

# 1 **Environmental parasitology: stressor effects on aquatic parasites**

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15

## 16 **Abstract**

17 Anthropogenic stressors are causing fundamental changes in aquatic habitats and to the

18 organisms inhabiting these ecosystems. Yet, we are still far from understanding the diverse

19 responses of parasites and their hosts to these environmental stressors and predicting how these

20 stressors will affect host-parasite communities. Here, we provide an overview of the impacts of

21 major stressors affecting aquatic ecosystems in the Anthropocene (habitat alteration, global

22 warming, and pollution) and highlight their consequences for aquatic parasites at multiple levels

23 of organisation, from the individual to the community level. We provide directions and ideas

24 for future research to better understand responses to stressors in aquatic host-parasite systems.

25

## 26 **Aquatic parasites in the Anthropocene**

27 Human impacts on the world are manifold, many of them being linked to negative effects on  
28 the global ecology. Such anthropogenic influences have increased greatly in recent decades,  
29 which is why this era is often summarised as the Anthropocene [1]. Although it is still being  
30 debated whether this epoch constitutes an official geological unit of time, it is characterised by  
31 the fact that humans have become the most influential species on the planet and have caused  
32 fundamental changes in the atmosphere and the entire ecology of the Earth [1], with far-  
33 reaching consequences for all levels of organisation of life, including parasites [2]. Freshwater  
34 habitats are particularly affected by human impact and subsequent species loss [3,4]. Evaluation  
35 of historical trends has revealed that freshwaters are diminishing and that these ecosystems are  
36 degrading faster than their terrestrial equivalents [5]. Consequently, freshwater environments  
37 have higher rates of biodiversity loss than terrestrial ecosystems [3,6]. Accordingly, the recent  
38 study by Wood et al. [2] for the first time clearly demonstrated a dramatic loss of aquatic  
39 parasite diversity in recent decades, which has gone largely unrecognised. In the current review,  
40 we therefore focus on possible reasons for human-induced or enhanced aquatic parasite decline  
41 and changes in parasite dynamics, with a focus on habitat alteration, global warming, and  
42 pollution [4], and highlight the effects of these **stressors** (see Glossary) on the fate of aquatic  
43 parasites and their interactions with the associated hosts at different levels of organisation (i.e.  
44 from the individual to the community level). This provides an up-to-date synthesis of the  
45 advancements, novel findings, and perspectives in environmental parasitology during the last  
46 decade, and points out key research questions and directions that will significantly advance this  
47 field of research.

48 The effects of environmental stressors on host-parasite associations can affect the life cycle of  
49 metazoan parasites at various points depending on the characteristics of host-parasite  
50 associations such as host specificity, life cycle complexity, transmission strategy, location on  
51 the host (endo- vs ectoparasites) and distribution range, to name a few. Parasites may either

52 directly (stressor effects on parasite stages) or indirectly (stressor effects on hosts) respond to  
53 an increase or decrease of stressors (**Box 1**). Overall, the persistence of a parasite species and  
54 its population in an ecosystem is determined by the weakest link in the chain: the most sensitive  
55 and specific host, or the most delicate parasite life stage. According to theory and recent  
56 findings, the diversity of **heteroxenous** parasites with complex (multi-host) life cycles (e.g.  
57 Digenea, Cestoda, Acanthocephala) is thus more likely to decrease in stressful environments  
58 than the diversity of **monoxenous** parasites (**Box 2**; e.g. Monogenea, Microsporidia) ([2,7–10]  
59 and references therein). In contrast to heteroxenous parasites, monoxenous parasites might in  
60 fact benefit from the presence of stressors, e.g. if stressors impair the host's defence against  
61 pathogens [11]. Additionally, an increase in environmental stressors can favour populations of  
62 tolerant host species, while populations of more sensitive species disappear. The resulting  
63 higher host population density increases the likelihood of transmission of monoxenous parasites  
64 between hosts [7,12].

65 Furthermore, specialist parasites will rely on hosts with large and stable populations, as they  
66 are not able to switch to other host species, and therefore face a higher risk of secondary  
67 extinction [13]. Accordingly, it can be assumed that parasites with simple life cycles  
68 (monoxenous, generalist) prevail in stressful environments, while parasites with complex life  
69 cycles (heteroxenous, specialists) will be more successful under more stable conditions (**Box**  
70 **2**). For heteroxenous parasites, the most sensitive host will be the limiting factor for the  
71 extinction risk [14]. There is evidence that parasite diversity and overall prevalence decline  
72 with increasing stressor intensity (e.g., [2,8,15] and that an increase in parasite richness and  
73 overall prevalence occurs with the recovery from stressors [16–18]. Due to their complex  
74 interaction with stressors or environmental conditions in general, parasites reflect the state and  
75 complexity of ecosystems and can therefore eventually be used as **bioindicators** to assess  
76 environmental conditions [19].

77 In the following sections, we will focus on selected stressors that characterise the  
78 Anthropocene, i.e. habitat alteration, global warming and pollution, and highlight their impact  
79 on the qualitative and quantitative responses of parasites (**Figure 1**). We also provide  
80 perspectives and ideas for future research, which will expand the knowledge in the field of  
81 aquatic environmental parasitology and will help to fill the missing gaps.

82

### 83 **Habitat alteration and the occurrence of parasites**

84 Freshwater habitats are particularly affected by degradation and subsequent species loss [3,4].  
85 Numerous human activities lead to habitat alteration and thereby jeopardise freshwater  
86 ecosystems and their species, including habitat modification, river diversion, fragmentation and  
87 flow regulation as well as agricultural and urban landscape expansion [5,20,21]. Accordingly,  
88 freshwater ecosystems are degrading faster and have higher rates of biodiversity loss than  
89 terrestrial ones [3,5,6]. In contrast, functional and resilient ecosystems are characterised by high  
90 habitat diversity and species richness (e.g.[22]), which should also be mirrored by a high  
91 parasite diversity as the association between parasite and host species richness suggests [23,24].  
92 More specifically, there is indication that parasite species richness is low and total abundance  
93 is high in stressed ecosystems, while parasite abundance decreases and diversity increases under  
94 conditions with absent or low stressor impact (see **Box 2**; [7]). Based on these findings, the idea  
95 of parasites as indicators of biodiversity or ‘ecosystem health’ was developed [12,25,26], as  
96 high parasite diversity is always dependent on diverse and complex interactions among free-  
97 living species [23]. The indicative value of parasites relates to their need of one to several host  
98 species as a prerequisite of their occurrence (see a trematode life cycle in **Figure 2** as an  
99 example). Therefore, life cycle-related traits of parasites are key to understanding and  
100 explaining stressor effects on parasite diversity [27]. Particular promising life cycle traits are  
101 the number of required obligate host species (life cycle complexity) as well as the specialisation  
102 of the parasites regarding the host range (generalists vs. specialists) [28].

103 In contrast to aquatic systems, terrestrial systems are rather well studied regarding the effects  
104 of habitat alterations on host-parasite assemblages (e.g. [29,30]). For example, a recent long-  
105 term study of terrestrial host-parasite systems has shown that habitat loss and fragmentation are  
106 likely to have severe impacts on parasites. Food web models predict that parasites with multiple  
107 obligate hosts are at greater risk of extinction, as local extinction, or reduction in abundance of  
108 one host leads to a bottleneck in the parasite's life cycle. Imbalances in the abundance of  
109 multiple hosts over time are likely to be common following disturbance, making parasites with  
110 complex life cycles particularly vulnerable to habitat fragmentation and other disturbances [29].  
111 Although these results originate from a terrestrial study, they are most likely transferable in  
112 their broad outlines to aquatic habitats. One of the few aquatic studies that supports this  
113 hypothesis is based on the premise that low host abundance and diversity due to environmental  
114 degradation and anthropogenic habitat alterations lead to a reduction or even extirpation of  
115 heteroxenous and specialised parasites [9]. Schwelm et al. [9] studied the trematode fauna of a  
116 protected natural reserve in Germany and found a tendency towards higher parasite diversity  
117 and prevalence under near-natural conditions. Furthermore, a comparison with other similarly  
118 large-scale faunal studies from Europe and North America revealed that life cycle complexity  
119 (number of obligate hosts involved in the life cycle) is higher in near-natural areas than in those  
120 that are more anthropogenically influenced [9]. Global warming might further exacerbate these  
121 dynamics [2]. In contrast, no clear pattern was found when investigating monoxenic  
122 microsporidian-host associations among near-natural and restored habitats at two German river  
123 catchments [31]. Microsporidians may have found a way to persist even in a degraded habitat  
124 despite low host abundance via resistant spores in the environment and to re-colonise it after  
125 stressor release. The ability of host switching [28] and different transmission mechanisms could  
126 also contribute to the persistence of members of this parasite group [31].  
127 The evidence to date on the relationship between parasites and habitat fragmentation is diverse  
128 and sometimes contradictory (see [28,29] and references therein), which is not surprising given

129 the complexity of possible links between habitat alteration, biodiversity loss and parasite  
130 prevalence [32,33]. But at the same time this also highlights the importance and necessity of  
131 differentiated approaches and investigation of various traits of parasites, their host associations  
132 and ecological requirements at an individual, local and global level [29].

133 In view of the loss of biodiversity with all its devastating consequences, long-term planning  
134 and implementation of countermeasures are now urgently needed. Restoration and the  
135 establishment and expansion of protected areas, such as the recently agreed global expansion  
136 of protected areas to a minimum of 30% ([https://www.cbd.int/article/cop15-cbd-press-release-](https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022)  
137 [final-19dec2022](https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022)) are just a few examples. Parasites are usually ignored in such large-scale  
138 projects. However, if one follows the assumptions discussed in this chapter, it seems reasonable  
139 to assume that protection and restoration measures may lead to an increase not only in free-  
140 living biodiversity in restored and protected areas, but also in parasite diversity. From an  
141 ecological perspective, this is of course to be welcomed, as parasites generally not only  
142 contribute to biodiversity, but can also show other positive effects on ecosystems (e.g. [34,35]).  
143 However, even from a disease ecology perspective, this should not be a concern in principle, as  
144 it is likely that **dilution effects** increase parasite diversity but not abundance per se [36].  
145 Fortunately, issues such as parasite extinction and conservation have received more attention  
146 recently (e.g. [2,35,37]) and even a global plan for their protection and inclusion in conservation  
147 programmes has been developed lately [35].

148

### 149 **Global warming**

150 Global warming is probably the most drastic and far-reaching result of anthropogenic activity  
151 on our planet [38]. Climate change encompasses many related and associated effects beyond  
152 temperature increases, ranging from changes in the occurrence and severity of extreme weather  
153 events to modulation of stratification, water levels, flow regimes or ocean currents [39,40].  
154 However, warming as such has been identified as one of the main drivers of the increased

155 frequency of parasite disease risks across terrestrial and aquatic ecosystems [41]. Temperature-  
156 driven modifications of parasite life cycles and their possible interactions with other abiotic and  
157 biotic parameters are expected to have serious ramifications for aquatic parasites and their hosts,  
158 but are hard to predict due to the inherent complexity of host-parasite systems [39]. Various  
159 studies have explored the possible impacts of temperature changes on host-parasite interactions,  
160 and the implications for disease dynamics, ecological communities, and whole ecosystems. In  
161 this section, we summarise recent key findings on the diverse, and sometimes unexpected,  
162 impacts of temperature changes on individual host-parasite interactions, parasite transmission  
163 dynamics and life histories, and ecosystem-wide consequences for aquatic systems.

164 The more complex a parasite life cycle is (i.e., the more steps that are required to complete it),  
165 the more susceptible the parasite is expected to react to environmental and climate changes,  
166 which might lead to neutral, positive, or negative effects on the parasite transmission and  
167 population dynamics [13]. Among metazoan parasites, digenean trematodes have some of the  
168 most complex life histories, often requiring multiple vertebrate and invertebrate hosts, and  
169 direct and indirect transmission pathways to complete their life cycle (**Figure 2**). The exposed  
170 free-living transmission stages (miracidia and cercariae) are susceptible to direct environmental  
171 influences. Moreover, the asexual production and emergence of cercariae in the first  
172 intermediate mollusc host as well as the infectivity in the second **intermediate host** are strongly  
173 positively correlated with temperature [42–45]. However, while increases in temperature  
174 positively affect cercarial transmission dynamics (e.g., cercarial emission and dispersal  
175 activity), these impacts can vary substantially between sympatric trematode species, and  
176 warming temperatures might shift parasite community structures in ecosystems rather than  
177 favour multiple species equally [46]. It remains questionable if these temperature-induced  
178 increases in cercarial emergence can be maintained over longer periods of time or are just short-  
179 term peaks that level off after host acclimation (see [47,48]).

180 Various non-host organisms can interfere with the free-living parasite transmission stages, e.g.,  
181 via predation that leads to a dilution of parasites in the system (e.g., [49,50]). Recent studies  
182 have highlighted that temperature-mediated increases in parasite productivity and infectivity  
183 can be counteracted by predation on free-living parasite stages, which might potentially offset  
184 increases in disease risk under climate change [51]. However, it remains uncertain to what  
185 extent the elimination of trematode larvae by filter-feeders can compensate for increased  
186 transmission rates, and if these processes can mitigate disease risks in ecosystems under  
187 temperature shifts [52]. Although trematode transmission and infectivity are typically expected  
188 to increase under warmer temperatures [39,41,42] with concomitant decreases in host resistance  
189 to infection [53], trematode transmission windows in coastal systems have been shown to be  
190 negatively affected under higher temperatures, which can hinder the possibility for trematodes  
191 to flourish in warming oceans [45]. Accordingly, the question which parasites will be able to  
192 profit in warming marine and freshwater systems will depend on a wide variety of biotic and  
193 abiotic factors as well as the ecology of the specific host-parasite systems. Similar varying  
194 patterns have been observed for parasitic protists with direct (monoxenous) life cycles in  
195 aquatic systems, where the direction and magnitude of the changes in disease occurrence is  
196 strongly influenced by the ecological features of each disease [54]. This brings into question  
197 the generality of the susceptibility of complex vs. simple life cycles to temperature changes and  
198 will require further testing in the future that takes the net effect of temperature on a parasite's  
199 entire life cycle into account (see [55]).

200 Temperature significantly influences the outcome and strength of species interactions across  
201 ecosystems (see [56]). Accordingly, not only parasite transmission dynamics of free-living  
202 parasite stages are strongly temperature-dependent, but also the effects of parasitic infections  
203 on their hosts and their involvement in food webs can be drastically modulated by temperature.  
204 For instance, trematode-infected snails have been shown to change their thermal preference,  
205 which likely increases parasite proliferation and transmission [57]. Many parasites that rely on



206 trophic transmission at some point during their life cycle can modify the behaviour of their  
207 hosts to facilitate such transmission processes. The plerocercoid stages of the cestode  
208 *Schistocephalus solidus* grow faster in their fish host at higher water temperature, enhancing  
209 trophic transmission to final bird hosts as well as parasite reproduction and fecundity, while at  
210 the same time shifting their host's thermal preference to warmer temperatures [58]. Different  
211 and diverging temperature optima of hosts and parasites have been shown for a range of  
212 *Schistocephalus*-stickelback systems, with potentially negative impacts on the hosts and drastic  
213 fitness gains for the parasites [59]. Understanding the thermal mismatches between hosts and  
214 parasites and identifying the underlying mechanisms of these processes are central requirements  
215 to improve our predictions of parasite and disease dynamics in warming ecosystems [60].  
216 Contrastingly, field studies from the same host parasite system found little evidence that  
217 temperature modified host-parasite interaction, and highlighted the possible difference between  
218 laboratory experiments and natural settings [61]. Likewise, studies from acanthocephalan host-  
219 parasite systems have shown that temperature changes within existing and predicted  
220 distribution ranges appear to have no impact on these behavioural changes in hosts and  
221 subsequent transmission outcomes [62,63]. Altogether, these findings emphasise the stark  
222 differences across various host-parasite associations. Moreover, even within the same host-  
223 parasite system, host genotypes from different geographical regions can show highly varied  
224 temperature responses, highlighting that disease and infection dynamics may be difficult to  
225 predict within individual parasite species [64,65].

226 Remarkably, experimental exposure of blue mussels infected with the trematode *Himasthla*  
227 *elongata* revealed a complex parasite-temperature interaction. While moderate parasite loads  
228 and increased temperature showed synergistic detrimental effects on mussel survival, high  
229 infection intensities appeared to nullify the negative effects of temperature stress on mussels  
230 [66]. Other studies revealed that warming and trematode infection increased HSP70 levels and  
231 changed the snail's biochemical condition but concluded that this might make them more

232 susceptible to thermal stress [67]. It therefore remains to be tested if, and under which  
233 conditions, some parasite infections could provide even a beneficial effect for their hosts under  
234 thermal stress, which would contradict our common view that parasites are exclusively harmful  
235 to their hosts. Besides these possible impacts of established infections on hosts, recent studies  
236 have highlighted the role of non-consumptive or avoidance (i.e., pre-infection) effects that can  
237 significantly alter host behaviour and performance in aquatic ecosystems and are potentially  
238 strongly temperature dependent [68–70]. Overall, these examples underline the complex and  
239 sometimes unexpected outcomes of individual host-parasite interactions in warming aquatic  
240 ecosystems.

241 These individual-level effects on host-parasite systems can translate into ecosystem-wide  
242 impacts that structure and regulate populations and communities. Existing outdoor mesocosm  
243 approaches could demonstrate strong detrimental synergistic effects of elevated temperature  
244 and parasitism on the diversity and structure of coastal crustacean communities with potentially  
245 negative impacts on the whole coastal habitat [56]. Likewise, recent mesocosm studies from  
246 freshwater systems showed similarly complex interactions between parasites and elevated  
247 temperature on invertebrate community composition and host abundance that had the potential  
248 to significantly alter the structure and dynamics in the affected ecosystem [71]. However, such  
249 community-level studies that test how parasites and temperature can shape and regulate the  
250 functional structure of aquatic ecosystems under climate change pressure remain scarce.  
251 Although the examples highlight that temperature effects on parasites and their hosts can have  
252 far-reaching ecological impacts, the actual relationship between temperature and disease is  
253 often complex and the varying underlying mechanisms are only understood for individual  
254 parasites and disease agents [51] and references therein. Moreover, the first century-scale time  
255 series of fish parasite abundance in North American coastal ecosystems revealed a drastic  
256 decline of parasite taxa with complex life cycles (>10% decline per decade) as the result of  
257 increasing temperature [2]. Future work must therefore continue to bring together experimental

258 approaches investigating mechanistic interactions between host-parasite systems and  
259 environmental changes with ecosystem-level studies of climate change effects on populations  
260 and communities in aquatic systems [55]. Such approaches will allow to better integrate this  
261 knowledge with modelling approaches to more accurately anticipate, monitor and mitigate the  
262 impacts of climate-driven disease dynamics in natural ecosystems [72].

263

## 264 **Pollution**

265 Elevated pollutant concentrations in aquatic systems are mostly of anthropogenic origin, but  
266 **geogenic sources** (e.g. various metals) might also pose a threat to organisms, including  
267 parasites. On a global scale, the diversity of environmental contaminants has increased over the  
268 last decades in the course of industrialisation and is still increasing every year [73]. As  
269 environmental contaminants, a broad spectrum of chemicals of different origin such as organic  
270 compounds (e.g. PAHs, PCBs, pesticides, drugs, micropollutants, etc.) and their metabolites,  
271 as well as nutrients, salts, various metals, organometallic compounds and others are known (e.g.  
272 [74,75]). The impact of pollutants as stressors on parasites and their associated hosts depends  
273 largely on their concentration. As summarised by Sures and Nachev [10] using the example of  
274 fish parasites, the mode of action of contaminants can be direct or indirect (see **Box 1**) which  
275 applies not only to fish parasites and their hosts but also to other taxonomic host groups. As a  
276 result of pollution impact, parasites respond with changes in their community structure (e.g.  
277 considering the ratio of heteroxenous to monoxenous parasites; for details see [15]) and  
278 diversity [55,76,77], which can be used in environmental parasitology as a measure for  
279 assessing stressor intensity. Thus, healthy and diverse aquatic ecosystems (free from pollution  
280 and other stressors) are generally assumed to have a greater diversity of parasites ([26], see also  
281 previous sections).

282 **Aqueous pollutants** can be accumulated to a high degree by parasites, making them promising  
283 sentinels for pollution (summarised by [8,10]). Accordingly, parasites provide valuable

284 information on the **bioavailability** of pollutants and might help in their detection and  
285 quantification when pollutants are present in very low concentrations in the environment but  
286 are accumulated to an enormous degree in the parasites. Various parasitic taxa have been  
287 studied in terms of their accumulation capacity, with acanthocephalans, cestodes and nematodes  
288 in particular being very sensitive sentinels for metals (see e.g.[8] and references therein).  
289 Similarly, a high accumulation capacity has also been demonstrated for some organic  
290 compounds such as PCBs [78,79]. The use of parasites such as cestodes and acanthocephalans  
291 to demonstrate the bioavailability of substances can represent a promising tool for  
292 ecotoxicological studies. Detection of certain substances in the body of these taxa is proof that  
293 these substances must be considered biologically available because they had to cross teguments  
294 and membranes due to the lack of a digestive tract in cestodes and acanthocephalans. If micro-  
295 or nanoparticles can be detected in these gutless helminths as shown for particulate platinum-  
296 group metals (e.g. [80]), they must be bioavailable. In addition to metallic nanoparticles, this  
297 could also be a promising approach to study the uptake, accumulation, and effects of nano- and  
298 microplastic particles in the aquatic environment. Additionally, the high accumulation potential  
299 of parasites was found to be beneficial for the hosts by reducing the pollutant burdens within  
300 the host body and thereby decreasing harmful effects on the physiology (reviewed by [8]; see  
301 also [81,82]).

302 However, high pollutant levels in the environment represent also a driving evolutionary force,  
303 as studies on the adaptation of fish populations to high Hg levels reveal (e.g. [83]). It therefore  
304 seems possible that various parasite taxa might have adapted to specific pollutants and  
305 developed tolerance to contamination although evidence from the literature is lacking so far.  
306 For example, in contrast to the expected patterns of reduced diversity, higher diversity of  
307 parasite communities of the intertidal klipfish, *Clinus superciliosus*, was found at marine sites  
308 that had relatively high metal concentrations due to geogenic conditions [84]. In this study,  
309 acanthocephalans, cestodes and parasitic isopods were more abundant at sites with higher

310 element levels. It therefore can be assumed that the fish hosts involved, as well as their parasites,  
311 have a high tolerance to geogenic background concentrations if the host-parasite systems could  
312 evolve adaptation measures. Similarly, higher abundance and prevalence of acanthocephalans  
313 was found at sites with poorer ecological status according to biological indices and bacterial  
314 loads when comparing different river sections [85].

315 Besides individual effects due to contaminants, there may also be interactive effects of climate  
316 change and/or habitat degradation in combination with pollutants. For example, acidification  
317 has a significant influence on bioavailability and toxicity of pollutants, both of which increase  
318 for metals at lower pH levels [86]. More diverse microhabitats and a higher diversity of free-  
319 living organisms (especially plant communities) on the other hand may act as pollutant sinks  
320 (e.g. [87]) and thereby reduce concentrations of available pollutants. Extreme weather events  
321 (periods of droughts or higher precipitation) can increase the pollution loads as well. For  
322 example, higher precipitation intensifies the process of erosion within drainage areas of aquatic  
323 habitats and contaminants of anthropogenic and geogenic origin can enter the water bodies with  
324 surface run-off [75,88]. Several studies on aquatic parasites showed that parasites react  
325 sensitively to anthropogenic activities in the drainage area such as increased urbanisation and  
326 pollution [89] and to extended land (habitat) destruction such as clearcutting [90]. Marcogliese  
327 et al. [90] already provided evidence of the effects of precipitation events on the composition  
328 of parasite communities of fish, which were associated with changes in discharge, flow velocity  
329 and overall water quality. Such qualitative and quantitative changes can be expected to affect  
330 the composition, bioavailability and toxicity of pollutants. The latter can be similarly affected  
331 by droughts, with high evaporation rates leading to an increase of concentrations in the water  
332 column of small aquatic ecosystems. In addition to this, high temperatures lead to reduced  
333 aqueous oxygen concentrations and changes in the redox potential, which results in different  
334 speciation of metals and an increase of their bioavailability as well [86]. In such scenarios, a  
335 complex set of stressors (high temperatures, anoxia and elevated pollution) might impose severe

336 effects on free-living communities and their associated parasites (see e.g. [91]). Although a  
337 large number of studies related to pollution and parasites have been published in the last  
338 decades, there are still various knowledge gaps, which represent a good starting point for future  
339 studies on the interaction between parasites and pollutants (see **Box 3**).

340

### 341 **Future perspectives**

342 Many of the stressors outlined above affect host-parasite systems on the molecular and  
343 biochemical level and the parasitized hosts often show a pattern of response different from  
344 uninfected hosts. Numerous studies addressed this topic in the last decades to obtain a more  
345 general understanding of the combined effects of environmental stressors and parasites on the  
346 hosts involved in the life cycle. The outcomes largely depend on the host-parasite system and  
347 the respective stressors studied, with increasing and decreasing effects of the parasites on the  
348 stressor response (see reviews by [8,92]). Even for the same group of parasites (trematodes) the  
349 response to a stressor (herbicide) in the same snail host species, can be opposite regarding  
350 cercarial emergence and host mortality [93]. Parasites not only affect the response of their hosts  
351 to stressors but vice versa, specific stressors can also change the host response to parasites. For  
352 example, the thiol concentrations increased with the abundance of a parasitic nematode  
353 (*Oswaldocruzia* sp.) in Northern leopard frogs if atrazine exposure was low but decreased in  
354 infected frogs under high atrazine exposure levels [94]. Even though the individual results  
355 obtained are highly valuable, we are still far from a general understanding of the physiological  
356 response of parasitised hosts that are additionally affected by other stressors and related  
357 community effects. Therefore, we highlight the suggestions for future research in this field  
358 shown in **Box 3** to achieve deeper insight into host-parasite interactions under multiple stressor  
359 exposure.

### 360 **Concluding remarks**

361 Although recent studies have brought major advancements in our understanding of the effects  
362 of stressors on host-parasite systems, there are still major challenges to face. For many  
363 ecosystems, our knowledge on the parasite communities remains limited and life cycles of many  
364 parasites are not fully known. Taking all research approaches into account, the overarching  
365 vision should be to understand why the responses of the hosts to the combination of parasite  
366 and other stressors are sometimes contradictory in different species and to be able to generalise  
367 the results to build models that allow predictions of stressor impacts (see **Outstanding**  
368 **questions**). Ultimately, these findings will guide us on the path to preserve biodiversity, both  
369 free-living and parasitic, from further decline.

370

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627 **Glossary**

628 **Aqueous pollutants:** Pollutants solved in surface or groundwaters.

629 **Bioavailability:** The bioavailability describes which proportion of a pollutant present in the  
630 environment can be taken up by organisms.

631 **Bioindicator:** Organisms that show a measurable reaction to environmental impact (stressors)  
632 at the individual (molecular, cellular, tissue) or population level (e.g. population decline).

633 **Dilution effect:** Removal of free living parasite stages from the environment by non-target-  
634 hosts that can be infected but where the parasite cannot be propagated further, or via predation  
635 of parasite stages. Leading to a decrease of infection pressure on target hosts.

636 **Geogenic sources:** Source of pollutants (e.g. metals) originating from weathering of bedrock.

637 **Heteroxenous life cycle:** Parasite life cycle involving two or more host species (indirect life  
638 cycle).

639 **Intermediate/final (definitive) hosts:** In the intermediate host, the parasite can grow and  
640 develop and it can multiply asexually. In the final (definitive) host the parasite reaches the  
641 mature adult stage and reproduces sexually.

642 **Microcosm, Mesocosm:** Experimental systems that mimics natural conditions in a controlled  
643 setup by using multiple species. Link between field study and highly controlled laboratory  
644 experiment.

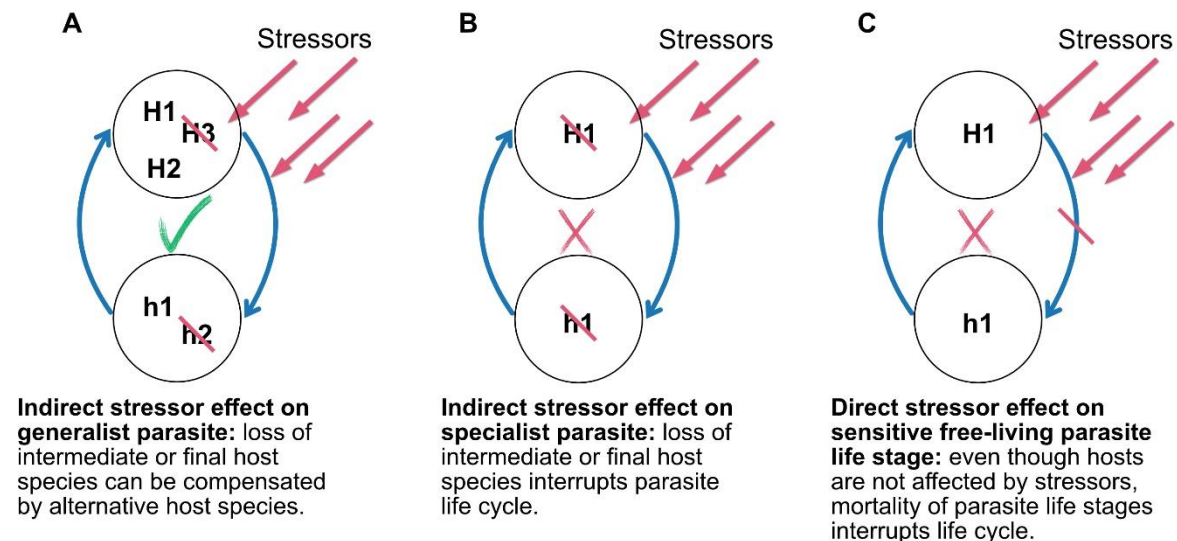
645 **Monoxenous life cycle:** Parasite life cycle involving a single host species (direct life cycle).

646 **Stressor:** Any impact that leads to environmental variables, individuals, populations,  
647 communities, or ecosystem functions exceeding the range of normal variation relative to  
648 undisturbed reference conditions.

649

### Box 1. Effects of environmental stressors on host-parasite associations

If generalist host-parasite systems are exposed to deleterious stressors, alternative hosts can take over the role of intermediate or **final hosts** when individual host species fail (indirect effect on parasite) (**Figure IA**), while for specialised parasites the harmful effects of stressors always disrupt the life cycle (**Figure IB**). Besides stressor effects on hosts, the survival and presence of parasites in ecosystems may be determined by direct stressor effects on the parasitic stages (e.g. temperature effects on parasite stages in poikilothermic hosts) or on the free-living larval stages of parasites species (e.g. coracidia, miracidia, cercariae or other larval stages; see **Figure IC**).



**Figure I (in Box 1).** Hypothetical life cycles of parasites using final (Hx) and intermediate hosts (hx). The different scenarios (A-C) show possible consequences of severe stressor impacts. Red lines: host lost from system, ✓ life-cycle maintained, X: life cycle interrupted.

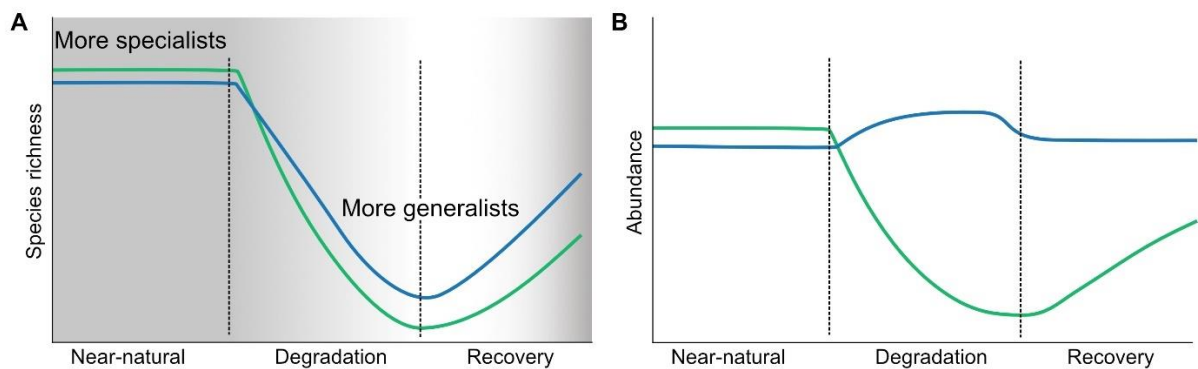
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653 **Box 2. Assumed development of parasite dynamics over time**

654 In a scenario of environmental degradation (e.g. increasing pollutant concentration in the  
 655 water), species numbers, but also community composition, will change with varying  
 656 environmental conditions from proportionally more complex life cycles and higher numbers of  
 657 host specialists under near-natural conditions to lower life cycle complexity and more host  
 658 generalists under degraded conditions (**Figure IA**). After stressor release (phase of recovery),  
 659 the composition of the parasite community is still different from the near-natural situation with  
 660 a dominance of few species with less complex life cycles, whereas specialists with complex life  
 661 cycles can only establish once the habitats allow for recolonization with the required host  
 662 species (**Figure IA**). The relative abundance of mono- and heteroxenous parasites will also  
 663 change. Monoxenous parasite communities will become species poor, with few but abundant  
 664 species that parasitise the remaining hosts during stressor impact (degradation phase) (**Figure**  
 665 **IB**). Relative abundance of heteroxenous parasites will decrease in degraded environments. The  
 666 relative abundance of both mono- and heteroxenous parasites will return to the pre-degradation-  
 667 state, but with delay for heteroxenous species (**Figure IB**). The observed development of the  
 668 parasite communities can vary for some stressors (e.g. nutrients) that might, for example, lead  
 669 to an increase of the abundance of heteroxenous parasites due to increasing numbers of  
 670 intermediate hosts.



671  
 672 **Figure I (in Box 2). Hypothetical development of parasite communities before (Near-**  
 673 **natural), during (Degradation) and after the occurrence of a stressor (Recovery) in an**

674 **aquatic system.** A: Changes in species richness. B: Changes in parasite abundance. Green line:  
675 heteroxenous parasites. Blue line: monoxenous parasites. Grey areas indicate higher number of  
676 host specialist parasites, while more light areas indicate higher numbers of generalists.  
677 The graphs show a hypothetical situation of a stressor intensity that is strong enough to affect  
678 communities but without complete eradication of all parasite species.

679



**Box 3. Directions for future research***Research foci on model host-parasite systems*

Studies applying different stressors to the same host-parasite system or the same stressor to a different host-parasite system with an identical experimental setup will allow the comparison of results and will reveal general trends. This would require more cooperative research projects that allow the development of coordinated experimental protocols between different working groups. A prerequisite is the reliable identification of the studied parasites by appropriate taxonomy specialists including molecular vouchers that prevent the use of morphologically similar, but genetically distinguishable cryptic species in subsequent work [95]. Methodologically, **microcosm** and **mesocosm** studies might bridge the gap between field and mere laboratory studies as they provide controlled and replicated conditions, but at the same time allow to study biotic interactions of different species. To our knowledge there are to date only few studies addressing stressor (temperature) effects in a multi-host and multi-parasite setting in experiments [45,56,71]. The responses of different host species were complex and contradictory due to interactions of the species among each other and presence or absences of the parasite in the system had a fundamental effect on the free-living community. Similar studies are required to assess ecosystem effects of parasites that cannot be elucidated when studying single host species.

*Clearly defined parasite life strategies*

There is a huge variety of life strategies among parasites that differ greatly in their effect on the host. For example, there is a major difference between parasites that are adsorptive feeders (e.g. adult cestodes, acanthocephalans) and those that actively feed on host tissue (e.g. nematodes, monogeneans) which is also reflected by the trophic position of these parasites

[96,97]. Similarly, effects on the hosts are also largely dependent on the developmental stage of a given parasite species. Usually, larval parasites inside their intermediate hosts are more detrimental to their hosts than adult parasites within their **definitive hosts** in order to facilitate transmission to the final host (e.g., via trophic transmission, host manipulation, or by producing large numbers for parasite transmission stages). Such differences exist not only between the major groups of parasites, but may also be important for more closely related species (e.g. trematodes forming sporocysts or rediae in the snail intermediate host). Therefore, studies should be designed using parasites with different life strategies under similar conditions (ideally same host, same stressor exposure) with precise descriptions of the relevant life cycle traits (e.g. life cycle complexity, specialisation of the parasites regarding the host range).

#### *Field studies on re-emergence and community formation of parasites after restoration*

Theoretical considerations would suggest that host diversity and abundance will be reduced with increasing stressor presence and effects. As a consequence, parasite richness will decrease ([2]; ecosystem degradation, **Box 2**). If stressors reach a threshold level, parasite life cycles will collapse and consequently, parasites will disappear. Upon stressor release and recovery of the system, the number and diversity of generalist parasites with less complex life cycles can be expected to increase, while specialists with complex multi-host life cycles are assumed to re-establish later, after conditions and host populations have recovered (**Box 2**). These theoretical predictions should be tested under “real world conditions” by including analyses of parasite abundance and prevalence data at field sites which had been subjected to ecological restoration.

#### *Description of processes involved in pollutant uptake by parasites*

Basic aspects regarding the uptake, storage and detoxification of contaminants by parasites as well as a deeper mechanistic understanding of how pollution and parasites interact require further elucidation. Additionally, there is still a limited number of studies on marine host parasite systems as well as on pollutant accumulation potential of parasites of bird and mammalian hosts. Apart from metal accumulation, studies on uptake of micropollutants (organic compounds and their metabolites) and various micro- and nanoparticles (e.g. plastic, metals) by parasites still remain scarce. Likewise, the role of parasites as sinks for organic pollutants needs to be further investigated, as few initial studies demonstrated the beneficial effects of parasites on concentrations in infected fish [78] and on host physiology [81,82].

*Study host transcriptomes to detect the target genes and metabolic pathways affected by stressors and parasites*

“Omics” based applications, mainly transcriptomics, have been used successfully to study parasites of medical or veterinarian significance (e.g. [98,99]). However, transcriptome sequencing to detect differential expression of genes in infected or stressor exposed hosts is also suitable for ecological questions. The major advantage to measuring a preselected set of biomarkers via qPCR or using biochemical assays is that genes or pathways regulated during parasite infection or exposure to stressors can be identified. This is particularly relevant if there is no prior knowledge on the effects of the parasite or stressor applied. To date, only few studies have applied transcriptomics to study stressor effects (temperature, pollution or combinations of both) on parasitized hosts in aquatic ecosystems [100–102]. Further research efforts are needed to increase the number of sequenced genomes of relevant hosts and parasites, to improve interpretation and functional annotation of the transcripts. Besides transcriptomes, next generation sequencing can provide further valuable tools e.g. for the

assessment of parasite biodiversity using environmental DNA (eDNA) or the identification of (micro-)parasite communities by metabarcoding (e.g. [103–106]).

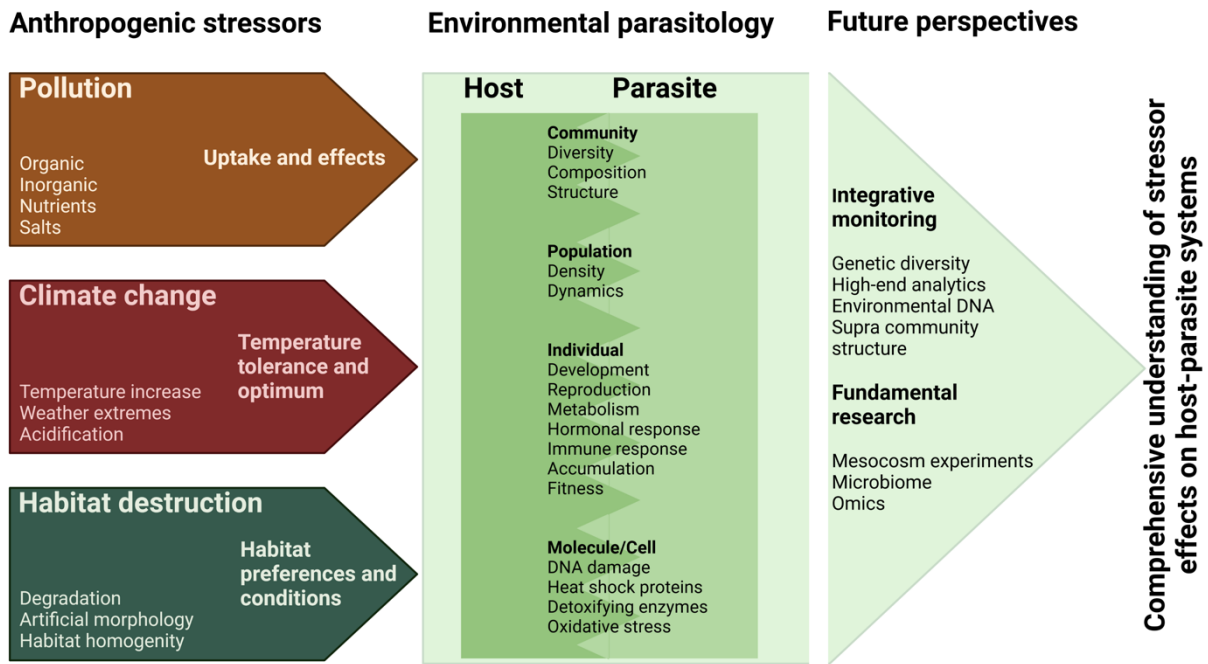
*Considering host and parasite microbiomes*

Part of the current research is focusing on the study of host and parasite microbiomes [107], which will add another layer of complexity to the research related to environmental parasitology. Differences in the microbiome of host and/or parasite individuals changes their phenotype and might also alter their response to stressors [108]. Therefore, microbiomes might be a promising approach to understand cases of seemingly contradictory results when studying the effects of stressors on hosts and parasites.

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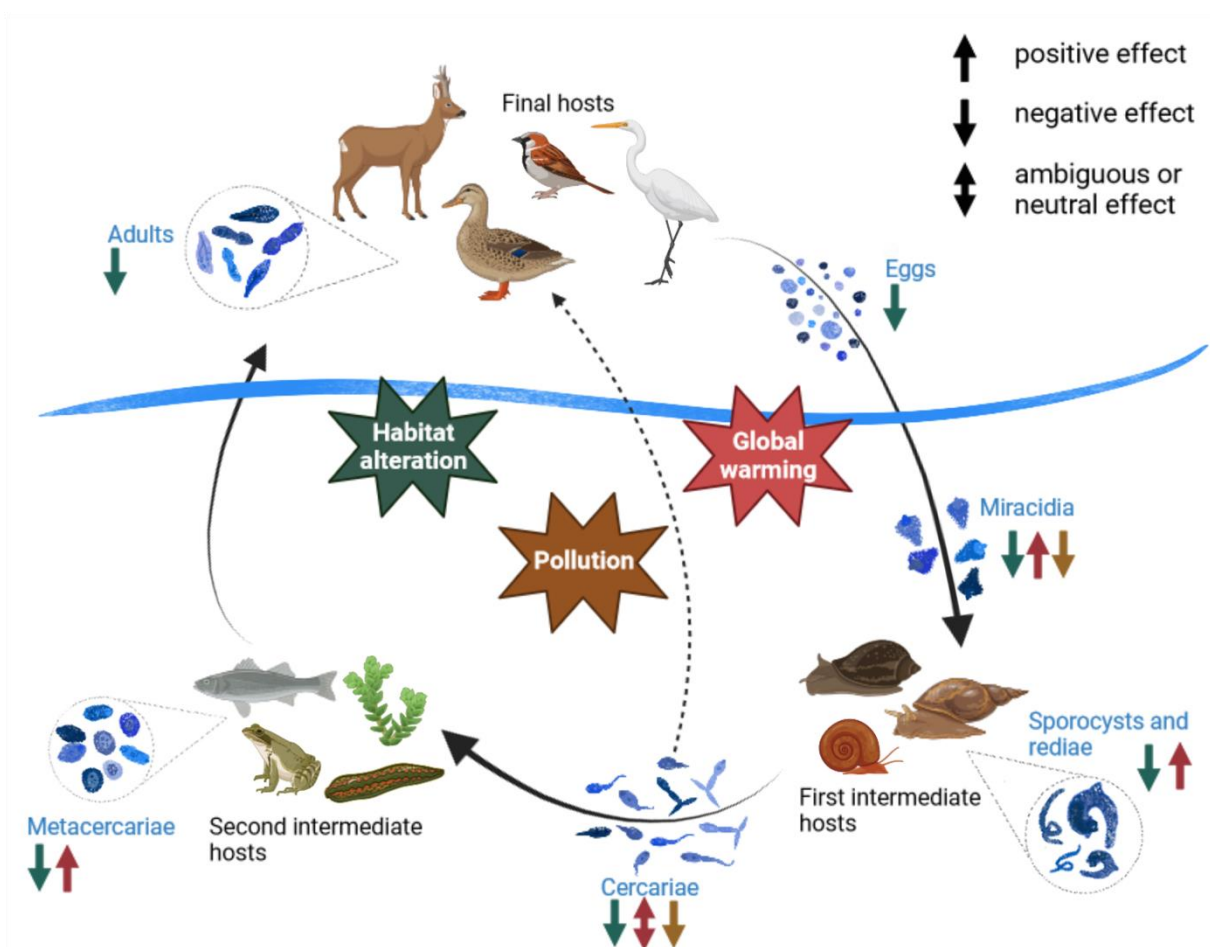
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685 **Figure 1. Relevance of `Environmental Parasitology` for ecosystem research in times of**  
 686 **increasing anthropogenic pressure (Anthropocene).** Figure created with BioRender.com

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691 **Figure 2. Generalised life cycle of digenean trematodes with final vertebrate hosts,**  
 692 **invertebrate and vertebrate intermediate hosts incorporating environmental stressors**  
 693 **(habitat alteration, global warming, pollution) and their effects on the parasite stages of**  
 694 **the life cycle.** Environmental stressors can directly and indirectly (via their hosts) affect parasite  
 695 reproduction, transmission, abundance and pathogenicity (see examples in text). These stressors  
 696 can have negative, neutral or positive effects (see arrows, colours represent respective stressors)  
 697 on the individual steps in the parasite's complex life cycle, highlighting our need to understand  
 698 both the mechanistic processes and the net effects of environmental stressors on parasite life  
 699 cycles. Figure created with BioRender.com

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