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Small lakes in big landscape: Multi-scale drivers of littoral ecosystem in alpine lakes

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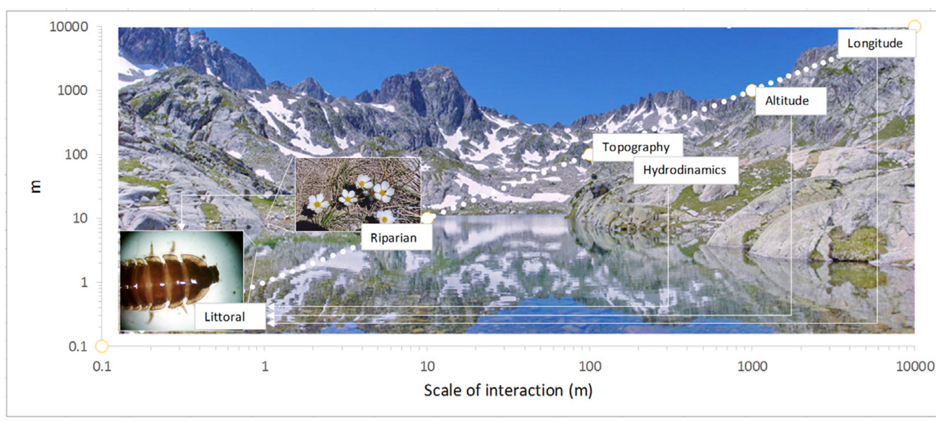
HIGHLIGHTS

- Understanding alpine ecosystem response to landscape heterogeneity is vital.
- Littoral zoobenthos, catchment and geolocation variates were studied in 113 lakes.
- Dataset illustrates biosphere, geosphere, hydrosphere and atmosphere interaction.
- Fuzzy Set models characterised ecosystem-landscape interactions at various scales.
- Ecosystem responded to catchment heterogeneity at scales beyond that of the lake.
- This underpins lakes role as sensors of local-to-large scale environmental changes.

GRAPHICAL ABSTRACT



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ABSTRACT

In low nutrient alpine lakes, the littoral zone is the most productive part of the ecosystem, and it is a biodiversity hotspot. It is not entirely clear how the scale and physical heterogeneity of surrounding catchment, its ecological composition, and larger landscape gradients work together to sustain littoral communities.

A total of 113 alpine lakes from the central Pyrenees were surveyed to evaluate the functional connectivity between littoral zoobenthos and landscape physical and ecological elements at geographical, catchment and local scales, and to ascertain how they affect the formation of littoral communities. At each lake, the zoobenthic composition was assessed together with geolocation, catchment hydrodynamics, geomorphology and topography, riparian vegetation composition, the presence of trout and frogs, water pH and conductivity.

Multidimensional fuzzy set models integrating benthic biota and environmental variables revealed that at geographical scale, longitude unexpectedly surpassed altitude and latitude in its effect on littoral ecosystem. This reflects a sharp transition between Atlantic and Mediterranean climates and suggests a potentially high horizontal vulnerability to climate change. Topography (controlling catchment type, snow coverage and lakes connectivity) was the most influential catchment-scale driver, followed by hydrodynamics (waterbody size, type and volume

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Vertebrate predation
Environmental change

of inflow/outflow). Locally, riparian plant composition significantly related to littoral community structure, richness and diversity. These variables, directly and indirectly, create habitats for aquatic and terrestrial stages of invertebrates, and control nutrient and water cycles. Three benthic associations characterised distinct lakes. Vertebrate predation, water conductivity and pH had no major influence on littoral taxa.
This work provides exhaustive information from relatively pristine sites, and unveils a strong connection between littoral ecosystem and catchment heterogeneity at scales beyond the local environment. This underpins the role of alpine lakes as sensors of local and large-scale environmental changes, which can be used in monitoring networks to evaluate further impacts.

1. Introduction

Integrative efforts linking landscape-scale biogeochemical, hydrological and ecological processes have been intensified in the last decade, and true whole-catchment perspectives are starting to crystalize (Richter and Billings, 2015). Alpine catchments are of increased relevance, partly because they are younger than the average landscape, and they are major drivers of hydrological and biogeochemical cycles affecting the wider biosphere. Their high topography, remoteness and climate allow for the formation of waterbodies of unmatched water quality, which are ecological, biogeochemical and aesthetic hotspots.

Only across Europe, there are over 50,000 remote mountain lakes (Kernan et al., 2009), of which the Pyrenees, a relatively low-density lacustric region, accounts for an estimated 4000 (Castillo-Jurado, 1992). The littoral and riparian zones of these lakes are critical mediators between sediment and nutrient fluxes from the surrounding terrestrial area and lake internal processes. Littoral surfaces also experience cross-ecosystem water and nutrient exchanges (both, autochthonous and allochthonous) with riparian zones, and provide habitat and resources for both aquatic and emerging stages of many aquatic taxa, such as most benthic insects (Gregory et al., 1991; Jonsson and Wardle, 2009; Kopacek et al., 2000). The Pyrenees are estimated to have >797 km of littoral zone in lakes above 1000 m, which are of at least 0.5 ha (Castillo-Jurado, 1992), meaning that littoral processes represent a great portion of the nutrient fluxes in the catchment.

The topography, the hydrology, the bedrock geology and the climate control the intensity of bedrock weathering and nutrient transport into alpine lakes; this influences water and sediment chemistry, and ultimately their ecosystems (Vollenweider, 1968). Even though the littoral zone is just a fraction of the total lake area, it harbours the vast majority of species in a lake, and the littoral nutrient productivity is vital for aquatic food webs, contributing substantially to the whole lake ecosystem energy budget (Vander-Zanden et al., 2006; Vadeboncoeur et al., 2011).

The challenges from inhabiting shallow lake areas at high elevation, range from high solar radiation and water level fluctuations, to low food availability, a short growing season, irregular freezing periods and strong seasonal temperature variation (Bretschko, 1995). Most of the aquatic invertebrates are at their distributional boundaries, and they are highly sensitive to environmental change (Bandyopadhyay et al., 1997). For example, winter mortality is a major factor regulating alpine lake macroinvertebrate populations (Oswood et al., 1991). Food availability and duration of ice/snow cover during winter are other factors affecting littoral macroinvertebrate communities (Bretschko, 1995), as there are also nitrate concentrations (from acid deposition), fish presence, lake morphology (Kernan et al., 2009) and type of shore coverage (Füreder et al., 2006).

Elevated topography and low available nutrients generally support simple littoral ecosystems, which are characterised by a limited number of species and trophic levels (as compared with lowland lakes; Magnea et al., 2013), and are highly adapted to local environment. Research has shown that in mountain lakes, variability in terrestrial conditions can affect littoral macroinvertebrate abundances, through relative control on the proximal environment (Kernan et al., 2009). Moreover, geographical location can have a greater influence on macroinvertebrate communities than local environment (Kernan et al., 2009). It is expected that these topographical and climate restrictions introduce strong biogeographical variability and segregation of littoral macroinvertebrates into distinct communities. Climate/environmental change would further disrupt this natural heterogeneity, through mechanisms that alter the temperature, water and nutrient fluxes, significantly changing lake ecosystem balances. For example the functional diversity of alpine stream benthic invertebrate communities can be particularly affected by climate change-driven glacier retreat (Khamis et al., 2014).

Despite a great ecological and geochemical importance of the alpine lakes' littoral zone, the scale and complexity of its connectivity to surrounding landscape remains an open question. To better anticipate its response to environmental change it is, therefore, imperative to integrate the littoral surfaces into the mechanistic understanding of how physical and ecological heterogeneity of the catchment and littoral ecosystem interact across spatial scales before major alterations occur. This study attempts to evaluate the magnitude of the influence catchment attributes have on littoral macrozoobenthos community composition at scales from a lake to large geographical gradients. A second aim was to assess how these interactions determine the formation of littoral associations, which can potentially serve as sensors of environmental change. We hypothesize that while local littoral environment directly mediates the macroinvertebrate community, its composition is also sensitive to landscape processes at scales beyond that of the lake, through mechanisms that can affect both aquatic and terrestrial phases of its taxa. The study area has the advantages of being at the confluence of four major biogeographical regions: Atlantic, Continental, Mediterranean, and Alpine, which should facilitate capturing the large-scale heterogeneity in a relatively narrow region.

2. Methodology

2.1. The lakes under study

A total of 113 lakes were surveyed in July 2001 in the axial Pyrenees, between degrees: 42°51′34.76″-42°43′8.19″N and 0°29′44.39″W-0° 8′ 40.29″E (Fig. 1, Supplementary List 1). Their selection was largely dictated by their accessibility, and comprised a range of typical alpine ponds and lakes, with surface area varying between 9.4 and 107,068 m^2. The area is within the boundaries of the Central Pyrenees National Park, France, and comprises a series of postglacial catchments on cirque and valley floors. Catchment geology varied between the various valleys and it was dominated by two large geologic units: in the central area and at the extreme east, lake catchments lie on acidic bedrock (granite batholith) while in between, granitic batholiths are surrounded by metasedimentary and sedimentary materials such as slate, limestone and sandstone (Zaharescu, 2011).

Most of the study lakes are above the tree line (altitudes ranged from 1580–2501 m a.s.l.; mean = 2212 m a.s.l.), and they are largely undisturbed by human activity. Low-level agro-pastoral activities, leisure fishing and trekking are among the very few activities allowed in the park. Two of the sampled lakes were transformed into reservoirs (lakes Artouste and Ossoue), and they are being used as freshwater reserve. The great majority of study lakes are oligotrophic. Their proximal catchment area (roughly 10–20 m around the lake) has generally low