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A Multiscale Framework for Deconstructing the Ecosystem Physical Template of High-Altitudes Lakes

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Lake Bassia at 2275m a.s.l. in the Pyrenees National Park, France, is one of the millions of remote high altitude lakes worldwide whose catchments are likely to experience severe effects due to climate change. Photo credit: Antonio Palanca-Soler.

ABSTRACT

An ecosystem is generally sustained by a set of integrated physical elements forming a functional landscape unit - ecotope, which supplies nutrients, microclimate, and exchanges matter and energy with the wider environment. To better predict environmental change effects on ecosystems, particularly in critically sensitive regions such as high altitudes, it is imperative to recognise how their natural landscape heterogeneity works at different scales to shape habitats and sustain biotic communities prior to major changes.

We conducted a comprehensive survey of catchment physical, geological and ecological properties of 380 high altitude lakes and ponds in the axial Pyrenees at a variety of scales, in order to formulate and test an integrated model encompassing major flows and interactions that drive lake ecosystems.

Three composite drivers encompassed most of the variability in lake catchment characteristics. In order of total percentage of variance explained they were: (i) hydrology/hydrodynamics- responsible for type and discharge of inlets/outlets, and for water body size; (ii) bedrock geomorphology, summarizing geology, slope and fractal order- all dictating vegetation cover of catchment slope and lake shore, and the presence of aquatic vegetation; and, (iii) topography, i.e. catchment formation type- driving lakes connectivity, and the presence of summer snow deposits. While driver (i) appeared to be local, (ii) and (iii) showed gradient changes along altitude and latitude. These three drivers differentiated several lake ecotopes based on their landscape similarities. The three-driver model was successfully tested on a riparian vegetation composition dataset, further illustrating the validity and fundamental nature of the concept.

The findings inform on the relative contribution of scale-dependent catchment physical elements to lake ecotope and ecosystem formation in high altitude lakes, which should be considered in any assessment of potentially major deleterious effects due to environmental/climate change.

Keywords: high altitude lakes; ecotope; ecosystem; scale; landscape function; lake classification; (categorical) principal component analysis; fuzzy set ordination.

1. INTRODUCTION

One of the first conceptual ideas illustrating ecosystem-landscape interdependence was Vernadsky's theory of Earth's surface evolution, which recognized the synergetic relationships and transfer of nutrients between geosphere and biosphere (Vernadsky 1926). Recent research in the critical zone framework (i.e. Earth’s near-surface environment influenced by life; Richter and Billings 2015) advances this understanding by providing high spatial and temporal resolution details of landscape physiology at a variety of scales.

From a landscape perspective, a lake is a structural and physiological unit that draws energy and nutrients from its surrounding catchment. A lake ecosystem is therefore sustained by its physical template (ecotope, the lake’s life support system), which incorporates elements of catchment geomorphology, land cover and climate, all directly and indirectly affecting the flows of water and nutrients resulting from bedrock weathering. Predicting how changes in physical environment control ecosystems in high altitude catchments is generally challenging, due to their remoteness, the complexity of their landscape, and the many direct and indirect linkages between landscape features and processes operating at different scales. For example abiotic factors such as water resilience and cycling, primary productivity and nutrient availability are all key aquatic factors shaping community/ ecosystem development (Van der Molen and others 2003).

Of more than 300 million lakes on the Earth's surface, a great abundance occur at mid-to-high altitudes (Downing and others 2006). In the Pyrenees, a relatively low-density lacustric region, there are an estimated 1030 lakes of > 0.05ha above 1000m altitude (Castillo-Jurado 1992), meaning that high altitude lakes mediate a great portion of ecological and geochemical processes in mountain catchments. Due to their remoteness and high topography, most of these lakes host pristine or semi-pristine ecosystems, and are under increasing attention worldwide as clean water repositories, hotspots of biodiversity (Gopal and others 2000), sensors of long-range transported pollutants (Andrea and others 2007) and global climate change (Williamson and others 2009). Moreover, their location in headwater basins implies that they are the first to collect and redistribute bedrock-derived nutrients to the wider biosphere. These waterbodies and surrounding catchments are therefore ideal for studying how physical environments sustain their ecosystems, before climate change can induce major deleterious effects.

Environmental influence on species richness in mountain-top lakes has been discussed in the conceptual framework of Equilibrium Theory of Island Biogeography (Vuilleumier 1970; Barbour and Brown 1974; Brown and Dinsmore 1988). The theory predicts species composition at equilibrium, in a suitable habitat, being a function of habitat isolation, size and composition (MacArthur and Wilson 1963; Losos and Ricklefs 2009). For example general trends in fauna and flora functional composition can be predicted by local physical characteristics, including geology, geomorphology, waterbody size, slope and land cover (Della Bella and others 2005; Mazerolle and others 2005; Goebel and others 2006).

At any given time, a lake/pond can be assumed to support a type of vegetation and fauna whose composition is constrained by substrate and ecotope characteristics. This could result in a particular configuration of nutrient distribution, microclimate, and a local ecosystem succession/evolution in time. It is therefore critical to understand the relative contribution of the physical elements of an ecosystem to biota development, and how they connect to regional, continental and global gradients in substrate and climate. This could address a major need in ecology, to better model how physical heterogeneity within an ecosystem predicts current and future ecological dynamics, particularly in human-induced climate and habitat stress scenarios.

We will use the term "ecotope" to represent the lake/pond and its proximal catchment area as an integrated physiological unit that supports an ecosystem. Similar to spatial patches in landscape ecology (Forman 1995), we assume this unit to represent unique combinations of hierarchically organised abiotic drivers that interact and drive the flow of energy/nutrients at multiple spatial scales, ultimately feeding and shaping the development of a lake ecosystem. The ecotope concept allows considering all such features and their spatial heterogeneity, including how they may be connected to large-scale gradients in substrate and climate, and thus has the potential to incorporate and predict their function. This concept has been used variously in the scientific literature, particularly in the framework of geographic information systems (GIS) as surface ecotope patterns for environmental conservation and in human impact scenarios (Whittaker and others 1973; Van der Molen and others 2003; Yue and Li 2010; Gwata and Mzezewa 2013; Liu and Pan 2014; Sorosjinda-Nunthawarasilp and Bhumiratana 2014). However, the concept is still confusing, and we lack sufficient empirical examples that integrate the ecosystem and its underlying abiotic drivers (ecotope) in clear conceptual models/units that would better fit into the current (interdisciplinary) paradigm of Earth function as a life support system.

The main aim of this work was to identify the main landscape elements assumed to sustain a lake ecosystem in high altitude basins, and model how they organise at different scales to produce a coherent ecosystem functioning. We also postulated that a lake's physical template is not formed randomly. Rather, it is a geomorphic inheritance left by the past major transformations of the landscape, particularly following the last glaciation. The work is based on a survey of 380 waterbodies in the axial Pyrenees. The strong E - W orientation of this mountain range, together with large blocks of distinct geology provide sharp contrasts in climate and biogeography, that makes the concept easier to test against large geographical gradients.

A secondary aim was to identify and define a number of ecotope types, supporting distinct lake ecosystems, which integrate related physical drivers. The lake ecotope concept is ultimately validated by showing its effect on lake riparian ecosystem composition.

2. METHODS

2.1 Study area and geology

The Pyrenees extend over roughly 430 km from the Atlantic to the Mediterranean Sea and separate the Iberian Peninsula from the rest of continental Europe. The area under study extends over about 80 km in the axial part of Pyrénées National Park (Atlantic Pyrenees), France (Fig. 1). This area, under reinforced protection, is restricted to recreational hiking, angling, and seasonal livestock grazing. Due to their location, the majority of the waterbodies could be considered to reflect mostly natural processes.

Bedrock geology is marked by the outcrop of Cauterets-Panticosa igneous (granitic) batholith in the central part, flanked by metasedimentary (shale) and sedimentary (limestone) materials (Fig. 1). The abundance of granite, which is particularly resistant to erosion, gives the region a characteristic steep-sloping aspect. The contact zone between the granitic outcrop and the low-grade metamorphic material includes ore deposits, some of which have been exploited for metalliferous mining in the past (Paegelow 2008). Mineral springs are abundant in this area, particularly the hot springs at the contact of granite with the stratified rocks.

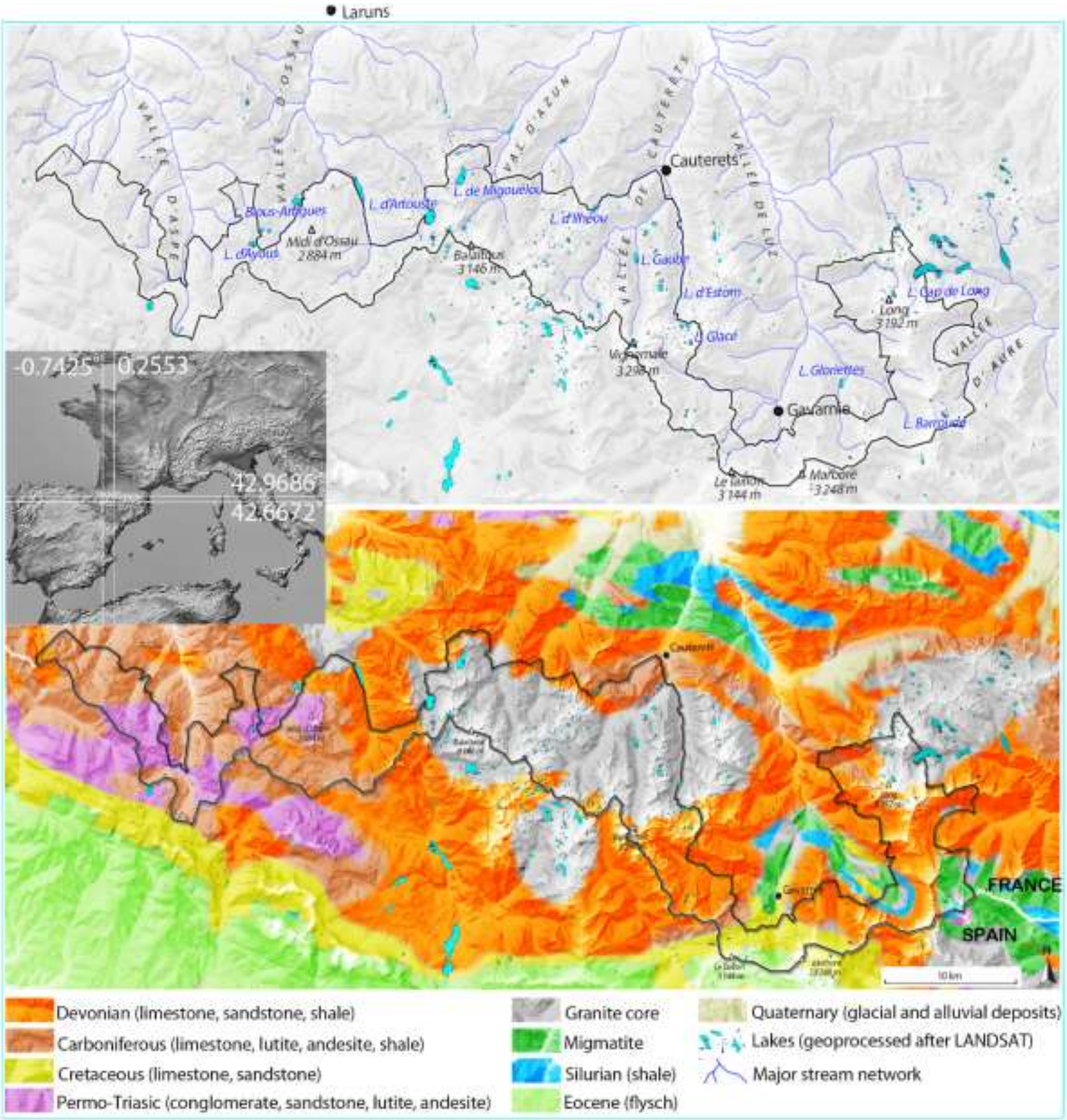


Figure 1. Study area (axial Pyrénées National Park, outlined in dark green) together with major hydrological and geological formations on digital elevation model. Lake representations are after LANDSAT imagery; inset radar map is after JPL (2000); Pyrenees digital elevation model is after Geoportail (http://www.geoportail.fr/); geological representation is after SGN (1996).

2.2 Climatology

The main air masses are from the W - NW, bringing precipitation (i.e. rain, snow and moist air) mainly from the Atlantic and the Bay of Biscay (oceanic-suboceanic climate; Mate 2002). This leads to a marked contrast between different sections/valleys of the region with glacial formations being formed mainly on the N-oriented slopes of the western and the central parts of the range. Some of the glaciers are still active and are the source of major streams. Precipitation averages 100-160cm year^{-1} in the area while mean annual temperature is 13-14°C

Table 1: Description of geographical and ecological variables used in the analysis of 380 altitude lakes from the central Pyrenees

Parameter	Values
Latitude^{+}	Geographic coordinates
Longitude^{+}	Geographic coordinates
Altitude^{+}	Meters a.s.l.
Catchment type^{+++}	Plain, U shape valley, slope, mountain pass, V shape valley, head of glacial valley
Main geology^{+++}	Conglomerate-sandstone-claystone, limestone (+sandstone-marlstone-schist enclaves), schist (+andesite-sandstone-claystone and granite-limestone), granite (+schist)
Size^{++}	Pool (<315±333m^2), pond (1566±1985m^2), small lake (9157±10267m^2), medium size lake (41127±31820m^2), large lake (91441±37307m^2)
Fractal order^{++}	1-4 scale
Visible connectivity with other^{+++}	Absent, surrounded by another lake, with another one, in chain
Nature of water input^{+++}	Meteoric, spring, stream/waterfall
Tributary discharge^{++}	Absent, low discharge, medium discharge, high discharge
Nature of water output^{+++}	Absent, temporary, surface-small, surface-medium, surface-large, subterranean, dam output
Aquatic vegetation^{++}	Absent, Absent but water flooding the grassland, scarce, abundant
% grass covered shore^{++}	<10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-100
% grass covered slopes^{++}	<10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-100
Slope of lake perimeter^{++}	Plain, plain in alternation with medium slopes, medium slopes, steep in alternation with medium/plain, steep in >50% of perimeter
Shore snow coverage^{++}	Absent, <10%, 11-50%, >51%, into the water
Snow deposits in the catchment^{++}	Absent, very scarce, scarce, abundant, very abundant
*Shape of lake/pond^{+++}	Circular, elliptic, elongate, irregular, triangular, rectangular, in 8, boomerang
*Modifications in lake's shape^{++}	Absent, one input/output stream, various input/output streams
*Color^{+++}	Blue-grey, opaline blue, opaline white, turquoise green
*Water level marks^{++}	Absent, < 50cm, > 50cm
*Damming^{++}	Absent, small dam, big dam
*Shore vegetation coverage^{++}	Most of it, partially, scarce
*Shore coverage^{+++}	Scarce vegetal cover (>50% cliffs, >50% slope drift, cliffs+slope drift, bedrock,

	bedrock+slope drift, bedrock+dispersed rocks, big granite blocks), medium vegetal cover (bedrock+grass patches, grassland+rocks, grassland+slope drift+rock blocks, cliffs+slope drift+ grassland, slope drift+grassland+scrubs, forest+cliffs+slope drift+grassland area) and dominant vegetal cover (>50% grassland, >50% scrubland, grassland+scrubs+forest, grassland+dispersed rocks, grassland+scrubs+rocks, grassland+bedrock+rocks, sheep field)
*Coverage of near catchment^{+++}	Scarce vegetal cover (>50% cliffs, >50% slope drift, cliffs and slope drift), medium vegetal cover (cliffs with slope drift and vegetated patches, grassland with scrubs and rocks, grassland with cliffs and slope drift, cliffs with slope drift, grass patches, scrubs and forest) and dominant vegetal cover (>50% grass land, grassland and scrubs, forest with grass land and scrubs)

Variable measure: $^{+}$ scale (numerical), $^{++}$ ordinal (categorical) and $^{+++}$ nominal. Variables proceeded by superscript (*) did not improve PCA total variance, and were removed from analyses.

(0°C isotherm oscillating between 1200m in January- 3300m in July/August). Tree line varies between 2000-2500m a.s.l. The snow cover above 2000m settles down in November and starts to thaw in April. The glacier forming line is relatively high, ranging between 2500 to 3200m a.s.l. (Kessler and Chambraud 1990).

2.3 Hydrology

There are more than 400 lakes and ponds within the boundaries of the Pyrénées National Park. The great majority of the lakes are of post-glacial origin and they are formed at valley head, in the axial part of the mountain range. They are relatively small water-bodies, as most (>90%) of the lakes on the Earth’s surface (Downing and others 2006). A large number of streams (>210), locally called *gaves*, drain the lake catchments, and give the hydrological network a dendritic structure (Fig. 1). These ‘gaves’ subdivide the area in six major units: Aspe, Ossau, Azun, Cauterets, Luz and Aure (Fig. 1 and Appendix S1). A total of 13 lakes in our dataset were transformed into reservoirs (Appendix S1), and are used for providing fresh-water and hydropower (Mate 2002).

2.4. Sampling and statistical methodology

In total 380 lakes/ponds were surveyed during the month of July in 2000, 2001 and 2002. The sampling was aimed to represent the majority of mountain lakes in the area and it was undertaken in an east-westward direction to minimize potential bias due to a generally late snow thaw in the western side. Appendix S1 lists the names and locations of the surveyed water-bodies. At each site a number of major landscape factors assumed to influence ecotope processes were visually approximated and scored according to dominant units. A detailed description of the variables surveyed is presented in Table 1. Lakes’ size categories were estimated from their surface area. This was approximated as the surface area of an ellipse whose major and minor diameters were measured in the field. A digital laser telemeter was used for this purpose.

Furthermore, a portable GPS device was used to record the latitude, longitude and altitude at each location.

A riparian vegetation survey was completed around each lake by visual inspection, at the same time when other environmental parameters were measured (Zaharescu 2011). The species were identified in the field using Grey-Wilson and Blamey (1979), Fitter and others (1984) and García-Rollán (1985) keys, and where not possible they were transported in a vasculum and identified in the laboratory.

Major statistical steps are summarised in Fig. 2. Principal Component Analysis (PCA) was used as an exploratory first step to disentangle the complex relationships between the large number of landscape variables, and reduce them to a small number of variable sets, termed principal components (PCs), that can reflect major environmental drivers of a lake ecotope. Each PC is composed of related variables and it is uncorrelated to the other PCs. Since PCA is not p-value driven, the technique is robust for non-normal data distributions. It also seemed to fair better than categorical PCA on our dataset, by producing more meaningful PCs. A Varimax rotation with Kaiser normalization was applied to the extracted axes (components) in order to maximize the captured variance, while keeping the uncorrelated nature of the PCs. Variables that did not improve the model i.e. they decreased the factor total explained variance, were excluded (Table 1). For this analysis name variables (e.g. geology) were re-coded on ordinal scales representing major transitional phases (e.g. from sedimentary, to metamorphic, to igneous bedrock) before using them in PCA. Results of PCA were interpreted using this encoding. The Kaiser-Meyer-Olkin measure of sampling adequacy in PCA was 0.72, and the Bartlett's test of sphericity, approx. χ^2= 1398.2 (P<0.001), indicating that the analysis was reliable and adequate.

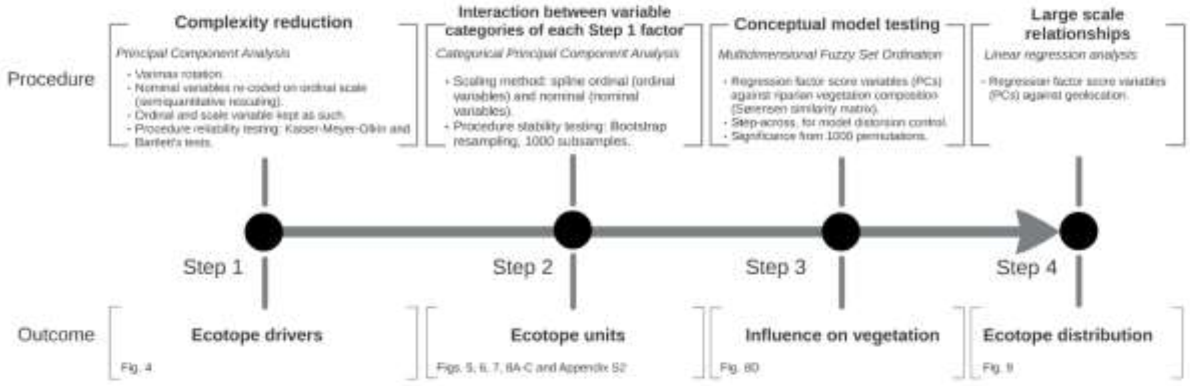


Figure 2. Flow chart illustrating the sequence of statistical steps supporting this work, and their outcomes.

To help identify and exemplify ecotope units, the spatial interaction between categories of variables in each extracted factor in step 1, and their vector projection on lakes in the ordination space were evaluated using categorical principal component analysis (CATPCA; Fig. 2). This is a nonparametric approach capable of finding relationships between a wide range of nonlinear variables (including numerical, categorical and nominal variables) and between variable categories and cases (lakes). Because CATPCA stability may be influenced by the sample characteristics, including sample number and scaling method, the degree of sensitivity to changes in the data was tested by bootstrap resampling. This procedure used 1000 random sets of subsamples from the original dataset and repeated CATPCA on each set. It determined the constancy of assignment (correlation) of the variables to the component vectors by producing 90% confidence regions of component loadings. If the results provided by CATPCA are stable, we expect narrow confidence ellipses.

The reliability of ecotope factors was tested for their influence on riparian vegetation composition using the logic of Multidimensional Fuzzy Set Ordination - MFSO (Roberts 2008). This approach related the explanatory PCA-derived composite factors (summarized into regression factor score variables) to riparian vegetation structure (response variables) by using a distance matrix of species incidence (calculated using Sørensen similarity index). Generally, this matrix gives a measure of similarity between sites based solely on biota composition. Multidimensional fuzzy set ordination is a more natural alternative to classical ordination methods based linear algebra logic, which assume objects to either belong (1) or not (0) to a given set or function. Instead, MFSO assumes that a case (element) can have partial membership values between 0 and 1, thus creating a range (fuzzy) of influences into the model. Since ecosystem-environment interactions are not always restricted to well-defined algebraic functions (they can be discontinuous), MFSO is particularly suitable to solving partial

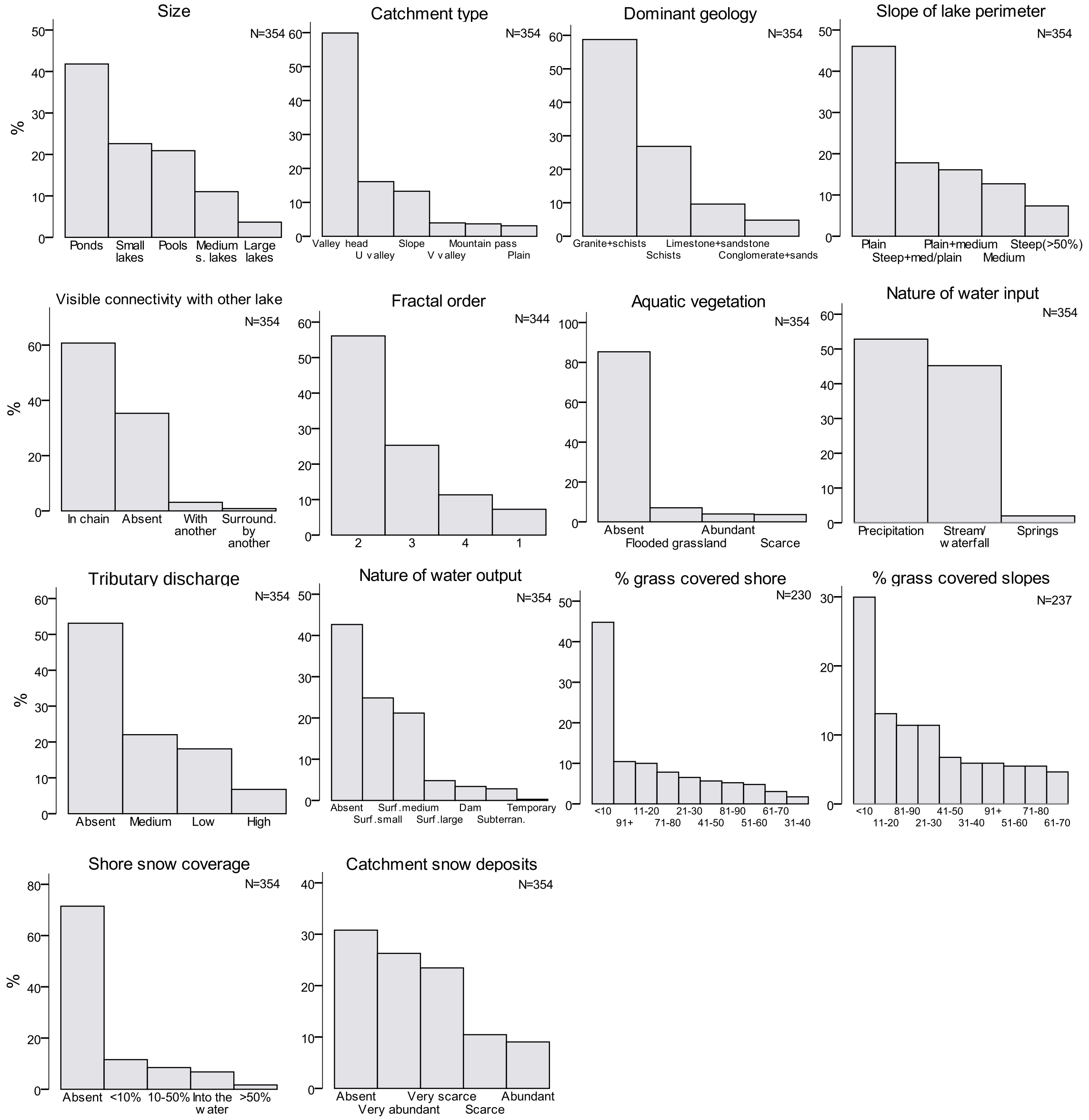


Figure 3. Frequency distribution (%) of sampled landscape variables in 380 altitude lake/pond locations from the Central Pyrenees.

relationship problems, which are more characteristic to real-world phenomena. Likewise, in MFSO factors have to be chosen beforehand and their contribution to the model is independent, therefore hypothesis testing of ecological/environmental processes (e.g. cause-effect relationships) is possible, for instance in gradient analyses (Roberts 1986). To improve the distortion effect given by sites with no species in common, a step-across function was used together with MFSO (Boyce 2009). This approximation procedure finds dissimilarities between sites (cases) above a threshold of missing data (no species in common) and replaces them with the shortest paths by stepping across intermediate sites. Visually, it produces an expansion of the data cloud at the distortion site (matrix dissimilarity before the procedure =1), improving therefore the fit. The significance of MFSO model was drawn after 1000 permutations.

As a final step, linear regression was used to examine the potential relationship between catchment-scale ecotope properties and large scale geographical gradients (Fig. 2). The variables were summarised as regression factor scores of the extracted principal components (PCs) before being used as response variables to geographical predictors in the regression analysis. Statistical treatment of the data was conducted in PASW for Windows (former SPSS, SPSS Inc. 2009). Bootstrap procedure was computed with macro file Categories CATPCA Bootstrap for PASW developed by Linting et al. (2007), available online at http://www.spss .com/devcentral/. Multidimensional Fuzzy Set Ordination was computed in R statistical language, using FSO (Roberts 2007) and LabDSV (Roberts 2012) packages. Step-across function was performed in VEGAN package (Oksanen and others 2012) for R (R Development Core Team 2005).

3. RESULTS AND DISCUSSION

The surveyed water-bodies spanned from 1161 to 2747 m altitude. Figure 3 presents the frequency distribution of the assessed landscape variables. As can be observed from this figure, most of the water-bodies can be included into pond and small lake categories. These water-bodies are mostly located on relatively flat surfaces at the head of glacial valleys; they have granite-dominated bedrock, and a great number of them are connected in chain with other lakes/ponds within their area. Likewise, the central Pyrenees lakes showed weakly developed riparian zones (as indicated by a high frequency of lakes with low fractal order, Fig. 3), which correspons to a relatively young age on a lake evolutionary time scale. With few exceptions aquatic vegetation was largely absent at the time of sampling. Most of the lakes/ponds are fed by precipitation or small surface streams of very low discharge, which is typical of high altitudes. Accordingly, a great number of them have visibly absent or small outputs. Water flowing from springs, on the other hand, seemed to have very little importance in their hydrodynamics. Shore/slopes vegetation coverage for most of the water-bodies was < 10%, and a mixed snow coverage was recorded in their near-catchment during the survey.

3.1 Deconstructing the main drivers of a lake physical template

The interaction between climate and geomorphology can potentially shape the formation of ecotopes. To examine the influence of catchment-scale landscape components on the structure of lake ecotopes, a PCA of all assessed variables (Table 1) was carried out. This reduced the variables to a limited number of key components (composite factors) which can explain the main environmental drivers of lake characteristics. The inherently complex nature of the high altitude environment meant the total PCA variance in our dataset was split over >3 uncorrelated composite factors (Fig. 4 inset). The first three components (PC1, PC2 and PC3) together accounted for more than 58% of the total variance in the lake and catchment characteristics (Fig. 4). The first component (PC1) accounted for 21.3% of the variation (Fig. 4). It, i.e. PC1 (interpreted hereafter as hydrodynamics), indicates a strong association between waterbody size and lake hydrology (type and volume of water input/output). This is important as aquatic macrophytes and invertebrates richness are likely to vary with the size of a lake (Oertli and others 2002; Biggs and others 2005), a core idea in the "ecological theory of island biogeography" (MacArthur and Wilson 1963; Losos and Ricklefs 2009).

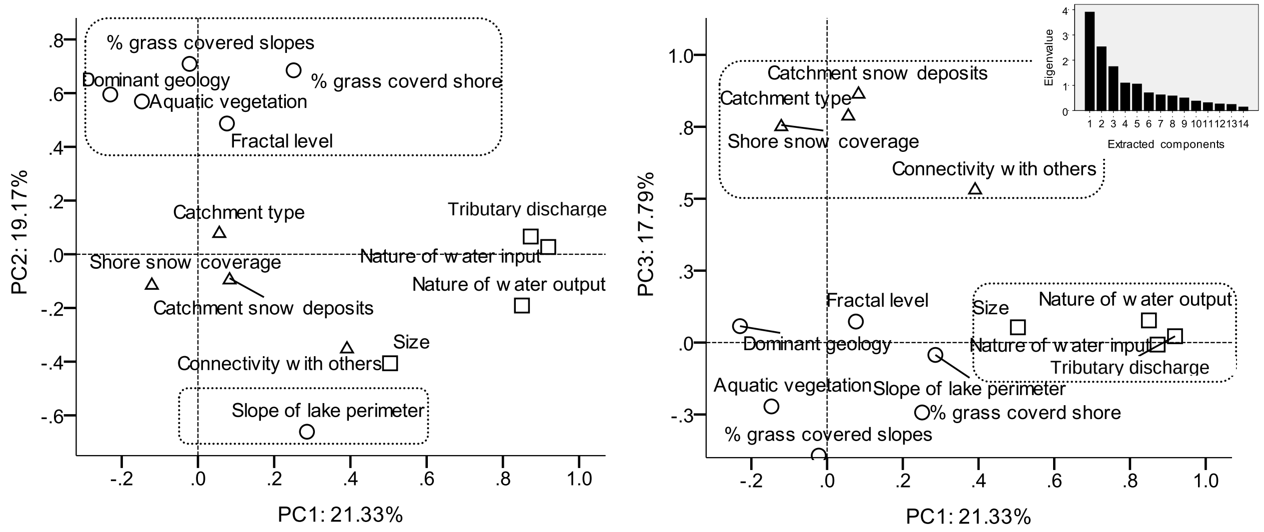


Figure 4. Relationships between landscape variables in their projections on principal components 1-2 and 1-3, of principal component analysis (PCA). Variables clustering with the PCs are enclosed in dash line. Figure symbols represent the variables with high loading on: (□) PC1, (○) PC2 and (Δ) PC3. Inset plot shows the number of extracted components. N=380 water-bodies.

The second component (PC2, explaining additional 19.2% of the total variance) had high loadings for the variables that would be determined by the main bedrock geology/ geomorphology, i.e. geology, shore sloping, % of slope/shore covered by grass, fractal order and the presence of aquatic vegetation (Fig. 4). Geerling et al. (2006) have shown that ecotope composition (riparian surface, vegetation coverage and composition) can change during rejuvenating hydro-geomorphological processes of rivers, i.e., meander progression, meander interruption and channel shift. Likewise, substrate geology and slope are recognised physical factors that can influence the characteristics of a lake through their effects on hydraulics, weathering and nutrient cycling processes which together shape its biological structure (EC 2000; Kamenik and others 2001). It seems therefore that geo-morphology is a second major driver of an altitude lake ecotope development and can influence not only the topographically-related high energy processes, such as slope erosion and runoff, but also the riparian development, its vegetation coverage and the development of aquatic vegetation. Lake shores' vegetation coverage is a crucial ecotope factor in high altitude waterbodies which has been found to control nutrient cycling in a lake and therefore its biotic composition (Kopacek and others 2000).

Finally, the third PC axis accounted for further 17.8% of the variability in the lakes' characteristics. The variables grouped under PC3 were: presence of snow deposits at shore level and in the near catchment, catchment type and visible connectivity with other lakes, together being interpreted as topographical formation (Fig. 4). The PC3 findings suggest that topography also has significant control over ecotope processes by its influence on important factors such as habitat connectivity and habitat snow coverage, the latter being important in shaping land-water interactions during the large periods a mountain lake catchment is snow-covered (Edwards and others 2007).

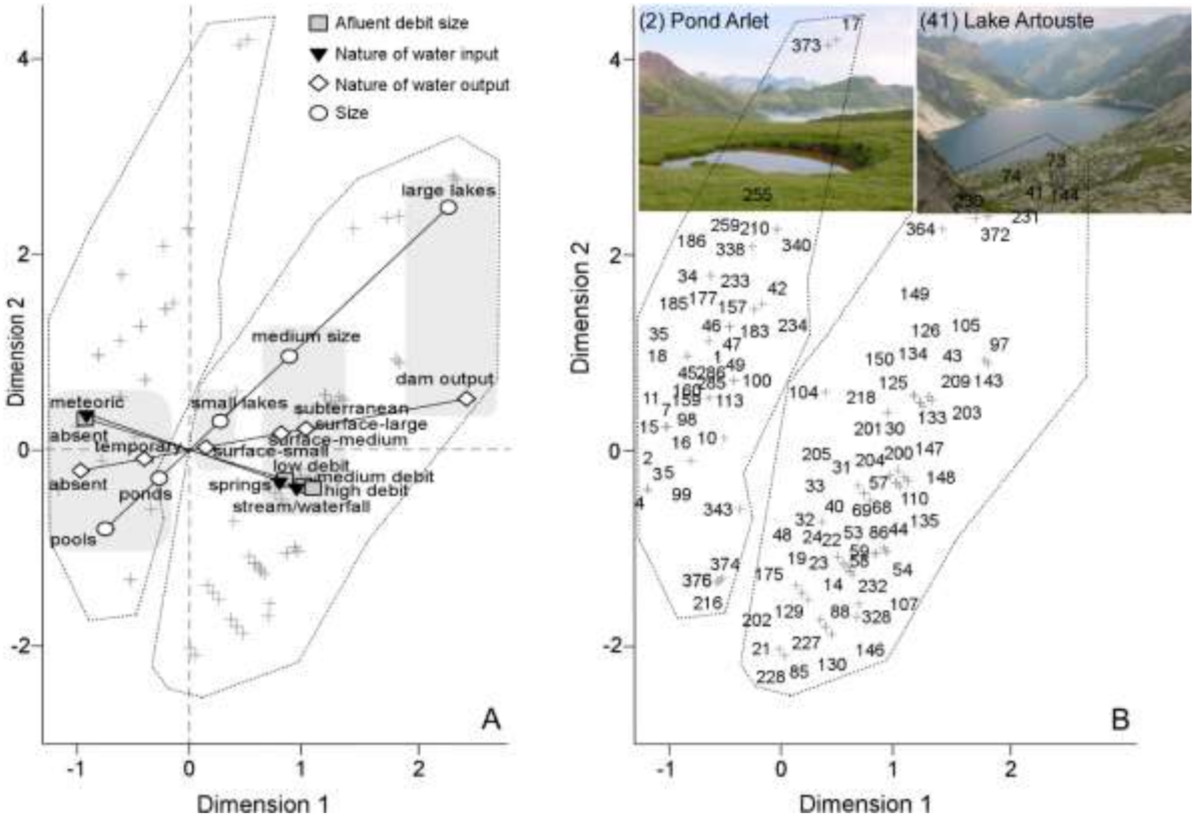


Figure 5. (A) Interaction between variable categories in hydrodynamics factor (i.e. PC1 in Fig. 4) and their association with lakes, as shown by CATPCA. To aid in interpretation, the associated categories were enclosed in grey, while their association to resulted lake groups is enclosed in dashed polygons. Lake grouping is further detailed and illustrated in (B). Lake coding corresponds to Appendix S1.

Evidence has shown that the patterns of snow distribution in rugged alpine terrain are the most visible consequence of topography and its interaction with climatic variables like precipitation, solar radiation and wind (Körner 1992, 2003; Gottfried and others 1999). The seasonal cycles of snow accumulation and ablation as well as snow coverage can have a crucial influence on high altitude ecosystems' composition at a variety of scales, with species capable of coping with the environmental conditions/stresses becoming more abundant (Walker and others 1993; Keller and others 2005). Habitat connectivity, on the other hand, is an important factor in maintaining the integrity of metapopulations of plant (Biggs and others 2005) and animals (Richards-Zawacki 2009), with species assemblages likely to be richer in areas that facilitate propagule dispersal and colonisation. This is a second important aspect of Island Biogeography Theory (MacArthur and Wilson 1963) which predicts an increase in species number with a decrease in remoteness of an island ecotope.

The remaining 42% variability in the dataset is accounted for by other numerous factors, individually each accounting for a small amount of the variability (Fig. 4 inset).

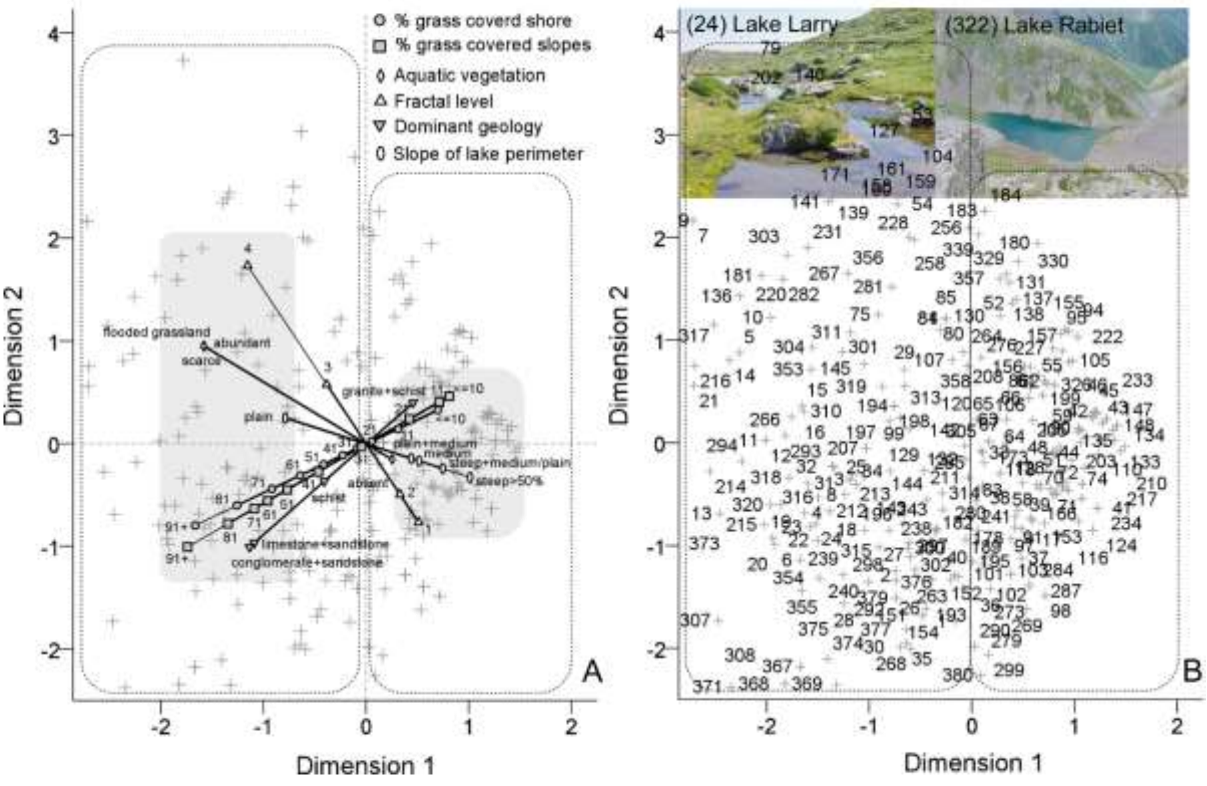


Figure 6. (A) CATPCA interactions between variable categories of the second extracted component (geo-morphology in Fig. 4), and their association to lakes. Category groups are highlighted on grey and lake groups are surrounded by dashed polygons. (B) Grouped lakes, with coding detailed in Appendix S1.

3.2 Integrated physical drivers determine lake basin types

Further analysis of the three PCs, individually, can help uncover the influence they have on ecotope development. To classify the waterbodies into ecotope types we studied the interaction between the variable categories within individual PCs previously discussed, i.e. hydrodynamics (PC1, Fig. 5), geo/morphology (PC2, Fig. 6A and B) and topographical formation (PC3, Fig. 7A and B). The analysis yielded a considerable degree of stability, as shown by relatively narrow 90% confidence ellipses of the bootstrap component loadings (Appendix S2), and can therefore be used confidently.

As displayed in Figure 4A, the interaction between hydrodynamics variables (PC1) shows that small waterbodies such as pools and ponds are fed principally by meteoric water, e.g. snow and rain, and such water-bodies either lack or have temporary tributaries/outputs. They represent a lake ecotope category. A second category is represented by small and medium-size lakes. They are characterized by various forms of water input, including springs and streams/waterfalls of low to high discharge; this category is also associated to a diverse output nature, e.g. surface and subterranean (Fig. 5A). On the other side, large lakes plot further apart and are represented by dam lakes (Fig. 5A). The analysis also shows the cross-point where major lake properties change, with variable vectors plotting onto two well-defined waterbody clusters: the first cluster, pools and ponds of low water turnover, plotting on the negative side of the first dimension. And the second cluster, represented by small to large lakes of a relatively

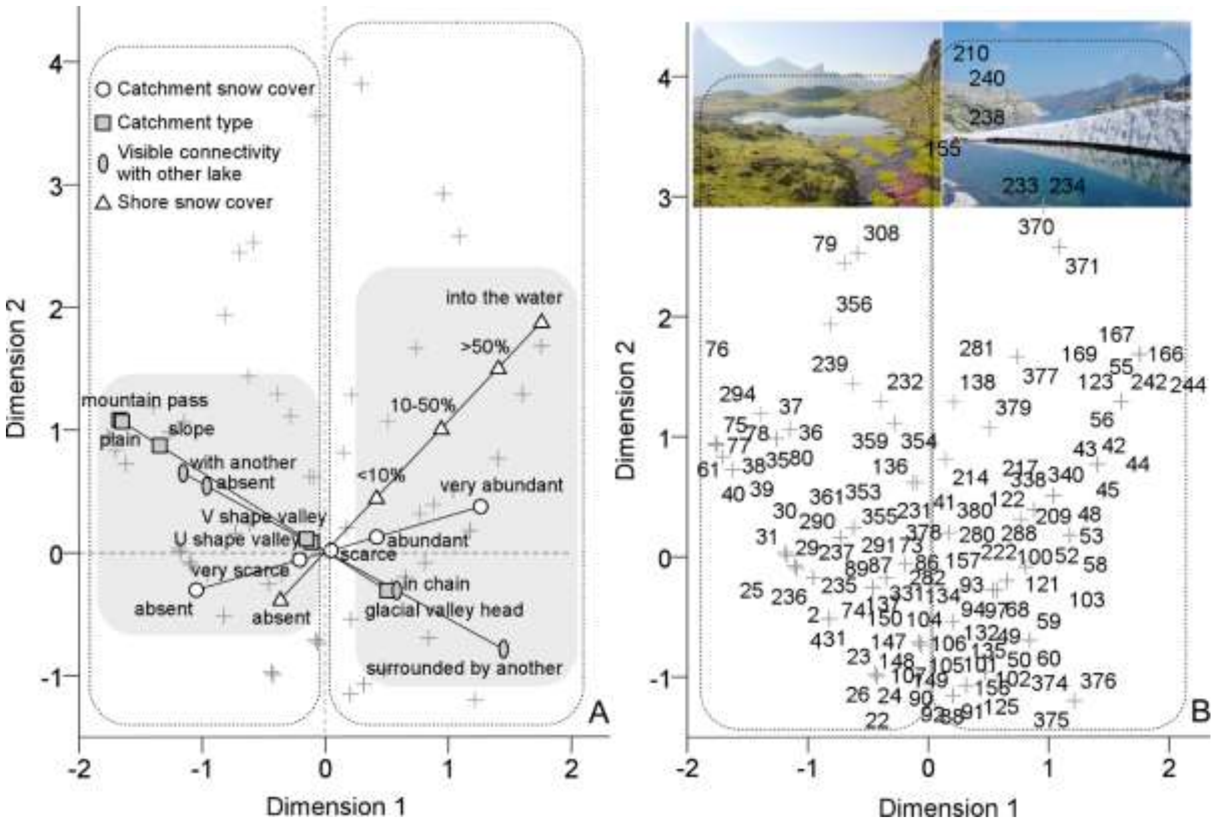


Figure 7. (A) Interactions (CATPCA) between variable categories of the third principal component (topographical formation, Fig. 4) and their associations to lakes. In grey are associated categories, while dashed polygons highlight resulted lake groups. (B) Lake grouping, with lakes listed in Appendix S1.

large tributary/output, plotting on the positive side in the ordination space (Fig. 5B). This is an important finding since waterbodies which receive significant runoff can have different biotic composition compared with the mainly rain-fed ones, as they can receive more nutrients from the catchment (EC 2000; Kamenik and others 2001). Riera et al. (2000), Saros et al. (2005) and Robinson and Kawecka (2005) provide illustrative examples of how nutrient availability/drainage type can shape phytoplankton, crayfish and fish development in oligotrophic alpine lakes.

The plot of interaction between PC2 variables, representing geo/morphological processes, shows that bedrock categories such as limestone/sandstone/conglomerates associate with lakes surrounded by a relatively flat topography, >50% grass covered shore/slopes, a highly developed riparian zone and the presence of aquatic vegetation (Fig. 6A). On the other hand, granite-schist bedrock plots together with medium to steep lake shore slopes, <20% grass covered shore/slopes, a poorly developed riparian zone and lack of aquatic vegetation (Fig. 6A). These two lake categories, i.e. formed on limestone and granite, point out to a spatial segregation of lake ecotopes according to the two main geomorphological units in the Pyrenees. That is, the Paleozoic-Mezozoic sedimentary bedrock and the metasedimentary-igneous outcrops (Fig. 1) which influence biota settling at these sites. Plotting of the surveyed sites by cluster analysis, however, did not form well-defined groups, suggesting rather transient ecotope

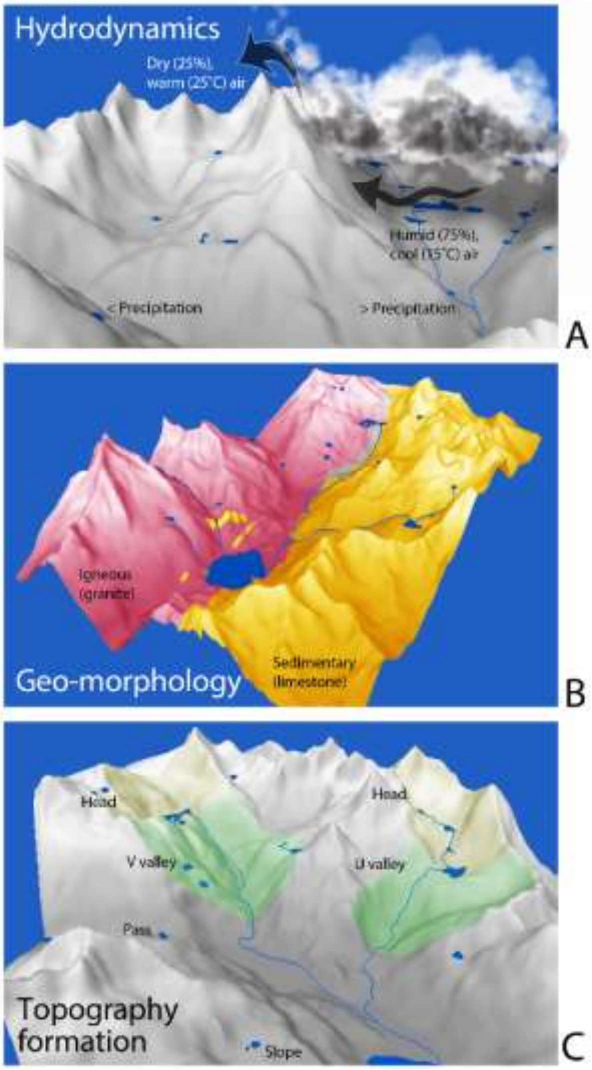
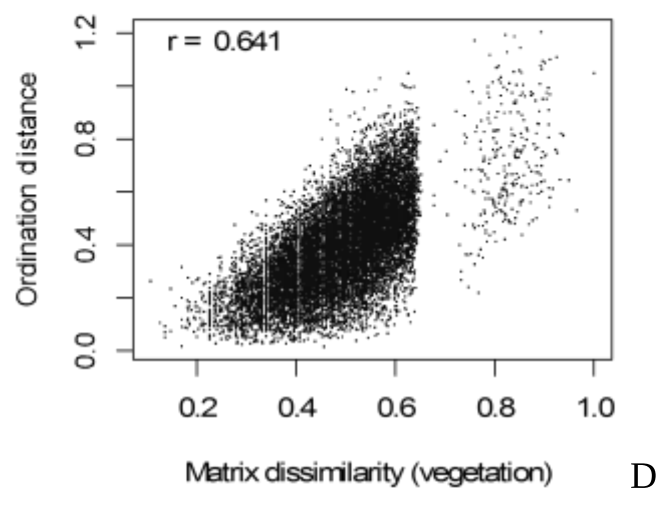


Figure 8. Conceptualization of lake ecotope development at high altitudes and its principal drivers, i.e. hydrodynamics (A), geo-morphology (B) and topography (C). A digital elevation model of upper Tena Valley (catchment of Lake Respomuso), central Pyrenees exemplifies this



concept. The hydrodynamic gradient is represented here as a typical mountain Foehn cloud leaving the precipitation on one slope, then it is dispersed as it comes in contact with warm, dry air masses on the opposite slopes. Colours in geo-morphology and topography models represent distinct bedrock geology and glacial valley sections, respectively. A test of the conceptualized model performed by Multidimensional Fuzzy Set Ordination (D) shows the joint effect of the 3 main ecotope drivers on riparian vegetation species composition recorded at each lake. Number of permutations in this model = 1000.

features between the two main categories (Fig. 6B), possibly owing to the influence of mixed geological compositions.

An analysis of the third composite factor, i.e. topographical formation (PC3; Fig. 7A and B) reveals two major ecotope forms. On one hand, there are lakes at the head of glacial valleys. These are generally either interconnected in chain with other lakes, or are in a basin in the vicinity of a major lake, and have a high proportion of summer snow deposits on their shores/near-catchment (Fig. 7A). Secondly, there are lakes on flat terrain, mountain passes and V/U shaped valleys, which are generally isolated or connected to a neighbouring lake, and have very scarce or no summer snow cover in their surroundings (Fig. 7A). The geomorphic changes resulted from the last glaciation and their location in the landscape (through the extent of their influence) are likely the main drivers of this factor. This is supported by Riera and others (2000) who found differences in biota assemblages inhabiting different geomorphic settings in the Northern Highland Lake District, Wisconsin, USA.

Our analysis helped individualise and classify key physical drivers in terms of their influence on lake ecotope development. A conceptualised form of the analysis's outcome was used to further simplify ecotope processes/forms that may be used to assess the relationship between key ecotope drivers and ecosystem functioning, e.g. vegetation structure (see below).

3.3 Conceptualisation and testing of a lake ecotope and its drivers

A conceptualization of the three major ecotope factors, i.e. hydrodynamics, geomorphology and topography is presented in Fig. 8. This figure illustrates different types of climate, geology and topography of the mountain terrain that are responsible for the development of different ecotopes. For example, differences in precipitation received by two slopes of a mountain as a result of Foehn cloud formation - typical of high altitudes (Fig. 8A), influence the amount of water that a lake receives as a result of a sharp drop in air moisture and an elevation of the cloud as it meets dry, warm air masses from the opposite slopes. This is a typical phenomenon found along the N-S (wet, Atlantic-dry, Mediterranean) climate gradient in the Pyrenees. Similarly, contrasting differences in substrate geo/morphology, e.g. limestone and siliceous, are fundamental for lake ecotope development (Fig. 8B). A conceptualisation of the third composite factor, i.e., topography formation (Fig. 8C) shows in a simplified way that different topographical forms or glacial formations underlie different lake types. Such influence of hydrodynamics, geomorphology and topography on ecotope formation, in *sensu amplo*, have been exemplified for other water and terrestrial environments by Van der Molen and others 2003; Hong and others 2004.

This conceptual model was tested on a dataset representing a complete survey of riparian vegetation composition in the study area (Zaharescu 2011). The effect magnitude of the three identified principal ecotope drivers on riparian plant species composition is cumulatively presented in Fig. 8D. The figure shows that with increasing vegetation similarity between sites (or decreasing dissimilarity), the environmental variability, as predicted by vegetation composition, decreases and sites become more similar in terms of their ecotope composition. There are also a fair number of sites with no species in common (the discontinuity in the data cloud), which is expected given the contrasting combination of climate, topography and geology of the study area. This means that the three drivers (PCs) identified and conceptualised in this work had a strong cummulative influence in determining the riparian vegetation species composition (cumulative Spearman $r=0.64$, $p<0.05$). The strongest influence on vegetation came from the composite factor topography formation ($r=0.43$); this was independently followed by hydrodynamics ($r=0.12$) and geo-morphology ($r=0.09$). These results imply that the conceptualised model is based on a valid identification of the key ecotope forming factors and their influence in determining ecosystem development. The approach thus

Table 2: Spearman rank correlation coefficients (Coef.) between geo-position variables (as predictors) and summarised landscape variables (i.e. regression factor scores of principal components) resulting from PCA, together with regression slope and intercept values for the significant correlations. PCA factors represent: hydrodynamics, PC1, geo-morphology, PC2 and, topographical formation, PC3. Variables summarised by these composite factors are presented in Figure 3.

	Hydro- dynamics			Geo-morphology			Topographical formation		
	Coef.	Slope	Intercept	Coef.	Slope	Intercept	Coef.	Slope	Intercept
Altitude	-0.11	n.a.	n.a.	-0.31*	-0.0013	2.76	0.64*	0.0025	-5.52
Latitude	0.26*	0.06	-291	-0.40*	-0.073	344	-0.15*	-0.026	125
Longitude	0.07	n.a.	n.a.	0.05	n.a.	n.a.	0.17*	0.0097	-7.1

*, correlation is significant at < 0.05 level (2-tailed).

N (number of cases) = 234.

n.a. = data not available.

has the potential to be used as a tool to predict the response of flora, fauna or other ecosystem components to changes in their life support environment.

3.3 Connection with large geographical gradients

The three ecotope forming factors while fundamental to ecotope development, they may follow large scale gradients of altitude, latitude and longitude. An analysis of hydrology/hydrodynamics, PC1, geo-morphology, PC2, and topographical formation, PC3 (Fig. 4) in concert with altitudinal, latitudinal and longitudinal (macroclimate) gradients (Table 2) identified elevation as a primary gradient explaining lake ecotopes development, with local effects of the variables associated with topography, i.e. PC3 (Fig. 9A). Altitude is a geographical constraint with known influences on catchment development through its main effects on glacial processes such as cirque and valley formation. This can influence water and nutrient cycling and photosynthesis, and can lead to biota compositional differences along aquatic gradients, for example cryon/crenon - rhithron - potamon. Such examples of altitudinal effect on biota composition have been reported for various taxa, including zoobenthos, macrophyte and amphibian species (Hinden and others 2005).

Latitude was the second most important (broad-scale) gradient for lake ecotope variation, with local effects of variables related to bedrock geo-morphology (regression factor score of the second PC) (Fig. 9B). Latitude apparently also had some effect on the variables associated to lake hydrodynamics, as shown by its relatively weak, but significant relationship with PC1 regression score (Spearman ρ=0.26; Table 2). The association of latitude to geological constraints is potentially reflective of some major N-S geomorphological gradient involved in lake ecotope development. However, the variation in lake hydrodynamics across latitude could be explained by the rates at which the catchments receive moisture-charged air masses from the Atlantic Ocean along a N-S direction, which lose moisture as they advance toward the (drier) axial part of the mountain range.

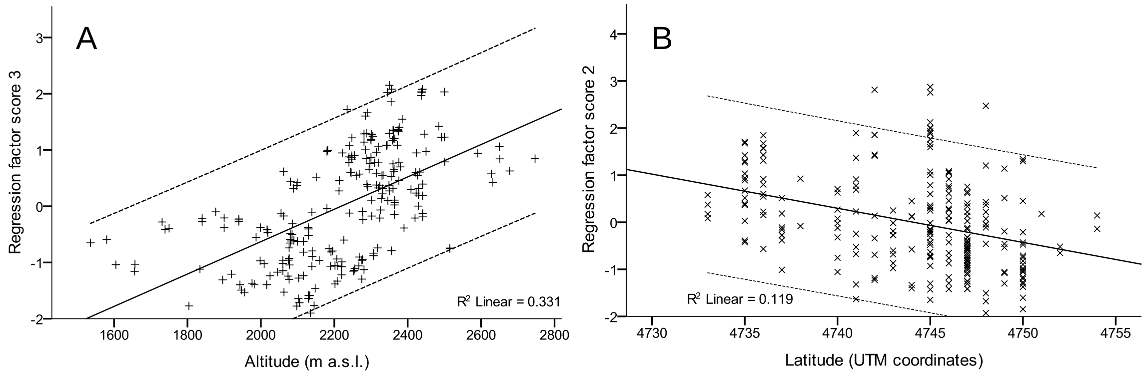


Figure 9. (A) Linear relationship between topographical formation (i.e. regression factor scores of PC 3: catchment type, connectivity with other lakes, catchment and shore snow coverage – see Fig. 4) and altitudinal gradient. (B) Relationship between geo-morphology (i.e. regression factor scores of PC 2: dominant bedrock geology, % grass

covered slopes, % grass covered shore, aquatic vegetation and fractal development) and latitude. Confidence intervals (95%) are dashed.

4. CONCLUSIONS

In headwater basins of the central Pyrenees, the development of a lake ecosystem's physical support (ecotope) was scale dependent, and was driven primarily by basin's hydrodynamics, seconded by geo/morphology and topographical formation. These major drivers resulted in a number of lake types, which shared similarities in their catchment physical properties, and provided distinctive abiotic settings for riparian plant communities.

Except hydrodynamics, which appeared to be mostly a local factor, the identified drivers were connected to large-scale geographical gradients, of which altitude and latitude were the most influential. The relationship between a lake ecosystem and its physical template is therefore expected to change along large horizontal and vertical gradients, in connection to major substrate units, and continental-to-global climate gradients. Changes in climate factors may therefore affect not only lake ecosystem composition, as previously shown, but also many of its physical and chemical processes, such as water energy and weathering, that feed and shape fauna and flora development and their structure. Our work provides compelling empirical support of these cross-scale linkages in remote natural catchments. We interpret this as confirmation of local-to-large scale landscape evolution in the postglacial period starting 11,000 years ago, which created the major elements of the physical landscape that drove biota settling and diversification.

We conceptualised and successfully tested how hydrodynamics, geo/morphology and topography interact to support ecotope and riparian vegetation composition development. Our conceptualised template could be a common feature in mountain ranges, therefore providing an integrated and fundamental conceptual framework for hypothesis testing and experimentation in ecological modelling studies where scale and landscape properties and fluxes are important.

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AUTHOR CONTRIBUTION

Sampling campaign design, A Palanca-Soler; data collection, A Palanca-Soler and DG Zaharescu; study design and data analysis, DG Zaharescu; manuscript preparation, DG Zaharescu, PS Hooda and CI Burghelea.

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A Multiscale Framework for Deconstructing the Ecosystem Physical Template of High-Altitudes Lakes

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SUPPLEMENTARY INFORMATION

Appendix S1: Lakes surveyed in this study

Lakes and ponds from the axial area of Pyrénées National Park (France) analysed in this study. Altitude is in m a.s.l.; latitude and longitude are in decimal coordinates. Main valleys, locally called *gaves*, give structure to the topography.

Lake ID	Sampling year	Name	Main valley	Altitude	Latitude	Longitude
1	2002	Lake Arlet	Aspe	1987	42.4955	-0.3735
2	2002	Pond Arlet 1	Aspe	1999	42.4955	-0.3735
3	2002	Pond Arlet 2	Aspe	1999	42.4955	-0.3735
4	2002	Pond Lurbe 1	Aspe	1900	42.4955	-0.3651
5	2002	Pond Lurbe 2	Aspe	1900	42.4955	-0.3651
6	2002	Pond Lurbe 4	Aspe	1900	42.4955	-0.3651
7	2002	Pond Lurbe 5	Aspe	1880	42.4955	-0.3651
8	2002	Pond Lurbe 3	Aspe	1990	42.4955	-0.3651
9	2002	Pond Caillaous	Aspe	1877	42.4954	-0.3607
10	2002	Pond Caillaous 1	Aspe	1877	42.4954	-0.3607
11	2002	Lake Gourgue	Aspe	1840	42.4954	-0.3607
12	2002	Pond Gourgue 1	Aspe	1840	42.4954	-0.3607
13	2002	Pond Gourgue 2	Aspe	1840	42.4954	-0.3607
14	2002	Lake Banasse 1	Aspe	1940	42.4954	-0.3607
15	2002	Lake Banasse 2	Aspe	1940	42.4954	-0.3607
16	2002	Lake Banasse 3	Aspe	1940	42.4954	-0.3607
17	2001	Lake Berseau	Ossau	2082	42.4959	-0.3015
18	2001	Lake Berseau 1	Ossau	2080	42.4959	-0.3015
19	2001	Lake Berseau 2	Ossau	2100	42.4959	-0.3015
20	2001	Pond Berseau 1	Ossau	2085	42.4959	-0.3015
21	2001	Pond Berseau 2	Ossau	2086	42.4959	-0.3015
22	2001	Lake Larry 1	Ossau	2077	42.5018	-0.3014
23	2001	Lake Larry 2	Ossau	2077	42.5018	-0.3014
24	2001	Lake Larry 3	Ossau	2077	42.5018	-0.3014
25	2001	Lake Larry 4	Ossau	2077	42.5018	-0.3014
26	2001	Lake Ayous 1	Ossau	2060	42.5018	-0.2929
27	2001	Lake Ayous 2	Ossau	2060	42.5018	-0.2929
28	2001	Lake Ayous 3	Ossau	2060	42.5018	-0.2929
29	2001	Lake Gentau 1	Ossau	1982	42.5018	-0.2929

30	2001	Lake Gentau	Ossau	1947	42.5018	-0.2929
31	2001	Lake Miey	Ossau	1920	42.5018	-0.2929
32	2001	Lake Roumassot	Ossau	1845	42.5018	-0.2929
33	2001	Lake Castérau	Ossau	1943	42.4945	-0.2931
34	2001	Lake Paradis	Ossau	1976	42.4945	-0.2931
35	2001	Lake Peyreget	Ossau	2074	42.4942	-0.2719
36	2001	Lake Peyreget 3	Ossau	2159	42.4941	-0.2635
37	2001	Pond Peyreget	Ossau	2180	42.4941	-0.2635
38	2001	Lake Col de Peyreget 1	Ossau	2220	42.4941	-0.2635
39	2001	Lake Col de Peyreget 2	Ossau	2208	42.4941	-0.2635
40	2001	Lake Pombie	Ossau	2025	42.4941	-0.2635
41	2001	*Lake Artouste	Ossau	1989	42.5110	-0.2039
42	2001	Lake Arrémoulit Supérieur	Ossau	2281	42.5005	-0.1957
43	2001	*Lake Arrémoulit	Ossau	2285	42.5037	-0.1956
44	2001	Lake Arrémoulit (bellow dam)	Ossau	2255	42.5037	-0.1956
45	2001	Lake Palas	Ossau	2359	42.5037	-0.1956
46	2001	Lake Palas 1	Ossau	2365	42.5037	-0.1956
47	2001	Lake Palas 2	Ossau	2362	42.5037	-0.1956
48	2001	Lake Arrémoulit Superior 1	Ossau	2300	42.5037	-0.1956
49	2001	Lake Arrémoulit Superior 2	Ossau	2295	42.5037	-0.1956
50	2001	Lake Arrémoulit Superior 3	Ossau	2297	42.5037	-0.1956
51	2001	Lake Arrémoulit Superior 4	Ossau	2300	42.5037	-0.1956
52	2001	Lake Arrémoulit Superior 5	Ossau	2300	42.5037	-0.1956
53	2001	Lake Arrémoulit Superior 6	Ossau	2305	42.5037	-0.1956
54	2001	Lake Arrémoulit Superior 6A	Ossau	2305	42.5037	-0.1956
55	2001	Lake Arrémoulit Superior 7	Ossau	2290	42.5037	-0.1956
56	2001	Lake Arrémoulit Superior 8	Ossau	2285	42.5037	-0.1956
57	2001	Lake Arrémoulit Inférieur	Ossau	2241	42.5037	-0.1956
58	2001	Lake Arrémoulit Inferior 1	Ossau	2248	42.5037	-0.1956
59	2001	Lake Arrémoulit Inferior 2	Ossau	2246	42.5037	-0.1956
60	2001	Lake Arrémoulit Inferior 3	Ossau	2244	42.5037	-0.1956
61	2001	Lake Arrémoulit Inferior 4	Ossau	2256	42.5037	-0.1956
62	2001	Lake Arrémoulit Inferior 5A	Ossau	2254	42.5037	-0.1956
63	2001	Lake Arrémoulit Inferior 5B	Ossau	2254	42.5037	-0.1956
64	2001	Lake Arrémoulit Inferior 5C	Ossau	2254	42.5037	-0.1956
65	2001	Lake Arrémoulit Inferior 5D	Ossau	2254	42.5037	-0.1956
66	2001	Lake Arrémoulit Inferior 6	Ossau	2252	42.5037	-0.1956
67	2001	Lake Arrémoulit Inferior 7	Ossau	2248	42.5037	-0.1956
68	2001	Lake Arrémoulit Inferior 8	Ossau	2100	42.5037	-0.1956
69	2002	Lake Carnau 1	Ossau	2208	42.5213	-0.1908
70	2002	Lake Carnau 2	Ossau	2202	42.5213	-0.1908
71	2002	Lake Carnau 3A	Ossau	2202	42.5213	-0.1908
72	2002	Lake Carnau 3B	Ossau	2202	42.5213	-0.1908
73	2000 (74/2002)	*Lake Migouélou	Azun	2278	42.5212	-0.1824
75	2000	Pond Migouélou_1	Azun	2420	42.5212	-0.1824
76	2000	Pond Migouélou_2	Azun	2420	42.5212	-0.1824
77	2000	Pond Migouélou_3	Azun	2420	42.5212	-0.1824
78	2000	Pond Migouélou_4	Azun	2420	42.5212	-0.1824
79	2000	Pond Migouélou_5	Azun	2420	42.5212	-0.1824
80	2000	Pond Migouélou_6	Azun	2420	42.5212	-0.1824
81	2000	Pond Migouélou_7	Azun	2420	42.5212	-0.1824
82	2000	Pond Migouélou_8	Azun	2420	42.5212	-0.1824
83	2000	Pond Migouélou_9	Azun	2420	42.5212	-0.1824
84	2000	Pond Migouélou_10	Azun	2420	42.5212	-0.1824

85	2000	Pond Migouélou_11	Azun	2420	42.5212	-0.1824
86	2000 (87/2002)	Lake Amont Migouélou	Azun	2301	42.5003	-0.1829
88	2002	Pond Amont Migouélou_1	Azun	2301	42.5003	-0.1829
89	2002	Pond Amont Migouélou_2	Azun	2301	42.5003	-0.1829
90	2002	Lake Les Lacarrats_1	Azun	2441	42.5212	-0.1824
91	2002	Lake Les Lacarrats_2	Azun	2441	42.5212	-0.1824
92	2002	Lake Les Lacarrats_3	Azun	2429	42.5212	-0.1824
93	2002	Lake Les Lacarrats_4	Azun	2430	42.5212	-0.1824
94	2002	Lake Les Lacarrats_5	Azun	2430	42.5212	-0.1824
95	2002	Lake Les Lacarrats_6	Azun	2441	42.5212	-0.1824
96	2002	Pond Les Lacarrats_6	Azun	2441	42.5212	-0.1824
97	2000	*Lake Pouey Laun	Azun	2346	42.5316	-0.1737
98	2000	Lake Pic de Hautafulhe	Azun	2361	42.5316	-0.1737
99	2000	Pond Puey Laun	Azun	2350	42.5316	-0.1737
100	2000	Lake Amount Puey Laun	Azun	2355	42.5316	-0.1737
101	2000	Pond above Puey Laun 1	Azun	2354	42.5316	-0.1737
102	2000	Pond above Puey Laun 2	Azun	2353	42.5316	-0.1737
103	2000	Pond above Puey Laun 3	Azun	2352	42.5316	-0.1737
104	2000	Pond down Migouélou	Azun	2226	42.5243	-0.1738
105	2000	*Lake Lassiédouat	Azun	2202	42.5211	-0.1740
106	2000	Pond Lassiédouat-1	Azun	2356	42.5211	-0.1740
107	2000	Pond Lassiédouat-2	Azun	2356	42.5211	-0.1740
108	2000	Lake Lassiédouat 1	Azun	2220	42.5211	-0.1740
109	2000	Lake Lassiédouat 2	Azun	2268	42.5211	-0.1740
110	2000	Lake Lassiédouat 3	Azun	2267	42.5211	-0.1740
111	2000	Pond Lasiedouat 3a	Azun	2267	42.5211	-0.1740
112	2000	Pond Lasiedouat 3b	Azun	2267	42.5211	-0.1740
113	2000	Lake Tramasaygues Supérieur 1	Azun	2277	42.5211	-0.1740
114	2000	Lake Tramasaygues Supérieur 2	Azun	2277	42.5211	-0.1740
115	2000	Lake Tramasaygues Supérieur 3	Azun	2277	42.5211	-0.1740
116	2000	Lake Tramasaygues Supérieur 4	Azun	2277	42.5211	-0.1740
117	2000	Lake Tramasaygues Supérieur 5	Azun	2277	42.5211	-0.1740
118	2000	Pond Touest	Azun	2016	42.5210	-0.1656
119	2000	Lake Touest	Azun	1955	42.5210	-0.1656
120	2001	Lake Micoulaou 1	Azun	2302	42.5034	-0.1744
121	2000	Lake Micoulaou 2	Azun	2333	42.5001	-0.1745
122	2000 (123/2001)	Lake Micoulaou 3	Azun	2362	42.5001	-0.1745
124	2001	Lake Micoulaou 4	Azun	2375	42.5001	-0.1745
125	2001 (126/2000)	Lake Batcrabère Supérieur	Azun	2180	42.5034	-0.1744
127	2001	Lake Batcrabère Supérieur 1	Azun	2182	42.5034	-0.1744
128	2001	Lake Batcrabére Milieu	Azun	2130	42.5034	-0.1744
129	2001	Pond Batcrabére Milieu 1	Azun	2130	42.5106	-0.1743
130	2000	Pond Batcrabére Milieu 2	Azun	2140	42.5034	-0.1744
131	2000	Lake above Batcrabére Milieu	Azun	2140	42.5034	-0.1744
132	2001	Lake bellow Batcrabére Milieu	Azun	2129	42.5034	-0.1744
133	2001 (134/2000)	Lake Batcrabère Inférieur	Azun	2116	42.5106	-0.1743
135	2001	Lake Batcrabère Inférieur 1	Azun	2116	42.5106	-0.1743
136	2001	Pond next to Larribet Refuge	Azun	2055	42.5106	-0.1743
137	2001 (138/2000)	Pond Pabat	Azun	2062	42.5106	-0.1743
139	2001	Lake La Claou Supérieur	Azun	1750	42.5210	-0.1656
140	2001 (141/2000)	Lake La Claou	Azun	1739	42.5210	-0.1656
142	2001	Lake Doumblas	Azun	1580	42.5209	-0.1612
143	2000	*Lake Suyen	Azun	1536	42.5137	-0.1613
144	2000	*Lake Tech	Azun	1207	42.5417	-0.1522

145	2001	Pond Pluviometre	Azun	1731	42.5135	-0.1529
146	2000	Pond Labassa	Azun	1750	42.5135	-0.1529
147	2000 (148/2001)	Lake Remoulis Inférieur	Azun	2017	42.5031	-0.1532
149	2000 (150/2001)	Lake Remoulis Supérieur	Azun	2019	42.5031	-0.1532
151	2000 (152/2001)	Pond Casteric	Azun	2080	42.4958	-0.1533
153	2000 (154/2001)	Pond Toue	Azun	2090	42.4958	-0.1533
155	2000	Pond Chemin du Portet de Heche	Azun	2380	42.4926	-0.1535
156	2000	Lake Houns De Heche Inférieur	Azun	2213	42.4957	-0.1449
157	2000	Lake Houns De Heche Supérieur	Azun	2214	42.4957	-0.1449
158	2000	Pond Liantran 2	Azun	1824	42.4957	-0.1449
159	2000	Pond Liantran 1	Azun	1824	42.4957	-0.1449
160	2000	Pond Liantran 3	Azun	1824	42.4957	-0.1449
161	2000	Pond Liantran 4	Azun	1824	42.4957	-0.1449
162	2000	Pond Plaa de Prat 1	Azun	1657	42.5133	-0.1401
163	2000	Pond Plaa de Prat 2	Azun	1657	42.5133	-0.1401
164	2000	Lake Prat	Azun	1656	42.5133	-0.1401
165	2000	Lake Langle	Azun	1605	42.5133	-0.1401
166	2001	Lake Col de Cambalés	Cauterets	2582	42.4925	-0.1451
167	2001	Lake Crete Du Cambalés	Cauterets	2440	42.4925	-0.1451
168	2001	Lake Peyregnets de Cambalés Grand	Cauterets	2492	42.4925	-0.1451
169	2001	Lake Peyregnets de Cambalés Petit	Cauterets	2453	42.4925	-0.1451
170	2001	Lake Cambalés 2	Cauterets	2424	42.4924	-0.1407
171	2001	Pond Cambalés 2	Cauterets	2424	42.4924	-0.1407
172	2001	Pond Cambalés Grand	Cauterets	2380	42.4924	-0.1407
173	2001	Pond Cambalés Grand 1	Cauterets	2386	42.4924	-0.1407
174	2001	Pond Cambalés Grand 2	Cauterets	2390	42.4924	-0.1407
175	2001	Pond Cambalés Grand 3	Cauterets	2441	42.4924	-0.1407
176	2001	Lake Cambalés Grand	Cauterets	2342	42.4924	-0.1407
177	2000	Lake Fache Supérieur	Cauterets	2427	42.4819	-0.1410
178	2000	Lake Fache Inférieur	Cauterets	2332	42.4819	-0.1410
179	2000	Lake Sentier Fache	Cauterets	2291	42.4850	-0.1324
180	2001	Pond Opale	Cauterets	2222	42.4923	-0.1323
181	2001	Pond Opale 1	Cauterets	2248	42.4923	-0.1323
182	2001	Pond Opale 2	Cauterets	2260	42.4923	-0.1323
183	2000 (184/2001)	Lake Opale Petit Inférieur	Cauterets	2287	42.4923	-0.1323
185	2000 (186/2001)	Lake Opale Supérieur	Cauterets	2320	42.4923	-0.1323
187	2001	Pond Petit Laquet	Cauterets	2360	42.4923	-0.1323
188	2001	Lake Petit Laquet	Cauterets	2350	42.4923	-0.1323
189	2001	Lake Costalade Supérieur	Cauterets	2320	42.4923	-0.1323
190	2001	Pond Cambalés	Cauterets	2315	42.4923	-0.1323
191	2001	Lake Costalade Inférieur	Cauterets	2310	42.4923	-0.1323
192	2000	*Lake Staing	Azun	1161	42.5413	-0.1226
193	2000	Lake Long	Azun	2326	42.5059	-0.1235
194	2000	Pond Long 1	Azun	2350	42.5059	-0.1235
195	2000	Pond Long 2	Azun	2360	42.5059	-0.1235
196	2000	Pond Long 3	Azun	2365	42.5059	-0.1235
197	2000	Pond Pic Arrouy	Azun	2370	42.5059	-0.1235
198	2000	Pond Pic Arrouy 1	Azun	2370	42.5059	-0.1235
199	2000	Lake Pic Arrouy	Azun	2376	42.5059	-0.1235
200	2000	Lake Nère de Arrouy	Azun	2241	42.5131	-0.1233
201	2002	Lake Nère de Bassia	Cauterets	2309	42.5026	-0.1236
202	2002	Pond Nére	Cauterets	2400	42.5026	-0.1236
203	2002	Lake Pourtet	Cauterets	2420	42.5026	-0.1236
204	2002	Lake Pourtet 1	Cauterets	2307	42.5025	-0.1152

205	2002	Lake Pourtet 2	Cauterets	2307	42.5025	-0.1152
206	2000 (207/2002)	Lake Embarrat 2	Cauterets	2139	42.5025	-0.1152
208	2002	Lake Embarrat 1	Cauterets	2078	42.5024	-0.1108
209	2001	Lake Badéte	Cauterets	2344	42.5024	-0.1108
210	2001	Lake Col d'Arratille	Cauterets	2501	42.4709	-0.1033
211	2001	Pond Arratille 1	Cauterets	2363	42.4741	-0.1031
212	2001	Pond Arratille 2	Cauterets	2330	42.4741	-0.1031
213	2001	Pond Arratille 3	Cauterets	2315	42.4741	-0.1031
214	2001	Pond Arratille 4	Cauterets	2289	42.4741	-0.1031
215	2001	Pond Arratille 5	Cauterets	2315	42.4741	-0.1031
216	2001	Pond Arratille 6	Cauterets	2268	42.4741	-0.1031
217	2001	Lake Arratille	Cauterets	2247	42.4741	-0.1031
218	2000	Lake Ilhéou	Cauterets	1998	42.5128	-0.1021
219	2000	Lake Noir d'Ilheou 1	Cauterets	1896	42.5200	-0.1020
220	2000	Pond Arras	Cauterets	2070	42.5233	-0.1018
221	2000	Pond Col d’Ilhéou	Cauterets	2242	42.5234	-0.1102
222	2002	Lake Chabarrou Supérieur	Cauterets	2422	42.4813	-0.0946
223	2002	Pond Chabarrou Supérieur	Cauterets	2400	42.4813	-0.0946
224	2002	Lake Chabarrou	Cauterets	2302	42.4812	-0.0902
225	2002	Lake Chabarrou Inférieur	Cauterets	2390	42.4812	-0.0902
226	2002	Pond Chabarrou 1	Cauterets	2364	42.4812	-0.0902
227	2002	Pond Chabarrou 2	Cauterets	2364	42.4812	-0.0902
228	2002	Pond Chabarrou 3	Cauterets	2364	42.4812	-0.0902
229	2002	Pond Chabarrou 4	Cauterets	2364	42.4812	-0.0902
230	2002	Lake Gaube	Cauterets	1725	42.4949	-0.0858
231	2001	Oulettes. glacier runoff	Cauterets	2151	42.4707	-0.0905
232	2001	Pond Arraillé Inférieur	Cauterets	2441	42.4706	-0.0821
233	2001	Lake Arraillé Milieu	Cauterets	2450	42.4706	-0.0821
234	2001	Lake Arraillé Supérieur	Cauterets	2485	42.4706	-0.0821
235	2002	Lake Estibe Aute 1	Cauterets	2515	42.4737	-0.0736
236	2002	Lake Estibe Aute 2	Cauterets	2515	42.4737	-0.0736
237	2002	Lake Estibe Aute 3	Cauterets	2515	42.4737	-0.0736
238	2001	Pond Baysselance	Luz	2555	42.4632	-0.0739
239	2001	Pond Baysselance 2	Luz	2378	42.4632	-0.0739
240	2001	Pond Baysselance 1	Luz	2236	42.4632	-0.0739
241	2001	Pond Montferrat	Luz	2207	42.4455	-0.0743
242	2001	Lake Montferrat	Luz	2374	42.4455	-0.0743
243	2001	Pond Montferrat 1	Luz	2372	42.4455	-0.0743
244	2001	Pond Montferrat 2	Luz	2440	42.4455	-0.0743
245	2001	Lake Montferrat 1	Luz	2438	42.4455	-0.0743
246	2001	Lake Montferrat 3	Luz	2438	42.4455	-0.0743
247	2001	Lake Montferrat 4	Luz	2437	42.4455	-0.0743
248	2001	Lake Montferrat 5	Luz	2437	42.4455	-0.0743
249	2001	Lake Montferrat 6	Luz	2440	42.4455	-0.0743
250	2001	Lake Montferrat 7	Luz	2440	42.4455	-0.0743
251	2001	Lake Montferrat 8	Luz	2440	42.4455	-0.0743
252	2002	Lake Estibet d'Estom	Cauterets	2470	42.4809	-0.0734
253	2002	Lake Estibet d'Estom 2	Cauterets	2464	42.4809	-0.0734
254	2002	Pond Estibet d'Estom	Cauterets	2464	42.4809	-0.0734
255	2002	Lake Estibe Aute Inférieur	Cauterets	2324	42.4842	-0.0733
256	2002	Pond Estibe Aute Supérieur	Cauterets	2324	42.4842	-0.0733
257	2002	Lake Estibe Aute Milieu	Cauterets	2324	42.4842	-0.0733
258	2002	Pond Estibe Aute Milieu	Cauterets	2324	42.4842	-0.0733
259	2002	Lake Estibe Aute Supérieur	Cauterets	2328	42.4842	-0.0733

260	2002	Pond Estibe Aute Supérieur	Cauterets	2328	42.4842	-0.0733
261	2002	Pond Estibe Aute Supérieur 1	Cauterets	2331	42.4842	-0.0733
262	2002	Pond Estibe Aute Supérieur 2	Cauterets	2331	42.4842	-0.0733
263	2001	Lake Estom	Cauterets	1804	42.4808	-0.0650
264	2001 (265/2002)	Pond Sentier d’Estom 1	Cauterets	2235	42.4703	-0.0653
266	2001 (267/2002)	Pond Sentier d’Estom 2	Cauterets	2240	42.4703	-0.0653
268	2001 (269/2002)	Pond Sentier d’Estom 3	Cauterets	2240	42.4703	-0.0653
270	2001 (271/2002)	Pond Sentier d’Estom 4	Cauterets	2248	42.4703	-0.0653
272	2001 (273/2002)	Lake Labas	Cauterets	2281	42.4702	-0.0609
274	2001 (275/2002)	Lake Oulettes d'Estom	Cauterets	2360	42.4702	-0.0609
276	2001 (277/2002)	Lake Couy	Cauterets	2445	42.4702	-0.0609
278	2001 (279/2002	Lake Turon Couy	Cauterets	2485	42.4630	-0.0611
280	2002	Pons Turon Couy 1	Cauterets	2487	42.4630	-0.0611
281	2001 (282/2002)	Pond Turon Couy 2	Cauterets	2492	42.4630	-0.0611
283	2001 (284/2002)	Lake Couy Supérieur	Cauterets	2500	42.4630	-0.0611
285	2001 (286/2002)	Pond Couy Supérieur	Cauterets	2500	42.4630	-0.0611
287	2001 (288/2002)	Lake Glace	Cauterets	2678	42.4630	-0.0611
289	2002	Lake Petit Lac Du Col	Cauterets	2650	42.4630	-0.0611
290	2002	Lake Gentianes	Luz	2642	42.4630	-0.0611
291	2001	*Lake Ossue	Luz	1834	42.4525	-0.0614
292	2002	Lake Cardal	Luz	2221	42.4348	-0.0618
293	2002	Pond Col de la Bernatoire	Luz	2045	42.4348	-0.0618
294	2002	Pond Col de la Bernatoire 1	Luz	2393	42.4316	-0.0620
295	2001	Lake Especiérès	Luz	2195	42.4240	-0.0409
296	2001	Lake Especiérès Infèrieur	Luz	2186	42.4240	-0.0409
297	2001	Pond Plaiteau de Saint André	Luz	2075	42.4239	-0.0326
298	2001	Ponds Labas Blanc	Luz	2009	42.4239	-0.0326
299	2002	*Lake Gloriettes	Luz	1668	42.4513	0.0149
300	2002	Laquet de Bassia	Luz	2275	42.4613	0.0448
301	2001	Pond Bassia 1	Luz	2277	42.4613	0.0448
302	2002	Pond Bassia 2	Luz	2275	42.4613	0.0448
303	2002	Pond Le Cot 1	Luz	2063	42.4402	0.0525
304	2002	Pond Le Cot 2	Luz	2130	42.4402	0.0525
305	2002	Pond Le Cot 3	Luz	2130	42.4402	0.0525
306	2002	Pond Le Cot 4	Luz	2130	42.4402	0.0525
307	2001	Pond Serre Longue	Luz	2190	42.4330	0.0523
308	2001	Pond Esbarris	Luz	2139	42.4329	0.0607
309	2001	Lake Aires Supérieur	Luz	2089	42.4329	0.0607
310	2001	Lake Aires Inférieur 1	Luz	2081	42.4329	0.0607
311	2001	Lake Aires Inférieur 2	Luz	2081	42.4329	0.0607
312	2001	Lake Comble 2	Luz	2099	42.4327	0.0651
313	2001	Lake Comble 1	Luz	2098	42.4327	0.0651
314	2001	Lake Troumouse 1	Luz	2098	42.4329	0.0607
315	2001	Pond Troumouse 1	Luz	2105	42.4329	0.0607
316	2001	Pond Troumouse 2	Luz	2102	42.4329	0.0607
317	2001	Pond Troumouse 3	Luz	2133	42.4329	0.0607
318	2001	Lake Troumouse 2	Luz	2135	42.4329	0.0607
319	2001	Lake Troumouse3	Luz	2145	42.4329	0.0607
320	2001	Lake Troumouse 4	Luz	2148	42.4329	0.0607
321	2002	Lake Pourtet	Luz	2411	42.4959	0.0459
322	2002	Lake Rabiet	Luz	2191	42.4927	0.0457
323	2002	Lake Couvela det Mey	Luz	2273	42.4855	0.0456
324	2002	Lake Bugarret	Luz	2281	42.4853	0.0540
325	2002	Lake Glere	Luz	2103	42.5103	0.0546

326	2002	Lake Coume Escuree	Luz	2150	42.5103	0.0546
327	2002	Lake Mourele	Luz	2297	42.5031	0.0544
328	2002	Pond Mourele	Luz	2340	42.5031	0.0544
329	2002	Lake Mail	Luz	2350	42.5031	0.0544
330	2002	Lake Oueil Nègre	Luz	2349	42.5031	0.0544
331	2002	Pond Mail 1	Luz	2652	42.5031	0.0544
332	2002	Pond Mail 2	Luz	2652	42.5031	0.0544
333	2002	Pond Mail 3	Luz	2652	42.5031	0.0544
334	2002	Pond Mail 4	Luz	2652	42.5031	0.0544
335	2002	Lake La Manche	Luz	2351	42.5031	0.0544
336	2002	Lake Estelat Inférieur	Luz	2399	42.4958	0.0543
337	2002	Lake Estelat Supérieur	Luz	2423	42.4958	0.0543
338	2002	Lake Glacé de Maniportet	Luz	2747	42.4926	0.0541
339	2002	Pond Maniportet	Luz	2720	42.4926	0.0541
340	2002	Lake Bleu De Maniportet	Luz	2651	42.4958	0.0543
341	2002	Pond Bleu De Maniportet 1	Luz	2651	42.4958	0.0543
342	2002	Pond Bleu De Maniportet 2	Luz	2651	42.4958	0.0543
343	2002	Lake Maniportet Infèrieur	Luz	2650	42.4958	0.0543
344	2002	Pond Bleu	Luz	2665	42.4957	0.0627
345	2002	Lake Vert Maniportet Long	Luz	2632	42.4957	0.0627
346	2002	Lake Vert Maniportet Rond	Luz	2626	42.4957	0.0627
347	2002	Pond Vert Maniportet Rond	Luz	2628	42.4957	0.0627
348	2002	Lake Vert Inférieur	Luz	2465	42.4957	0.0627
349	2002	Pond Vert Inférieur 1	Luz	2465	42.4957	0.0627
350	2002	Pond Vert Inférieur 2	Luz	2465	42.4957	0.0627
351	2002	Lake Breche 2	Luz	2433	42.4957	0.0627
352	2002	Lake Breche 1	Luz	2409	42.4957	0.0627
353	2001	Pond Aguilous	Luz	2318	42.4506	0.0612
354	2001	Pond Aguilous 1	Luz	2240	42.4506	0.0612
355	2001	Pond Agulious 2	Luz	2255	42.4506	0.0612
356	2002	Runoff Cap de Long 3	Aure	2602	42.4746	0.0704
357	2002	Pond Cap de Long 2	Aure	2591	42.4819	0.0706
358	2002	Pond Cap de Long 1	Aure	2179	42.4851	0.0707
359	2002	*Lake Cap de Long	Aure	2160	42.4851	0.0707
360	2002	Pond Neuvelle reserve	Aure	2471	42.5101	0.0714
361	2002	*Lake Aubert	Aure	2154	42.5101	0.0714
362	2002	Lake Aumar	Aure	2193	42.5101	0.0714
363	2001	Lake Badet	Aure	2084	42.4536	0.0742
364	2001	Pond Barroude 6	Aure	2345	42.4326	0.0735
365	2001	Pond Barroude 5	Aure	2350	42.4326	0.0735
366	2001	Pond Barroude 4	Aure	2356	42.4326	0.0735
367	2001	Pond Barroude 3	Aure	2374	42.4326	0.0735
368	2001	Pond Barroude 2	Aure	2375	42.4326	0.0735
369	2001	Pond Barroude 1	Aure	2376	42.4325	0.0819
370	2001	Pond Barroude	Aure	2385	42.4325	0.0819
371	2001	Pond Barraode refuge	Aure	2377	42.4325	0.0819
372	2001	Lake Barroude Grand	Aure	2355	42.4325	0.0819
373	2001	Lake Barroude Petit	Aure	2377	42.4325	0.0819
374	2001	Pond Barroude Petit 1	Aure	2377	42.4325	0.0819
375	2001	Pond Barroude Petit 2	Aure	2377	42.4325	0.0819
376	2001	Pond Barroude Petit 3	Aure	2377	42.4325	0.0819
377	2001	Pond Barroude Grand 1	Aure	2458	42.4325	0.0819
378	2001	Pond Barroude Grand 2	Aure	2458	42.4325	0.0819
379	2001	Pond Barroude Grand 3	Aure	2458	42.4325	0.0819

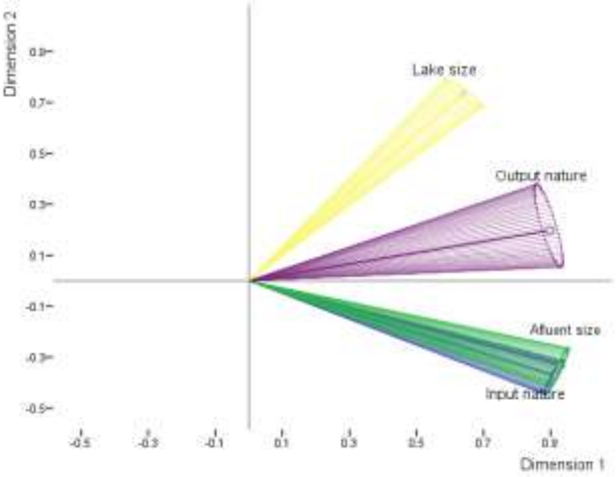
380	2001	Pond Barroude Grand 4	Aure	2440	42.4325	0.0819

Notes: some of the nameless lakes/ponds were given the name of their surrounding area. The largest lake in an area has no suffix. (*) represents lakes with various degrees of dam closing. Lakes sampled multiple years have their alternative IDs in brackets. Toponyms are in French.

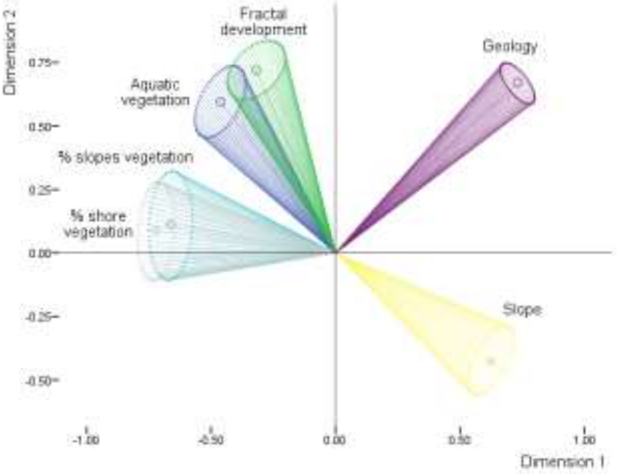
Appendix S2: CATPCA model testing

Plots showing the stability of CATPCA results (i.e. variables loading on first 2 extracted dimensions), for hydrodynamics, geo-morphology and topography factors (as summarized by PCA), as given by Bootstrap resampling. Component loadings are displayed together with their 90% confidence intervals. The procedure shows a good level of stability, which is illustrated by generally narrow confidence interval

HYDRODYNAMICS



GEO-MORPHOLOGY



TOPOGRAPHY FORMATION