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1 The role of abiotic variables in an emerging global amphibian 2 fungal disease in mountains

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14 Abstract

15 The emergence of the chytridiomycete fungal pathogen *Batrachochytrium dendrobatidis*
16 (*Bd*), causing the disease chytridiomycosis, has caused collapse of amphibian communities
17 in numerous mountain systems. The health of amphibians and of mountain freshwater
18 habitats they inhabit is also threatened by ongoing changes in environmental, and
19 anthropogenic factors such as climate, hydrology, and pollution. Climate change is causing
20 more extreme climatic events, shifts in ice occurrence, and changes in the timing of snow-
21 melt and pollutant deposition cycles. All of these factors impact both pathogen and host, and
22 disease dynamics. Here we review abiotic variables, known to control *Bd* occurrence and
23 chytridiomycosis severity, and discuss how climate change may modify them. We propose
24 two main categories of abiotic variables that may alter *Bd* distribution, persistence, and

25 physiology: 1) climate and hydrology (temperature, precipitation, hydrology, ultraviolet
26 radiation (UVR); and, 2) water chemistry (pH, salinity, pollution). For both categories, we
27 identify topics for further research. More studies on the relationship between global change,
28 pollution and pathogens in complex landscapes, such as mountains, are needed to allow for
29 accurate risk assessments for freshwater ecosystems and resulting impacts on wildlife and
30 human health. Our review emphasizes the importance of using data of higher spatiotemporal
31 resolution and uniform abiotic metrics in order to better compare study outcomes. Fine-scale
32 temperature variability, especially of water temperature, variability of moisture conditions and
33 water levels, snow, ice and runoff dynamics should be assessed as abiotic variables shaping
34 the mountain habitat of pathogen and host. A better understanding of hydroclimate and
35 water chemistry variables, as co-factors in disease, will increase our understanding of
36 chytridiomycosis dynamics.

37 Keywords

38 Freshwater ecosystems; *Batrachochytrium dendrobatidis*; Climate change; Hydrology;
39 Aquatic pollution; Interdisciplinary research

40 1. Introduction

41 Wildlife diseases caused by fungal pathogens lead to an attrition of biodiversity, putting at
42 risk ecosystem health and food security (Fisher et al., 2012; Scheele et al., 2019). Aquatic
43 pathogens can affect entire freshwater ecosystems when they cause local extinctions of key
44 biological elements such as amphibians (Hocking and Babbitt, 2014; Whiles et al., 2013).
45 Declines of such key species related to disease and environmental stress should be seen as
46 warning system for global ecosystem change, degradation, and health repercussions for
47 ecosystems, wildlife and the human population (Hopkins, 2007).

48 The chytridiomycete fungus *Batrachochytrium dendrobatidis* (hereafter *Bd*), causing the
49 disease chytridiomycosis, has been linked to the decline of a dramatically increasing number

50 of amphibian species globally (Lambert et al., 2020; Scheele et al., 2019; Wake and
51 Vredenburg, 2008). *Bd* has been described as a generalist pathogen and is showing
52 extraordinary virulence among amphibian species in a wide range of biogeographical and
53 climatic contexts (Daszak et al., 1999; Fisher et al., 2009; Fisher and Garner, 2020).
54 Increasingly globalized trade (Auliya et al., 2016), and the resulting intended or unintended
55 release of amphibian hosts into the wild, is facilitating invasion of highly virulent *Bd* lineages
56 into naïve host populations (Garner et al., 2006; Vredenburg et al., 2013). The *Bd* global
57 pandemic lineage (*Bd*-GPL) is the main driver of epizootic mass mortalities of amphibians
58 and may go back to lineages from Asia. In Asia, coevolution of endemic *Bd* lineages with
59 amphibian hosts may have occurred over millions of years, allowing Asian species to control
60 *Bd* infections and maintain infection burdens at enzootic levels (O’Hanlon et al., 2018).
61 Although *Bd* has been reported to affect amphibians at low and high elevations, severe
62 mass mortalities due to *Bd* have been observed mainly in mountain populations (Lips et al.,
63 2008; Vredenburg et al., 2010a; Catenazzi et al., 2011).

64 The disease expression caused by *Bd* or other pathogens is the result of complex biotic and
65 abiotic interactions, recently conceptualized in a disease pyramid (Bernardo-Cravo et al.,
66 2020). Abiotic variables that impact disease outcome are environmental factors that affect
67 the host, the pathogen, and host microbiome. Mountain freshwaters integrate catchment
68 responses to both global changes and local stressors and can therefore be seen as sentinel
69 ecosystems (Adrian et al., 2009). Future distribution of *Bd* and other aquatic pathogens will
70 depend crucially on pathogen, host and microbiome responses to resulting changes in
71 abiotic variables (Bernardo-Cravo et al., 2020). Effective disease management for
72 conservation of freshwater biodiversity relies on accurately predicting and communicating
73 these results (Schmeller et al., 2018).

74 Here we review abiotic variables that can affect chytridiomycosis disease dynamics in
75 freshwater ecosystems, and discuss them for mountain freshwaters and in the context of
76 global change. Based on the existing knowledge of their importance on infection dynamics,

77 we defined climate, hydrology and water chemistry as abiotic variables. Our review seeks to
78 facilitate interdisciplinary collaboration by proposing a framework for abiotic variables that
79 control *Bd*, and focuses on mountain freshwater ecosystems where global change is
80 expected to have the most extensive impacts on ecosystems and wildlife.

81 2. Abiotic variables controlling *Bd*

82 2.1 Climate and Hydrology

83 Climate affects the physiology of all organisms in the disease pyramid: the pathogen, the
84 host, the host microbiome and biotic factors known to interact with the pathogen, such as
85 nano-, micro- and macro-zooplankton (Bernardo-Cravo et al., 2020). Concerning impacts on
86 hydroclimatic variables on *Bd*, the majority of research has been focusing on temperature,
87 while fewer studies have been investigating the role of precipitation, ultraviolet radiation
88 (UVR) and hydrology.

89 2.1.1 Temperature

90 In culture, optimal growth of *Bd* cultures is between 17°C and 25°C, while temperatures
91 below 17°C slow down fungal growth rates (Piotrowski et al., 2004). Exposure to higher
92 temperatures from 27°C and above were shown to kill *Bd* within hours to days (Johnson et
93 al., 2003; Piotrowski et al., 2004; Schmidt et al., 2011), while *Bd* produced more zoospores
94 at temperatures of 7°C to 10°C (Woodhams et al., 2008). *Bd* exhibits a broad thermal
95 tolerance with differences between *Bd* lineages, where lineages may show differences in
96 fitness related to temperature (Voyles et al., 2017). The general pattern observed in
97 experimental and field studies shows that temperatures below its optimum growth range
98 rarely limit *Bd*, whereas temperatures above the upper tolerance limit of around 26°C can
99 restrict or kill the fungus and thus may offer hosts refuge from infection. Complex controls of
100 temperature on *Bd*, host and host microbiome may explain differences in disease dynamics

101 observed in the laboratory and in the field and may also play a role in the different disease
102 outcomes between mountain sites (Table 1, Figures 1 and 2).

103 Temperatures in the *Bd* optimal range and wet climate were early on related to outbreaks of
104 chytridiomycosis in mountains of Australia (Berger et al., 2004). While the role of climate as
105 single driver of *Bd*-related amphibian epidemics has since been ruled out, climatic variation,
106 temperature extremes and large-scale climatic events such as El Niño are potentially
107 negatively affecting immune defences of amphibians towards infection in favour of the
108 pathogen (Raffel et al., 2015; Rohr and Raffel, 2010). Climate change may be a driver of *Bd*
109 epidemics in mountains, if the altered climatic conditions enlarge the available habitat for the
110 pathogen and affect host immune reactions (Catenazzi et al., 2014). Global and regional
111 species distribution models predict current and future suitable habitats for *Bd* by taking into
112 account its climatic niche, habitat variables such as vegetation and the potential of new
113 introductions (Ron, 2005; Xie et al., 2016). Simulations of future distributions of *Bd* and its
114 sister species *Batrachochytrium salamandrivorans* (*Bsal*) suggest expansions to higher
115 latitudes and elevations, especially on the northern hemisphere (Beukema et al., 2018; Xie
116 et al., 2016). Warming can benefit *Bd* by providing optimal growth temperatures across
117 larger areas and access to more amphibian hosts (Adams et al., 2017).

118 Because amphibians are ectotherms, their physiology (e.g., immunity and growth) is directly
119 linked to environmental temperature. Host resistance to infection is temperature-dependant,
120 and thus host populations can find refuge from disease if temperatures are limiting *Bd*
121 survival or growth (Brannelly et al., 2021). A so-called “behavioural fever” is a defence
122 mechanism for amphibians to fight pathogen infection by raising body temperatures through
123 choosing warm microhabitat (Richards-Zawacki, 2010). The amphibian strategy to seek
124 warm microhabitat may reduce *Bd* infection load (Daversa et al., 2018; Forrest and
125 Schlaepfer, 2011), especially when body temperatures are above 25°C (Rowley and Alford,
126 2013). Increasing amounts of short-term exceedance of daily maximum temperatures above
127 *Bd* tolerance limits or warm microclimates may also decrease infection loads of hosts

128 (Becker et al., 2012; Sonn et al., 2019). These thermal refugia in mountain freshwaters that
129 exist due to topographic heterogeneity may shield freshwater species from rapid warming
130 (Isaak et al., 2016). Thus, amphibian exposure to climatic stress with potential impacts on
131 disease dynamics has to be evaluated taking into account macroclimatic trends and
132 microclimate responses to climate change.

133 More severe infection outcomes might be a consequence of thermal stress lowering
134 amphibian immune responses (Cohen et al., 2017; McMillan et al., 2019). Rising
135 temperatures in mountain freshwaters related to climate warming may impact health and
136 survival of amphibians, especially of early life stages that are restricted to aquatic habitat
137 and have low heat tolerance (Enriquez-Urzelai et al., 2019; Fernández-Loras et al., 2019).
138 While high winter temperatures may favour amphibian resistance to *Bd* (McCaffery and
139 Maxell, 2010), low temperatures in more severe winters can lead to low immune reactivity
140 which may favour severe outbreaks of chytridiomycosis (Rollins-Smith et al., 2011).
141 Temperature effects on the expression of chytridiomycosis (prevalence, infection burden) will
142 crucially depend on how the amphibian host species' thermal optimum relates to
143 experienced temperature change and sudden temperature shifts, as those are likely to
144 favour *Bd* over host adaptability, which is also termed "thermal mismatch hypothesis"
145 (Cohen et al., 2017).

146 These direct impacts of temperature on the host-pathogen relationship are complemented by
147 indirect effects. Such an indirect effect is e.g. driven by zoospore predation by zooplankton
148 that may reduce infection pressure on amphibians (Schmeller et al., 2014). Water
149 temperature being a major factor for determining the growth and species composition of
150 micropredatory zooplankton communities (Schmeller et al., 2018), changes in water
151 temperature have indirect effects on host-pathogen interactions. With changes in
152 temperature regimes, the differences in plankton egg hatching may profoundly differ
153 between years. As there are differences in zooplankton ability to consume *Bd* zoospores
154 (Schmeller et al. 2014), such temperature regimes may constitute or not a zooplankton

155 community able to protect amphibian tadpoles from *Bd* infection. Hence, between years and
156 breeding seasons, amphibian hosts may find very different conditions under which they
157 breed and thus face very different *Bd* infection pressures.

158 In addition, it has been stated that the protective amphibian skin microbiome is also
159 impacted by temperature (Catenazzi et al., 2018). Temperature fluctuations may create
160 opportunities for bacterial replacement on the amphibian skin, which attenuate pathogen
161 transmission and improve host persistence against pathogen infection (Longo and Zamudio,
162 2017). More research is needed on the ecology of the amphibian skin microbiome, but
163 seasons and temperature appear to be important determinants of the composition of
164 amphibian skin microbiome determining disease outcome (Bernardo-Cravo et al. 2020).

165 **2.1.2 Precipitation**

166 It is known that *Bd* is adversely affected and potentially is killed from desiccation (Johnson et
167 al., 2003; Piotrowski et al., 2004). Precipitation regime and vegetation density were shown to
168 be a significant predictor of global pathogen distribution (Liu et al., 2012) and humid climate
169 has been related to more severe chytridiomycosis (Puschendorf et al., 2011) (Table 1).
170 Amphibians in continuous contact with water are more likely to develop lethal
171 chytridiomycosis (Bustamante et al., 2010; Murphy et al., 2011), while dry environments lead
172 to lower mortality (Raffel et al., 2015; Scheele et al., 2015). Precipitation deficits in
173 combination with thermal stress may lower the amphibian capacity of an immune response
174 under climate change (Lertzman-Lepofsky et al., 2020) and thus lower their resistance to
175 infection. This may explain the severe disease outcomes that have led to mass mortalities in
176 some mountain settings (Lampo et al., 2006) (Table 1).

177 **2.1.3 Hydrology**

178 Global warming impacts on precipitation, ice and snow regimes, water levels and
179 hydroperiod of freshwater habitat (Adam et al., 2009; Bavay et al., 2009; Preston et al.,
180 2016; Stewart, 2009), which can be important variables in freshwater pathogen and host

181 distribution, health and life cycles. *Bd* new habitat colonization and inter-annual
182 chytridiomycosis dynamics have been related to glacier melt (Seimon et al., 2017) and
183 changes in lake ice phenology (Clare et al., 2016) (Table 1).

184 Transport by water in streams is a potential directional and long-distance dispersal
185 mechanism for microorganisms (Hohl et al., 2014). Streams may transport pathogens over
186 greater distances downstream in a catchment (Meentemeyer et al., 2012; Rinaldo et al.,
187 2018). The mechanisms of abiotic dispersal of *Bd* in complex landscapes such as mountains
188 are still largely unknown, but dispersal over smaller distances by rain, water movements in
189 lakes or via downstream transport has been suggested (E. A. Courtois et al., 2017; Hagman
190 and Alford, 2015; Kolby et al., 2015; Sapsford et al., 2013) (Table 1). *Bd* dispersal and host
191 reinfections may further be facilitated by short distances between freshwater habitats
192 (Padgett-Flohr and Hopkins, 2010) (Table 1).

193 Freshwater ecosystems with seasonal regimes can be a pathogen-free refuge for
194 amphibians if *Bd* has not been able to colonize them or to survive their dry-out (Scheele et
195 al., 2015). But seasonal and extreme climatic events may put amphibians inhabiting
196 mountain freshwaters at higher risk, when they change the availability of breeding habitats
197 and impact on the density of tadpoles due to changes in the volume of water bodies
198 (McMillan et al., 2019; Scheele et al., 2015). *Bd* may further profit from drought through
199 higher presence of reservoir species, hosts weakened by hydric stress (Adams et al., 2017;
200 Catenazzi et al., 2013; Walls et al., 2013) or crowding of hosts causing higher pathogen
201 transmission rates (Adams et al., 2017; Elodie A. Courtois et al., 2017). Changes in snow
202 amount and snow cover duration are potential additional negative effects on amphibian
203 health when they lead to shifts breeding phenology, with earlier breeding start due to earlier
204 snowmelt (Corn, 2003). Climate warming will continue to have far-reaching consequences
205 for the mountain hydro- and cryosphere and potentially influence disease dynamics in
206 mountain freshwater ecosystems.

207 **2.1.4 Ultraviolet radiation**

208 High UVR levels in mountain freshwaters may induce *Bd* mortality (Hite et al., 2016) and
209 radiation in the UV-B spectrum was found to lower *Bd* infection levels in hosts (Ortiz-
210 Santaliestra et al., 2011) (Table 1). However, sublethal effects of UV-B may also hamper
211 immune responses of amphibians to pathogen infection (Cramp and Franklin, 2018).
212 Negative effects of UVR on amphibians have mostly been studied for radiation in the UV-B
213 spectrum and can depend on sensitivity of amphibian species to radiation (Blaustein et al.,
214 1994; Blaustein and Belden, 2003) and on the presence of cofactors such as pathogens,
215 contaminants or low temperatures that characterize their mountain habitats (Blaustein and
216 Kiesecker, 2002; Davidson et al., 2002; Kiesecker and Blaustein, 1995; Morison et al.,
217 2020).

218 It has been shown that UV-B changes the aquatic microscopic species composition due to
219 different radiation sensitivity of species (Sommaruga, 2001). Hence, UV-B radiation intensity
220 may lower the presence, abundance, and diversity of zooplankton micropredators of *Bd*,
221 increasing the infection pressure on amphibians (Hite et al., 2016). Currently, we know little
222 about the effect of UV-B on the amphibian skin microbiome as a first immune response
223 capacity of amphibians against infections. We can therefore only suggest that earlier findings
224 (Ortiz-Santaliestra et al., 2011) may be linked to UV-B impacts on the amphibian skin
225 microbiome.

226 The threat of damaging UV-B for biota, including mountain amphibians threatened by
227 disease, is likely to persist in the future. Besides the potential damage to atmospheric ozone
228 by new ozone depleting agents (Fang et al., 2019), a larger threat of UV-B exposure to
229 mountain freshwater organisms can be a change in freshwater ice phenology, leading to
230 earlier annual exposures to high radiation levels in spring (Williamson et al., 2014).
231 Especially in freshwater habitats that offer only limited protection from UV-B radiation, for
232 example due to shallow water levels or low dissolved organic carbon (DOC) in water,
233 freshwater organisms may face radiative stress (Kiesecker et al., 2001; Sommaruga, 2001).
234 On the other hand, upwards shifts of the treeline (Gottfried et al., 2012), glacier melt

235 (Sommaruga, 2015) or extreme precipitation events (Sadro and Melack, 2012; Williamson et
236 al., 2014) may potentially increase future import of DOC in water, which would lead to lower
237 UV-B levels in water.

238 2.2 Water chemistry and pollution

239 Water chemistry, including pH, salinity and the presence of environmental pollutants in water
240 may impact chytridiomycosis outcomes through their effects on pathogen, host or the
241 aquatic microbiome. Water chemistry and pollution impacts on *Bd* and chytridiomycosis
242 occurrence in a mountain context are still largely lacking evidence (but see Chestnut et al.,
243 2014, Table 1).

244 **2.2.1 Acidity and salinity**

245 Water acidity and salinity levels in water affect both *Bd* and amphibian hosts. *Bd* has been
246 suggested to be limited in its habitat by pH 6 - 7 (Johnson and Speare, 2005; Piotrowski et
247 al., 2004). So far, only a few studies have investigated the effect of salinity on pathogen
248 infections, including *Bd*. It is known that elevated salinity of more than 2 ppt in water can
249 hamper *Bd* growth by disturbing osmotic balance (Stockwell et al., 2015), reduce *Bd*
250 infection loads in saline ponds and wetlands at low elevation study sites (Heard et al., 2014;
251 Stockwell et al., 2015), or block *Bd* transmission altogether (Clulow et al., 2018). Amphibians
252 can adapt to environments with low pH (Räsänen et al., 2003). Nevertheless, low pH in
253 water may lead to increased micropollutant concentrations with potential lethal to sublethal
254 effects (e.g. stress, malformations, slow growth) on amphibians (Freda, 1991; Havas and
255 Rosseland, 1995). Aquatic zooplankton community composition is as well influenced by
256 acidity (Hořická et al., 2006) and salinity (Gutierrez et al., 2018). Thus, impacts of pH on the
257 pathogen-host system are possibly indirect via the effects of those variables on host
258 susceptibility and planktonic predators of *Bd*.

259 Many mountain freshwaters have recovered from acidification related to reduced deposition
260 of acid pollutants (Catalan et al., 2013). Present-day acidification can play a role if mountains

261 are located downwind of Nitrogen or Sulphur emission sources buffering capacity of
262 freshwater is low (Nodvin et al., 1995). Higher rates of erosion and weathering as a result of
263 increased events of heavy precipitation may on the other hand lead to a higher import of
264 base cations to freshwaters, thus to potential increase in pH (Kopáček et al., 2017). Salinity
265 fluctuations in water may play a role when hurricanes occur in wetlands of coastal mountains
266 (Walls et al., 2013). Due to direct and indirect effects of acidity and salinity changes on the
267 physiology of *Bd*, and on physiology and community composition of amphibians and
268 microbiome, those abiotic variables should be assessed in chytridiomycosis surveys.

269 **2.2.2 Pollutants**

270 Organic micropollutants, including many pesticides, have been shown to be detrimental to
271 *Bd* and amphibian health. Fungicides and different commonly used pesticides lead to *Bd*
272 mortality and were shown to inhibit *Bd* zoospore production (Johnson et al., 2003).
273 Fungicides and pesticides show adverse effects on amphibian health but due to potential
274 effects on hosts and *Bd* their effect on infection dynamics can be equivocal (Battaglin et al.,
275 2016). Exposure to pesticides at the tadpole stage can have a long-term negative impact on
276 the amphibian immune system (Rohr et al., 2014). Differential responses of disease
277 dynamics to pesticides have been related to the importance of changes in sensitivity of
278 amphibians during their lifecycle (Rumschlag and Rohr, 2018). Exposure timing and type of
279 pesticide may affect tadpole survival chances in case of simultaneous pathogen infection
280 (Hanlon and Parris, 2014). While pesticides in water might be limiting *Bd*, they may favour
281 *Bd* infections of tadpoles and mortality due to *Bd* infection in metamorphic or adult
282 amphibians at a later, terrestrial life stage (Rohr et al., 2017). The impact of presence of
283 inorganic compounds on *Bd* growth and survival may be depending on their concentration in
284 water. For example, high concentrations of copper due to mining or agriculture were
285 hypothesized to locally limit *Bd* growth (Boisvert and Davidson, 2011). Inorganic
286 micropollutants such as potentially harmful trace elements may accumulate in amphibian
287 tissue and lead to poor amphibian health and higher amphibian mortality (Unrine et al., 2007,

288 2004). As such, mercury (Hg) bioaccumulation was found in amphibian populations close to
289 local pollution hotspots originating from historical mining spots (Hothem et al., 2010) or
290 industrial sites (Bergeron et al., 2010).

291 Catchment sources of pollutants may be increasingly mobilized by extreme climate, such as
292 longer hot and dry periods and heavy rain (Zaharescu et al., 2016b). Remote sources deliver
293 pollutants to mountain freshwater ecosystems. For example, pesticides originating from
294 downwind agriculture have been found in mountain amphibians and have been suspected to
295 play a role in amphibian declines (Davidson and Knapp, 2007; Fellers et al., 2004). In
296 addition, emerging pollutants are currently being introduced into mountains with their effects
297 on freshwater organisms still widely unknown (Brahney et al., 2020; Catalan et al., 1992;
298 Reid et al., 2019).

299 3. Future research directions

300 The usage of more uniform metrics and spatiotemporal data resolutions should be
301 considered for future studies of climate impacts on chytridiomycosis dynamics, as they allow
302 for a higher comparability between studies and places when investigating disease
303 expression under climate change. Different abiotic variables and metrics with different
304 spatiotemporal resolutions used in studies (see also references in Table 1) may each relate
305 to different responses of freshwater ecosystems, pathogens and hosts.

306 Widely available are climatic data of spatial resolution in the km-range, and with annual or
307 monthly temporal resolution (James et al., 2015; Muths et al., 2008; Rohr and Raffel, 2010;
308 Sette et al., 2015). Compared to other vertebrates, the importance of microclimates (cm-
309 scale) increases significantly for ectotherms such as amphibians (Enriquez-Urzelai et al.,
310 2019), which may be one explanation for heterogeneous responses of disease dynamics to
311 climate change (Slavich et al., 2014). Despite the importance of micro- and topoclimate,
312 regional climate variables (>100 m spatial resolution) are essential as they allow for long-
313 term studies of climatic variables in order to approximate climate effects on *Bd* and its host.

314 We should take advantage of high-resolution data and models to assess climate and
315 hydrology at spatiotemporal scales relevant for amphibian host, host microbiome and
316 pathogen. For disease dynamics, climate extremes and sudden temperature shifts may be
317 more important than long-term mean temperature changes, as they generally favour
318 pathogens over hosts according to the thermal mismatch hypothesis (Cohen et al., 2017).
319 Data with fine temporal resolution of at least daily resolution are needed to describe these
320 climatic variations sufficiently well. The availability of small and inexpensive data loggers has
321 made it more feasible to track microclimatic variables such as air and water temperature and
322 its short-term variability (Bramer et al., 2018). Recent microclimate models can even take
323 into account amphibian heat- or moisture budget and allow to model water temperatures as
324 mechanistic variable (Catenazzi et al., 2014; Enriquez-Urzelai et al., 2019).

325 Temperature changes should be studied together with changes in moisture conditions, as
326 the interaction of both variables defines amphibian behaviour and physiological vulnerability
327 to warming (Lertzman-Lepofsky et al., 2020) and will impact their response capacities to
328 disease. Hydrological changes relevant to *Bd* and host, such as changing soil moisture
329 conditions, accumulation of surface water, snow melt and runoff dynamics need to be
330 tracked at high, at least daily, temporal resolution. We need to include hydroperiod and
331 water level changes of mountain freshwaters in sampling for *Bd* due to their importance for
332 disease dynamics in mountain amphibians. Here, high-resolution remote sensing may allow
333 to study changes in catchment surface water levels, and for example monitor hydroperiods
334 of ephemeral or permanent wetlands, but also changes in the volumes of water bodies
335 (Lertzman-Lepofsky et al., 2020; Maclean et al., 2017; Raffel et al., 2015). Metrics such as
336 the topographic wetness index and the topographic position index can help to indicate water
337 saturated areas or wetlands in topographic depressions, facilitating mapping of intermediate
338 or ephemeral ponds (Riley et al., 2017). Mountain freshwater ecosystems should further be
339 evaluated in terms of their hydrological and landscape connectivity, in order to identify
340 freshwater sites at risk for infection spill-over (Hagman and Alford, 2015; Sapsford et al.,

341 2013; Scheele et al., 2015). Similar hydrological functioning of different mountain
342 catchments, for example due to climate, geological and topographical setting may help to
343 extrapolate freshwater habitat characteristics from one mountain setting to another
344 (Zaharescu et al., 2016a). Further, hydrologic models, remote sensing and new ground-
345 based monitoring techniques may also allow transfer of parameters and conceptual models
346 of hydrologic functioning between different catchments (Hrachowitz et al., 2013). Increasing
347 our knowledge on functioning and changes of hydrology will enable further understanding of
348 chytridiomycosis dynamics in mountain freshwater ecosystems.

349 A better knowledge of the complex interactions between UVR (UVB) and the host-pathogen
350 system in mountain freshwaters is crucial. More work on post-hatching effects of UVR on
351 hosts (Vance T. Vredenburg et al., 2010) and on indirect effects on host infection dynamics
352 has been recommended (Hite et al., 2016). We need more understanding of the
353 immunosuppressive effects of UVR in amphibians and on the amount of radiation necessary
354 to produce adverse effects (Cramp and Franklin, 2018). Further, DOC concentrations and
355 changes in water levels or hydroperiod of shallow freshwater habitat should be included in
356 sampling, as both variables regulate UVR exposure to *Bd* and amphibians in mountains as a
357 potential cofactor in disease vulnerability and disease outcomes in mountains.

358 The interactions between water chemistry and disease in amphibians are still poorly
359 understood and we therefore call for more research attention and more studies to assess
360 those stressors in mountain amphibian populations. Changes in weathering and element
361 cycles, persisting accumulation of atmospheric pollution and mobilization of legacy pollution
362 are threats to freshwater ecosystems that are likely to exacerbate stress to mountain
363 amphibian populations in the future. We need to identify the types of pollutants present in
364 mountain freshwaters and the local pollution fingerprint (Schmeller et al., 2018). New
365 dynamics of pollutant transfer to freshwater ecosystems (Bogdal et al., 2010; Hansson et al.,
366 2017; Le Roux et al., 2020) and new types of pollutants (Allen et al., 2019; Reid et al., 2019)
367 call for experimental and field studies in mountain ecosystems that evaluate local pollution

368 threats as additional stressors to amphibians facing disease. Finally, timing of changes in
369 water chemistry is crucial for amphibians as their life stages show different sensitivities
370 towards changes in water chemistry (Hanlon and Parris, 2014; Rumschlag and Rohr, 2018).
371 We therefore need more frequent and increased sampling efforts to collect water samples
372 during periods when amphibians are most vulnerable and when the aquatic environment is
373 most dynamic, for example during spring snowmelt (McClain et al., 2003) to better
374 understand how anthropogenic pollution may drive disease.

375 4. Conclusions

376 It is vital that we acknowledge the role of amphibian health as an early warning system for
377 current degradations in freshwater and environmental health. Amphibian mortalities due to
378 chytridiomycosis disease are evidence of profound changes in mountain aquatic
379 ecosystems. Mountains are complex and dynamic environments, which translates into
380 differences of observed disease between global mountain ranges. Climate, hydrology and
381 water chemistry can either directly impact *Bd* distribution, growth and virulence, or act as co-
382 factors impacting amphibian health and exposure to potential infection. Our review reveals
383 that interdisciplinary research is critical to advance disease ecology and conservation efforts
384 for amphibians in mountains, which extends to freshwater health at low elevations. Global
385 climatic changes with more frequently expected climate extremes and the response of
386 microclimates, hydrologic processes, water chemistry and pollutant levels in freshwater
387 ecosystems represent important leverages in disease dynamics. While mountains can offer
388 climatic refuges for freshwater organisms in microhabitats due to topographic heterogeneity
389 (Isaak et al., 2016), amphibians are likely to be negatively affected by climate warming at the
390 same time as pathogens may experience advantages over hosts (Cohen et al., 2017). The
391 usage of data with high spatiotemporal resolution will benefit future epidemiology models
392 and will lead to better predictions of environmental controls on wildlife disease dynamics. In
393 order to achieve effective and preventive conservation management, *Bd* occurrence and
394 disease dynamics should be studied in different mountain settings, using the same abiotic

395 metrics with comparable spatiotemporal data resolution. Interdisciplinary formulated,
396 spatially transferable models for landscape epidemiology will facilitate risk assessment and
397 conservation efforts in the perspective of present and future environmental change.

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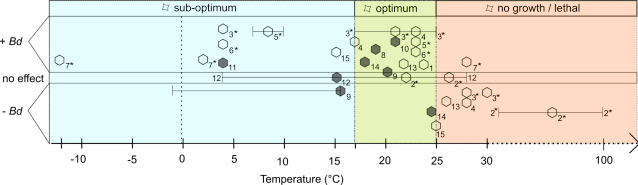
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Figure captions:

Figure 1: Temperature effects on *Batrachochytrium dendrobatidis* (*Bd*) from selected studies (studies represented by hexagons). Temperature effect on *Bd* infection intensity / *Bd* zoospore count, divided into favouring *Bd* (+ *Bd*, *rectangle upper half*) limiting/eliminating *Bd* (- *Bd*, *rectangle lower half*) or with no effect on observed *Bd* status on host / in culture (no effect, *rectangle between upper and lower half*). Studies on *Bd* growth in culture are marked with asterix (*). Open hexagons: experimental study; closed diamonds: field study. The vertical location of studies (hexagons) within each of the divisions (+*Bd* / -*Bd* / no effect) has no significance. Horizontal bars connected to hexagons represent a temperature range that was used in the respective study. References in subscripts: 1 Berger et al., 1998; 2 Johnson et al., 2003 ; 3 Piotrowski et al., 2004; 4 Berger et al., 2004 ; 5 Woodhams et al., 2008; 6 Voyles et al., 2012 ; 7 Voyles et al., 2017; 8 Pounds et al., 2006 ; 9 Muths et al., 2008; 10 Bosch et al., 2007; 11 Walker et al., 2010 ; 12 Knapp et al., 2011; 13 Schmidt et al., 2011 ; 14 Becker et al., 2012; 15 Raffel et al., 2015. (The studies for this figure were selected in order to represent the general pattern of temperature effects on *Bd*, and are not an exhaustive list of all studies on this subject.)

Figure 2: The disease pyramid (modified, after Bernardo-Cravo et al., 2020), illustrating the role of temperature as abiotic variable impacting all corners of the disease pyramid: host, pathogen, host microbiome, and their habitat as part of the environment. Temperature regulates growth, immune system and behaviour of the host, growth and virulence of the pathogen as well as growth and species composition of the host microbiome (dashed axes). We stress the importance of temporal variability of abiotic variables such as temperature on disease dynamics (represented by a clock: short-term variations and long-term change, extreme events, seasonal changes).



Environment



Temperature

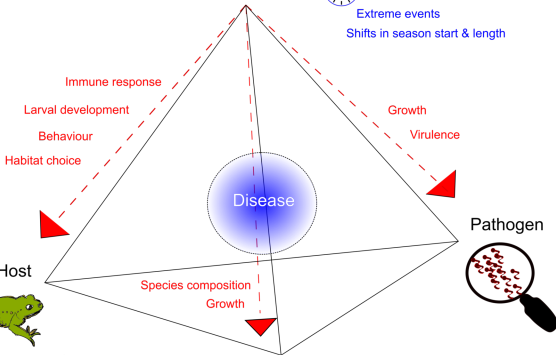


Short-term variability

Long-term change

Extreme events

Shifts in season start & length



Immune response

Larval development

Behaviour

Habitat choice

Host



Disease

Growth

Virulence

Pathogen



Species composition

Growth

Host microbiome



Table 1: Mountain field studies relating abiotic variables of categories climate, hydrology, UVR and water chemistry to observed *Bd* distribution and/or infection severity or outcomes.

Abiotic Category	Abiotic Variable	Study location / mountain range	Variable range / conditions in experiment / environment	Effect on <i>Bd</i>	Study on <i>Bd</i> only / <i>Bd</i> & host (species)	Reference
Climate	Temperature (Water)	Great Dividing Range & coast, Eastern Australia	<i>Bd</i> infected hosts, Laboratory infection experiments at 17 °C; 23 °C; 27 °C	Chytridiomycosis surveys in the field show higher amphibian mortalities in winter	<i>Bd</i> & host (34 amphibian species in field surveys and <i>Mixophyes fasciolatus</i> in infection experiment)	Berger et al., 2004
Climate	Temperature (Air)	Central & South American tropical mountain sites	Field surveys, daily minimum and maximum temperatures converge towards 17 – 25 °C (<i>Bd</i> optimum growth)	Chytrid thermal optimum hypothesis: observed daytime cooling and nighttime warming suggest <i>Bd</i> epidemics related to recent shifts of daily temperature range towards <i>Bd</i> optimum	<i>Bd</i> & host (<i>Incilius periglenes</i>)	Pounds et al., 2006

Climate	Temperature (Air)	Rocky Mountains, USA	Field surveys, daily maximum temperature < 17 – 25 °C (<i>Bd</i> optimum growth)	Lower <i>Bd</i> infection intensities observed at higher altitudes explained by low maximum temperatures	<i>Bd</i> & host (<i>Anaxyrus</i> <i>boreas boreas</i>)	Muths et al., 2008
Climate	Temperature (Air)	Peñalara Natural Park, Guadarrama Mountains, Spain	Field surveys of mountain ponds, Increasing number of days with maximum temperature > 21 – 27 ° C	Increased <i>Bd</i> infection intensity explained by warmer temperatures related to recent regional warming	<i>Bd</i> & host (<i>Alytes</i> <i>obstetricans</i>)	Bosch et al., 2007
Climate	Temperature (Air)	Guadarrama Mountains & Pyrenees, Spain	Field surveys of mountain ponds, average / minimum temperature warmest quarter & minimum temperature coldest month	No evidence for temperature control on <i>Bd</i> prevalence; weak relationship of infected sites and temperatures < <i>Bd</i> optimum	<i>Bd</i> & host (<i>Alytes</i> <i>obstetricans</i>)	Walker et al., 2010
Climate	Temperature (Water)	Sierra Nevada, California, USA	Field surveys, Mountain lakes, temperature range of 4 – 28 °C; metrics: average annual temperatures and	No <i>Bd</i> limitation by lower water temperatures with increasing altitude	<i>Bd</i> & host (<i>Rana</i> <i>sierrae</i>)	Knapp et al., 2011

			number of days between 15 – 25 °C (for 0 – 100 d/year)			
Climate	Temperature (Water)	Adirondack Mountains, USA	Field surveys, Mountain Ponds, metrics: average daily temperature & average daily minimum and maximum temperature, average daily maximum temperature frequently above > 25 °C	Highest <i>Bd</i> infection intensities observed at closed canopy sites with lower water temperature	<i>Bd</i> & host (<i>Craugastor fitzingeri</i> , <i>Litoria lesueuri</i>)	Becker et al., 2012
Climate	Precipitation (drought)	Andes, Venezuela	Survey of museum specimen for signs of infection, Analysis of precipitation records revealed deficit of annual accumulated rainfall	Suggested climatic forcing of chytridiomycosis: Severe drought event coincides with epidemics due to <i>Bd</i> infection	<i>Bd</i> & host (<i>Atelopus carbonerensis</i> , <i>Atelopus mucubajensis</i> , <i>Atelopus sorianoi</i> , <i>Mannophryne cordilleriana</i>)	Lampo et al., 2006
Climate	Precipitation (Humid climate)	Queensland, Australia	Field surveys, mountain river, lack of canopy cover, low annual precipitation, dry	<i>Bd</i> suggested to be limited by drier and warmer	<i>Bd</i> & host (<i>Litoria lorica</i> , <i>Litoria nannotis</i>);	Puschendorf et al., 2011

	vs. dry climate)		conditions at dry sclerophyll forest site vs wet conditions in rainforest	microclimatic conditions and favored by wet conditions		
Hydrology	Lake ice regime	Pyrenees, France	Field survey, timing of lake thaw from water temperature data, mountain lake	Early timings of lake spring thaw followed by high prevalence of infection	<i>Bd</i> & host (<i>Alytes obstetricans</i> , <i>Bufo spinosus</i> , <i>Rana temporaria</i>)	Clare et al., 2016
Hydrology	Habitat availability	Cordillera Vilcanota, Andes, Peru	Field survey, deglaciation ponds	Recently developed deglaciation ponds allowing <i>Bd</i> and host to extend habitat range to higher altitudes	<i>Bd</i> & host (<i>Pleurodema marmorata</i> , <i>Bufo spinulosus</i> , <i>Telmatobius marmoratus</i> , <i>Rhinella spinulosa</i>)	Seimon et al., 2017
Hydrology	<i>Bd</i> dispersal via water (Hydrological connectivity)	Cusuco National Park, Honduras	Field survey, <i>Bd</i> in rainwater samples	Short-distance dispersal of <i>Bd</i> zoospores by rainwater as possible spreading mechanism	<i>Bd</i>	Kolby et al., 2015

Hydrology	<i>Bd</i> dispersal via water (Hydrological connectivity)	Queensland, Australia	Field experiment & survey, rainforest streams,	Transport of <i>Bd</i> zoospores in streams as downstream transmission mechanism	<i>Bd</i> & host (<i>Litoria rheocola</i>); <i>Bd</i> & host (<i>Litoria serrata</i>);	Sapsford, Alford, & Schwarzkopf, 2013; Hagman and Alford, 2015;
Hydrology	<i>Bd</i> dispersal via water (Hydrological connectivity)	Pyrenées, France	Field experiment & survey, Co-housing of infected & non-infected hosts, mountain lake	<i>Bd</i> zoospore dispersal in water as a means of passive transmission of the pathogen	<i>Bd</i> & host (<i>Alytes obstetricans</i>)	Courtois et al. 2017
Hydrology	Habitat density / habitat connectivity	Sierra Nevada, USA	Field survey, distance between ponds	Perennial ponds and ephemeral ponds in spatial proximity (1000 – 1500 m) are <i>Bd</i> hotspots in the landscape	<i>Bd</i> & host (<i>Anaxyrus boreas halophilus</i> , <i>Ambystoma Californiense</i> , <i>Pseudacris regilla</i> , <i>Taricha torosa torosa</i> , <i>Rana draytonii</i> , <i>Rana catesbeiana</i>)	Padgett-Flohr and Hopkins, 2010

UVR	UV-B (280-315 nm)	Peñalara Natural Park, Guadarrama Mountains, Spain	Field experiment & survey, full or no exposure to UV-B, mountain pond	<i>Bd</i> prevalence lower in hosts exposed than those not exposed to UV-B	<i>Bd</i> & host (<i>Bufo Bufo</i>)	Ortiz-Santaliestra et al., 2011
UVR	UVR (250–399 nm)	Peñalara Natural Park, Guadarrama Mountains, Spain	Field experiment & survey, full or no exposure to UVR, mountain pond	UVR exposure reduced <i>Bd</i> survival by 50 %; suggested further controls on UVR and thus on disease are hydroperiod, pond depth, dissolved organic carbon (DOC)	<i>Bd</i> & host (<i>Salamandra salamandra</i> , <i>Alytes obstetricans</i>)	Hite et al., 2016
Water chemistry	pH	Western US field sites (100 – 2500 m elevation)	Field survey, pH 6.5 – 10.4	Negligible effect of pH range on detection probability of free <i>Bd</i> zoospores	<i>Bd</i>	Chestnut et al., 2014

