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Dirk Schmeller, Davnah Urbach, Kieran Bates, Jordi Catalan, Dan Cogălniceanu, Matthew Fisher, Jan Friesen, Leopold Füreder, Veronika Gaube, Marilen Haver, et al.

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Scientists' Warning of Threats to Mountains

AUTHORS :

[Dirk S.Schmeller^a](#), [DavnahUrbach^b](#), [KieranBates^{cde}](#), [JordiCatalan^{fg}](#), [DanCogălniceanu^h](#), [Matthew C.Fisher^d](#), [JanFriesenⁱ](#), [LeopoldFüreder^j](#), [VeronikaGaube^k](#), [MarilenHaver^a](#), [DeanJacobsen^l](#), [Gael Le Roux^a](#), [Yu PinLin^m](#), [Adeline Loyau^a](#), [Oliver Machateⁱ](#), [Andreas Mayer^k](#), [Ignacio Palomoⁿ](#), [Christoph Plutzer^k](#), [Hugo Sentenac^a](#), [Ruben Sommarugaⁱ](#), [Rocco Tiberti^o](#), [William J.Ripple^p](#)

^a LEFE, Université de Toulouse, INPT, UPS, Toulouse, France

^b Global Mountain Biodiversity Assessment, Institute of Plant Sciences, University of Bern, Bern, Switzerland

^c Department of Zoology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK

^d MRC Centre for Global Infectious Disease Analysis, Department of Infectious Disease Epidemiology, School of Public Health, Imperial College London, London W2 1PG, UK

^e Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

^f CREAM Campus UAB, Edifici C, Cerdanyola Del Valles, Spain

^g CSIC, Campus UAB, Cerdanyola Del Valles, Spain

^h Ovidius University Constanța, Faculty of Natural Sciences and Agricultural Sciences, Al. Universității 1, 900470 Constanța, Romania

ⁱ Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany

^j Department of Ecology, University of Innsbruck, Technikerstr. 25, 6020 Innsbruck, Austria

^k University of Natural Resources and Life Sciences, Vienna, Department of Economics and Social Sciences, Institute of Social Ecology (SEC), Schottenfeldgasse 29, Austria

^l Freshwater Biological Section, Dept. Biology, University of Copenhagen, Denmark

^m Department of Bioenvironmental Systems Engineering, National Taiwan University, Taiwan

ⁿ Univ. Grenoble-Alpes, IRD, CNRS, Grenoble INP*, IGE, 38000 Grenoble, France

^o

46 Department of Earth and Environmental Sciences – DSTA, University of Pavia, Via
47 Ferrata 9, 27100 Pavia, Italy

48 ^P
49 Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR,
50 USA

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54 **Abstract**

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

75

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

78

79 **Main text**

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

111 Mountains cover a large part of the Earth's terrestrial surface and host a larger proportion
112 of biodiversity than expected by area (Körner et al., 2011). They hold an estimated one-third of

113 terrestrial species diversity (Körner, 2004), and represent 18 of the 36 global biodiversity
114 hotspots (Chape et al., 2005). Nevertheless, even in remote areas human impact is strong, as
115 mountains are part of the global socio-ecological systems which have been shaped by
116 geological forces and by human activities (Turner et al., 1990). In mountains, these impacts and
117 the resulting threats remain largely understudied (Schmeller et al., 2018). Generally, people are
118 unaware of the threats to mountain ecosystems and the services mountains provide to humanity.
119 Mountain ecosystems sequester CO₂, clean waters and the air, regulate climate, provide
120 biomedical resources, and regulate floods (Martín-López et al., 2019). Mountains also provide
121 for the livelihoods of more than half of humanity (Grêt-Regamey et al., 2012; Grêt-Regamey and
122 Weibel, 2020). All these goods and services are provided by mountain ecosystems through
123 complex processes that are maintained by communities of species interacting with each other
124 and with the abiotic environment (Bestion et al., 2021). These mountain communities are
125 comprised of prokaryotic and eukaryotic microbes, fungi, plankton species, woody and non-
126 woody plants, as well as invertebrates and vertebrates. By destructing, rebuilding, changing, and
127 shaping the environment, these species produce organic matter and oxygen as well as bind
128 CO₂.

129 The mountain environment is characterized by extreme temperature regimes, severe
130 weather events and short growing seasons at high altitudes to which species have adapted
131 (Körner, 2019; Payne et al., 2020). In temperate mountains, comparably few species have been
132 able to widely colonize the diverse habitats with montane conditions during the short time
133 window given by the recent demise of glaciers at the end of the last glacial period about 11,000
134 years ago (McCain and Colwell, 2011; Schabetsberger et al., 2013; Valbuena-Ureña et al.,
135 2018). Mountain ecosystems have evolved in partial isolation, separated by a variety of
136 biogeographic barriers. The gradients and dynamics in climate, hydrology, and water chemistry
137 contributed to the formation of a high diversity of microhabitats, harboring numerous species in
138 comparably small areas (McCain and Colwell, 2011), which also explains the high levels of
139 endemism detected in mountains (Rahbek et al., 2019a; b; Swanson et al., 1988). With
140 increasing elevation, montane climates become more extreme, providing habitat for fewer
141 species. System redundancies (i.e. different species with similar functions), available in
142 ecosystems at low altitudes, are increasingly scarce in mountain ecosystems with increasing
143 elevation. Such redundancies usually provide stability to ecosystems (Fonseca and Ganade,
144 2001). The absence of these redundancies renders mountain ecosystem particularly vulnerable
145 to the impacts of global change (Moser et al., 2019). However, multiple threats to mountains are
146 arising from climate change alone. Moreover, interactions with socio-cultural, economic and

147 political developments, such as the exploitation of mountains, e.g. for timber, food production,
148 including fish and livestock, tourism, and hydro-electricity, exacerbate these threats, calling for
149 urgent consideration by policymakers (Figure 1).

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

161 **Climate Change in Mountains**

162 Mountains are defined by rugged terrain and unique climate regimes distinguishing them
163 from lowlands (Körner et al., 2017). The climatic complexity created by mountain topography
164 also influences insolation and air circulation (Dobrowski et al., 2009). Elevation gradients in
165 particular, have a strong impact on many abiotic variables in mountains, and their geographic
166 location is the main control on moisture gradients or seasonality in climate (Körner, 2007). On a
167 regional scale, mountain climate is influenced by large-scale synoptic patterns, proximity to
168 oceans, and the range's longitudinal or latitudinal orientation (Del Barrio et al., 1990). In synergy
169 with climate change impacts, we see important changes in precipitations, temperatures, and
170 frequency of extreme events, such as droughts and floods. Therefore, climate change might be
171 considered the most basic and far-reaching threat to mountains, impacting mountain biodiversity
172 and ecosystems way more intensively as compared to lowland regions (Rangwala and Miller,
173 2012; Scarano, 2019).

174 Precipitation dynamics are not the same in all mountains, and for example, mountains in
175 tropical regions show precipitation maxima at lower and mid-elevations. Temperate mountains
176 typically have an orographic effect and show increased precipitation towards the top, largely
177 driven by different seasonal dynamics in precipitation intensity (Roe, 2005). These precipitation
178 regimes are also regulated by geology, soils, vegetation, and human land use, leading to a large
179 variety of hydrological behaviors and stream flow regimes in global mountain catchments
180 (Dierauer et al., 2018; Zuecco et al., 2018). Climate change-driven precipitation regimes and

181 their increasing variability, especially in mountains, determine long-term change on soil moisture
182 conditions and are important controls on water levels and on the hydroperiods of shallow lakes,
183 ponds and wetlands (Catalan and Bartumeus, 2006; Stephan et al., 2021). As such they are
184 particularly important variables for mountain habitats. Climate change will increase the
185 unpredictability of precipitation patterns (Myhre et al., 2019). Generally, water availability and its
186 predictability is expected to decrease in the future due to lower water storage capacities in areas
187 with glacier cover and higher outflows of excess water during periods of extreme precipitation
188 and melting events (Rajczak and Schär, 2017). These changes will jeopardize the role of
189 mountains as global water towers and the drinking water supply for billions of people (Viviroli et
190 al., 2007) as well as for plants and animals.

191 Trends in warming of mountain surface air temperatures become more and more
192 apparent (López-Moreno et al., 2008; Niedrist et al., 2018; Niedrist and Füreder, 2021), and
193 high-latitude mountains are projected to warm much faster than temperate and tropical
194 mountains (Negi et al., 2021; Nogues-Bravo et al., 2007). Further, warming is accentuated at
195 higher altitudes (Pepin et al., 2015). The intensity of warming depends on the mountain climatic
196 zone, elevation and season (Pepin and Lundquist, 2008). In the Alps, the mean annual
197 temperature has already increased by 1.5 - 2°C since 1970, and future projections predict an
198 additional rise of 0.25 - 0.36 °C per decade within the next century (Einhorn et al., 2015). Similar
199 increases have been projected in other mountain ranges (Urrutia and Vuille, 2009; Valdivia et
200 al., 2013). Increasing temperatures have decreased the annual snow deposition volume with
201 most impacts observed at mid- and lower elevations (Laternser and Schneebeli, 2003), has
202 caused important shifts to earlier snow melt (Kapnick and Hall, 2012), earlier lake-ice melt
203 (Franssen and Scherrer, 2008), and globally accelerated the deglaciation process (Zemp et al.,
204 2015). Yearly, world-wide cumulative glacier mass balance data have been showing significant
205 decreasing trends in glacier thickness (Ripple et al., 2021). The shorter period of snow cover will
206 therefore also shorten the time during which the Albedo effect is active and during which 85% to
207 90% of sunlight is reflected. Hence, further acceleration of the temperature rise in alpine
208 mountain regions needs to be expected. Droughts and extreme precipitation events will globally
209 increase in mountains (Gobiet et al., 2014; Urrutia and Vuille, 2009; Valdivia et al., 2013). For
210 the European Alps, climate projections predict more summer droughts and more extreme rainfall
211 events (Rajczak and Schär, 2017). Subtropical mountains tend to experience more frequent
212 summer droughts (McCullough et al., 2016), while for example the Hindu Kush and the Himalaya
213 have been experiencing increased amounts of extreme rainfall events (Hartmann and Andresky,
214 2013; Wester et al., 2019). Droughts in mountains also lead to an increase of the probability of

215 wildfires in mountain grasslands and forest as the probability of ignition of dry plant material by
216 lightning increases (Stephens et al., 2018). Such wildfires are difficult to extinguish due to the
217 difficult terrain and result in the loss of very large areas (i.e. thousands of hectare) of mountain
218 vegetation with large and long-lasting effects on mountain ecosystems due to low pre-fire
219 production of seeds due to drought and the generally low recovery speed with increasing altitude
220 (Werner et al., 2022).

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

243 Generally, decreasing amounts of annual snow and retreating glaciers have been and
244 will continue to profoundly reshape mountain freshwater habitats and also the terrestrial
245 communities depending on them, threatening mountain species and communities (Jacobsen and
246 Dangles, 2017; Sommaruga, 2015), but also providing new habitats for colonization (Ficetola et
247 al., 2021). Impacts on lowland human populations include difficult to predict water supply (Huss
248 et al., 2017; Viviroli et al., 2007) and destruction of infrastructure through more frequent extreme

249 floods and/or landslides. Climate change will drive the disappearance of many intermediate and
250 ephemeral habitats in mountains due to droughts, with potential severe consequences for
251 mountain biodiversity and biological processes e.g. carbon storage. Climate change will also
252 impact the water regime of many peatlands. Due to the importance of mountain peat- and
253 wetlands as global carbon sinks, the loss of these habitats may further accentuate climate
254 change (De Jong et al., 2010) and UVR impacts (Barnes et al. 2019).

255 **Pollutants in Mountains**

256 Sources of pollution are manifold in mountain ecosystems (Lei and Wania, 2004; Noyes
257 et al., 2009; Shunthirasingham et al., 2010) and we generally lack a global approach to observe
258 environmental pollution and its impact (Brack et al., 2022). Global atmospheric transport of
259 micropollutants (Hussain et al., 2019; Wania and Mackay, 1993; Yang et al., 2010) and local
260 human activities such as mining, logging, agriculture, pastoralism and tourism are the main
261 pollution sources in mountain environments. Increasing pastoralism and livestock units have
262 been shown to put the health of mountain lakes at risk by introducing highly toxic organic
263 pollutants into mountain lakes (Machate et al., 2022). Further, fish stocking introduced heavy
264 metals such as mercury in mountain ecosystems (Hansson et al., 2017b). Other sources of
265 pollution include extreme weather events releasing legacy pollutants from mining, tourists
266 introducing UV blockers as part of personal care products, and atmospheric transport of
267 pollutants releasing a plethora of different molecules (Gross, 2022; Le Roux et al., 2020; Pozo et
268 al., 2007). Mountains are also at risk of acidification when they are located downwind of Nitrogen
269 or Sulphur emission sources and buffering capacity of freshwater is low. In addition, seasonal
270 events such as snowmelt can change pH up to a full unit (Nodvin et al., 1995). Acidic pulses
271 may co-occur with spikes of toxic element concentrations in water (Havas and Rosseland,
272 1995). Further, higher rates of erosion and weathering, as a result of more frequent events of
273 heavy precipitation, may also lead to a higher import of base cations and increase the pH of
274 mountain freshwater and soil (Kopáček et al., 2017). Finally, global change-driven eutrophication
275 and elevated temperatures lead to an increased growth of cyanobacteria, which can produce
276 toxins (e.g. cyanotoxins), with known negative impacts on human health (Catherine et al., 2013;
277 Funari and Testai, 2008; Zanchett and Oliveira-Filho, 2013).

278 The scavenging of atmospheric organic and inorganic pollutants is pronounced at high
279 altitudes and can take the form of dry and wet deposition of aerosols to the ground surface (Daly
280 and Wania, 2005; Le Roux et al., 2016; Le Roux et al., 2020). Atmospheric pollutants in
281 mountains include trace elements (Camarero et al., 2009) (Yang et al., 2010), organic and

282 synthetic pollutants (i.e. current-use and legacy pesticides), polycyclic aromatic hydrocarbons
283 (PAHs), endocrine disrupting compounds (EDCs; Rockström et al., 2009; Meire et al., 2012),
284 and polychlorinated biphenyls (PCBs) or microplastics (Allen et al., 2019; Brahney et al., 2020;
285 Reid et al., 2019). These compounds are introduced into the atmosphere via evaporation, or
286 binding to particles light enough to be carried by wind. Volatile compounds tend to evaporate in
287 warmer environments at lower altitudes and condensation progressively takes place with
288 decreasing temperature as air masses travel over mountain slopes (Blais et al., 1998). Less
289 volatile compounds, such as most of the currently used agricultural pesticides, are not prone to
290 directly evaporate into the atmosphere, but are still transported into the mountain environment
291 as they bind to soil particles, which can be uplifted and carried over longer distance during more
292 extreme wind events (Silva et al., 2018). As a consequence, organic and inorganic
293 micropollutants can be introduced to mountains via the atmosphere and over long distances
294 (Camarero et al., 2009; Bradford et al., 2010; 2013; Fig. 2).

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

305 Despite the accumulated knowledge on global pollution, we still know little about the toxic
306 cocktail accumulating in mountains and its impact on biodiversity (but see Catalan, 2015). There
307 are very few studies that analyzed a broad set of pollutants or even conduct non-target
308 monitoring in a mountain context (Machate et al., 2022), rendering our current knowledge on
309 global mountain pollution patterns largely incomplete. We also know little about each
310 (detectable) compound's physico-chemical characteristics, e.g. the water-air constant (K_{wa}),
311 without which it is difficult to make predictions on future pollution patterns in mountains.
312 Generally, the introduction of new pollutants and changes in pollutant mobilization due to climate
313 change may challenge mountain ecosystem health and increase the vulnerability of species and
314 humans to pathogens, increasing health risks (Brack et al., 2022; Schmeller et al., 2020; 2018).
315 Concerns about adverse toxic effects have especially been raised about, but are not limited to,

316 pollutants introduced from local activities (Machate et al., 2022). In the future, these health risks
317 might further increase, by shifting e.g. pastures to higher altitudes (Mayer et al., 2022), where
318 ecosystems are already under high pressures due to climate change (Herzog and Seidl, 2018)).
319 Tourism and expansion of infrastructure create yet additional pressures on mountain
320 biodiversity.

321 **Vegetation and land use changes in Mountains**

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

349 **Introduced species in mountains**

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

358 For example, tourism drives fish stocking of naturally fishless lakes. In such naturally
359 fishless mountain lakes fish introductions have an outsized impact and drive profound ecological
360 change as a highly efficient aquatic predator is introduced in a naïve environment (Miró and
361 Ventura, 2020). Stocking montane lakes with fish for subsistence purposes has been occurring
362 since the Neolithic, through fish translocations from nearby lakes and rivers. However, before
363 1950 such introductions had limited geographic extent and their impacts were rather local
364 (Moser et al., 2019). Since 1950, introductions of fish increased dramatically as a consequence
365 of the increasing popularity of recreational angling, both in large and relatively small lakes as
366 well as in adjacent wetlands (Hansson et al., 2017b). In addition, the use of small fish, mainly
367 minnows *Phoxinus* sp. (Fam. Cyprinidae), as live baits for trout fishing is causing a new and
368 detrimental wave of invasion (Miró and Ventura, 2015). These introduced fish dramatically affect
369 native communities of mountain lakes. Initially considered ecologically harmless and
370 economically beneficial, introductions continued even when their serious ecological
371 consequences became clear (Knapp et al., 2001). Supported by institutional stocking campaigns
372 and non-authorized translocations by anglers, fish spread rapidly in mountain deep-ponds and
373 lakes of all sizes, as well as in all the colonizable downstream habitats (Ventura et al., 2017),
374 with a long list of negative impacts: i) decline/elimination of native species (e.g., invertebrates
375 and amphibians; (Knapp et al., 2001; Tiberti et al., 2014); ii) cascading effects in the trophic
376 network (Schindler et al., 2001), affecting the chemical/microbiological quality of waters, and the
377 ecological linkages with surrounding terrestrial habitats (Epanchin et al., 2010); iii) impacts such
378 as predation, competition, transmission of pathogens and hybridization on native fish inhabiting
379 downstream habitats (Adams et al., 2001), and iv) further collateral introductions of fish used as
380 live bait (Miró and Ventura, 2015). Hence, fish stocking in mountain lakes is particularly
381 detrimental to water quality and biodiversity, especially as now nearly all these ecosystems are

382 affected, including large lakes, small lakes, ponds, connecting streams and their adjacent
383 mountain wetlands (Ventura et al., 2017).

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

401 **Water abstraction from Mountains**

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

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

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

433 **Threats to and from Mountain Micro-Biodiversity**

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

444 Despite their small size, microbial communities drive major processes in and on animals,
445 plants, as well as in ecosystems (Bates et al., 2022; Bernardo-Cravo et al., 2020; Lin et al.,
446 2021). In a nutrient poor environment such as mountains, microbial communities likely play an
447 important role in synthesizing vital nutrients, thereby increasing energy uptake and growth of
448 plants and animals (Bernardo-Cravo et al., 2020; Schmeller et al., 2020; Sentenac et al., 2022).
449 Similarly, micro-organisms stabilize whole ecosystems by buffering against change through the

450 maintenance of biodiversity and ecosystem processes. For example, the interactions between
451 micro-organisms and plankton constitute the basis of aquatic food webs and determine the
452 functioning of biogeochemical cycles, accounting for more than half of global carbon fixation
453 (Cavicchioli et al., 2019; Purcell et al., 2022). Any kind of disturbance to microbial communities
454 can therefore impact on mountain species and ecosystems.

455 Pathogens, and other microorganisms, can be easily introduced to mountains through
456 pastoralism, tourism or wind drift. However, we remain largely oblivious to how the complexity of
457 the abiotic and biotic environment in mountain ecosystems influences beneficial microbe-species
458 interactions (e.g. microbial loop, mycoloop; (Kagami et al., 2014), host-pathogen interactions
459 (Frenken et al., 2017; Haver et al., 2021; Fisher and Garner, 2020) and health risks for the
460 human population (Schmeller et al., 2018). For example, the transport of microbial pathogens is
461 of special concern for human and livestock health, but also for wildlife and keystone species
462 groups such as amphibians. In particular, fungi and bacteria with resistant aerosolised spores
463 are capable of long-distance transport of e.g. dust (Dadam et al., 2019; Sultan et al., 2005).
464 Global dust dispersion is a natural phenomenon, and occurs when topsoil is transported into the
465 troposphere and carried over long distances by wind currents. However, global warming and
466 changes in land use practices (e.g. deforestation and overgrazing) have accelerated
467 desertification in many areas, resulting in increased dust dispersion even to remote places
468 (Moulin and Chiapello, 2006; Tegen et al., 2004), particularly to high elevation sites (Dong et al.,
469 2020). Further anthropogenic impacts via air pollution can intensify both the abundance and
470 community composition of aerial microbes (Yan et al., 2016), but also for vector-borne diseases
471 (Caminade et al., 2019): Malaria has been found at higher altitudes in mountains in Ethiopia and
472 Colombia (Siraj et al., 2014), incidences of Malaria and Dengue are increasing in Nepal's
473 mountains (Dhimal et al., 2015a), altitudinal upward shifts of Dengue and Chikungunya (Dhimal
474 et al., 2015b), and also ticks have been reported, the latter e.g. leading to increased occurrence
475 of Lyme borreliosis in the Alps (Garcia-Vozmediano et al., 2020).

476 Recent data also suggest that we currently see an increase in eutrophication of mountain
477 lakes globally with an upsurge of the diversity of Cyanobacteria (Ho et al., 2019). Cyanobacteria
478 produce a range of toxins (e.g. microcystins, cyanotoxins, Catherine et al., 2013), which have an
479 important impact on the quality of water (Du et al., 2019; Ho et al., 2019), therewith increasing
480 risks of intoxications for humans and livestock. Epilithic biofilms are a highly reactive component
481 in freshwater systems that play a crucial role in the provision of many ecosystem services
482 (Catalan and Donato Rondon, 2016). Especially in smaller mountain lakes, streams and other
483 waterbodies, epilithic biofilms must be considered the major player in carbon cycling and

484 ecosystem productivity (Vadeboncoeur et al., 2008). A better understanding of the risks of
485 proliferation of potentially harmful microbial groups, pathogenic fungi, bacteria and protists due
486 to human-driven input of phosphorus, nitrogen through atmospheric fertilization and microbial
487 pollution is necessary to improve our predictive abilities for human and wildlife risks. For
488 mountain ecosystems, in particular, our predictive abilities are poor for forecasting pathogen
489 proliferation, the dynamics of potentially harmful microorganisms, and for identifying threatened
490 species and habitats. In a mountain context that could mean that resources of clean drinking
491 water will diminish at a much faster rate than currently predicted (Schmeller et al., 2018) and the
492 important ecosystem services such as CO₂ sequestration and nitrogen retention will be
493 suboptimal or absent (Saunders and Kalff, 2001).

494 **Threats to Mountain Macro-Biodiversity**

495 Mountain areas host many species that live in a delicate balance or at the edge of their
496 distribution and are therefore very susceptible to environmental changes and local extinction.
497 Top predators, such as large carnivores, but also large herbivores play important roles in
498 maintaining mammal, avian, invertebrate, and herpetofauna abundance and richness. Many of
499 these species are threatened with extinction (Ripple et al., 2014) and nearing global collapse
500 (Ripple et al., 2015). Threats to macro-biodiversity in mountains come from chemical pollution,
501 nutrient influx through atmospheric processes and local sources such as livestock (Machate et
502 al., 2022), introduction of non-native taxa, but most importantly from overexploitation and habitat
503 loss (Maxwell et al., 2016). These threats drive the decline of already threatened species
504 (Maxwell et al., 2016) and will change the communities of species, which do not all have the
505 same possibilities of dispersal, recovery and reproduction to avoid disturbances (Kerr and
506 Deguise, 2004; Pimm, 2008). For example, among aquatic organisms, the possibility of dispersal
507 and life traits such as the mode of reproduction are very different among taxonomic groups.
508 Some zooplankton species can reproduce sexually or parthenogenetically, and can produce
509 resting eggs, which can survive for a long time in sediment egg banks (Brendonck and De
510 Meester, 2003; Nielsen et al., 2012). Benthic invertebrates increase their dispersal capacity by
511 producing winged adults. Both strategies may allow a speedy recovery through hatching from
512 resting stages or recolonization by flying. Complete recovery after local extinction, however, is
513 unlikely, and restoration and recovery processes in mountains take a long time (Tiberti et al.,
514 2019). For example, recovery from fish impacts took 11-20 years to obtain a similar food web
515 structure. In the same studies, it was evident that recolonization efficiency of species with a
516 parthenogenetic reproduction mode was higher than for sexual reproduction (Knapp and
517 Sarnelle, 2008; Knapp et al., 2001). In any case, for many species dispersal and recolonization

518 can be limited, when the remaining seed pool is not abundant or found too distant or beyond
519 barriers in the land- or waterscape in mountains, due to their relief. Hence, connectivity between
520 different populations of the same mountain species is reduced, hampering recolonization after
521 disturbance (Heino, 2013). Further, upward shifts of distribution areas are not the same for all
522 mountain species, disrupting long-established communities and their interactions. For example,
523 we understand only inadequately, if the observed upward shift of some mountain plant species
524 due to climate change is met by associated microbes and invertebrates (Grabherr et al., 1994;
525 Steinbauer et al., 2018). Other factors leading to unequal dispersal of formerly associated
526 species might be driven by reduced oxygen availability with increasing elevation (Jacobsen,
527 2020), differences in temperature and drought tolerance (Forero-Medina et al., 2011;
528 Schai-Braun et al., 2021), different adaptation abilities through e.g. seasonality or phenology
529 (Parmesan and Yohe, 2003), or different abilities to change depth distribution. Dysfunctional
530 ecosystems, with lower resilience to further impacts, are the likely outcome (Körner, 2019; Pecl
531 et al., 2017). Due to the non-linear loss of biodiversity (Trisos et al., 2020), the expected
532 extinction of endemic plant and animal species after tipping points have been met (Dullinger et
533 al., 2012), may further increase the dysfunctioning of mountain ecosystems. When this will
534 happen and what will be the outcome will be difficult to predict due to the multitude of factors
535 impacting different species in a community.

536 **Threats to mountain ecosystem services**

537 Negative impacts on mountain biodiversity threatens ecosystem integrity and functioning,
538 and hence also the multiple ecosystem services provided to local communities, populations
539 downstream and local stakeholders, including tourists (Grêt-Regamey et al., 2012; Martín-López
540 et al., 2019; Schirpke et al., 2019). The capacity of mountain ecosystems to provide ecosystem
541 services is deteriorating due to biodiversity loss driven by global change (Palomo, 2017). There
542 is an alarming set of negative consequences from those changes, in stark contrast to the few
543 positive effects that have been reported (Hobbs et al., 2009). These changes will jeopardize
544 water use of at least 1.9 billion people (Immerzeel et al., 2020). Moreover, as a result of glacier
545 decline, water availability will be severely reduced in the dry season, affecting millions of farmers
546 globally (Biemans et al., 2019). Mountains will therefore not remain the reliable and highly
547 important source of water they have been for thousands of years. Even in humid mountain
548 regions, such as the European Alps, droughts have become a problem (Stephan et al., 2021)
549 due to the increasing irregularity of water discharging rates and increasing flood events (Ragetti
550 et al., 2021). The irregularity of water discharging rates in combination with land use and land
551 cover changes can also have synergistic effects on ecosystem functioning, rendering mountains

552 more vulnerable to climate change impacts (Chiang et al., 2014). For the central mountain range
553 of Taiwan, it was shown that these combined effects lead to a relocation or loss of ecosystem
554 services and therefore need to be considered in conservation planning (Lin et al., 2019; Lin et
555 al., 2017).

556 Net primary production (NPP), the amount of biomass or carbon produced by primary
557 producers per unit area and time, is the basis of all ecosystem services and is being altered due
558 to climate change (Haberl et al., 2007; Kastner et al., 2022; Melillo et al., 1993). Overall, there is
559 evidence that increasing temperatures and CO₂ concentrations have increased the NPP of
560 forests when water was not a limiting factor (Boisvenue and Running, 2006). In the Alps,
561 changes in NPP of grasslands on which cattle depend show contrasting regional trends (Jäger
562 et al., 2020). A study combining experimentation and meta-analysis reported stabilization of NPP
563 of grasslands under climate change due to changes in species and increasing allocation towards
564 belowground biomass to resist drought (Liu et al., 2018). Despite a limited body of evidence,
565 local models predict that NPP will increase under climate change in the forests of the mountain
566 region of Changbai in China (Gao et al., 2020).

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

580 **Conclusions**

581 Mountain ecosystems are complex, dynamic, exceptionally fragile and are highly
582 sensitive to global change. They are therefore considered sentinels of change (Schmeller et al.,
583 2018). We are only beginning to understand the functional ecology of mountain ecosystems, but
584 international research already suggests that changing species communities will be detrimental to
585 the environment, to biodiversity and therefore to a critical part of Earth's life-support system.

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

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

615 In this light, and in that of the challenging objectives set by global agendas, including the
616 UN Sustainable Development Agenda, the Convention on Biological Diversity, the recently
617 launched EU Biodiversity Strategy for 2030 or the UN Decade on Ecosystem Restoration 2021-
618 2030, investments are needed for the delivery of policy-relevant science on mountain
619 ecosystems (Körner, 2019), closely following recommendations given in the global biodiversity

620 framework (CBD/WG2020/3/3). Only if we maintain a high ecosystem resilience will we be able
621 to maintain ecosystem functioning and ecosystem services. Threats to mountains are numerous
622 and the repercussions to humanity demand conservation and restoration of mountain
623 ecosystems, as they are an essential and highly sensitive part of the global life-support system.
624

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637

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