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

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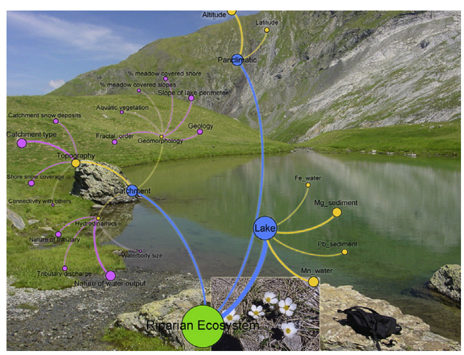
HIGHLIGHTS

- We explored the functional connectivity in riparian vegetation–landscape elements.
- Plant composition, lake and catchment variates were assessed in 189 alpine lakes.
- Vegetation structure was shaped by local, catchment and panclimatic drivers.
- Landscape structure was responsible for the formation of four ecosystem types.
- They are potential keystone sensors for changes in the alpine environment.

GRAPHICAL ABSTRACT



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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

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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.

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 al., 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 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.

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.,