Environmental parasitology: stressor effects on aquatic parasites

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Abstract

Anthropogenic stressors are causing fundamental changes in aquatic habitats and to the organisms inhabiting these ecosystems. Yet, we are still far from understanding the diverse responses of parasites and their hosts to these environmental stressors and predicting how these stressors will affect host-parasite communities. Here, we provide an overview of the impacts of major stressors affecting aquatic ecosystems in the Anthropocene (habitat alteration, global warming, and pollution) and highlight their consequences for aquatic parasites at multiple levels of organisation, from the individual to the community level. We provide directions and ideas for future research to better understand responses to stressors in aquatic host-parasite systems.
Aquatic parasites in the Anthropocene

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

The effects of environmental stressors on host-parasite associations can affect the life cycle of metazoan parasites at various points depending on the characteristics of host-parasite associations such as host specificity, life cycle complexity, transmission strategy, location on the host (endo- vs ectoparasites) and distribution range, to name a few. Parasites may either
directly (stressor effects on parasite stages) or indirectly (stressor effects on hosts) respond to an increase or decrease of stressors (Box 1). Overall, the persistence of a parasite species and its population in an ecosystem is determined by the weakest link in the chain: the most sensitive and specific host, or the most delicate parasite life stage. According to theory and recent findings, the diversity of heteroxenous parasites with complex (multi-host) life cycles (e.g. Digenea, Cestoda, Acanthocephala) is thus more likely to decrease in stressful environments than the diversity of monoxenous parasites (Box 2; e.g. Monogenea, Microsporidia) ([2,7–10] and references therein). In contrast to heteroxenous parasites, monoxenous parasites might in fact benefit from the presence of stressors, e.g. if stressors impair the host’s defence against pathogens [11]. Additionally, an increase in environmental stressors can favour populations of tolerant host species, while populations of more sensitive species disappear. The resulting higher host population density increases the likelihood of transmission of monoxenous parasites between hosts [7,12].

Furthermore, specialist parasites will rely on hosts with large and stable populations, as they are not able to switch to other host species, and therefore face a higher risk of secondary extinction [13]. Accordingly, it can be assumed that parasites with simple life cycles (monoxenous, generalist) prevail in stressful environments, while parasites with complex life cycles (heteroxenous, specialists) will be more successful under more stable conditions (Box 2). For heteroxenous parasites, the most sensitive host will be the limiting factor for the extinction risk [14]. There is evidence that parasite diversity and overall prevalence decline with increasing stressor intensity (e.g., [2,8,15] and that an increase in parasite richness and overall prevalence occurs with the recovery from stressors [16–18]. Due to their complex interaction with stressors or environmental conditions in general, parasites reflect the state and complexity of ecosystems and can therefore eventually be used as bioindicators to assess environmental conditions [19].
In the following sections, we will focus on selected stressors that characterise the Anthropocene, i.e. habitat alteration, global warming and pollution, and highlight their impact on the qualitative and quantitative responses of parasites (Figure 1). We also provide perspectives and ideas for future research, which will expand the knowledge in the field of aquatic environmental parasitology and will help to fill the missing gaps.

Habitat alteration and the occurrence of parasites

Freshwater habitats are particularly affected by degradation and subsequent species loss [3,4]. Numerous human activities lead to habitat alteration and thereby jeopardise freshwater ecosystems and their species, including habitat modification, river diversion, fragmentation and flow regulation as well as agricultural and urban landscape expansion [5,20,21]. Accordingly, freshwater ecosystems are degrading faster and have higher rates of biodiversity loss than terrestrial ones [3,5,6]. In contrast, functional and resilient ecosystems are characterised by high habitat diversity and species richness (e.g.[22]), which should also be mirrored by a high parasite diversity as the association between parasite and host species richness suggests [23,24]. More specifically, there is indication that parasite species richness is low and total abundance is high in stressed ecosystems, while parasite abundance decreases and diversity increases under conditions with absent or low stressor impact (see Box 2; [7]). Based on these findings, the idea of parasites as indicators of biodiversity or ‘ecosystem health’ was developed [12,25,26], as high parasite diversity is always dependent on diverse and complex interactions among free-living species [23]. The indicative value of parasites relates to their need of one to several host species as a prerequisite of their occurrence (see a trematode life cycle in Figure 2 as an example). Therefore, life cycle-related traits of parasites are key to understanding and explaining stressor effects on parasite diversity [27]. Particular promising life cycle traits are the number of required obligate host species (life cycle complexity) as well as the specialisation of the parasites regarding the host range (generalists vs. specialists) [28].
In contrast to aquatic systems, terrestrial systems are rather well studied regarding the effects of habitat alterations on host-parasite assemblages (e.g. [29,30]. For example, a recent long-term study of terrestrial host-parasite systems has shown that habitat loss and fragmentation are likely to have severe impacts on parasites. Food web models predict that parasites with multiple obligate hosts are at greater risk of extinction, as local extinction, or reduction in abundance of one host leads to a bottleneck in the parasite's life cycle. Imbalances in the abundance of multiple hosts over time are likely to be common following disturbance, making parasites with complex life cycles particularly vulnerable to habitat fragmentation and other disturbances [29]. Although these results originate from a terrestrial study, they are most likely transferable in their broad outlines to aquatic habitats. One of the few aquatic studies that supports this hypothesis is based on the premise that low host abundance and diversity due to environmental degradation and anthropogenic habitat alterations lead to a reduction or even extirpation of heteroxenous and specialised parasites [9]. Schwelm et al. [9] studied the trematode fauna of a protected natural reserve in Germany and found a tendency towards higher parasite diversity and prevalence under near-natural conditions. Furthermore, a comparison with other similarly large-scale faunal studies from Europe and North America revealed that life cycle complexity (number of obligate hosts involved in the life cycle) is higher in near-natural areas than in those that are more anthropogenically influenced [9]. Global warming might further exacerbate these dynamics [2]. In contrast, no clear pattern was found when investigating monoxenic microsporidian-host associations among near-natural and restored habitats at two German river catchments [31]. Microsporidians may have found a way to persist even in a degraded habitat despite low host abundance via resistant spores in the environment and to re-colonise it after stressor release. The ability of host switching [28] and different transmission mechanisms could also contribute to the persistence of members of this parasite group [31]. The evidence to date on the relationship between parasites and habitat fragmentation is diverse and sometimes contradictory (see [28,29] and references therein), which is not surprising given
the complexity of possible links between habitat alteration, biodiversity loss and parasite prevalence [32,33]. But at the same time this also highlights the importance and necessity of differentiated approaches and investigation of various traits of parasites, their host associations and ecological requirements at an individual, local and global level [29].

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

Global warming

Global warming is probably the most drastic and far-reaching result of anthropogenic activity on our planet [38]. Climate change encompasses many related and associated effects beyond temperature increases, ranging from changes in the occurrence and severity of extreme weather events to modulation of stratification, water levels, flow regimes or ocean currents [39,40]. However, warming as such has been identified as one of the main drivers of the increased
frequency of parasite disease risks across terrestrial and aquatic ecosystems [41]. Temperature-driven modifications of parasite life cycles and their possible interactions with other abiotic and biotic parameters are expected to have serious ramifications for aquatic parasites and their hosts, but are hard to predict due to the inherent complexity of host-parasite systems [39]. Various studies have explored the possible impacts of temperature changes on host-parasite interactions, and the implications for disease dynamics, ecological communities, and whole ecosystems. In this section, we summarise recent key findings on the diverse, and sometimes unexpected, impacts of temperature changes on individual host-parasite interactions, parasite transmission dynamics and life histories, and ecosystem-wide consequences for aquatic systems.

The more complex a parasite life cycle is (i.e., the more steps that are required to complete it), the more susceptible the parasite is expected to react to environmental and climate changes, which might lead to neutral, positive, or negative effects on the parasite transmission and population dynamics [13]. Among metazoan parasites, digenean trematodes have some of the most complex life histories, often requiring multiple vertebrate and invertebrate hosts, and direct and indirect transmission pathways to complete their life cycle (Figure 2). The exposed free-living transmission stages (miracidia and cercariae) are susceptible to direct environmental influences. Moreover, the asexual production and emergence of cercariae in the first intermediate mollusc host as well as the infectivity in the second intermediate host are strongly positively correlated with temperature [42–45]. However, while increases in temperature positively affect cercarial transmission dynamics (e.g., cercarial emission and dispersal activity), these impacts can vary substantially between sympatric trematode species, and warming temperatures might shift parasite community structures in ecosystems rather than favour multiple species equally [46]. It remains questionable if these temperature-induced increases in cercarial emergence can be maintained over longer periods of time or are just short-term peaks that level off after host acclimation (see [47,48]).
Various non-host organisms can interfere with the free-living parasite transmission stages, e.g.,
via predation that leads to a dilution of parasites in the system (e.g., [49,50]. Recent studies
have highlighted that temperature-mediated increases in parasite productivity and infectivity
can be counteracted by predation on free-living parasite stages, which might potentially offset
increases in disease risk under climate change [51]. However, it remains uncertain to what
extent the elimination of trematode larvae by filter-feeders can compensate for increased
transmission rates, and if these processes can mitigate disease risks in ecosystems under
temperature shifts [52]. Although trematode transmission and infectivity are typically expected
to increase under warmer temperatures [39,41,42] with concomitant decreases in host resistance
to infection [53], trematode transmission windows in coastal systems have been shown to be
negatively affected under higher temperatures, which can hinder the possibility for trematodes
to flourish in warming oceans [45]. Accordingly, the question which parasites will be able to
profit in warming marine and freshwater systems will depend on a wide variety of biotic and
abiotic factors as well as the ecology of the specific host-parasite systems. Similar varying
patterns have been observed for parasitic protists with direct (monoxenous) life cycles in
aquatic systems, where the direction and magnitude of the changes in disease occurrence is
strongly influenced by the ecological features of each disease [54]. This brings into question
the generality of the susceptibility of complex vs. simple life cycles to temperature changes and
will require further testing in the future that takes the net effect of temperature on a parasite’s
entire life cycle into account (see [55]).

Temperature significantly influences the outcome and strength of species interactions across
ecosystems (see [56]). Accordingly, not only parasite transmission dynamics of free-living
parasite stages are strongly temperature-dependent, but also the effects of parasitic infections
on their hosts and their involvement in food webs can be drastically modulated by temperature.
For instance, trematode-infected snails have been shown to change their thermal preference,
which likely increases parasite proliferation and transmission [57]. Many parasites that rely on
trophic transmission at some point during their life cycle can modify the behaviour of their 
hosts to facilitate such transmission processes. The plerocercoid stages of the cestode 
Schistocephalus solidus grow faster in their fish host at higher water temperature, enhancing 
trophic transmission to final bird hosts as well as parasite reproduction and fecundity, while at 
the same time shifting their host’s thermal preference to warmer temperatures [58]. Different 
and diverging temperature optima of hosts and parasites have been shown for a range of 
Schistocephalus-stickelback systems, with potentially negative impacts on the hosts and drastic 
fitness gains for the parasites [59]. Understanding the thermal mismatches between hosts and 
parasites and identifying the underlying mechanisms of these processes are central requirements 
to improve our predictions of parasite and disease dynamics in warming ecosystems [60]. 
Contrastingly, field studies from the same host parasite system found little evidence that 
temperature modified host-parasite interaction, and highlighted the possible difference between 
laboratory experiments and natural settings [61]. Likewise, studies from acanthocephalan host-
parasite systems have shown that temperature changes within existing and predicted 
distribution ranges appear to have no impact on these behavioural changes in hosts and 
subsequent transmission outcomes [62,63]. Altogether, these findings emphasise the stark 
differences across various host-parasite associations. Moreover, even within the same host-
parasite system, host genotypes from different geographical regions can show highly varied 
temperature responses, highlighting that disease and infection dynamics may be difficult to 
predict within individual parasite species [64,65]. 
Remarkably, experimental exposure of blue mussels infected with the trematode Himasthla 
elongata revealed a complex parasite-temperature interaction. While moderate parasite loads 
and increased temperature showed synergistic detrimental effects on mussel survival, high 
infection intensities appeared to nullify the negative effects of temperature stress on mussels 
[66]. Other studies revealed that warming and trematode infection increased HSP70 levels and 
changed the snail’s biochemical condition but concluded that this might make them more
susceptible to thermal stress [67]. It therefore remains to be tested if, and under which conditions, some parasite infections could provide even a beneficial effect for their hosts under thermal stress, which would contradict our common view that parasites are exclusively harmful to their hosts. Besides these possible impacts of established infections on hosts, recent studies have highlighted the role of non-consumptive or avoidance (i.e., pre-infection) effects that can significantly alter host behaviour and performance in aquatic ecosystems and are potentially strongly temperature dependent [68–70]. Overall, these examples underline the complex and sometimes unexpected outcomes of individual host-parasite interactions in warming aquatic ecosystems.

These individual-level effects on host-parasite systems can translate into ecosystem-wide impacts that structure and regulate populations and communities. Existing outdoor mesocosm approaches could demonstrate strong detrimental synergistic effects of elevated temperature and parasitism on the diversity and structure of coastal crustacean communities with potentially negative impacts on the whole coastal habitat [56]. Likewise, recent mesocosm studies from freshwater systems showed similarly complex interactions between parasites and elevated temperature on invertebrate community composition and host abundance that had the potential to significantly alter the structure and dynamics in the affected ecosystem [71]. However, such community-level studies that test how parasites and temperature can shape and regulate the functional structure of aquatic ecosystems under climate change pressure remain scarce. Although the examples highlight that temperature effects on parasites and their hosts can have far-reaching ecological impacts, the actual relationship between temperature and disease is often complex and the varying underlying mechanisms are only understood for individual parasites and disease agents [51] and references therein. Moreover, the first century-scale time series of fish parasite abundance in North American coastal ecosystems revealed a drastic decline of parasite taxa with complex life cycles (>10% decline per decade) as the result of increasing temperature [2]. Future work must therefore continue to bring together experimental
approaches investigating mechanistic interactions between host-parasite systems and environmental changes with ecosystem-level studies of climate change effects on populations and communities in aquatic systems [55]. Such approaches will allow to better integrate this knowledge with modelling approaches to more accurately anticipate, monitor and mitigate the impacts of climate-driven disease dynamics in natural ecosystems [72].

Pollution

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

Aqueous pollutants can be accumulated to a high degree by parasites, making them promising sentinels for pollution (summarised by [8,10]). Accordingly, parasites provide valuable
information on the bioavailability of pollutants and might help in their detection and quantification when pollutants are present in very low concentrations in the environment but are accumulated to an enormous degree in the parasites. Various parasitic taxa have been studied in terms of their accumulation capacity, with acanthocephalans, cestodes and nematodes in particular being very sensitive sentinels for metals (see e.g. [8] and references therein).

Similarly, a high accumulation capacity has also been demonstrated for some organic compounds such as PCBs [78, 79]. The use of parasites such as cestodes and acanthocephalans to demonstrate the bioavailability of substances can represent a promising tool for ecotoxicological studies. Detection of certain substances in the body of these taxa is proof that these substances must be considered biologically available because they had to cross teguments and membranes due to the lack of a digestive tract in cestodes and acanthocephalans. If micro- or nanoparticles can be detected in these gutless helminths as shown for particulate platinum-group metals (e.g. [80]), they must be bioavailable. In addition to metallic nanoparticles, this could also be a promising approach to study the uptake, accumulation, and effects of nano- and microplastic particles in the aquatic environment. Additionally, the high accumulation potential of parasites was found to be beneficial for the hosts by reducing the pollutant burdens within the host body and thereby decreasing harmful effects on the physiology (reviewed by [8]; see also [81, 82]).

However, high pollutant levels in the environment represent also a driving evolutionary force, as studies on the adaptation of fish populations to high Hg levels reveal (e.g. [83]). It therefore seems possible that various parasite taxa might have adapted to specific pollutants and developed tolerance to contamination although evidence from the literature is lacking so far. For example, in contrast to the expected patterns of reduced diversity, higher diversity of parasite communities of the intertidal klipfish, Clinus superciliosus, was found at marine sites that had relatively high metal concentrations due to geogenic conditions [84]. In this study, acanthocephalans, cestodes and parasitic isopods were more abundant at sites with higher...
element levels. It therefore can be assumed that the fish hosts involved, as well as their parasites, have a high tolerance to geogenic background concentrations if the host-parasite systems could evolve adaptation measures. Similarly, higher abundance and prevalence of acanthocephalans was found at sites with poorer ecological status according to biological indices and bacterial loads when comparing different river sections [85].

Besides individual effects due to contaminants, there may also be interactive effects of climate change and/or habitat degradation in combination with pollutants. For example, acidification has a significant influence on bioavailability and toxicity of pollutants, both of which increase for metals at lower pH levels [86]. More diverse microhabitats and a higher diversity of free-living organisms (especially plant communities) on the other hand may act as pollutant sinks (e.g. [87]) and thereby reduce concentrations of available pollutants. Extreme weather events (periods of droughts or higher precipitation) can increase the pollution loads as well. For example, higher precipitation intensifies the process of erosion within drainage areas of aquatic habitats and contaminants of anthropogenic and geogenic origin can enter the water bodies with surface run-off [75,88]. Several studies on aquatic parasites showed that parasites react sensitively to anthropogenic activities in the drainage area such as increased urbanisation and pollution [89] and to extended land (habitat) destruction such as clearcutting [90]. Marcogliese et al. [90] already provided evidence of the effects of precipitation events on the composition of parasite communities of fish, which were associated with changes in discharge, flow velocity and overall water quality. Such qualitative and quantitative changes can be expected to affect the composition, bioavailability and toxicity of pollutants. The latter can be similarly affected by droughts, with high evaporation rates leading to an increase of concentrations in the water column of small aquatic ecosystems. In addition to this, high temperatures lead to reduced aqueous oxygen concentrations and changes in the redox potential, which results in different speciation of metals and an increase of their bioavailability as well [86]. In such scenarios, a complex set of stressors (high temperatures, anoxia and elevated pollution) might impose severe
effects on free-living communities and their associated parasites (see e.g. [91]). Although a large number of studies related to pollution and parasites have been published in the last decades, there are still various knowledge gaps, which represent a good starting point for future studies on the interaction between parasites and pollutants (see Box 3).

**Future perspectives**

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

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

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**Glossary**

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

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

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

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

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

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

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

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

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

**Stressor**: Any impact that leads to environmental variables, individuals, populations, communities, or ecosystem functions exceeding the range of normal variation relative to undisturbed reference conditions.
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.
In a scenario of environmental degradation (e.g. increasing pollutant concentration in the water), species numbers, but also community composition, will change with varying environmental conditions from proportionally more complex life cycles and higher numbers of host specialists under near-natural conditions to lower life cycle complexity and more host generalists under degraded conditions (Figure IA). After stressor release (phase of recovery), the composition of the parasite community is still different from the near-natural situation with a dominance of few species with less complex life cycles, whereas specialists with complex life cycles can only establish once the habitats allow for recolonization with the required host species (Figure IA). The relative abundance of mono- and heteroxenous parasites will also change. Monoxenous parasite communities will become species poor, with few but abundant species that parasitise the remaining hosts during stressor impact (degradation phase) (Figure IB). Relative abundance of heteroxenous parasites will decrease in degraded environments. The relative abundance of both mono- and heteroxenous parasites will return to the pre-degradation-state, but with delay for heteroxenous species (Figure IB). The observed development of the parasite communities can vary for some stressors (e.g. nutrients) that might, for example, lead to an increase of the abundance of heteroxenous parasites due to increasing numbers of intermediate hosts.

Figure I (in Box 2). Hypothetical development of parasite communities before (Near-natural), during (Degradation) and after the occurrence of a stressor (Recovery) in an...
aquatic system. A: Changes in species richness. B: Changes in parasite abundance. Green line: heteroxenous parasites. Blue line: monoxenous parasites. Grey areas indicate higher number of host specialist parasites, while more light areas indicate higher numbers of generalists.

The graphs show a hypothetical situation of a stressor intensity that is strong enough to affect communities but without complete eradication of all parasite species.
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
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.
Figure 1. Relevance of `Environmental Parasitology` for ecosystem research in times of increasing anthropogenic pressure (Anthropocene). Figure created with BioRender.com
Figure 2. Generalised life cycle of digenean trematodes with final vertebrate hosts, invertebrate and vertebrate intermediate hosts incorporating environmental stressors (habitat alteration, global warming, pollution) and their effects on the parasite stages of the life cycle. Environmental stressors can directly and indirectly (via their hosts) affect parasite reproduction, transmission, abundance and pathogenicity (see examples in text). These stressors can have negative, neutral or positive effects (see arrows, colours represent respective stressors) on the individual steps in the parasite’s complex life cycle, highlighting our need to understand both the mechanistic processes and the net effects of environmental stressors on parasite life cycles. Figure created with BioRender.com