and weathering of natural metal stores, increased fragmentation and competition from lowland species.

The riparian-aquatic and riparian-terrestrial connections shown by this study clearly illustrate how physical, geochemical and hydrological elements of the alpine landscape aggregate into major ecotope drivers, and operate at different scale to shape the composition and distribution of the overlying ecosystem. It remains to be seen how the environmental change affects the functional connectivity of these water-sensitive ecosystems with the supporting ecotope, at its manifold of scales.

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AUTHORS CONTRIBUTION

Research grant design, A. Palanca-Soler; field data collection, R.N. Lester (plant taxonomy), C. Tanase (plant taxonomy), 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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SUPPORTING INFORMATION

Riparian vegetation in the alpine connectome. Terrestrial-aquatic and terrestrial-terrestrial interactions

D.G. Zaharescu, A. Palanca-Soler, P.S. Hooda, C. Tanase, C.I. Burghelea, R. N. Lester

Table S1. Lakes from the axial region of the Pyrenees National Park (France) surveyed for this study, their geographical position and surface area. A Google Earth map file with a representative subset of lakes is available on the article webpage. Major lakes in a catchment have no suffix, while waterbodies lacking names were given the name of their surrounding area. (*) represents dam closing. Multiple year sampling is illustrated in brackets.

Lake ID	Sampling year	Name	Main valley	Altitude (m)	Latitude	Longitude	Area (m^2)
1	2002	Lake Arlet	Aspe	1987	42.5021	-0.3653	31037.00
9	2002	Pond Caillaous	Aspe	1877	42.4954	-0.3607	108.19
10	2002	Pond Caillaous 1	Aspe	1877	42.4954	-0.3607	388.77
11	2002	Lake Gourgue	Aspe	1840	42.4954	-0.3607	1295.91
14	2002	Lake Banasse 1	Aspe	1940	42.4954	-0.3607	742.20
15	2002	Lake Banasse 2	Aspe	1940	42.4954	-0.3607	1178.10
16	2002	Lake Banasse 3	Aspe	1940	42.4954	-0.3607	2450.44
17	2001	Lake Bersau	Ossau	2082	42.4959	-0.3015	79223.11
18	2001	Lake Berseau 1	Ossau	2080	42.4959	-0.3015	1484.40
19	2001	Lake Berseau 2	Ossau	2100	42.4959	-0.3015	2419.81
20	2001	Pond Berseau 1	Ossau	2085	42.4959	-0.3015	127.23
21	2001	Pond Berseau 2	Ossau	2086	42.4959	-0.3015	180.64
22	2001	Lake Larry 1	Ossau	2077	42.5018	-0.3014	1162.39

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23	2001	Lake Larry 2	Ossau	2077	42.5018	-0.3014	293.74
24	2001	Lake Larry 3	Ossau	2077	42.5018	-0.3014	414.69
25	2001	Lake Larry 4	Ossau	2077	42.5018	-0.3014	306.31
26	2001	Lake Ayous 1	Ossau	2060	42.5018	-0.2929	722.57
27	2001	Lake Ayous 2	Ossau	2060	42.5018	-0.2929	753.96
28	2001	Lake Ayous 3	Ossau	2060	42.5018	-0.2929	769.69
29	2001	Lake Gentau 1	Ossau	1982	42.5018	-0.2929	1850.40
30	2001	Lake Gentau	Ossau	1947	42.5018	-0.2929	107068.62
31	2001	Lake Miey	Ossau	1920	42.5018	-0.2929	9324.25
32	2001	Lake Roumassot	Ossau	1845	42.5018	-0.2929	55694.15
33	2001	Lake Castérau	Ossau	1943	42.4945	-0.2931	15013.67
34	2001	Lake Paradis	Ossau	1976	42.4945	-0.2931	9495.97
35	2001	Lake Peyreget	Ossau	2074	42.4942	-0.2719	10568.01
38	2001	Lake Col de Peyreget 1	Ossau	2220	42.4941	-0.2635	1473.41
39	2001	Lake Col de Peyreget 2	Ossau	2208	42.4941	-0.2635	3758.13
42	2001	Lake Arrémoulit Supérieur	Ossau	2281	42.5005	-0.1957	39654.75
43	2001	*Lake Arrémoulit	Ossau	2285	42.5037	-0.1956	72184.37
44	2001	Lake Arrémoulit (bellow dam)	Ossau	2255	42.5037	-0.1956	9680.03
45	2001	Lake Palas	Ossau	2359	42.5037	-0.1956	6856.53
46	2001	Lake Palas 1	Ossau	2365	42.5037	-0.1956	2511.70
47	2001	Lake Palas 2	Ossau	2362	42.5037	-0.1956	1226.79
48	2001	Lake Arrémoulit Superior 1	Ossau	2300	42.5037	-0.1956	1272.35
49	2001	Lake Arrémoulit Superior 2	Ossau	2295	42.5037	-0.1956	208.92
50	2001	Lake Arrémoulit Superior 3	Ossau	2297	42.5037	-0.1956	23.56
51	2001	Lake Arrémoulit Superior 4	Ossau	2300	42.5037	-0.1956	2104.08
52	2001	Lake Arrémoulit Superior 5	Ossau	2300	42.5037	-0.1956	1503.25
53	2001	Lake Arrémoulit Superior 6	Ossau	2305	42.5037	-0.1956	1237.00
55	2001	Lake Arrémoulit Superior 7	Ossau	2290	42.5037	-0.1956	384.85
56	2001	Lake Arrémoulit Superior 8	Ossau	2285	42.5037	-0.1956	144.51
57	2001	Lake Arrémoulit Inférieur	Ossau	2241	42.5037	-0.1956	9671.11
58	2001	Lake Arrémoulit Inferior 1	Ossau	2248	42.5037	-0.1956	292.17
59	2001	Lake Arrémoulit Inferior 2	Ossau	2246	42.5037	-0.1956	2831.36
60	2001	Lake Arrémoulit Inferior 3	Ossau	2244	42.5037	-0.1956	4970.00
61	2001	Lake Arrémoulit Inferior 4	Ossau	2256	42.5037	-0.1956	523.85
62	2001	Lake Arrémoulit Inferior 5A	Ossau	2254	42.5037	-0.1956	282.74
63	2001	Lake Arrémoulit Inferior 5B	Ossau	2254	42.5037	-0.1956	271.74
64	2001	Lake Arrémoulit Inferior 5C	Ossau	2254	42.5037	-0.1956	278.02
65	2001	Lake Arrémoulit Inferior 5D	Ossau	2254	42.5037	-0.1956	266.24
66	2001	Lake Arrémoulit Inferior 6	Ossau	2252	42.5037	-0.1956	197.92
69	2002	Lake Carnau 1	Ossau	2208	42.5213	-0.1908	34321.90
70	2002	Lake Carnau 2	Ossau	2202	42.5213	-0.1908	9291.26
90	2002	Lake Les Lacarrats_1	Azun	2441	42.5212	-0.1824	490.87
91	2002	Lake Les Lacarrats_2	Azun	2441	42.5212	-0.1824	235.62
92	2002	Lake Les Lacarrats_3	Azun	2429	42.5212	-0.1824	4594.58
93	2002	Lake Les Lacarrats_4	Azun	2430	42.5212	-0.1824	9825.33
94	2002	Lake Les Lacarrats_5	Azun	2430	42.5212	-0.1824	7657.63
120	2001	Lake Micoulaou 1	Azun	2302	42.5034	-0.1744	706.84
126	2000 (125/2001)	Lake Batcrabère Supérieur	Azun	2180	42.5034	-0.1744	79168.13
127	2001	Lake Batcrabère Supérieur 1	Azun	2182	42.5034	-0.1744	285.88
128	2001	Lake Batcrabére Milieu	Azun	2130	42.5034	-0.1744	1923.44
129	2001	Pond Batcrabére Milieu 1	Azun	2130	42.5106	-0.1743	47.12
132	2001	Lake bellow Batcrabére Milieu	Azun	2129	42.5034	-0.1744	1755.31
134	2000 (133/2001)	Lake Batcrabère Inférieur	Azun	2116	42.5106	-0.1743	18606.08
135	2001	Lake Batcrabère Inférieur 1	Azun	2116	42.5106	-0.1743	3573.56
136	2001	Pond next to Larribet Refuge	Azun	2055	42.5106	-0.1743	1979.20

138	2000 (137/2001)	Pond Pabat	Azun	2062	42.5106	-0.1743	518.35
139	2001	Lake La Claou Supérieur	Azun	1750	42.521	-0.1656	2964.09
141	2000 (140/2001)	Lake La Claou	Azun	1739	42.521	-0.1656	2035.75
142	2001	Lake Doumblas	Azun	1580	42.5209	-0.1612	1796.99
145	2001	Pond Pluviometre	Azun	1731	42.5135	-0.1529	4546.54
148	2001 (147/2000)	Lake Remoulis Inférieur	Azun	2017	42.5031	-0.1532	5340.71
150	2001 (147/2000)	Lake Remoulis Supérieur	Azun	2019	42.5031	-0.1532	12801.99
152	2001 (151/2000)	Pond Casteric	Azun	2080	42.4958	-0.1533	659.73
154	2001 (153/2000)	Pond Toue	Azun	2090	42.4958	-0.1533	639.31
176	2001	Lake Cambalés Grand	Cauterets	2342	42.4924	-0.1407	13994.22
180	2001	Pond Opale	Cauterets	2222	42.4923	-0.1323	175.93
181	2001	Pond Opale 1	Cauterets	2248	42.4923	-0.1323	54.98
182	2001	Pond Opale 2	Cauterets	2260	42.4923	-0.1323	1412.15
184	2001 (183/2000)	Lake Opale Petit Inférieur	Cauterets	2287	42.4923	-0.1323	8466.59
186	2001 (185/2000)	Lake Opale Supérieur	Cauterets	2320	42.4923	-0.1323	32842.99
187	2001	Pond Petit Laquet	Cauterets	2360	42.4923	-0.1323	169.65
188	2001	Lake Petit Laquet	Cauterets	2350	42.4923	-0.1323	3765.98
189	2001	Lake Costalade Supérieur	Cauterets	2320	42.4923	-0.1323	9519.03
190	2001	Pond Cambalés	Cauterets	2315	42.4923	-0.1323	829.38
191	2001	Lake Costalade Inférieur	Cauterets	2310	42.4923	-0.1323	10148.92
203	2002	Lake Pourtet	Cauterets	2420	42.5026	-0.1236	80311.96
205	2002	Lake Pourtet 2	Cauterets	2307	42.5025	-0.1152	1374.45
207	2002 (206/2000)	Lake Embarrat 2	Cauterets	2139	42.5025	-0.1152	14278.54
208	2002	Lake Embarrat 1	Cauterets	2078	42.5024	-0.1108	35215.68
209	2001	Lake De la Badéte	Cauterets	2344	42.5024	-0.1108	58109.25
210	2001	Lake Col d'Arratille	Cauterets	2501	42.4709	-0.1033	2670.28
211	2001	Pond Arratille 1	Cauterets	2363	42.4741	-0.1031	141.37
212	2001	Pond Arratille 2	Cauterets	2330	42.4741	-0.1031	63.62
213	2001	Pond Arratille 3	Cauterets	2315	42.4741	-0.1031	3691.37
214	2001	Pond Arratille 4	Cauterets	2289	42.4741	-0.1031	31.42
215	2001	Pond Arratille 5	Cauterets	2315	42.4741	-0.1031	731.21
216	2001	Pond Arratille 6	Cauterets	2268	42.4741	-0.1031	1165.53
217	2001	Lake Arratille	Cauterets	2247	42.4741	-0.1031	70038.67
222	2002	Lake Chabarrou Supérieur	Cauterets	2422	42.4813	-0.0946	1406.02
224	2002	Lake Chabarrou	Cauterets	2302	42.4812	-0.0902	34150.98
225	2002	Lake Chabarrou Inférieur	Cauterets	2390	42.4812	-0.0902	617.93
226	2002	Pond Chabarrou 1	Cauterets	2364	42.4812	-0.0902	412.33
229	2002	Pond Chabarrou 4	Cauterets	2364	42.4812	-0.0902	14.01
231	2001	Oulettes. glacier runoff	Cauterets	2151	42.4707	-0.0905	2434.66
232	2001	Pond Arraillé Inférieur	Cauterets	2441	42.4706	-0.0821	714.71
233	2001	Lake Arraillé Milieu	Cauterets	2450	42.4706	-0.0821	2544.69
235	2002	Lake Estibe Aute 1	Cauterets	2515	42.4737	-0.0736	12935.51
237	2002	Lake Estibe Aute 3	Cauterets	2515	42.4737	-0.0736	24864.92
241	2001	Pond Montferrat	Luz	2207	42.4455	-0.0743	109.96
242	2001	Lake Montferrat	Luz	2374	42.4455	-0.0743	10445.80
243	2001	Pond Montferrat 1	Luz	2372	42.4455	-0.0743	1313.19
244	2001	Pond Montferrat 2	Luz	2440	42.4455	-0.0743	1011.59
245	2001	Lake Montferrat 1	Luz	2438	42.4455	-0.0743	2111.15
246	2001	Lake Montferrat 3	Luz	2438	42.4455	-0.0743	302.38
247	2001	Lake Montferrat 4	Luz	2437	42.4455	-0.0743	319.66
249	2001	Lake Montferrat 6	Luz	2440	42.4455	-0.0743	500.30
255	2002	Lake Estibe Aute Inférieur	Cauterets	2324	42.4842	-0.0733	45356.74
256	2002	Pond Estibe Aute Supérieur	Cauterets	2324	42.4842	-0.0733	614.97
259	2002	Lake Estibe Aute Supérieur	Cauterets	2328	42.4842	-0.0733	125663.71
261	2002	Pond Estibe Aute Supérieur 1	Cauterets	2331	42.4842	-0.0733	435.90
263	2001	Lake Estom	Cauterets	1804	42.4808	-0.065	67122.71

264	2001 (265/2002)	Pond Sentier d’Estom 1	Cauterets	2235	42.4703	-0.0653	320.44
266	2001 (267/2002)	Pond Sentier d’Estom 2	Cauterets	2240	42.4703	-0.0653	247.39
268	2001 (269/2002)	Pond Sentier d’Estom 3	Cauterets	2240	42.4703	-0.0653	243.47
270	2001 (271/2002)	Pond Sentier d’Estom 4	Cauterets	2248	42.4703	-0.0653	388.76
272	2001 (273/2002)	Lake Labas	Cauterets	2281	42.4702	-0.0609	49542.92
274	2001 (275/2002)	Lake Oulettes d'Estom	Cauterets	2360	42.4702	-0.0609	95504.42
276	2001 (277/2002)	Lake Couy	Cauterets	2445	42.4702	-0.0609	92909.86
278	2001 (279/2002	Lake Turon Couy	Cauterets	2485	42.463	-0.0611	4712.39
281	2001 (282/2002)	Pond Turon Couy 2	Cauterets	2492	42.463	-0.0611	471.24
283	2001 (284/2002)	Lake Couy Supérieur	Cauterets	2500	42.463	-0.0611	4712.39
285	2001 (286/2002)	Pond Couy Supérieur	Cauterets	2500	42.463	-0.0611	4712.25
288	2002 (287/2001)	Lake Glace	Cauterets	2678	42.463	-0.0611	136030.96
289	2002	Lake Petit Lac Du Col	Cauterets	2650	42.463	-0.0611	21650.29
291	2001	*Lake Ossoue	Luz	1834	42.4525	-0.0614	38954.60
292	2002	Lake Cardal	Luz	2221	42.4348	-0.0618	4618.14
293	2002	Pond Col de la Bernatoire	Luz	2045	42.4348	-0.0618	144.51
294	2002	Pond Col de la Bernatoire 1	Luz	2393	42.4316	-0.062	3166.73
295	2001	Lake Especiérès	Luz	2195	42.424	-0.0409	27876.89
296	2001	Lake Especiérès Infèrieur	Luz	2186	42.424	-0.0409	1658.71
297	2001	Pond Plaiteau de Saint André	Luz	2075	42.4239	-0.0326	94.25
298	2001	Ponds Labas Blanc	Luz	2009	42.4239	-0.0326	989.60
300	2002	Laquet de Bassia	Luz	2275	42.4613	0.0448	22855.09
301	2001	Pond Bassia 1	Luz	2277	42.4613	0.0448	967.61
302	2002	Pond Bassia 2	Luz	2275	42.4613	0.0448	3104.68
303	2002	Pond Le Cot 1	Luz	2063	42.4402	0.0525	125.66
304	2002	Pond Le Cot 2	Luz	2130	42.4402	0.0525	673.87
305	2002	Pond Le Cot 3	Luz	2130	42.4402	0.0525	824.67
306	2002	Pond Le Cot 4	Luz	2130	42.4402	0.0525	353.43
307	2001	Pond Serre Longue	Luz	2190	42.433	0.0523	537.21
308	2001	Pond Esbarris	Luz	2139	42.4329	0.0607	694.29
309	2001	Lake Aires Supérieur	Luz	2089	42.4329	0.0607	14953.98
310	2001	Lake Aires Inférieur 1	Luz	2081	42.4329	0.0607	1865.32
311	2001	Lake Aires Inférieur 2	Luz	2081	42.4329	0.0607	7314.41
312	2001	Lake Comble 2	Luz	2099	42.4327	0.0651	3758.13
313	2001	Lake Comble 1	Luz	2098	42.4327	0.0651	6660.18
314	2001	Lake Troumouse 1	Luz	2098	42.4329	0.0607	433.54
315	2001	Pond Troumouse 1	Luz	2105	42.4329	0.0607	11.78
316	2001	Pond Troumouse 2	Luz	2102	42.4329	0.0607	9.42
317	2001	Pond Troumouse 3	Luz	2133	42.4329	0.0607	25.13
318	2001	Lake Troumouse 2	Luz	2135	42.4329	0.0607	687.22
319	2001	Lake Troumouse3	Luz	2145	42.4329	0.0607	5006.91
320	2001	Lake Troumouse 4	Luz	2148	42.4329	0.0607	1209.51
322	2002	Lake Rabiet	Luz	2191	42.4927	0.0457	13469.58
324	2002	Lake Bugarret	Luz	2281	42.4853	0.054	86079.64
325	2002	Lake Glere	Luz	2103	42.5103	0.0546	41563.27
329	2002	Lake Det Mail	Luz	2350	42.5101	0.0623	65426.81
330	2002	Lake Oueil Nègre	Luz	2349	42.5031	0.0544	753.98
337	2002	Lake Estelat Supérieur	Luz	2423	42.4958	0.0543	34086.28
338	2002	Lake Glacé de Maniportet	Luz	2747	42.4926	0.0541	12126.03
340	2002	Lake Bleu De Maniportet	Luz	2651	42.4958	0.0543	26295.13
345	2002	Lake Vert Maniportet Long	Luz	2632	42.4957	0.0627	6408.85
347	2002	Pond Vert Maniportet Rond	Luz	2628	42.4957	0.0627	6872.23
351	2002	Lake Breche 2	Luz	2433	42.4957	0.0627	2209.33
352	2002	Lake Breche 1	Luz	2409	42.4957	0.0627	1845.69
354	2001	Pond Aguilous 1	Luz	2240	42.4506	0.0612	141.37
355	2001	Pond Agulious 2	Luz	2255	42.4506	0.0612	268.61

357	2002	Pond Cap de Long 2	Aure	2591	42.4819	0.0706	1969.78
364	2001	Pond Barroude 6	Aure	2345	42.4326	0.0735	400.55
365	2001	Pond Barroude 5	Aure	2350	42.4326	0.0735	1157.68
366	2001	Pond Barroude 4	Aure	2356	42.4326	0.0735	1762.43
367	2001	Pond Barroude 3	Aure	2374	42.4326	0.0735	668.37
368	2001	Pond Barroude 2	Aure	2375	42.4326	0.0735	186.92
369	2001	Pond Barroude 1	Aure	2376	42.4325	0.0819	803.46
372	2001	Lake Barroude Grand	Aure	2355	42.4325	0.0819	53603.42
373	2001	Lake Barroude Petit	Aure	2377	42.4325	0.0819	62682.63

Table S2. Variables (and their measurement units) collected from the 189 lakes and ponds of the central region of the Pyrenees National Park (France) at different scales. Superscripts represent [a]numerical, [b]categorical and [c]nominal variables.

	Variable type	
Local	Catchment (reduced to composite factors by PCA)	Panclimatic
[a]**Riparian vegetation** Species presence	[c]**Catchment type** Plain, U - shape valley, slope, mountain pass, V - shape valley, head of glacial valley	[a]**Longitude** Geographic degrees
[a]**Lake sediment C, N, Na, Mg, Al, Si, P, S, Cl, K, Ca, Ti, and Fe** % mass-mass	[c]**Main geology** Conglomerate-sandstone-claystone, limestone (+sandstone-marlstone-schist enclaves), schist (+andesite-sandstone-claystone and granite-limestone), granite (+schist)	[a]**Latitude** Geographic degrees [a]**Altitude** Meters above sea level
[a]**Lake sediment V, Cr, Mn, Co, Ni, Cu, Zn, As, Rb, Sr, Ba and Pb** mg kg^{-1}	[b]**Snow deposits in the catchment** Absent, very scarce, scarce, abundant, very abundant	
[a]**Lake water pH** (surface and bottom)	[c]**Visible connectivity with other lake** Absent, surrounded by another lake, with another one, in chain	
[a]**Lake water conductivity** (surface and bottom) μS cm^{-1}	[c]**Nature of tributary** Meteoric, spring, stream/waterfall [b]**Tributary discharge** Absent, low discharge, medium discharge, high discharge	
[a]**Lake water Li, B, Na, Mg, Al, K, Ca, Mn, Fe, Ni, Cu, Ga, Se, Sr, Ba, Rb and Pb** mg L^{-1}	[c]**Nature of water output** Absent, temporary, surface-small, surface-medium, surface-large, subterranean, dam output	
	[b]**% grass covered slopes** <10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-100	
	[b]**Slope of lake perimeter** Plain, plain in alternation with medium slopes, medium slopes, steep in alternation with medium/plain, steep in >50% of perimeter	
	[b]**Lake size** Pool (<315±333m^2), pond (1566±1985m^2), small	

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	lake (9157±10267m^2), medium size lake (41127±31820m^2), large lake (91441±37307m^2) [b]**Lake fractal development order** 1, 2, 3, 4 [b]**Shore snow coverage** Absent, <10%, 11-50%, >51%, into the water [b]**% grass covered shore** <10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-100 [b]**Aquatic vegetation** Absent, absent but water flooding the grassland, scarce, abundant

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

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

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Carex frigida	*Juncus articulatus*	*Primula farinosa*	*Trifolium repens*
Carex hallerana	*Juncus filiformis*	*Primula integrifolia*	*Vaccinium myrtillus*
Carex macrostylon	*Juncus inflexus*	*Primula viscosa*	*Vaccinium uliginosum*
Carex nigra	*Juniperus communis ssp. nana*	*Prunella vulgaris*	*Veratrum album*
Carex pulicaris	*Kobresia myosuroides*	*Pulsatilla sp.*	*Veronica alpina*
Carex riparia	*Kobresia simpliciuscula*	*Ranunculus alpestris*	*Veronica beccabunga*
Carex rostrata	*Leontodon autumnalis*	*Ranunculus aquatilis*	*Veronica fruticans*
Carex sempervirens	*Leontopodium alpinum*	*Ranunculus pyrenaeus*	*Veronica nummularia*
Carum carvi	*Leucanthemopsis alpina*	*Ranunculus repens*	*Veronica officinalis*
Chara foetida	*Linaria alpina*	*Ranunculus reptans*	*Viola biflora*
Chenopodium bonus-henricus	*Lotus alpinus*	*Rhamnus pumilus*	*Viola palustris*
Cochlearia officinalis	*Luzula alpinopilosa*		

N (number of species) = 168.