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Scientists' Warning of Threats to Mountains

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Abstract

Mountains are an essential component of the global life-support system. They are characterized by a rugged, heterogenous landscape with rapidly changing environmental conditions providing myriad ecological niches over relatively small spatial scales. Although montane species are well adapted to life at extremes, they are highly vulnerable to human derived ecosystem threats. Here we build on the manifesto 'World Scientists' Warning to Humanity', issued by the Alliance of World Scientists, to outline the major threats to mountain ecosystems. We highlight climate change as the greatest threat to mountain ecosystems, which are more impacted than their lowland counterparts. We further discuss the cascade of "knock-on" effects of climate change such as increased UV radiation, altered hydrological cycles, and altered pollution profiles; highlighting the biological and socio-economic consequences. Finally, we present how intensified use of mountains leads to overexploitation and abstraction of water, driving changes in carbon stock, reducing biodiversity, and impacting ecosystem functioning. These perturbations can provide opportunities for invasive species, parasites and pathogens to colonize these fragile habitats, driving further changes and losses of micro- and macro-biodiversity, as well further impacting ecosystem services. Ultimately, imbalances in the normal functioning of mountain ecosystems will lead to changes in vital biological, biochemical, and chemical processes, critically reducing ecosystem health with widespread repercussions for animal and human wellbeing. Developing tools in species/habitat conservation and future restoration is therefore essential if we are to effectively mitigate against the declining health of mountains.

Keywords: Pollution, climate change, environmental health, sustainable development goals, policy

Main text

Following the onset of the industrial revolution and the use of fossil energy, humans can indisputably be seen as major geological agents (Gałuszka et al., 2014) and as global pathogen vectors (Small et al., 2019). Due to the increase in human activities over the last 300 years, human impact has become at least as strong a force as natural processes (Crutzen, 2006), marking the geological era of the Anthropocene (Gałuszka et al., 2014). Already in 1972, scientists lined out that there are limits to human population growth (Meadows et al., 1972). Twenty years later, scientists warned about ozone depletion in the stratosphere, availability of drinking water, climate change, exponential human population growth, and degradation of the environment and biodiversity (Scientists, 1992). This early warning remained largely unheard and unrecognized, and the progress of humanity towards a sustainable lifestyle has been largely insufficient. This insufficiency ushered in a second warning to humanity 25 years later, arguing that our life-support system is on the brink of collapse (Ripple et al., 2017). Scientists are now largely aware of humanity approaching important tipping points (Lenton, 2011) and planetary boundaries (Steffen et al., 2015). A policy-led reaction was the development of 17 Sustainable Development Goals (https://sdgs.un.org/goals) and 20 Aichi targets (https://www.cbd.int/sp/targets/), the creation of the Intergovernmental Panel for Climate Change (IPCC) and the Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES, Schmeller et al., 2017). However, all recent global reviews of the state of the planet conducted by the United Nations, IPCC and IPBES univocally lay out the dire state of Earth (Bridgewater et al., 2019). The direct drivers of the observed changes, as outlined in the global assessment on biodiversity and ecosystem services by IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019), include climate change, pollution, and increasing demands for energy and materials due to a growing human population. As a response, the UN Convention on Biological Diversity (CBD), developed a global biodiversity framework with 21 targets and 10 milestones to be achieved by 2030 to ‘living in harmony with nature’ by 2050 (CBD/WG2020/3/3). Goals include reducing threats to biodiversity (8 targets), meeting people’s needs through sustainable use and benefit-sharing (5 targets), developing tools and solutions for implementation and mainstreaming (8 targets; CBD/WG2020/3/3). In line with these goals and targets, IPBES, during its 8th plenary, decided to advance with an assessment on the transformative change needed to indicate ways out of the current global crisis (Schmeller and Bridgewater, 2021).

Mountains cover a large part of the Earth’s terrestrial surface and host a larger proportion of biodiversity than expected by area (Körner et al., 2011). They hold an estimated one-third of terrestrial species diversity (Körner, 2004), and represent 18 of the 36 global biodiversity hotspots (Chape et al., 2005). Nevertheless, even in remote areas human impact is strong, as mountains are part of the global socio-ecological systems which have been shaped by geological forces and by human activities (Turner et al., 1990). In mountains, these impacts and the resulting threats remain largely understudied (Schmeller et al., 2018). Generally, people are unaware of the threats to mountain ecosystems and the services mountains provide to humanity. Mountain ecosystems sequester CO_2, clean waters and the air, regulate climate, provide biomedical resources, and regulate floods (Martín-López et al., 2019). Mountains also provide for the livelihoods of more than half of humanity (Grêt-Regamey et al., 2012; Grêt-Regamey and Weibel, 2020). All these goods and services are provided by mountain ecosystems through complex processes that are maintained by communities of species interacting with each other and with the abiotic environment (Bestion et al., 2021). These mountain communities are comprised of prokaryotic and eukaryotic microbes, fungi, plankton species, woody and non-woody plants, as well as invertebrates and vertebrates. By destructing, rebuilding, changing, and shaping the environment, these species produce organic matter and oxygen as well as bind CO_2.

The mountain environment is characterized by extreme temperature regimes, severe weather events and short growing seasons at high altitudes to which species have adapted (Körner, 2019; Payne et al., 2020). In temperate mountains, comparably few species have been able to widely colonize the diverse habitats with montane conditions during the short time window given by the recent demise of glaciers at the end of the last glacial period about 11,000 years ago (McCain and Colwell, 2011; Schabetsberger et al., 2013; Valbuena-Ureña et al., 2018). Mountain ecosystems have evolved in partial isolation, separated by a variety of biogeographic barriers. The gradients and dynamics in climate, hydrology, and water chemistry contributed to the formation of a high diversity of microhabitats, harboring numerous species in comparably small areas (McCain and Colwell, 2011), which also explains the high levels of endemism detected in mountains (Rahbek et al., 2019a; b; Swanson et al., 1988). With increasing elevation, montane climates become more extreme, providing habitat for fewer species. System redundancies (i.e. different species with similar functions), available in ecosystems at low altitudes, are increasingly scarce in mountain ecosystems with increasing elevation. Such redundancies usually provide stability to ecosystems (Fonseca and Ganade, 2001). The absence of these redundancies renders mountain ecosystem particularly vulnerable to the impacts of global change (Moser et al., 2019). However, multiple threats to mountains are arising from climate change alone. Moreover, interactions with socio-cultural, economic and political developments, such as the exploitation of mountains, e.g. for timber, food production, including fish and livestock, tourism, and hydro-electricity, exacerbate these threats, calling for urgent consideration by policymakers (Figure 1).

Here, we highlight the diversity of global threats impacting mountain ecosystems. We focus on the direct drivers climate change, pollution, and land use following earlier science-policy reports (IPBES 2019) to compel stakeholders and decision makers of the urgency to act on all of these different threats. We detail how different drivers interact, creating pressures that degrade and destroy valuable mountain ecosystems and their biodiversity. We further outline, how this impacts the services provided by mountains and creates emerging risks for humans. We treat threats to mountains largely equally, as a ranking of threats in regard to their severity appears elusive based on current knowledge. Finally, we provide recommendations for mitigation actions to be taken to preserve mountains, their biodiversity and the ecosystem services they provide to humanity, as well as describing ways of averting detrimental trajectories.

Climate Change in Mountains

Mountains are defined by rugged terrain and unique climate regimes distinguishing them from lowlands (Körner et al., 2017). The climatic complexity created by mountain topography also influences insolation and air circulation (Dobrowski et al., 2009). Elevation gradients in particular, have a strong impact on many abiotic variables in mountains, and their geographic location is the main control on moisture gradients or seasonality in climate (Körner, 2007). On a regional scale, mountain climate is influenced by large-scale synoptic patterns, proximity to oceans, and the range’s longitudinal or latitudinal orientation (Del Barrio et al., 1990). In synergy with climate change impacts, we see important changes in precipitations, temperatures, and frequency of extreme events, such as droughts and floods. Therefore, climate change might be considered the most basic and far-reaching threat to mountains, impacting mountain biodiversity and ecosystems way more intensively as compared to lowland regions (Rangwala and Miller, 2012; Scarano, 2019).

Precipitation dynamics are not the same in all mountains, and for example, mountains in tropical regions show precipitation maxima at lower and mid-elevations. Temperate mountains typically have an orographic effect and show increased precipitation towards the top, largely driven by different seasonal dynamics in precipitation intensity (Roe, 2005). These precipitation regimes are also regulated by geology, soils, vegetation, and human land use, leading to a large variety of hydrological behaviors and stream flow regimes in global mountain catchments (Dierauer et al., 2018; Zuecco et al., 2018). Climate change-driven precipitation regimes and their increasing variability, especially in mountains, determine long-term change on soil moisture conditions and are important controls on water levels and on the hydroperiods of shallow lakes, ponds and wetlands (Catalan and Bartumeus, 2006; Stephan et al., 2021). As such they are particularly important variables for mountain habitats. Climate change will increase the unpredictability of precipitation patterns (Myhre et al., 2019). Generally, water availability and its predictability is expected to decrease in the future due to lower water storage capacities in areas with glacier cover and higher outflows of excess water during periods of extreme precipitation and melting events (Rajczak and Schär, 2017). These changes will jeopardize the role of mountains as global water towers and the drinking water supply for billions of people (Viviroli et al., 2007) as well as for plants and animals.

Trends in warming of mountain surface air temperatures become more and more apparent (López-Moreno et al., 2008; Niedrist et al., 2018; Niedrist and Füreder, 2021), and high-latitude mountains are projected to warm much faster than temperate and tropical mountains (Negi et al., 2021; Nogues-Bravo et al., 2007). Further, warming is accentuated at higher altitudes (Pepin et al., 2015). The intensity of warming depends on the mountain climatic zone, elevation and season (Pepin and Lundquist, 2008). In the Alps, the mean annual temperature has already increased by 1.5 - 2°C since 1970, and future projections predict an additional rise of 0.25 - 0.36 °C per decade within the next century (Einhorn et al., 2015). Similar increases have been projected in other mountain ranges (Urrutia and Vuille, 2009; Valdivia et al., 2013). Increasing temperatures have decreased the annual snow deposition volume with most impacts observed at mid- and lower elevations (Laternser and Schneebeli, 2003), has caused important shifts to earlier snow melt (Kapnick and Hall, 2012), earlier lake-ice melt (Franssen and Scherrer, 2008), and globally accelerated the deglaciation process (Zemp et al., 2015). Yearly, world-wide cumulative glacier mass balance data have been showing significant decreasing trends in glacier thickness (Ripple et al., 2021). The shorter period of snow cover will therefore also shorten the time during which the Albedo effect is active and during which 85% to 90% of sunlight is reflected. Hence, further acceleration of the temperature rise in alpine mountain regions needs to be expected. Droughts and extreme precipitation events will globally increase in mountains (Gobiet et al., 2014; Urrutia and Vuille, 2009; Valdivia et al., 2013). For the European Alps, climate projections predict more summer droughts and more extreme rainfall events (Rajczak and Schär, 2017). Subtropical mountains tend to experience more frequent summer droughts (McCullough et al., 2016), while for example the Hindu Kush and the Himalaya have been experiencing increased amounts of extreme rainfall events (Hartmann and Andresky, 2013; Wester et al., 2019). Droughts in mountains also lead to an increase of the probability of wildfires in mountain grasslands and forest as the probability of ignition of dry plant material by lightning increases (Stephens et al., 2018). Such wildfires are difficult to extinguish due to the difficult terrain and result in the loss of very large areas (i.e. thousands of hectare) of mountain vegetation with large and long-lasting effects on mountain ecosystems due to low pre-fire production of seeds due to drought and the generally low recovery speed with increasing altitude (Werner et al., 2022).

Ultraviolet radiation (UVR) both affects and is affected by climate change. These modifications of UV exposure are affecting how people and ecosystems respond to UV, with more pronounced effects in the future (Barnes et al. 2019). UVR reaching mountain ecosystems increases with elevation (Sommaruga et al., 1999). In many high mountain freshwaters, the limited catchment sources of DOC, which results in crystal clear water, facilitates the penetration of radiation far into the water column (Catalan and Donato Rondon, 2016; Laurion et al., 2000; Rose et al., 2009). High levels of UVR in the UV-B spectrum (wavelength range 280-320 nm) have been studied with regard to their effects on aquatic organisms at higher elevations. Colored dissolved organic carbon (DOC) and phytoplankton may attenuate the penetration of UV underwater, shielding freshwater species from negative effects of this radiation (Sommaruga et al., 1999). Variability in UVR reaching mountain freshwaters depends on factors such as cloud cover and air pollution (Brooks et al., 2005; de Oliveira et al., 2021; Diamond et al., 2005; Obertegger and Flaim, 2021; Sommaruga, 2001). Long-term changes in UV-B in turn are due to changes in atmospheric ozone levels, and despite the recovery of atmospheric ozone layers since the Montreal protocol was implemented (Barnes et al., 2019), new reports of ongoing lower stratospheric ozone depletion (Ball et al., 2018) and new ozone depleting agents in the atmosphere have been issued (Fang et al., 2019). We may also see potential opposite effects of global warming in mountains, as for aquatic or semi-aquatic species UVR stress may increase due to earlier snow and ice-cover melt, but may decrease due to higher DOC import from catchment reforestation (Sommaruga et al., 1999). The impact of UVR and stress avoidance behavior remains an understudied field, but may drive further changes in mountain biodiversity and perturb mountain ecosystems (Häder et al., 2011).

Generally, decreasing amounts of annual snow and retreating glaciers have been and will continue to profoundly reshape mountain freshwater habitats and also the terrestrial communities depending on them, threatening mountain species and communities (Jacobsen and Dangles, 2017; Sommaruga, 2015), but also providing new habitats for colonization (Ficetola et al., 2021). Impacts on lowland human populations include difficult to predict water supply (Huss et al., 2017; Viviroli et al., 2007) and destruction of infrastructure through more frequent extreme floods and/or landslides. Climate change will drive the disappearance of many intermediate and ephemeral habitats in mountains due to droughts, with potential severe consequences for mountain biodiversity and biological processes e.g. carbon storage. Climate change will also impact the water regime of many peatlands. Due to the importance of mountain peat- and wetlands as global carbon sinks, the loss of these habitats may further accentuate climate change (De Jong et al., 2010) and UVR impacts (Barnes et al. 2019).

Pollutants in Mountains

Sources of pollution are manifold in mountain ecosystems (Lei and Wania, 2004; Noyes et al., 2009; Shunthirasingham et al., 2010) and we generally lack a global approach to observe environmental pollution and its impact (Brack et al., 2022). Global atmospheric transport of micropollutants (Hussain et al., 2019; Wania and Mackay, 1993; Yang et al., 2010) and local human activities such as mining, logging, agriculture, pastoralism and tourism are the main pollution sources in mountain environments. Increasing pastoralism and livestock units have been shown to put the health of mountain lakes at risk by introducing highly toxic organic pollutants into mountain lakes (Machate et al., 2022). Further, fish stocking introduced heavy metals such as mercury in mountain ecosystems (Hansson et al., 2017b). Other sources of pollution include extreme weather events releasing legacy pollutants from mining, tourists introducing UV blockers as part of personal care products, and atmospheric transport of pollutants releasing a plethora of different molecules (Gross, 2022; Le Roux et al., 2020; Pozo et al., 2007). Mountains are also at risk of acidification when they are located downwind of Nitrogen or Sulphur emission sources and buffering capacity of freshwater is low. In addition, seasonal events such as snowmelt can change pH up to a full unit (Nodvin et al., 1995). Acidic pulses may co-occur with spikes of toxic element concentrations in water (Havas and Rosseland, 1995). Further, higher rates of erosion and weathering, as a result of more frequent events of heavy precipitation, may also lead to a higher import of base cations and increase the pH of mountain freshwater and soil (Kopáček et al., 2017). Finally, global change-driven eutrophication and elevated temperatures lead to an increased growth of cyanobacteria, which can produce toxins (e.g. cyanotoxins), with known negative impacts on human health (Catherine et al., 2013; Funari and Testai, 2008; Zanchett and Oliveira-Filho, 2013).

The scavenging of atmospheric organic and inorganic pollutants is pronounced at high altitudes and can take the form of dry and wet deposition of aerosols to the ground surface (Daly and Wania, 2005; Le Roux et al., 2016; Le Roux et al., 2020). Atmospheric pollutants in mountains include trace elements (Camarero et al., 2009) (Yang et al., 2010), organic and synthetic pollutants (i.e. current-use and legacy pesticides), polycyclic aromatic hydrocarbons (PAHs), endocrine disrupting compounds (EDCs; Rockström et al., 2009; Meire et al., 2012), and polychlorinated biphenyls (PCBs) or microplastics (Allen et al., 2019; Brahney et al., 2020; Reid et al., 2019). These compounds are introduced into the atmosphere via evaporation, or binding to particles light enough to be carried by wind. Volatile compounds tend to evaporate in warmer environments at lower altitudes and condensation progressively takes place with decreasing temperature as air masses travel over mountain slopes (Blais et al., 1998). Less volatile compounds, such as most of the currently used agricultural pesticides, are not prone to directly evaporate into the atmosphere, but are still transported into the mountain environment as they bind to soil particles, which can be uplifted and carried over longer distance during more extreme wind events (Silva et al., 2018). As a consequence, organic and inorganic micropollutants can be introduced to mountains via the atmosphere and over long distances (Camarero et al., 2009; Bradford et al., 2010; 2013; Fig. 2).

Transfer of inorganic and organic pollutants to mountain freshwaters can also originate from legacy and recent local human activities. Fish stocking (Hansson et al., 2017b), present and historic mining activities (Hansson et al., 2017a) or forestry, agriculture and tourism (Alpers et al., 2016) introduce pollutants or mobilize their catchment sources such as soils and sediments. Evidence for the introduction of potentially harmful trace elements (PHTE, for example the metals As, Hg, Pb, Se, Sb, Zn, Cu) from distant or local sources is found in mountain lake sediments, peatlands and in snow (Bacardit and Camarero, 2010). Furthermore, glacier melt and snowmelt can mobilize legacy atmospheric pollution and catchment sources of pollutants (Bogdal et al., 2009; Meyer and Wania, 2008), which may increase exposure of mountain species to micropollutants.

Despite the accumulated knowledge on global pollution, we still know little about the toxic cocktail accumulating in mountains and its impact on biodiversity (but see Catalan, 2015). There are very few studies that analyzed a broad set of pollutants or even conduct non-target monitoring in a mountain context (Machate et al., 2022), rendering our current knowledge on global mountain pollution patterns largely incomplete. We also know little about each (detectable) compound's physico-chemical characteristics, e.g. the water-air constant (K_{wa}), without which it is difficult to make predictions on future pollution patterns in mountains. Generally, the introduction of new pollutants and changes in pollutant mobilization due to climate change may challenge mountain ecosystem health and increase the vulnerability of species and humans to pathogens, increasing health risks (Brack et al., 2022; Schmeller et al., 2020; 2018). Concerns about adverse toxic effects have especially been raised about, but are not limited to, pollutants introduced from local activities (Machate et al., 2022). In the future, these health risks might further increase, by shifting e.g. pastures to higher altitudes (Mayer et al., 2022), where ecosystems are already under high pressures due to climate change (Herzog and Seidl, 2018)). Tourism and expansion of infrastructure create yet additional pressures on mountain biodiversity.

Vegetation and land use changes in Mountains

Recent mountain vegetation is largely shaped by historical and current land use (Körner et al., 1997; Lavorel et al., 2017), with the degree of influence depending mainly on the accessibility of the area (Tasser and Tappeiner, 2002). Vegetation and changes in rates of carbon sequestration due to shifts in land use can occur through a change in land cover, through intensification or extensification of existing land use practices (Niedertscheider et al., 2017) and acidification (Bowman et al., 2012). Most of these changes are driven by pastoral activities, such as livestock grazing, which is the major agricultural activity in most mountains. Pastoral activities in many mountain regions have a long history. However, especially for European countries it is known that livestock units are increasing, partly as a result of the EU subvention policy, partly as strategy to evade climate change impacts and reduced availability of fodder in lowlands (Mayer et al. 2022). Another (illegal) activity related to pastoralism is slash and burn to avoid expansion of forest areas. The clearing intensity and frequency increases with increasing pastoral pressure. In addition, novel non-native crops have been planted to increase local food availability under optimal environmental conditions. However, plantations of species that are well-adapted to the environment of a particular mountain range, such as cardamom in the Hindu Kush region (Eklabya et al., 2000), provide a larger genetic reservoir and thus a greater buffer against environmental pressures such as climate change (Kelty, 2006). Other land use changes include logging of forest stands (Latty et al., 2004), afforestation (Liu et al., 2021), vegetation regrowth in abandoned lands (Aide et al., 2019). All these changes intervene deeply in the existing ecosystem (Hinojosa et al., 2016), altering and threatening underlying processes and associated ecosystem services (Chiang et al., 2014; Faccioni et al., 2019; Tasser and Tappeiner, 2002). An emerging land-use trend is the growing impact of tourism on ecosystems, where damage to vegetation can occur (Rodway-Dyer and Ellis, 2018) and is playing an increasing role in mountain regions (Niu and Cheng, 2019). In the Dongling Mountains (China), tourism led to a lower species richness, heterogeneity and evenness in impacted subalpine meadows (Zhang et al., 2012). Increasing pressures from land use changes will further accentuate the impacts of climate change and pollution on mountain biodiversity and the health of mountain ecosystems.

Introduced species in mountains

Biological invasions are increasingly exacerbated by human activities and are responsible for significant biodiversity decline as well as high economic losses to society (Diagne et al., 2021). In addition, they are exacerbated by globalization and climate change (Seebens et al., 2021). The harsh environmental conditions (e.g., high UV-B, low temperatures, variable water availability, poor soil) may limit alien plant invasion and expansion, especially in high mountain areas (Watermann et al., 2020). However, remote mountain areas have been reportedly impacted by the introduction of alien species (Pauchard et al., 2009), partly also through tourism (Hemp, 2008).

For example, tourism drives fish stocking of naturally fishless lakes. In such naturally fishless mountain lakes fish introductions have an outsized impact and drive profound ecological change as a highly efficient aquatic predator is introduced in a naïve environment (Miró and Ventura, 2020). Stocking montane lakes with fish for subsistence purposes has been occurring since the Neolithic, through fish translocations from nearby lakes and rivers. However, before 1950 such introductions had limited geographic extent and their impacts were rather local (Moser et al., 2019). Since 1950, introductions of fish increased dramatically as a consequence of the increasing popularity of recreational angling, both in large and relatively small lakes as well as in adjacent wetlands (Hansson et al., 2017b). In addition, the use of small fish, mainly minnows *Phoxinus* sp. (Fam. Cyprinidae), as live baits for trout fishing is causing a new and detrimental wave of invasion (Miró and Ventura, 2015). These introduced fish dramatically affect native communities of mountain lakes. Initially considered ecologically harmless and economically beneficial, introductions continued even when their serious ecological consequences became clear (Knapp et al., 2001). Supported by institutional stocking campaigns and non-authorized translocations by anglers, fish spread rapidly in mountain deep-ponds and lakes of all sizes, as well as in all the colonizable downstream habitats (Ventura et al., 2017), with a long list of negative impacts: i) decline/elimination of native species (e.g., invertebrates and amphibians; (Knapp et al., 2001; Tiberti et al., 2014); ii) cascading effects in the trophic network (Schindler et al., 2001), affecting the chemical/microbiological quality of waters, and the ecological linkages with surrounding terrestrial habitats (Epanchin et al., 2010); iii) impacts such as predation, competition, transmission of pathogens and hybridization on native fish inhabiting downstream habitats (Adams et al., 2001), and iv) further collateral introductions of fish used as live bait (Miró and Ventura, 2015). Hence, fish stocking in mountain lakes is particularly detrimental to water quality and biodiversity, especially as now nearly all these ecosystems are affected, including large lakes, small lakes, ponds, connecting streams and their adjacent mountain wetlands (Ventura et al., 2017).

For timber production, fast growing tree species of the genera *Pinus* and *Eucalyptus* have also been introduced in many mountain forests. These exotic tree plantations are subject to serious criticism due to their negative impact on water balance, soil fertility, and native biodiversity (Fahey and Jackson, 1997; Hofstede et al., 2002; Lundgren, 1978). A significant loss of soil carbon and a major reduction in taxonomic and functional diversity of soil invertebrates has been observed in pine tree plantations compared to native forests of very similar soil origins and topographies (Cifuentes-Croquevielle et al., 2020). These impacts may further be exaggerated by fast rotation speeds, which would not permit to increase floristic and hence also faunistic biodiversity (Hall et al., 2012). These changes therefore have the potential to aggravate both climate change impacts and biodiversity loss (but see (Balthazar et al., 2015). Further, exotic tree species can become highly invasive under the right environmental conditions, which might also be met by future climate change. Invasibility is also driven by seeds from exotic tree plantations leading to colonisation and replacement of surrounding natural vegetation (van Wilgen, 2012). Reversing impacts associated with those self-sown invasive stands has be proven to be very difficult (van Wilgen and Richardson, 2012), also because waste of e.g. pine harvesting is left at sites or even delivered to nearby rivers, delaying the natural regeneration of indigenous vegetation (Balthazar et al., 2015).

Water abstraction from Mountains

Most valley bottoms have been heavily altered by human activities that impact freshwater systems (Finlayson and D'Cruz, 2005). These activities include land drainage, dredging, flood protection, water abstraction for hydroelectric powerplants, and inter-basin water transfer, building dams to create reservoirs, and digging new canals for navigation. In mountains, which are increasingly used as recreational area, food and water source, but also as hydroelectric powerplants, water abstraction has been increased to excessive levels. Hydrological interventions include (hydroelectric) dams, pipelines and derivation channels, agricultural ponds, irrigation and snowmaking reservoirs, quarries, water removal, and flow regime alterations. Among their very many consequences, these interventions may lead to the gradual drying up of natural aquatic ecosystems due to excessive water extraction and diversion, as well as changes in the water level of (dammed) lakes, in the flow regime of streams, and in hydrological connectivity. These consequences in turn impact on the structure and function of the unique biodiversity that is characteristic of these habitats, and which includes many endemic and threatened species absent from the lowlands (Fait et al., 2020; Mayerhofer et al., 2021;

Schabetsberger et al., 2013). Importantly, ongoing modifications in high-mountain freshwater ecosystems may also directly and profoundly impact on the wellbeing and livelihoods of peoples (Schmeller et al., 2018).

Recent reports indicate that biodiversity in freshwater ecosystems is declining even faster than in oceans and forests and that the extent of human alteration and impairment of aquatic ecosystems is massive (Tickner et al., 2020). Mountain aquatic systems are no exception, particularly in high-mountain areas (Catalan et al., 2017). Human alterations to alpine aquatic ecosystems are of particular concern given that mountain aquatic habitats provide essential ecosystem services such as drinking water and renewable energy to much of humanity, and that they are of high aesthetic, recreational, and conservation value, particularly in their function as biodiversity reservoirs (Fait et al., 2020). Water abstraction in concert with climate driven changes in hydrological regimes will lead to a gradual drying up of aquatic mountain ecosystems, likely causing massive water shortages in cities that depend on drinking water from mountains (Viviroli et al., 2020; United Nations Environment Programme 2022). The desertification of these ecosystems will also be detrimental to their unique mountain biodiversity, leading to an irreversible degradation of these sensitive ecosystems, if no or too little action for their preservation are put in place immediately (Immerzeel et al., 2020).

Threats to and from Mountain Micro-Biodiversity

The unseen diversity of micro-organisms and their microbiomes, comprising the community of fungi, yeasts, bacteria, viruses and protists, and the impacts of climate change on them have already been subject to a previous warning (Cavicchioli et al., 2019). In short, micro-biodiversity plays a central role and is of global importance in climate change biology, particularly in extreme environments such as mountain ecosystems (Schmeller et al., 2018). Climate change impacts, relevant also for humanity, depend heavily on the responses of microorganisms, which are essential for achieving an environmentally sustainable future (Cavicchioli et al., 2019). Despite their importance, we still know little about the microbial communities or microbiomes, especially in mountain ecosystems (Kammerlander et al., 2015; Schmeller et al., 2018).

Despite their small size, microbial communities drive major processes in and on animals, plants, as well as in ecosystems (Bates et al., 2022; Bernardo-Cravo et al., 2020; Lin et al., 2021). In a nutrient poor environment such as mountains, microbial communities likely play an important role in synthesizing vital nutrients, thereby increasing energy uptake and growth of plants and animals (Bernardo-Cravo et al., 2020; Schmeller et al., 2020; Sentenac et al., 2022). Similarly, micro-organisms stabilize whole ecosystems by buffering against change through the maintenance of biodiversity and ecosystem processes. For example, the interactions between micro-organisms and plankton constitute the basis of aquatic food webs and determine the functioning of biogeochemical cycles, accounting for more than half of global carbon fixation (Cavicchioli et al., 2019; Purcell et al., 2022). Any kind of disturbance to microbial communities can therefore impact on mountain species and ecosystems.

Pathogens, and other microorganisms, can be easily introduced to mountains through pastoralism, tourism or wind drift. However, we remain largely oblivious to how the complexity of the abiotic and biotic environment in mountain ecosystems influences beneficial microbe-species interactions (e.g. microbial loop, mycoloop; (Kagami et al., 2014), host-pathogen interactions (Frenken et al., 2017; Haver et al., 2021; Fisher and Garner, 2020) and health risks for the human population (Schmeller et al., 2018). For example, the transport of microbial pathogens is of special concern for human and livestock health, but also for wildlife and keystone species groups such as amphibians. In particular, fungi and bacteria with resistant aerosolised spores are capable of long-distance transport of e.g. dust (Dadam et al., 2019; Sultan et al., 2005). Global dust dispersion is a natural phenomenon, and occurs when topsoil is transported into the troposphere and carried over long distances by wind currents. However, global warming and changes in land use practices (e.g. deforestation and overgrazing) have accelerated desertification in many areas, resulting in increased dust dispersion even to remote places (Moulin and Chiapello, 2006; Tegen et al., 2004), particularly to high elevation sites (Dong et al., 2020). Further anthropogenic impacts via air pollution can intensify both the abundance and community composition of aerial microbes (Yan et al., 2016), but also for vector-borne diseases (Caminade et al., 2019): Malaria has been found at higher altitudes in mountains in Ethiopia and Colombia (Siraj et al., 2014), incidences of Malaria and Dengue are increasing in Nepal´s mountains (Dhimal et al., 2015a), altitudinal upward shifts of Dengue and Chikungunya (Dhimal et al., 2015b), and also ticks have been reported, the latter e.g. leading to increased occurrence of Lyme borreliosis in the Alps (Garcia-Vozmediano et al., 2020).

Recent data also suggest that we currently see an increase in eutrophication of mountain lakes globally with an upsurge of the diversity of Cyanobacteria (Ho et al., 2019). Cyanobacteria produce a range of toxins (e.g. microcystins, cyanotoxins, Catherine et al., 2013), which have an important impact on the quality of water (Du et al., 2019; Ho et al., 2019), therewith increasing risks of intoxications for humans and livestock. Epilithic biofilms are a highly reactive component in freshwater systems that play a crucial role in the provision of many ecosystem services (Catalan and Donato Rondon, 2016). Especially in smaller mountain lakes, streams and other waterbodies, epilithic biofilms must be considered the major player in carbon cycling and ecosystem productivity (Vadeboncoeur et al., 2008). A better understanding of the risks of proliferation of potentially harmful microbial groups, pathogenic fungi, bacteria and protists due to human-driven input of phosphorus, nitrogen through atmospheric fertilization and microbial pollution is necessary to improve our predictive abilities for human and wildlife risks. For mountain ecosystems, in particular, our predictive abilities are poor for forecasting pathogen proliferation, the dynamics of potentially harmful microorganisms, and for identifying threatened species and habitats. In a mountain context that could mean that resources of clean drinking water will diminish at a much faster rate than currently predicted (Schmeller et al., 2018) and the important ecosystem services such as CO_2 sequestration and nitrogen retention will be suboptimal or absent (Saunders and Kalff, 2001).

Threats to Mountain Macro-Biodiversity

Mountain areas host many species that live in a delicate balance or at the edge of their distribution and are therefore very susceptible to environmental changes and local extinction. Top predators, such as large carnivores, but also large herbivores play important roles in maintaining mammal, avian, invertebrate, and herpetofauna abundance and richness. Many of these species are threatened with extinction (Ripple et al., 2014) and nearing global collapse (Ripple et al., 2015). Threats to macro-biodiversity in mountains come from chemical pollution, nutrient influx through atmospheric processes and local sources such as livestock (Machate et al., 2022), introduction of non-native taxa, but most importantly from overexploitation and habitat loss (Maxwell et al., 2016). These threats drive the decline of already threatened species (Maxwell et al., 2016) and will change the communities of species, which do not all have the same possibilities of dispersal, recovery and reproduction to avoid disturbances (Kerr and Deguise, 2004; Pimm, 2008). For example, among aquatic organisms, the possibility of dispersal and life traits such as the mode of reproduction are very different among taxonomic groups. Some zooplankton species can reproduce sexually or parthenogenetically, and can produce resting eggs, which can survive for a long time in sediment egg banks (Brendonck and De Meester, 2003; Nielsen et al., 2012). Benthic invertebrates increase their dispersal capacity by producing winged adults. Both strategies may allow a speedy recovery through hatching from resting stages or recolonization by flying. Complete recovery after local extinction, however, is unlikely, and restoration and recovery processes in mountains take a long time (Tiberti et al., 2019). For example, recovery from fish impacts took 11-20 years to obtain a similar food web structure. In the same studies, it was evident that recolonization efficiency of species with a parthenogenetic reproduction mode was higher than for sexual reproduction (Knapp and Sarnelle, 2008; Knapp et al., 2001). In any case, for many species dispersal and recolonization can be limited, when the remaining seed pool is not abundant or found too distant or beyond barriers in the land- or waterscape in mountains, due to their relief. Hence, connectivity between different populations of the same mountain species is reduced, hampering recolonization after disturbance (Heino, 2013). Further, upward shifts of distribution areas are not the same for all mountain species, disrupting long-established communities and their interactions. For example, we understand only inadequately, if the observed upward shift of some mountain plant species due to climate change is met by associated microbes and invertebrates (Grabherr et al., 1994; Steinbauer et al., 2018). Other factors leading to unequal dispersal of formerly associated species might be driven by reduced oxygen availability with increasing elevation (Jacobsen, 2020), differences in temperature and drought tolerance (Forero-Medina et al., 2011; Schai-Braun et al., 2021), different adaptation abilities through e.g. seasonality or phenology (Parmesan and Yohe, 2003), or different abilities to change depth distribution. Dysfunctional ecosystems, with lower resilience to further impact s, are the likely outcome (Körner, 2019; Pecl et al., 2017). Due to the non-linear loss of biodiversity (Trisos et al., 2020), the expected extinction of endemic plant and animal species after tipping points have been met (Dullinger et al., 2012), may further increase the dysfunctioning of mountain ecosystems. When this will happen and what will be the outcome will be difficult to predict due to the multitude of factors impacting different species in a community.

Threats to mountain ecosystem services

Negative impacts on mountain biodiversity threatens ecosystem integrity and functioning, and hence also the multiple ecosystem services provided to local communities, populations downstream and local stakeholders, including tourists (Grêt-Regamey et al., 2012; Martín-López et al., 2019; Schirpke et al., 2019). The capacity of mountain ecosystems to provide ecosystem services is deteriorating due to biodiversity loss driven by global change (Palomo, 2017). There is an alarming set of negative consequences from those changes, in stark contrast to the few positive effects that have been reported (Hobbs et al., 2009). These changes will jeopardize water use of at least 1.9 billion people (Immerzeel et al., 2020). Moreover, as a result of glacier decline, water availability will be severely reduced in the dry season, affecting millions of farmers globally (Biemans et al., 2019). Mountains will therefore not remain the reliable and highly important source of water they have been for thousands of years. Even in humid mountain regions, such as the European Alps, droughts have become a problem (Stephan et al., 2021) due to the increasing irregularity of water discharging rates and increasing flood events (Ragettli et al., 2021). The irregularity of water discharging rates in combination with land use and land cover changes can also have synergistic effects on ecosystem functioning, rendering mountains more vulnerable to climate change impacts (Chiang et al., 2014). For the central mountain range of Taiwan, it was shown that these combined effects lead to a relocation or loss of ecosystem services and therefore need to be considered in conservation planning (Lin et al., 2019; Lin et al., 2017).

Net primary production (NPP), the amount of biomass or carbon produced by primary producers per unit area and time, is the basis of all ecosystem services and is being altered due to climate change (Haberl et al., 2007; Kastner et al., 2022; Melillo et al., 1993). Overall, there is evidence that increasing temperatures and CO_2 concentrations have increased the NPP of forests when water was not a limiting factor (Boisvenue and Running, 2006). In the Alps, changes in NPP of grasslands on which cattle depend show contrasting regional trends (Jäger et al., 2020). A study combining experimentation and meta-analysis reported stabilization of NPP of grasslands under climate change due to changes in species and increasing allocation towards belowground biomass to resist drought (Liu et al., 2018). Despite a limited body of evidence, local models predict that NPP will increase under climate change in the forests of the mountain region of Changbai in China (Gao et al., 2020).

Further, as glaciers retreat and permafrost thaw, the decreased land-surface stability results in increased hazards in the form of landslides and rock fall, increasing risks for wildlife, tourists and livestock (Huss et al., 2017; Temme, 2015). Glacial lake outburst floods may also intensify due to glacier retreat and glacial lake formation, with potentially devastating consequences for populations downstream (Harrison et al., 2018; Milner et al., 2017; Vuille et al., 2018). Cultural ecosystem services are also impacted by climate change. For example, glaciers are considered sacred or have a strong symbolic meaning for several mountain communities, and thus spirituality is being affected (Allison, 2015) and has been documented in various countries in Africa, Asia, and the Americas (Allison, 2015; Mölg et al., 2008; Shijin and Dahe, 2015). Overall, the documented threats to mountain ecosystem services are a major concern worldwide, as they could lead to increased poverty, lower food production, higher health risks and a general decrease of human wellbeing, which may often affect not only mountains but also the populations living downstream.

Conclusions

Mountain ecosystems are complex, dynamic, exceptionally fragile and are highly sensitive to global change. They are therefore considered sentinels of change (Schmeller et al., 2018). We are only beginning to understand the functional ecology of mountain ecosystems, but international research already suggests that changing species communities will be detrimental to the environment, to biodiversity and therefore to a critical part of Earth’s life-support system.

Climate change might be considered the most impactful driver of change in mountain ecosystem, but all the outlined threats to mountains act in synergy. Climate change is modifying and will continue to modify the occurrence of extreme events, the amount of precipitations (rain and snow), as well as freeze and thaw cycles, with impacts on the onset of snow melt (and thus length of growing season) and water temperatures, aggravating impacts from inappropriate land use practices. Global change with all the different pressures outlined above causes imbalances in the functioning of mountain ecosystems, which lead to changes in vital biological, biochemical, and chemical processes, critically reducing ecosystem health with repercussions for animal and human health and wellbeing (Acevedo-Whitehouse and Duffus, 2009; Bradshaw et al., 2021; Lerner and Berg, 2017).

Humanity has a wide range of options in its hand to mitigate human-driven impacts on mountains and to change the current trajectory as humanity is at the nexus of it all. All relevant actors need to coordinate their efforts in extensive collaborations to achieve the necessary conservation measures: in mountain areas with a protection status conservation policy needs reinforcement; for mountain areas without a protection status, evaluation of its status, importance and future perspective need to be used to prioritize (i) protective measures, (ii) re-evaluations of impacts of touristic and pastoral activities, (iii) evaluation of sustainability management of natural resources, and (iv) development of early-warning systems of ecosystem degradation and biodiversity loss. These measures will then be able to inform about trajectories towards detrimental outcomes (pathogen emergence, ecosystem services; (Huber et al., 2013). As mountain stakeholders are numerous, regional networks and coordination mechanisms must urgently be installed, and a broad communication strategy needs to be developed to raise awareness about the threats to mountains and their complex consequences (Brunner and Grêt-Regamey, 2016; Drexler et al., 2016). These consequences may have also an important social component, as people may move out of mountain areas, if the conditions for cultivation and exploitation are unfavourable, not providing for their livelihood. These different aspects need to be included in comprehensive mountain ecosystem management plans, considering the cumulative and hierarchical context of disturbance regimes to prevent reductions in ecological variability and ecosystem resilience (Chiang et al., 2014).

In this light, and in that of the challenging objectives set by global agendas, including the UN Sustainable Development Agenda, the Convention on Biological Diversity, the recently launched EU Biodiversity Strategy for 2030 or the UN Decade on Ecosystem Restoration 2021-2030, investments are needed for the delivery of policy-relevant science on mountain ecosystems (Körner, 2019), closely following recommendations given in the global biodiversity framework (CBD/WG2020/3/3). Only if we maintain a high ecosystem resilience will we be able to maintain ecosystem functioning and ecosystem services. Threats to mountains are numerous and the repercussions to humanity demand conservation and restoration of mountain ecosystems, as they are an essential and highly sensitive part of the global life-support system.

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