People, pollution and pathogens - Global change impacts in mountain freshwater ecosystems

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Review

People, pollution and pathogens – Global change impacts in mountain freshwater ecosystems

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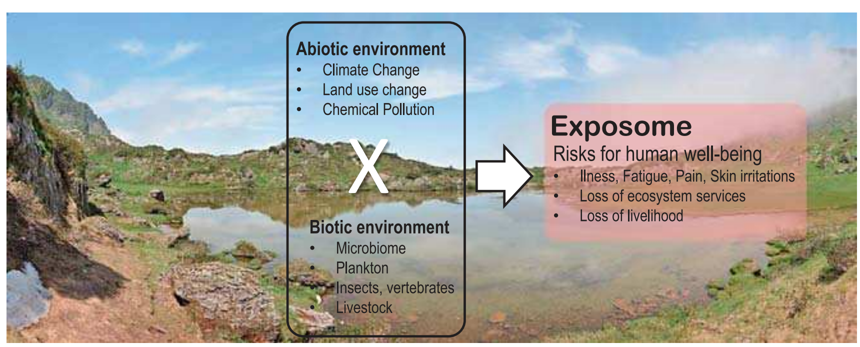
HIGHLIGHTS

- Mountain freshwater ecosystems are sensitive to global change.
- Microbiome composition indicates water quality.
- Dynamics of plankton reflects ecosystem health.
- Loss of ecosystem services
- Risks for human society through increased pathogen pressure

GRAPHICAL ABSTRACT

Interactions between the abiotic and biotic environment impact on human well-being in mountain freshwater ecosystems.



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ABSTRACT

Mountain catchments provide for the livelihood of more than half of humankind, and have become a key destination for tourist and recreation activities globally. Mountain ecosystems are generally considered to be less complex and less species diverse due to the harsh environmental conditions. As such, they are also more sensitive to the various impacts of the Anthropocene. For this reason, mountain regions may serve as sentinels of change and provide ideal ecosystems for studying climate and global change impacts on biodiversity. We here review different facets of anthropogenic impacts on mountain freshwater ecosystems. We put particular focus on micropollutants and their distribution and redistribution due to hydrological extremes, their direct influence on water quality and their indirect influence on ecosystem health via changes of freshwater species and their interactions. We show that those changes may drive pathogen establishment in new environments with harmful

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Chemical micro-pollutants
Potential harmful trace elements
Pesticides
Pathogens
Human impact
Pollution legacy
Anthropocene

consequences for freshwater species, but also for the human population. Based on the reviewed literature, we recommend reconstructing the recent past of anthropogenic impact through sediment analyses, to focus efforts on small, but highly productive waterbodies, and to collect data on the occurrence and variability of microorganisms, biofilms, plankton species and key species, such as amphibians due to their bioindicator value for ecosystem health and water quality. The newly gained knowledge can then be used to develop a comprehensive framework of indicators to robustly inform policy and decision making on current and future risks for ecosystem health and human well-being.

Contents

1. Introduction

Mountain catchments provide freshwater for more than half of humankind, provide the living space for an important number of animal and plant species, and have become a key destination for tourist and recreation activities globally (Grêt-Regamey et al., 2012). However, all forms of anthropogenic disturbance are damaging for freshwater biota (Lake et al., 2000; Revenga et al., 2005; Sala et al., 2000). For freshwater ecosystems, human activities causing water pollution, habitat loss and degradation, overexploitation, flow modifications and alien species invasions are common threats on all continents (Dudgeon et al., 2006; Malmqvist and Rundle, 2002) and contribute to quantitative and qualitative decreases of freshwater resources. All these activities interact to give rise to the two large-scale phenomena of biodiversity loss and climate change (Vitousek et al., 1997), the latter recognized as a major threat to wetlands worldwide (Schindler, 1981; Schindler and Hilborn, 2015). In mountains, freshwater ecosystems are key hotspots for climate vulnerability and ideal ecosystems for climate change studies, as they are influenced not only by altered average environmental conditions but also by climate and hydrological extremes (Millenium Ecosystem Assessment, 2005).

The importance of mountain catchments for the livelihood of humans asks for a higher effort to investigate and monitor biogeochemical and ecological processes. Particularly small but very numerous waterbodies (size between 1m^2 and 500 m^2) show a high susceptibility to climate change and hydrological extremes due to their shallow depth and low water volumes (Smol and Douglas, 2007; Smol et al., 2005; Wissinger et al., 2016). Such small waterbodies, especially when they are part of highland peatlands, play crucial roles in the biochemical cycling and retention due to their high productivity (Céréghino et al., 2008). Despite their high number and important role in freshwater catchments these water bodies remain largely understudied, especially in comparison to large mountain lakes, which they outnumber 100 to 1 (Birck et al., 2013; Hoffman and Huff, 2008; Oertli et al., 2005). Research on changes to the natural flow regimes, eutrophication, increasing temperature, and habitat loss in small mountain waterbodies and their microbial, plankton, plant and animal diversity is therefore important (Fenwick, 2006; Hudson et al., 2006; Johnson et al., 2010a; Middelboe et al., 2008; Okamura et al., 2011; Scholthof, 2006). More so, as small aquatic ecosystems, due to their susceptibility to climate events and increasing temperature, may also function as sentinels for long-term effects on larger aquatic systems, including whole catchments (Céréghino et al., 2008). Increasing temperatures, for example, may lead to changes in local and regional species richness with increased colonization events in mountain ponds due to an upward shift of species with a wide temperature tolerance and extinctions of stenothermal species (Oertli et al., 2008).

Research on change in mountain freshwater biodiversity and on the drivers and pressures causing those changes has a high value to inform policy and decision-making of local and regional stakeholders and administrations about the risks of climate change and the potential impact on human well-being. Here, we review current knowledge on the anthropogenic impact on mountain freshwater ecosystems, how anthropogenic pollution affects biodiversity (the eco-exposome) in mountain ecosystems and how those alterations may impact on human well-being (exposome) (Lioy and Smith, 2013).

2. Pollution through chemical micropollutants

Chemical micropollutants consist of mineral (=inorganic) as well as organic molecules. Micropollutants occur in low to very low concentrations (pg/l to ng/l) in water and their impact on freshwater ecosystems is much less understood in comparison to macropollutants (concentrations from mg/l or higher), such as acids, salts, nutrients, and natural organic matter (Schwarzenbach et al., 2006). However, the contamination of freshwater with chemical compounds is a key challenge humanity is facing, as it is closely linked to climate change and climate extremes (Whitehead et al., 2009). Global change, including climate change, plays a key role in the re-distribution of chemical micropollutants and is assumed to enhance release of micropollutants stored in ice, soils or sediments through e.g. flood events (Rockström et al., 2009). Also a range of other climate variables, such as rainfall, snowfall, length of growth season, and wind patterns may play an important but little understood role in distribution and re-distribution of micropollutants (Ferrario et al., 2017; Pavlova et al., 2014; Steffens et al., 2015). For example, temperature dependent partitioning between air and atmospheric particles, snow surface, or water droplets determine dry and wet deposition rates that may lead to a fractionation and preferential deposition of different compounds at different altitudes (Blais et al., 2006; Blais et al., 1998; Le Roux et al., 2008; Lei and Wania, 2004; Wania and Mackay, 1993; Weathers et al., 2000; Zhang et al., 2013). Mountain topography and land cover may further support the formation of hotspots of micropollutant concentrations, for example in snow fields, forest edges and wetlands (Bacardit and Camarero, 2010; Bacardit et al., 2012). Generally, the accumulation and release of micropollutants in the mountain watershed may be variable depending on the controlling parameters that include topography, dominating winds and type of vegetation (Le Roux et al., 2008; Lovett and

Kinsman, 1990). However, the fate of organic and inorganic pollutants in relation to long-term climate change or rapid environmental changes, as well as the impact of pollutants on the eco-exposome, remains poorly understood (Schwarzenbach et al., 2006).

Mineral (= inorganic) micropollutants include trace elements that have no biological function or have a harmful effect when exceeding a certain concentration, termed Potentially Harmful Trace Elements (PHTEs, Camizuli et al., 2014a, 2014b). Organic micropollutants include organic molecules with adverse effects and long persistence in the environment such as pesticides, hydrocarbons, etc. (Persistent Organic Pollutants = POPs). Both micropollutant groups have pollution sources of both local and/or global origin. The local sources are much influenced by localized human activities such as mining, smelting or forestry (Hansson et al., 2017). Due to the geological and ecological features of mountains, the legacy of ancient mines in mountains is also an important local source of contamination. For example, in the European Black Forest, >50% of lead in soils comes from pre-industrial human activities (Le Roux et al., 2005) and organic toxins might have been produced by human activities such as charcoal production or forest clearing using fire (Lemieux et al., 2004). Some micropollutants are also subject to long range atmospheric transport, which carries them over very long distances into remote areas (Bao et al., 2015; Camarero and Catalan, 1993; LeNoir et al., 1999; Noyes et al., 2009), including the arctic (Macdonald et al., 2000) and mountains (Lyons et al., 2014).

Especially peat lands, a recurring feature in mountainous environments, act as reservoirs of organic matter and therefore also for POPs and PHTEs binding to organic tissue. Due to their ability to retain micropollutants, these natural ecosystems can be considered a pollutant "sponge" which has accumulated contaminants and acted as a natural filter for toxic element (Rausch et al., 2005). Once these pollutants are released from surrounding soils, the watershed can be highly enriched in the bioavailable fraction of pollutants. Pollutants can also be bioaccumulated in a range of different species, including invertebrates and other biota (Monna et al., 2011). Despite an important number of organic and inorganic micropollutants in the environment, we know little of the toxicological effects of compound mixtures on biodiversity patterns (Schwarzenbach et al., 2006), especially in highly productive small water bodies. We know also little, how the bioavailable fraction of pollutants impacts on the quality of domestic water (Delpla et al., 2009) with implications for human well-being and ecosystem health and functioning (Kallenborn, 2006).

3. Human disturbance and food web dynamics

The altered atmospheric processes, driven by climate change, favor local weather extremes and may considerably modify the flux of micropollutants globally and in mountain catchments in particular (Catalan et al., 2006; Catalan et al., 2013). The influx of micropollutants together with other impacts of climate change will likely disturb biodiversity across all tropic levels, from microbes, plankton to higher animals with little understood consequences for the whole ecosystem. Recent theoretical and empirical work suggested that disturbances in a socio-ecological system that are correlated in space and time can have a more severe impact on biodiversity than random disturbances (Kallimanis et al., 2008). Along those lines, climate change effects correlated with habitat fragmentation may have severe impacts on the population dynamics of animals and plants, as habitat specialists and weak dispersers (such as some amphibians) are particularly prone to decline (Fahrig, 2003; Laurance and Williamson, 2001). Such weak disperser species, even where suitable climate space (= habitat within the climatic preferences of the species) increases, may lose current habitat due to their incapacity to disperse sufficiently fast into newly available and suitable sites. Hence, in those species reproduction is heavily impaired when climate change impacts on the temporally matched availability of suitable reproduction habitat conditions (Probst et al., 2009; Stoll et al., 2010) and/or the availability of certain food types during critical periods of offspring development (Stenseth and Mysterud, 2002). Especially in highly dynamic, small water bodies (<0.5 ha in size) we know yet little about the food web dynamics between microbes, plankton and higher animals, such as amphibians. It is therefore difficult to reveal and clarify mechanisms behind food web dynamics, infer cause-effect relationships between multiple food web components, estimate standing stocks and fluxes of materials, and/or forecast the future status of food webs and nutrient cycles (Frenken et al., 2017).

Despite their small size, microorganisms (protists and single-cell eukaryotes) drive important aquatic biogeochemical and nutrient cycles and hold crucial roles within aquatic food webs (Eiler et al., 2014; Hanson et al., 2014; McMahon and Read, 2013). Environmental surveys, recently largely driven by the development of high throughput sequencing technologies, have revealed the immense diversity of protists and bacteria in aquatic ecosystems (Eiler et al., 2013; Lie et al., 2014). Microbes in oligotrophic high-elevation lake environments are typically dominated by *Actinobacteria* and *Proteobacteria* and include many rare species (Hayden and Beman, 2016). These microbial communities will be increasingly exposed to higher temperatures (Beniston et al., 1997) and higher levels of pollution due to atmospheric deposition and the higher frequency of hydrological extremes (Clow et al., 2010). Despite being much less studied than prokaryotic microbes, molecular-based studies have also changed our perception of single-cell eukaryotic microorganisms (i.e., protists). Molecular studies have shown that only a tiny proportion of microbiotic taxa and functional diversity have been described so far, leaving a large knowledge gap in understanding ecosystem functioning at high altitudes and the impact pollution and climate change may have (Grossmann et al., 2016; Oikonomou et al., 2015). The few mountain lake surveys performed so far suggest a difference in microbial composition and diversity in regard to lake type and biogeographic region, corroborating results obtained for bacteria, multicellular animals and plants (Filker et al., 2016; Kammerlander et al., 2015; Triadó-Margarit and Casamayor, 2012). On a local and regional scale, environmental factors such as altitude (a proxy of environmental temperature), the concentration of ions, pH and nutrients (Triadó-Margarit and Casamayor, 2012; Wu et al., 2009) are structuring eukaryotic plankton communities, while differences at large distance scales are mainly due to historical contingencies (Filker et al., 2016). While these studies have increased our knowledge on the distribution, abundance and community structure of the freshwater microbiome, the complexity of interactions and interdependencies within and across microbial trophic levels driving ecosystem functions has not been comprehensively studied. Understanding trophic and non-trophic interactions are not only crucial in the context of the biodiversity-ecosystem functioning debate (Saleem et al., 2012), but also to better predict community responses to global change (Cabrerizo et al., 2017). In that regard, the novel statistical association network approaches using high throughput sequence data are important means in microbial ecology studies and allow exploring ecologically meaningful interactions and linking these networks to environmental parameters (Fuhrman et al., 2015; Lima-Mendez et al., 2015). For example, networks of multiple interacting populations are increasingly considered to be a key part in sustaining multiple ecosystem functions and buffering disturbance (Saint-Béat et al., 2015; Thrush et al., 2014) and thus these microbial co-occurrence patterns might be good indicators of ecosystem stability and health (Faust et al., 2015; Peura et al., 2015).

Microbes are also an important component of biofilms, which are a ubiquitous feature in nature. In contrast to free-living stages, microbial cells in a biofilm are enclosed, and thus also protected by an extracellular polymeric substance matrix (Donlan, 2002), which forms an external digestion system (Wingender and Flemming, 2011). The formation of a biofilm in an aqueous medium depends on e.g. the pH, ionic strength, temperature, trophic state, organic matter composition, phytoplankton, seasonality of the habitat, and food web structure (Donlan et al., 1994; Hall-Stoodley et al., 2004; Pernthaler, 2013; Pernthaler et al., 1998). Any change in these parameters will likely not only be reflected in the composition and structure of the biofilm but also in changes of ecosystem-relevant processes and functions, such as nitrate removal (Baker et al., 2009), ammonium production (Yavitt et al., 2012), or the self-cleaning potential of waterbodies (Wingender and Flemming, 2011). Apart of the self-cleaning potential, biofilms also support the trophic food chain and the occurrence and growth of protozoa, zooplankton, invertebrate and vertebrate species (Wingender and Flemming, 2011). Additionally, in mountain lakes biofilms are further considered important for the degradation and distribution of micropollutants such as organobromine (e.g. polybromodiphenyl ethers (PBDEs)) and organohalogen compounds (Bartrons et al., 2011, 2012). Generally, biofilms change in response to pollutants and were therefore discussed as indicator for the cleanliness of environmental water (White et al., 1998).

As a direct result of changes in the microbial community and biofilms, environmental changes or seasonality, freshwater plankton suffers direct and indirect hazardous impacts from micropollutants (Richards and Baker, 1993). The interactions between microbial species and plankton also constitute the base of aquatic food webs and determine the functioning of biogeochemical cycles, accounting for more than half of the global carbon fixation (Falkowski, 2012; Wolfe et al., 2003). Changes in these interactions and impacts on plankton may lead to an increased eutrophication of mountain lakes and changes in ecosystem services (Bergström and Jansson, 2006). Most mountain lakes are oligotrophic and over a season, planktonic organisms experience a range of dynamic changes in resource availability at different temporal and spatial scales due to seasonality and mixing regimes. It has also been reported that increasing climate change impacts and anthropogenic activities conduct changes in resource availability and therefore have the potential to profoundly change planktonic communities (Berger et al., 2014; Gruner et al., 2017; Tian et al., 2015). Plankton variability may therefore also be an important indicator of change (Winder and Sommer, 2012), but we need to better understand the inherent natural variability of plankton in order to make future predictions of the global change impact on aquatic ecosystem functioning (Chang et al., 2011; Ciszewski et al., 2013; Winder and Sommer, 2012). As phytoplankton growth is directly related to nutrient availability, effects to higher trophic levels are to be expected, e.g. zooplankton, insects and amphibian larvae (Moss, 2012; Sardans et al., 2012; Sterner and Elser, 2002; Van de Waal et al., 2010). Zooplankton density may be reduced through indirect effects of PHTEs and pesticides reducing algal productivity, thus affecting zooplankton food supply (Kasai and Hanazato, 1995; Salonen et al., 2006). Stoichiometric mismatches may become a bottleneck for the transfer of carbon and nutrients to higher trophic levels (Elser et al., 2010; Urabe et al., 2003) as they alter food webs and their dynamics, especially in regard to higher species, including amphibians.

In freshwater and adjacent ecosystems, amphibians are keystone species. For example, tadpoles are primary consumers, altering algal biomass, community composition and sedimentation, whereas adults prey on invertebrate communities and deposit energy-rich eggs that are consumed by many species. Amphibians also link the lowest and highest trophic levels in a community due to their ability to exploit energy poor resources as result of their ectothermic physiology. Such a link via the flux of energy and nutrients becomes obvious due to the enormous biomass amphibians represent in many aquatic and terrestrial ecosystems, especially in mountains (Hopkins, 2007). Therefore, amphibians are of high trophic importance and are critical components of both aquatic and terrestrial communities and ecosystems (Hocking and Babbitt, 2014). In addition, they are highly susceptible to a wide range of pollutants (Fryday and Thompson, 2012; Grillitsch and Chovanec, 1995; Kerby and Storfer, 2009; Quarles, 2015). They impact nutrient dynamics, influence the cycling of nutrients and energy flows between freshwater and terrestrial systems, and control populations of pest insects (Colón-Gaud et al., 2009; Connelly et al., 2008; Whiles et al., 2013, 2006). A change in amphibian communities likely reflects important impacts on entire ecosystems, yet we do not know how impacts on lower trophic levels in mountain lakes impact on amphibian populations (Hopkins, 2007; Lawler et al., 2010).

4. Diseases, parasites and pathogens

Climate change driven atmospheric processes, such as dust plumes and transport of airborne particles, not only disperse nutrients or pollutants, but have been shown to deliver microorganisms to distant high mountains despite the harsh environmental conditions during transport (Perfumo and Marchant, 2010). Especially in a mountain context, more frequent weather extremes with strong rain fall and wind gushes are expected due to climate change and may be an important mechanism of parasite and pathogen spread (Smith et al., 2011). Several individuals of the transported taxa have the potential to establish viable populations in the recipient lakes and might contribute to the freshwater bacterial biosphere (Peter et al., 2014). Further, dispersion of microorganisms to mountain areas by human activities, such as tourism, exploitation and pastoralism, is poorly understood so far. Such activities, however, are likely to have major ecological implications in mountain freshwater ecosystems, especially if microorganisms are or become pathogenic in the new environment due to interactions with hosts and the environment (Fenwick, 2006; Hudson et al., 2006; Johnson et al., 2010a; Middelboe et al., 2008; Okamura et al., 2011; Scholthof, 2006). Pathogens can be confronted to a new environment following host jump, enlargement of the initial distribution range, or human introduction in a new geographic area. The new environment may represent an enemy-free space, allowing pathogens to reallocate defense resources to growth and reproduction and thus increase their competitive ability and virulence (Frenken et al., 2017). However, establishment in a new environment may commonly be restrained by predators, parasitoids, parasites, and interspecific competition (Arndt, 1993; Johnson et al., 2010b; Sakai et al., 2001). Apart from theoretical frameworks, very few examples of biotic resistance to pathogens exist to date (Carlsson et al., 2009; Johnson et al., 2010b; Keesing et al., 2006; Lafferty et al., 2008; Randolph and Dobson, 2012). For example, local richness and abundance of zooplankton species was negatively correlated to the prevalence as well as the intensity of infection in two highly susceptible amphibian species, both in the lab and in the field (Schmeller et al., 2014).

Generally, the knowledge of parasites and pathogens in mountains is limited and does not allow for their active management nor for the understanding of interactions between pathogens, hosts, and environment. Therefore, our predictive abilities are poor for forecasting outbreaks and for identifying threatened species and habitats (Fisher et al., 2012). Further, our knowledge is also insufficient to predict impacts on human health by e.g. toxic cyanobacteria. Toxic cyanobacteria, which produce neurotoxic cyanotoxins, can be responsible for poisoning the drinking water for wild and domestic animals, as well as for humans. Cyanobacteria are therefore a growing concern worldwide (de Jong, 2015). Cyanobacteria blooms may be favored by the introduction of cyanobacteria in new environments, with the potential to profoundly alter the structure of native communities and to modify ecosystem functioning (Sukenik et al., 2015).

The complexity of the abiotic and biotic environment in mountain freshwater ecosystems shapes the interaction of pathogens and their hosts (Frenken et al., 2017). Seasonality and temperature, as well as hydrological events, may favor the spread of parasites and pathogens and their proliferation in and outside of hosts. To take the example of the pathogenic fungus *Batrachochytrium dendrobatidis* (*Bd*), which is related to global amphibian declines (Berger et al., 1998), temperature is among the controlling factors of pathogen spread and prevalence (Clare et al., 2016). *Bd* growth is supposed to be optimal in the temperature range between 17 and 25 °C (Piotrowski et al., 2004). But the success of the pathogen seems to be governed by complex interactions of environmental parameters when not cultivated under laboratory conditions. *Bd*-temperature dynamics show differing patterns in tropical and temperate high altitude environments and between latitudes, altitudes and seasons. In tropical and subtropical climates, amphibian decline due to *Bd* infection has been observed to be reduced in hot and dry conditions existing at lower altitudes (Woodhams and Alford, 2005), lower latitudes (Kriger and Hero, 2007) and during the warm seasons (Kriger et al., 2007), with cooler and wetter conditions favoring *Bd* spread (Clare et al., 2016; Courtois et al., 2017). Local temperature shifts (increase or decrease) together with cloud formation and precipitation patterns are able to influence these dynamics (Pounds et al., 2006). However, the relationship between different climate variables and *Bd* dynamics is not yet well explored for temperate mountain environments, where the pathogen is frequently at the lower end of its growth temperature tolerance. Contradicting studies are either suggesting a limitation of *Bd* spread (Muths et al., 2008) or no observable limitation of the pathogen at high altitude locations (Knapp et al., 2011). Pathogens might also be able to adapt their life cycle to augment their success at lower temperatures (Woodhams et al., 2008). Global climate warming will possibly impact pathogen occurrence and prevalence at high temperate altitudes by shifting the temperature towards the pathogens optimum.

5. Perspective

Here, we reviewed the multitude of harmful impacts on mountain ecosystems, their biodiversity and outlined potential risks to human society. Pollution by persistent organic pollutants and potentially harmful trace elements, carried to remote areas by climate extremes, interacting with local and introduced biota can alter mountain ecosystems profoundly. Such altered mountain ecosystems might be less stable, less healthy and less functional to provide ecosystem services to human society, such as clean drinking water. Despite the importance of mountain freshwater ecosystems to the livelihood of biodiversity and mankind, research efforts are impaired by budgetary restraints and the lack of comprehensive, multidisciplinary approaches to capture all facets of change. Only multidisciplinary approaches can deal with the complexity of interactions between the abiotic and biotic environment and the important societal components, and capture the non-linear behavior of natural and social systems (Folke et al., 2002; Gurung et al., 2012).

Research needs to better understand the pathways on how pollutants arrived in mountain freshwaters, both temporally and spatially (Fig. 1). Fine scale temporal analyses of sediment cores are therefore important to understand the intake, retention and release of pollutants over time. These must be linked with available climate data and data of human land use to analyse the drivers of pollution. Metagenomic and paleobotanic analyses would need to be done in parallel to retrieve currently missing data on historic biodiversity change and to set temporal baselines to which recent change can be compared to (Mihoub et al., 2017). Recent distribution of pollutants with sufficient seasonal resolution needs to be complemented by changes in freshwater biodiversity and human land use regimes. We opt for observation of fluctuations of a) biofilms, due to their value as an indicator of water quality (Burns and Ryder, 2001), b) the freshwater microbiome due to their important role in aquatic biogeochemical and nutrient cycles (Offre et al., 2013), c) planctonic species, indicating critical change and stoichiometric mismatches (Adrian et al., 2009), and d) key species such as amphibians, capable of exploiting energy poor resources, and indicating critical ecological change (Hopkins, 2007). Such observations would not only take place in large lakes, but need increased efforts to include the numerous highly productive small water bodies. Those are showing critical change much faster and if analysed along a space-for-time substitution to capture the altitudinal variability of biodiversity, climate change and pollution, are a highly performant sentinel ecosystem type (Downing, 2010). The retrieved data can then be used in food web analyses (Pickett, 1989) and refined in network analyses (Blüthgen, 2010) linked to recent and past data on climate, land use, and biotic variables. Indicators of change, based on microbiome and plankton variability, biofilm change, change in key species (together representing the eco-exposome) can then be produced to inform the policy arena and decision making on the impact on human well-being (the exposome; Fig. 1).

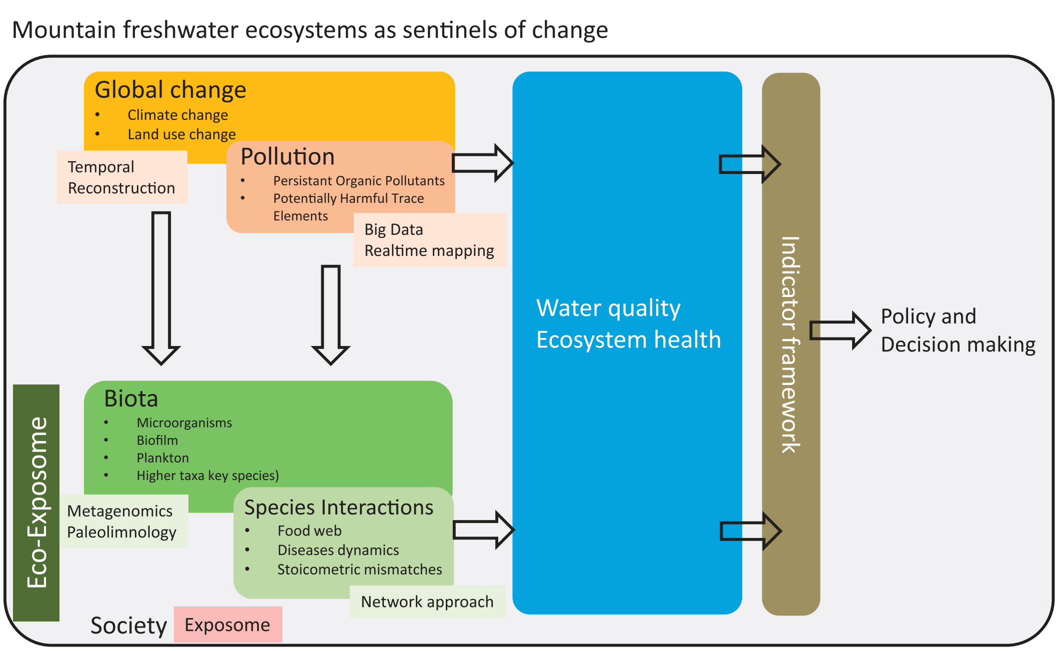

Fig. 1. A comprehensive research approach to establish mountain freshwater ecosystems as sentinels of change. Drivers and pressures (orange) of biodiversity change need to be reconstructed. Recent pollutant distributions need to be mapped in real-time. Apart of the direct impacts of pollution on the water quality, it has also an indirect impact via the eco-exposome (green). To analyse the eco-exposome, metagenomics approaches need to be complemented by temporal reconstruction via paleolimnologic analyses. Such analyses will allow investigating important species interactions, such as food webs, disease dynamics and stoicometric mismatches also via network analyses. These analyses will lead to the development of new indicators or refinement of existing ones for ecosystem health. Based on the results, the indicator framework (olive green) needs to be focussed on the provision of robust information to policy and decision-making. Only with robust information a valuable risk assessment for society can be made and mitigation strategies developed (grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Future comprehensive and multidisciplinary research in mountains must also be concerned about stakeholders' and the public's attitudes towards biodiversity and wildlife, as behavioral responses to conservation measures originate from attitudes and subjective norms, including the consideration of opinions from peers (Ajzen and Fishbein, 1977; Fischer and Young, 2007; Loyau and Schmeller, 2017; Moscovici and Duveen, 2000; Røskaft et al., 2007). The evaluation of public understanding, acceptance and impact of conservation actions is therefore important for the development of new management strategies to reduce the conflict potential between human society and wildlife and to reduce the lack of public support and even rejection of conservation measures (Buijs, 2009a, 2009b; Buijs et al., 2011, 2008; Stoll-Kleemann, 2001). Forced conservation measures, despite good intentions, may increase the unpopularity of conservation and counteract any positive effect.

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