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Major drivers of biodiversity loss and their impacts on helminth parasite populations and communities

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Abstract

The world's biodiversity is in peril. The major threats to biodiversity globally are habitat change, overexploitation, climate change, invasive species and pollution. Not only do these stressors impact free-living organisms, but they affect parasitic ones as well. Herein, this perspective examines the potential consequences of these anthropogenic perturbations on helminth populations and communities, with emphasis on significant developments over the past decade. Furthermore, several case studies are examined in more detail for each of these threats to biodiversity. While effects are widespread and diverse, for the most part all these environmental stressors have negative effects on parasite populations and communities. Those parasites with complex life cycles that are trophically transmitted are often more at risk, although larval parasites with a wide host spectrum, and directly transmitted ectoparasites, appear less threatened and may even benefit. However, differential effects on hosts and parasites, on parasite life cycle stages and on host–parasite interactions made specific predictions difficult and context-dependent. Experimental laboratory and mesocosm studies on specific parasites that test effects on the different life cycle stages, hosts and host–parasite interactions, permitting the determination of net effects of an environmental stressor, yield insightful and sometimes counterintuitive results, although they remain a simplification of real-world complexity. Recent advances in the use of parasites as bioindicators of effects also are discussed.

Introduction

The world's biodiversity is under siege. A high percentage of numerous groups of organisms are considered in danger of extinction (Díaz *et al.*, 2019). These include mammals, birds, reptiles, amphibians, fishes, insects and other arthropods, all of which are experiencing significant population declines (Stuart *et al.*, 2004; Ceballos *et al.*, 2015; Grant *et al.*, 2016; Rosenberg *et al.*, 2019; Seibold *et al.*, 2019; Albert *et al.*, 2021; Pacoureaux *et al.*, 2021; Lees *et al.*, 2022). While there are numerous causes of biodiversity loss, the major direct drivers, in order of importance, are habitat change, overexploitation, climate change, invasive species and pollution (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019; World Wide Fund for Nature, 2020). These, however, may vary among taxa (Pelletier & Coltman, 2018). In addition, they are not mutually exclusive or independent and may contribute synergistically to biodiversity loss (Brook *et al.*, 2008; Pelletier & Coltman, 2018). Furthermore, climate change can modulate habitat changes, host and parasite species' distributions, invasive species ranges and pollution (Marcogliese, 2001, 2008, 2016). Habitat change and overexploitation account for more than 50% of impacts in or on the land, fresh water and the oceans, although the relative importance due to these two drivers differs among those realms (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019).

Given that all species are considered to be infected with at least one parasite species (Price, 1980) and total parasite species numbers could account for one-third to over one-half of all the species on earth (Poulin, 2014), parasites undoubtedly make up an important component of biodiversity in any habitat. Focusing on helminths, estimates of the global species richness vary from 75,000–300,000 (Poulin & Morand, 2004). Dobson *et al.* (2008) tallied 76,930 described helminth species, and more recently, Carlson *et al.* (2020) tallied 103,078 described helminth species, which accounted for an estimated 15% of all helminths. In several ecosystems, parasite species richness was correlated with host species richness for a number of host taxa (Hechinger & Lafferty, 2005; Hechinger *et al.*, 2007; Kamiya *et al.*, 2014; Johnson *et al.*, 2016). Presuming this is a general relationship, a decline in the biodiversity of free-living organisms is expected to be accompanied by a decline in parasite diversity. Theoretical studies demonstrate that life cycle complexity and host specificity contribute to loss of parasites with a reduction in biodiversity (Lafferty, 2012). Food web models further suggest that parasite diversity declines

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more than previously believed with biodiversity loss, with parasites on specialist hosts and those high in the food chain being the most susceptible (Lafferty, 2012). Rohr *et al.* (2020) posited that multi-host parasites, especially those with complex life cycles and free-living infectious stages, should be affected by changes in biodiversity more than directly-transmitted specialists. These, of course, include the parasitic helminths. However, effects of biodiversity loss on individual parasites could be positive or negative (Keesing *et al.*, 2010; Rohr *et al.*, 2020). Indeed, parasites may increase or decrease in abundance and diversity in response to various stressors (Marcogliese, 2001, 2004, 2005, 2016).

The study of effects of anthropogenic environmental perturbations on host–parasite interactions has been considered a landmark advance in ecological parasitology (Poulin, 2021). Global changes resulting from anthropogenic activity affect host–parasite interactions at multiple scales of biological organization, ranging from the biochemical through physiological and immunological to the ecological (Wells & Flynn, 2022). In this perspective, concentrating on the higher organizational scales, I evaluate the potential ecological consequences of the five major drivers of biodiversity loss listed above for helminth parasite populations and communities, focusing on developments during the past decade or so. In addition, further insights will be derived from recent results of novel and informative studies on selected host–parasite systems.

Habitat change

Habitat change refers to loss of habitat, modifications in land use, degradation and fragmentation of habitats, or reduction in quality of key habitat for any specific species or group of organisms (Pelletier & Colman, 2018; World Wide Fund for Nature, 2020). For both terrestrial and freshwater ecosystems, this is considered the leading cause of biodiversity decline (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019).

While fragmentation is well-documented to affect numerous terrestrial and freshwater organisms such as birds (Lees *et al.*, 2022), amphibians (Stuart *et al.*, 2004), insects (Seibold *et al.*, 2019) and freshwater organisms in general (Albert *et al.*, 2021), its effects on helminth parasites are less well-studied. In a series of studies on gastrointestinal nematodes in wild primates, nematode prevalence generally was related negatively to fragment size or reduced in fragments compared to the main forest (Chapman *et al.*, 2006; Gillespie & Chapman, 2006; Mbora & McPeck, 2009; Valdespino *et al.*, 2010). It should be noted that most of these nematodes had direct life cycles. A study of gastrointestinal nematodes infecting four-striped mice (*Rhabdomys pumilio*) from fragmented habitats in agricultural landscapes and from natural areas revealed interesting patterns. Species richness and overall abundance of gastrointestinal helminths was higher in the fragmented habitats, an effect attributed to the high density of mice in these areas (Froeschke *et al.*, 2013), similar to results of studies on primates described above. Another pattern emerged from the mouse study: those species with high abundance were generalists with a free-living stage, while those that were less abundant in fragmented areas were more commonly associated with other species of definitive host (Froeschke *et al.*, 2013). Theoretically, for pathogens with direct life cycles, without considering confounding factors such as reservoir hosts, host density should increase at least in the initial stages in small fragments, promoting transmission (McCallum & Dobson, 2002).

In a rare experimental study of effects of fragmentation on parasites, a long-term study on the nematode *Hedruris wogwoensis* in intermediate host amphipods (*Arcitalitrus sylvaticus*) and definitive host skinks (*Lampropholis guichenoti*) yielded intriguing results. While establishing a pine (*Pinus radiata*) plantation, a forested area covered by *Eucalyptus* was cut back, but fragments of various sizes were left untouched within the pine plantation in the Wog Wog Habitat Fragmentation Experiment in south-eastern Australia (Bitters *et al.*, 2022). The experiment spanned three decades. During 1985–1999, nematodes had completely disappeared from the plantation and the skinks from the *Eucalyptus* fragments were rarely infected. By 2010–2013, there was only limited recovery of nematodes in the skinks in the forest fragments (Bitters *et al.*, 2022). Nematode abundance was lower in skinks in both the fragments and the plantation than in the continuous *Eucalyptus* forest during both time periods. The decline in infection in the plantation and forest fragments was attributed to a reduction in the abundance of the amphipod host during the first decade, due to loss of shade and drying in the modified landscape. However, amphipod populations recovered by 2010–2013, but skink populations declined in 2010–2013 due to increasing shadiness in the pine plantation (Bitters *et al.*, 2022). Thus, the decline in parasites following landscape fragmentation was due to the decline of one of the hosts in the life cycle, but these differed between the two time periods (Bitters *et al.*, 2022). These results support theoretical models, where life cycle complexity and host susceptibility to extinction were two important factors governing a parasite's ability to withstand biodiversity loss (Lafferty, 2012).

Agricultural development is the most widespread type of habitat change affecting terrestrial and freshwater ecosystems (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019) and thus a major threat to biodiversity. A series of studies from independent laboratories on the effects of the atrazine and other herbicides on parasites of anurans from agricultural wetlands also yielded significant relationships between helminth populations and communities and agricultural landscape variables. While these studies also examined the effects of pesticides on parasite populations and communities, the landscape relationships are emphasized in this section.

The combined prevalence of trematode infections in grey tree frog (*Hyla versicolor*) tadpoles correlated positively with agricultural activity in south-western Ontario wetlands (Koprivnikar *et al.*, 2006). While no cause could be determined, these effects may result from environmental effects resulting from agricultural practices, including pesticide application and nutrient runoff, enhancing conditions for intermediate hosts and/or parasite transmission. There was no relationship between total trematode infection and surrounding forest cover or road density. However, the prevalence of *Alaria* sp. correlated positively with forest cover at 100 m surrounding the ponds, an effect these authors presumed was the result of habitat suitability of forest cover for the canid definitive hosts (Koprivnikar *et al.*, 2006). A follow-up study in agricultural ponds in the same region demonstrated that prevalence of cercarial release of *Echinostoma trivolvis* from snails was positively related to area of forest cover within 100 m, which was attributed to habitat suitability for avian definitive hosts (Koprivnikar *et al.*, 2007). In a related study on agricultural localities exposed to the herbicide glyphosate, grey tree frogs from the non-agricultural ponds had higher levels of *Alaria* sp. than those from the agricultural localities, similar to results described above (Koprivnikar & Redfern, 2012). However,

echinostome trematodes, which are host generalists, were more abundant in the agricultural ponds (Koprivnikar & Redfern, 2012). In a subsequent study, larval grey tree frogs and spring peepers (*Pseudacris crucifer*) from agricultural sites had a higher prevalence, but lower mean abundance, of trematodes compared to those from non-agricultural sites (Koprivnikar *et al.*, 2017). The closer the nearest forest and the mean distance to forested areas, the greater was the occurrence of trematodes in tadpoles, but the lower in odonate intermediate hosts (Koprivnikar *et al.*, 2017). Furthermore, this study emphasized the importance of considering multiple hosts when assessing environmental impacts on parasites.

Another series of studies focusing on atrazine uncovered habitat effects on parasites of leopard frogs (*Lithobates pipiens*). Helminth infracommunity species richness was negatively correlated with the agricultural and urban areas surrounding ponds at a 500 m scale in south-western Quebec, Canada (King *et al.*, 2007). Furthermore, parasite species that matured in frogs or in birds or mammals tended to be much less abundant in agricultural wetlands (King *et al.*, 2007). Mean total parasite abundance was negatively correlated with forest area. Habitat modification through agriculture or urbanization may: (a) restrict access of vertebrate definitive hosts to wetlands due to a reduction in habitat suitability and accessibility; (b) reduce the diversity and abundance of invertebrate intermediate hosts due to loss of forest cover; and/or (c) reduce the diversity of amphibian hosts of those frog parasites with direct life cycles (King *et al.*, 2007, and references therein). The generalist echinostomes were common at all locations, regardless of agricultural status (King *et al.*, 2007). These parasites may be able to persist in degraded habitats because they can infect a wide variety of amphibian intermediate and mammalian definitive hosts (King *et al.*, 2007; Koprivnikar & Redfern, 2012). In a study of American bullfrog (*Lithobates catesbeianus*) parasites, also in south-western Quebec, parasite species richness and diversity were lower in agricultural wetlands compared to reference wetlands (King *et al.*, 2010). The number of parasite species per frog increased with forest area surrounding the ponds at a 500 m scale, while the number of species per locality decreased with the agricultural area at a 100 m scale. Notably, there were few parasites with birds or mammals as definitive hosts at the intensive agricultural sites, whereas they were common at forested localities (King *et al.*, 2010). These results are consistent with those of King *et al.* (2007) and support the notion that agricultural development leads to habitat fragmentation, restricting access of terrestrial vertebrate hosts. A seasonal study in the leopard frog system revealed that component community and infracommunity species richness in leopard frogs were lowest in the most developed agricultural and urban landscapes compared to a pristine wetland (King *et al.*, 2008). However, the abundance of monoxenous nematodes increased to a greater extent in agricultural wetlands (King *et al.*, 2008).

In another study on northern leopard frogs, parasites were examined from 18 wetlands in the Eastern Broadleaf Forest Province of Minnesota, United States (Schotthoefer *et al.*, 2011). In this part of the state, natural areas are highly fragmented due to agriculture and wetlands varied from low (<20%) to high (>35%) areas of surrounding farmland. Abundance, richness and diversity of helminths in frogs increased with the area of forested and woody wetland habitat, proximity to other woody wetlands and the occurrence of nearby small open water patches (Schotthoefer *et al.*, 2011). Larval trematodes appeared to be most

influenced by wetland and local (1 km) landscape factors, while adult helminths were affected by local and regional (10 km) landscape variables (Schotthoefer *et al.*, 2011). These authors concluded that the loss of habitat and reduced connectivity between them were associated with declines in helminth richness and abundance. In contrast to the studies described above, echinostomes appeared to be negatively associated with agriculture (Schotthoefer *et al.*, 2011). Importantly, all the anuran studies described above find some effects due to pesticide contamination, but also changes in parasite populations and communities due to changes in habitat at the landscape level.

In a major parasite survey of 846 amphibian populations belonging to 31 species from 448 lentic water bodies across the continental United States between 2000 and 2014, species richness was positively related to wetland area and land cover diversity, among other factors (Johnson & Haas, 2021). Combined parasite abundance also correlated with land cover diversity within 1 km as well as wetland area to some extent (Johnson & Haas, 2021). Land cover diversity was the area of land dedicated to either wetland, forest, or development. Heterogeneous landscapes are believed to promote spatial overlap and/or interactions among the various hosts involved in helminth life cycles (Johnson & Haas, 2021). Curiously, the amount of forested or developed area was not significant in the overall analysis. This may be due to the large spatial scale employed, compared to the studies described above. Landscape changes also have been shown to affect fish–parasite systems, particularly in rivers and streams (see Sures *et al.*, 2017).

In freshwater ecosystems, habitat alterations, fragmentation and loss imperil aquatic biodiversity and ecosystem function (Vörösmarty *et al.*, 2004). Dams and reservoir construction affect helminth populations and communities in fishes (Izyumova, 1987; Marcogliese, 2001; Morley, 2007). The formation of reservoirs is well known to increase the habitat of snails that are intermediate hosts for *Schistosoma* spp., the cause of schistosomiasis (Steinmann *et al.*, 2006). The prevalence of *Schistosoma haematobium* and especially *Schistosoma mansoni* in humans has increased drastically in numerous parts of Africa following dam construction. In some cases, *S. mansoni* has appeared in areas where it was previously absent (Steinmann *et al.*, 2006). However, the actual cause of the increase in snail habitat is unclear, in part due to the multitude of complex changes in aquatic ecosystems associated with dams (Sokolow *et al.*, 2017). Recently, an examination of published data associated with 14 dam projects in sub-Saharan Africa found that increases in schistosomiasis were associated with prawn habitat. Native river prawns (*Macrobrachium* spp.) consume the gastropod intermediate hosts of schistosomes. These prawns are migratory and their movements are blocked by dam construction, thus reducing predation on the snail intermediate hosts (Sokolow *et al.*, 2017). Furthermore, the prevention of biotic interactions that normally controlled snail abundance and thus parasite transmission ultimately leads to increased disease. This study also exemplifies the importance on indirect effects of habitat alterations on predators that are not involved in a parasite's life cycle on transmission.

A meta-analysis of effects of urbanization on parasitism in terrestrial mammals illustrates the importance of transmission mode and host type (Werner & Nunn, 2020). Specifically, prevalence of parasites with complex life cycles, including helminths, was lower in urban carnivores and primates compared to non-urban populations, while no effect was found on parasites of rodents or marsupials. In addition, there was no difference in prevalence of

parasites with direct life cycles between urban and non-urban populations of any host type (Werner & Nunn, 2020).

It appears that for the most part parasites with direct life cycles or those with a wide host spectrum are more common in disturbed and fragmented landscapes than those with complex life cycles or specialist host distributions. Nevertheless, results may vary with the nature of the disturbance and time since the disturbance occurred, as well as the life cycle stage of the parasite. Furthermore, indirect effects of any perturbation on other components of the ecosystem may affect helminth transmission.

Overexploitation

Overexploitation is the most important driver of biodiversity loss in the marine realm (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019). Indeed, fishing affects approximately 900 of 1271 marine species-at-risk (O'Hara *et al.*, 2021). Fishing not only drives declines in fish abundance, but affects marine mammals, sea turtles and seabirds (Burgess *et al.*, 2018). Biomass of large predatory fish in the coastal and open oceans are 10% that of pre-industrial levels (Myers & Worm, 2003) and the overall abundance of sharks and rays has declined 71% due to increased fishing pressure since 1970 (Pacoureau *et al.*, 2021). In marine realms, fishing has led to a shortening in food chain length due to removal of top predators (Pauly *et al.*, 1998, 2000; Dobson *et al.*, 2006). Subsequently, due to reduced availability, global fishing efforts have transitioned from piscivorous demersal fish found high in the food chain to invertebrates and pelagic fishes occurring lower down the food chain (Pauly *et al.*, 1998, 2000).

Clearly, shortening of food chain length and removal of top predators should have noticeable effects on parasite populations and transmission. Marcogliese (2002) proposed that fishing activities should affect parasites through their cascading effects on marine food webs. Predictions included changes in parasite species composition and declines in parasites using top predators as definitive hosts, along with increases in parasites of elasmobranchs and shifts in the parasite fauna from a speciose benthic fauna to a more impoverished pelagic assembly in certain North Atlantic fisheries (Marcogliese, 2002).

Fisheries that reduce host abundance should lead to a decline in disease transmission, especially those of directly transmitted parasites (McCallum *et al.*, 2005; Wood *et al.*, 2010). Several mechanisms have been proposed to explain how fishing can affect parasitism, either positively or negatively, in the world's oceans. In terms of host populations, fisheries: (a) may target hosts, reducing and/or fragmenting their populations, lowering infection rates; (b) may select infected hosts, reducing parasite populations; or (c) select uninfected hosts, which can either reduce host densities or increase the populations of infected hosts (Wood *et al.*, 2010). In terms of host communities, fishing may: (a) reduce food web complexity, limiting transmission opportunities of parasites with complex life cycles; (b) select for host prey, thus reducing host density; (c) select specific hosts, leading to compensatory increases in alternative host populations; or (d) select for a host's predators or competitors, increasing the host population (Wood *et al.*, 2010). A meta-analysis that compared parasite abundance and diversity in hosts between fished and unfished areas proved insightful. Parasite diversity was lower in hosts from exploited areas, but effects on abundance also varied depending on the parasite life cycle (Wood & Lafferty, 2015). For parasites with complex life cycles (helminths), abundance

decreased in fished hosts, but increased in unfished hosts, in exploited areas. For parasites with direct life cycles, including the monogeneans, abundance increased in exploited areas whether the host was fished or not (Wood & Lafferty, 2015). Thus, the response of fish parasites to fishing pressure varies with the type of life cycle and whether the host is exploited or not (Wood & Lafferty, 2015).

Most studies comparing fish parasites from exploited and unexploited areas are single species studies that are not replicated (Wood & Lafferty, 2015). However, there are a series of studies from the Line Islands chain in the central Pacific, with good replication and increasing complexity, that demonstrate the effect of fishing on fish-parasite communities. Lafferty *et al.* (2008) compared the parasite communities of five species of fish between two coral atolls in this island chain. For all host species, parasite species richness was higher at the relatively pristine atoll compared to the heavily fished atoll. Furthermore, at the pristine atoll, parasites tended to have higher infracommunity species richness, prevalence and abundance than parasites from fishes in the exploited atoll. These authors speculated that the reduced rates of infection at the exploited atoll reflected a simplified food web that resulted from overfishing (see above). Low biodiversity would hinder transmission of parasites with complex life cycles, particularly those of sharks, which were fished heavily (Lafferty *et al.*, 2008). These results were augmented by a more expansive study that examined parasites of seven fish species from three fished and three unfished islands (Wood *et al.*, 2014). Fish from exploited islands had lower parasite species richness, in part due to the presence of rare parasites at unfished localities (Wood *et al.*, 2014). However, parasite abundance in fish hosts varied between types of islands, depending on their life cycles. Parasites with direct life cycles were more common in fish from fished islands, while those with complex life cycles that were trophically transmitted were more abundant at unfished islands. Presumably, those with complex life cycles infected top predators whose populations were reduced by fishing, while those with direct life cycles responded to increases in host density, indirectly caused by harvesting their predators (Wood *et al.*, 2014). Curiously, cestodes and nematodes, but not trematodes, increased in abundance at unfished islands. Some trematodes (*Stephanostomum* spp.) responded positively to fishing, while others did not, possibly due to indirect effects of fishing on their molluscan intermediate hosts (Wood *et al.*, 2014). Further analysis across the archipelago showed that three of four nematode taxa and seven of nine trematode taxa, excluding *Stephanostomum* spp., occurred only at unfished islands (Wood *et al.*, 2018). In addition, parasite diversity was correlated with host diversity in unfished habitats, but not in exploited waters, driven mainly by the presence of cestodes and trematodes which were largely absent at the latter (Wood *et al.*, 2018). This result differed from previous studies where the abundance of trematodes, excluding *Stephanostomum* spp., was not affected by fishing. Overall, fishing pressure results in an impoverished fauna of directly transmitted parasites unrelated to changes in host diversity (Wood *et al.*, 2018).

Other studies also examined the effects of commercial fishing on parasites in exploited and protected areas, although degrees of replication and study design vary. Nevertheless, a few are worth examining in detail (see table 1 for other examples). Four exploited host species, two fishes and two invertebrates, were compared between three marine protected areas and three unprotected areas (Wood *et al.*, 2013). Almost all parasite species,

Table 1. Selected examples of parasitological studies of hosts residing outside and inside marine and freshwater protected areas.

| Protected area | Location | Host | Time protected | Main results | Reference |
|--|---------------------------------|--|--------------------------|--|---|
| Cerbère-Banyuls Marine Reserve | South-eastern France | Bucchich's goby (<i>Gobius bunchichi</i>) | Prior to 1979 | Only adult helminths considered. Results equivocal | Sasal <i>et al.</i> (1996) |
| Cerbère-Banyuls Marine Reserve | South-eastern France | White sea bream (<i>Diplodus sargus</i>) | Prior to 1979 | Only monogeneans (<i>Lamellodiscus</i> spp.) considered. Communities similar inside and out of protected area. Most common and least specific species more abundant in protected area | Sasal <i>et al.</i> (2004) |
| Scandola Nature Reserve | Corsica, France | 63 fish species | Since at least 1986 | Diversity of trematodes much greater than in other parts of the Mediterranean | Bartoli <i>et al.</i> (2005) |
| Bonifacio Strait Marine Reserve | Corsica, France | Six fish species | Reserve established 1999 | Parasite distribution did not appear to be affected by protection status, but by host specificity | Ternengo <i>et al.</i> (2009) |
| Medes Islands MPA | Catalonia, Spain | White seabream (<i>Diplodus sargus sargus</i>) | MPA established 1983 | Monoxenous parasite diversity higher in fished areas, but more abundant in NTZ. Richness and abundance of heteroxenous parasites higher in NTZ | Isbert <i>et al.</i> (2018) |
| Celestun Biosphere Reserve, Dzilam and Alacranes National Park | Yucatán, Gulf of Mexico | Black grouper (<i>Mycteroperca bonaci</i>) | Unknown | Three distinct intestinal helminth communities in the three areas varying in protection levels | Villegas-Hernández <i>et al.</i> (2022) |
| Bienener Altrhein Natural Reserve | North Rhine-Westphalia, Germany | 15 snail species | Unknown | Trematode diversity and prevalence similar to unprotected areas in Europe | Schwelm <i>et al.</i> (2021) |

MPA, marine protected area; NTZ, no take zone.

including some monogeneans and trematodes, had higher density (number of parasites/m²) in the protected areas. However, only one parasite (a monogenean on one of the fishes) had higher abundance on fish from the protected areas. These authors attributed the decline in parasite density to a reduction in parasite habitat and resources (host population) in fished host populations, although effects on abundance at the infrapopulation level were less common (Wood *et al.*, 2013).

Braicovich *et al.* (2021) used a different approach, comparing parasites of the Brazilian flathead (*Percophis brasiliensis*) before and after closure of a fishery off Argentina. They observed significant changes in parasite community structure and composition after several years of closure, resulting from increased abundances of several parasites, all of which were generalists. A number of these parasites infected elasmobranchs as definitive hosts, whose populations have benefitted from the closure (Braicovich *et al.*, 2021). Others use marine mammals, which have also benefitted from a cessation of harvesting (Braicovich *et al.*, 2021).

Overall, it appears that exploitation results in lower parasite species richness, a reduced abundance of trophically-transmitted parasites and an increased abundance of direct life cycle parasites. It is noteworthy that these results parallel general observations of effects of pollution on fish parasites, where parasite diversity decreases with increased pollution, with those parasites with

complex life cycles experiencing reductions and those directly-transmitted experiencing increases, although any particular parasite species may increase or decrease in abundance (Poulin, 1992; MacKenzie, 1999; Marcogliese, 2004, 2005).

Comparable studies do not exist for freshwater ecosystems, but results of managed fisheries yield information that highlights effects of fishing as well. For example, intensive fishing of whitefish (*Coregonus lavaretus*) and pike (*Esox lucius*) for three years successfully reduced levels of *Triaenophorus crassus*, but not *Dibothriocephalus ditremus* (formerly *Diphyllobothrium ditremum*), in whitefish (Amundsen & Kristoffersen, 1990). The former cestode matures in pike and the latter in birds. These authors concluded that *T. crassus* abundance declined following removal of the pike definitive host (Amundsen & Kristoffersen, 1990). These results parallel those above in that removal of a top predator reduced the abundance of a parasite with a complex life cycle. In another study that examined the effects of exploitation of a fish stock on parasitism, two of three trophically transmitted helminths increased in an intensively-fished population of brook trout (*Salvelinus fontinalis*) in northern Quebec, Canada (Albert & Curtis, 1991). This increase in parasite recruitment may have been due to increased feeding of younger fish cohorts due to competitive release following selective removal of an older cohort of fish (Albert & Curtis, 1991).

Climate change

Over the last two decades, there have been numerous reviews and perspectives on the effects of climate change on parasitism and disease (Dobson & Carper, 1992; Harvell *et al.*, 1999, 2002; Marcogliese, 2001, 2008, 2016; Lafferty, 2009; Altizer *et al.*, 2013; Dobson *et al.*, 2015; Byers, 2020, 2021; Cohen *et al.*, 2020; Rohr & Cohen, 2020; among others). Effects of climate change globally are complex and multi-faceted and vary regionally, with knock-on ramifications for myriad other environmental phenomena, including other drivers of biodiversity loss (Marcogliese, 2001, 2008, 2016). Among parasites, effects also can be species and stage specific. For example, temperature has different effects on the same life cycle stage of closely-related parasites, or even strains within a species (Marcogliese, 2001; Morley, 2011), as well as different stages within the same species' life cycle (Morley & Lewis, 2015).

Rohr & Cohen (2020) highlight major advancements in our understanding of climate change and disease. These include improved mechanistic disease models, the recognition of the importance of climate variability to disease dynamics and the significance and consequences of thermal mismatches between host and parasites. Predictive models describing the effects of climate change on helminth parasites of wildlife using a metabolic approach to generate thermal performance curves can be parameterized using body size of parasites and their hosts and temperature (Dobson *et al.*, 2015; Molnár *et al.*, 2017). For example, by incorporating the metabolic theory of ecology into host–macro-parasite population models, Molnár *et al.* (2013) were able to determine the fundamental thermal niche of an Arctic nematode (*Ostertagia gruehneri*), the most common gastrointestinal parasite of caribou (*Rangifer tarandus*), illustrating that climate change effectively partitions a continuous transmission season running from spring to autumn into two distinct transmission periods (see Marcogliese, 2001 for other examples of changing seasonal transmission dynamics).

Variability in temperature is an important consideration in elucidating host–parasite interactions because it better simulates natural conditions (Marcogliese, 2016). Temperature variability affects both parasite and host traits of trematodes infecting invertebrate and vertebrate hosts including cercarial productivity, cercarial infection rate, host survival and components of the host immune system, all of which affect parasite population dynamics (reviewed in Marcogliese, 2016). Climate change also leads to a decrease in diurnal temperature range, as night-time temperatures will warm faster than during the day (Rohr & Cohen, 2020).

The thermal mismatch hypothesis proposes that as environmental temperatures shift away from those normally experienced by parasites and hosts, parasites will often perform better than their hosts. In this case, parasites will achieve their highest infection levels at these temperatures rather than those where they do best in isolation. The hypothesis predicts that disease risk should increase with global warming in hosts from cooler climates (Rohr & Cohen, 2020). The thermal mismatch hypothesis received general support in a global analysis of parasitism and disease in over 7000 wildlife populations. Effects were observed in both terrestrial and freshwater host populations, but were stronger in ectotherms (Cohen *et al.*, 2020). Parasite prevalence was greatest when ectothermic hosts from cool and warm climates experienced warm and cool conditions, respectively. Effects were stronger in parasites with direct life cycles, compared to those with complex life cycles (Cohen *et al.*, 2020). Helminth prevalence was directly

related to temperature across all climatic zones, but effects were most apparent in the cool climates of the temperate zone. These authors suggested that helminths might benefit from climate change more than other types of parasites (Cohen *et al.*, 2020).

In addition to the conceptual and applied progress in climate change research into effects on parasites and disease eloquently described by Rohr & Cohen (2020), other important developments in our understanding of host–parasite interactions include the idea of phenological disruption of parasite and host life history traits under a changing climate (Marcogliese, 2001, 2016). Warming can affect timing of transmission events at key points in a parasite's life cycle. Laboratory experiments demonstrated that high temperatures promoted intermediate host snail growth, egg production and mortality, as well as egg development in the trematode *Ribeiroia ondatrae*, a parasite responsible for malformations in its intermediate hosts (Paull & Johnson, 2011). Such changes would result in earlier transmission of the trematode to snails and subsequently to the amphibian second intermediate host, termed a phenological mismatch. At these earlier life history stages, the anuran hosts are more susceptible to the pathological effects (limb deformities and mortality) of the parasite (Paull & Johnson, 2011). McDevitt-Galles *et al.* (2020) examined host–parasite interactions along an altitudinal cline to examine the phenological synchrony of *R. ondatrae* and Pacific chorus frogs (*Pseudacris regilla*) and subsequent parasite-induced pathology. At low elevations, synchrony was high and the probability of severe limb malformations caused by an established trematode increased by 33% compared to a high-elevation area. Consequently, after controlling for parasite intensity, the risk of pathology increased by 50% in the low-elevation habitat (McDevitt-Galles *et al.*, 2020). These authors concluded that climatic warming could lead to increased rate of malformations due to the interaction between infection intensity and phenological synchronicity.

Given that there are differential effects of temperature on the various stages of parasite life cycles, their hosts and host–parasite interactions in different hosts, it is imperative to examine net effects of temperature increases and variability on transmission dynamics across a parasite's life cycle and the subsequent host response (Marcogliese, 2016). Few studies have taken such a holistic perspective, but relevant examples were reviewed from both freshwater and marine ecosystems (Marcogliese, 2016). In a marine trematode that uses snails and amphipods as intermediate hosts, heat waves accounting for temperature variability should lead to increased cercarial productivity and establishment in the amphipod host (Studer & Poulin, 2013). In the freshwater *R. ondatrae*–amphibian system, experiments at the level of the gastropod intermediate host (*Planorbella trivolvis*) and the second intermediate anuran host (*P. regilla*) displayed differential effects on parasites and hosts at higher temperatures, revealing nonlinearities in pathological effects due to temperature (fig. 1; Paull & Johnson, 2011; Paull *et al.*, 2012). Snail growth and development increased with temperature, but survival declined. Development of parasite eggs and cercariae increased, but survival declined. Infected snail survival plateaued at the intermediate temperature (Paull & Johnson, 2011). Cercarial infectivity to tadpoles increased with temperature, but cercarial establishment and total numbers in tadpoles decreased at different rates (Paull *et al.*, 2012). Consequently, the level of malformations in tadpoles was highest at intermediate temperatures, while infection intensities were lowest at the highest temperature (fig. 1). These studies highlight the importance of examining effects of temperature at

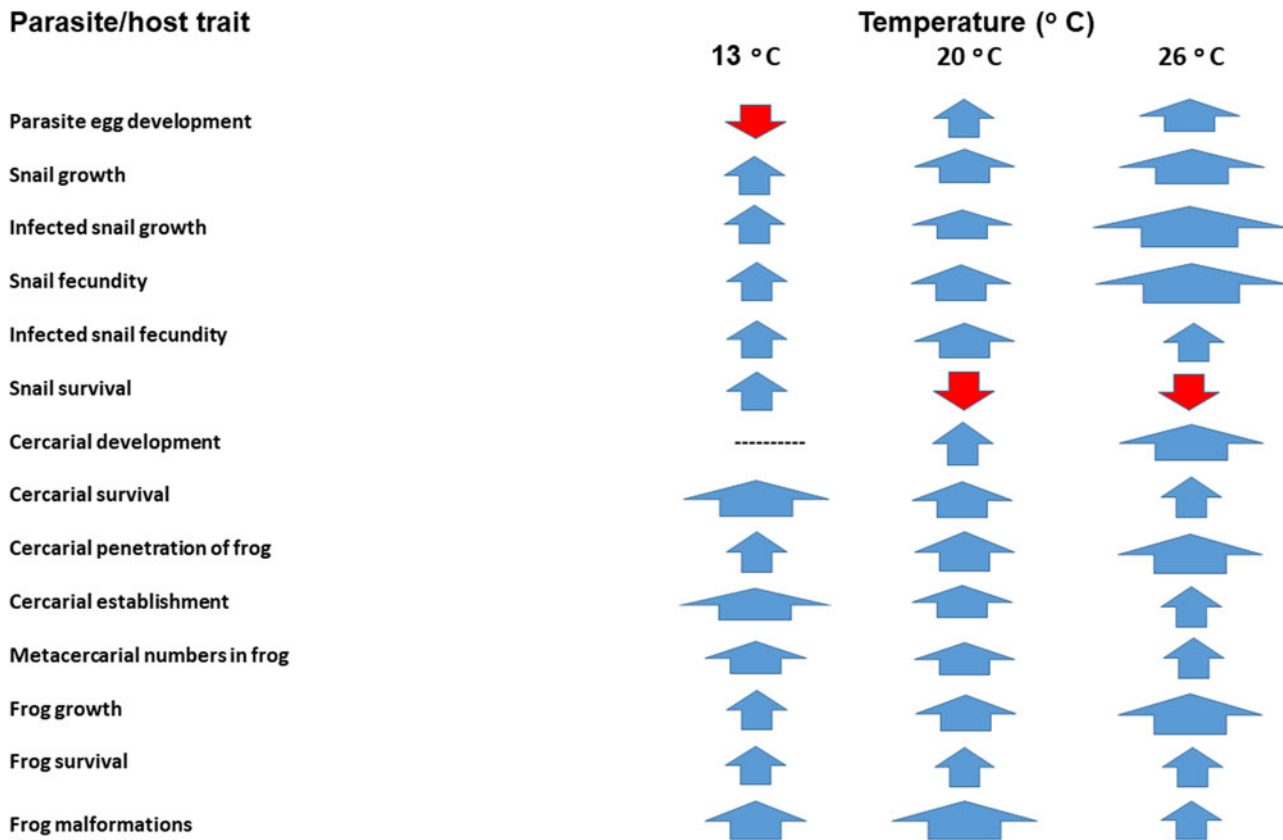


Fig. 1. Effects of temperature on parasite and host traits in the life cycle of the freshwater trematode *Ribeiroia ondatrae* in its gastropod first intermediate host (*Planorbella trivolvis*) and tadpoles of its anuran second intermediate host (*Pseudacris regilla*). The width of the arrow reflects the intensity of the effect. Net effects indicate that metacercarial numbers are lowest in tadpoles at the highest temperature, while pathology peaks at the intermediate temperature. A dashed line indicates no effect. Diagram based on table 2 in Marcogliese (2016) and the results from Paull & Johnson (2011) and Paull *et al.* (2012).

all parasite life cycle stages, on the host and on the host–parasite interactions in the different hosts (e.g. host resistance). Differential effects of temperature on development of parasites and hosts and on their interactions renders the predictability of effects of climate change on parasite infections and their consequences problematic (Paull *et al.*, 2012).

Few other studies on net effects of temperature on different stages and hosts within a parasite's life cycle have been undertaken. Another marine trematode, *Himasthla elongata*, infects the snail *Littorina littorina* as first intermediate host and the mussel *Mytilus edulis sensu lato* as the second intermediate host, with an avian final host (fig. 2). Snails died faster at the warmer temperatures (22°C and 28°C), and trematode infection further increased susceptibility of the snail to an elevated temperature (22°C) typical of warm summers in the south-western Baltic Sea (Díaz-Morales *et al.*, 2022). Furthermore, exposure of infected snails to that temperature optimized cercarial emergence and infectivity, although survival was reduced. Successful establishment in the mussels was maximized at 22°C and lowest at 28°C. Overall, higher temperatures resulted in net negative effects on trematode transmission to the second intermediate host mussel due to the snail first intermediate host's sensitivity to those temperatures, along with the accompanying reduced cercarial survival (Díaz-Morales *et al.*, 2022). These authors concluded that it is imperative to examine the most fragile links in a parasite's life cycle and that *H. elongata* performance may be reduced in a warming ocean.

Interestingly, using an innovative approach involving the examination of preserved hosts held in natural history collections, Wood *et al.* (2023) revealed a decline in parasite abundance in fishes from Puget Sound, Washington, United States, over a 100-year period. Declines in numerous species were correlated with an increase in temperature over the same period. Furthermore, population declines occurred in helminth parasites that had three or more hosts in their life cycles, but not those with only one or two hosts, suggesting that life cycle complexity is a contributing factor to parasite vulnerability to environmental change (Wood *et al.*, 2013).

A number of studies, mainly in intertidal ecosystems, demonstrate potential ecosystem-wide effects resulting from changes in parasite–host dynamics with increases in temperature (reviewed in Mouritsen & Poulin, 2002; Mouritsen *et al.*, 2005; Marcogliese, 2008; Byers, 2020, 2021). Using experimental mesocosms, Mouritsen *et al.* (2018) examined effects of increasing temperature on a diverse community of intertidal amphipods serving as second intermediate hosts for the trematode *Maritrema novaezealandensis*. A temperature increase from 17°C to 21°C resulted in huge changes in community structure. Density of four epibenthic amphipods, but not the two infaunal species, declined significantly, as did species diversity in the presence of the parasite. At 19°C, negative effects on the parasitized amphipod community were similar to those at 21°C on amphipods without parasites. A simulated heat wave at 25°C nearly eliminated the entire amphipod community in the presence of

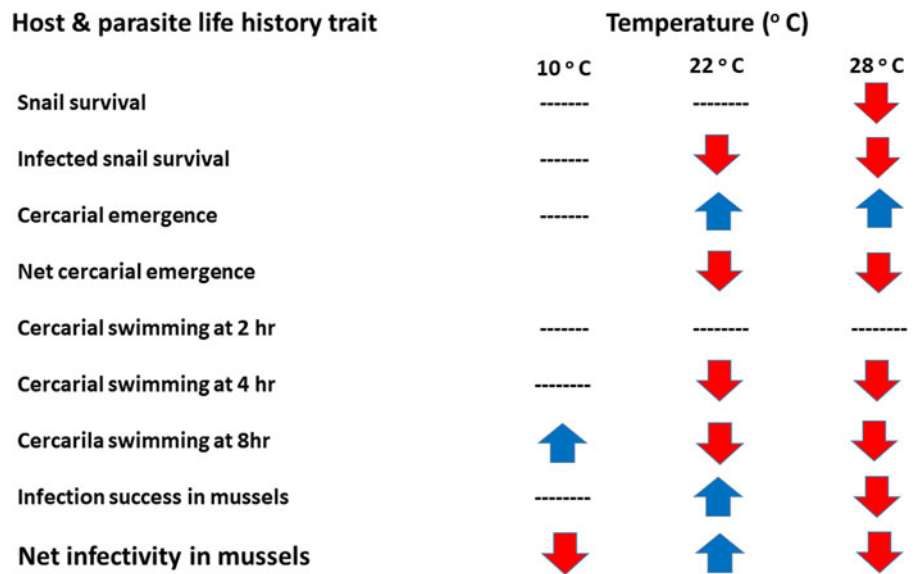


Fig. 2. Effects of temperature deviations on components of the life cycle and host–parasite interactions, relative to ambient temperature (18°C) in the trematode *Himasthla elongata*, infecting the first snail (*Littorina littorea*) and second mussel (*Mytilus edulis sensu lato*) intermediate hosts. Optimal temperature for transmission and infection success is 22°C. Dotted lines indicate no effect. Based on results from Díaz-Morales *et al.* (2022).

the trematode, favouring the infaunal species (Mouritsen *et al.*, 2018). Corroborative field studies showed that there was a significant negative relationship between amphipod species richness and prevalence of *M. novaezealandensis* in the first intermediate host mud snails (*Zeacumantus subcarinatus*) across a dozen sites (Mouritsen *et al.*, 2018). Although temperature and parasitism both had negative effects on amphipod diversity, these effects were not identical, and their combined effects were unpredictable. These authors predict that their synergistic effects will lead to drastic changes in the coastal amphipod community with climate change.

Another freshwater mesocosm experiment tested interactive effects of infection by two species of parasite larvae and temperature on four species of crustacean hosts (Friesen *et al.*, 2021). Hosts included two amphipods (*Paracalliope fluviatilis* and *Paracorophium excavatum*) and two isopods (*Austriodotea annectens* and *Austriodotea lacustris*). These hosts share four trematode species, two of which were used in this experiment (*Maritrema poulini* and *Coitocaeum parvum*). Both parasites use the mud snail *Potamopyrgus antipodarum* as first intermediate host and the former infects waterfowl as definitive host while the latter uses fish. Factors involved in the experiment included two temperatures (ambient and elevated) and continuous parasite exposure or no continuous exposure. Parasite exposure and temperature had interactive effects on community structure. Abundance of the amphipod *P. fluviatilis* declined significantly at elevated temperature and continuous parasite exposure. The other amphipod suffered parasite-induced mortality at the higher temperature. Comparatively, abundance of isopods was affected to a much lesser degree by parasite exposure or temperature (Friesen *et al.*, 2021). Results suggest that trematode parasitism in a warming climate will affect benthic invertebrate community structure by reducing the abundance of amphipods in the ecosystem, which could have knock-on effects on other organisms (Friesen *et al.*, 2021).

Invasive species

Global losses due to invasive species along with remediation and management expenses are estimated at 26.8 billion US\$ annually

(Diagne *et al.*, 2021). Agriculture, forestry and fisheries, along with other sectors of the economy, all have been impacted (Pimentel *et al.*, 2005). Invasive fishes alone in the United States have inflicted damage estimated at 5.4 billion US\$ annually (Pimentel *et al.*, 2005). Invasive species also include parasites. For example, there are numerous well-documented cases of parasites causing serious problems for fish and fisheries around the world. Among the best-known helminths are the monogenean *Gyrodactylus salmonis* in Norwegian salmonids, the swim bladder nematode *Anguillicoloides* (formerly *Anguillicola*) *crassus* in the European eel (*Anguilla anguilla*) and the Asian fish tapeworm *Schyzocotyle* (formerly *Bothriocephalus*) *acheiolognathi* in numerous freshwater fish globally. The parasitic problems associated with invasive species have been illustrated extensively in numerous excellent reviews (Prenter *et al.*, 2004; Taraschewski, 2006; Dunn, 2009; Peeler *et al.*, 2011; Poulin *et al.*, 2011; Dunn *et al.*, 2012; Hatcher *et al.*, 2012; Telfer & Bown, 2012; Goedknecht *et al.*, 2016; Médoc *et al.*, 2017). Although many of these focus on disease problems arising associated with invasive species, the sublethal and indirect effects of parasites on hosts, populations and ecosystems have been the focus of much attention.

In terms of helminth populations and communities, there are various outcomes associated with invasive species. They may establish without their native pathogens and parasites in their introduced range, having left their parasites behind in their native range (Torchin *et al.*, 2003; Torchin & Mitchell, 2004). Termed the enemy release hypothesis (ERH), such a phenomenon may be the result of small propagule pressure or unsuitable conditions for the parasite in the introduced range. However, invasive species may import invasive parasites, which then may be transferred to native hosts, termed spillover (Prenter *et al.*, 2004; Dunn, 2009; Tompkins *et al.*, 2011). Invasive species may acquire native parasites and successfully participate in their transmission, so that their populations are enhanced, termed amplification or spillback (Kelly *et al.*, 2009; Poulin *et al.*, 2011; Tompkins *et al.*, 2011). Lastly, they may not be competent hosts for native parasites and act as a sink or dead end, breaking the transmission cycle, termed dilution or transmission interference (Johnson & Thieltges, 2010; Tompkins *et al.*, 2011; Goedknecht *et al.*, 2016). These ideas were developed further by Chalkowski *et al.* (2018).

Invasive species also may contribute to spillback not only by amplification but indirectly, without being infected themselves, through habitat alteration or physical transfer by acting as mechanical vectors. In addition, the expansion and range of invasive species may be limited by a native or invasive parasite or pathogen, termed suppressive spillover (Chalkowski *et al.*, 2018). Herein, three case studies of helminth parasites in invasive fish and amphibians are presented to illustrate some key issues and developments for the consequences of species invasions for helminth populations and communities.

A series of studies examining patterns of aggregation in parasites of invasive and native hosts lends some insight into the mechanisms behind the ERH. The so-iuy mullet (*Liza haematocheilus*), native to the Amur River estuary and Sea of Japan, was deliberately introduced into the Black and Azov Seas in the 1970–1980s, where it lives sympatrically with the native flathead mullet (*Mugil cephalus*), and other mullets (Sarabev, 2015a). The so-iuy mullet displays reduced infracommunity species richness in the introduced range compared to its native range, in support of the ERH (Sarabev, 2015a). Truncated parasite abundance distributions suggested that parasite-induced host mortality of juvenile so-iuy mullet accounted for the low proportion of invasive mullets infected (Sarabev, 2015b). Total parasite mean abundance was over 15 times lower in mullets in the invasive range compared to their native range, although the difference was less for co-introduced monogeneans compared to acquired trematodes (Sarabev *et al.*, 2017). In addition, aggregation was lower for acquired endohelminths in the invasive mullets, but not co-introduced monogeneans, compared to their native range. Patterns of parasite aggregation may explain the success of the invasive hosts, with fewer susceptible hosts (Sarabev *et al.*, 2017). Both acquired mullet specialists and generalists infected a low proportion of invasive mullets at low abundance, unlike the co-introduced monogeneans. Essentially, there were fewer hosts in the invasive population susceptible to native parasites (Sarabev *et al.*, 2017, 2018). Strict host specificity and a direct life cycle were the parasite characteristics permitting exploitation of a large proportion of the invasive host population. These authors concluded that co-introduced and acquired parasites use invasive host populations in fundamentally different ways (Sarabev *et al.*, 2018). In a subsequent study, these authors conjectured that infection patterns were due to a high rate of host-induced parasite mortality in susceptible hosts along with

a high degree of resistance to acquired parasites among a large portion of the host population in the invaded range (Sarabev *et al.*, 2019). A network analysis showed that the invasive mullet played a peripheral role in host–parasite networks in the invaded range, compared to its native range as well as compared to another native mullet that inhabited both the invaded and native areas (Llopis-Belenguer *et al.*, 2020). Taking these data a step further, significant differences occurred between parasite networks of the so-iuy mullet in connectedness, nestedness and modularity in the invaded and native areas (Llberia-Robledillo *et al.*, 2022). These network properties differed between actively-transmitted and trophically-transmitted parasites, varying not only between the parasites themselves but between invaded and native ranges (Llberia-Robledillo *et al.*, 2022). Integrating data together at different organizational and hierarchical scales and comparing ectoparasite and endoparasite subsets between the regions in a macroecological approach, Sarabev *et al.* (2022) proposed fundamental differences in parasites between those co-introduced and those acquired in an invaded range that include abundance–variance and abundance–occupancy relationships, core-satellite species, patterns of aggregation and prevalence frequency distributions, infrapopulation size, and infracommunity species richness. Lastly, they interpreted results to support the idea that infections with acquired larval trematodes induce mortality in juvenile invasive fish, which essentially is suppressive spillover (Chalkowski *et al.*, 2018), while a large proportion of the population remained resistant to infection in the invaded area (Sarabev *et al.*, 2022).

Further insights can be derived from an examination of parasitological studies on another invasive species, the round goby (*Neogobius melanostomus*). This species has been a widespread invader in European waters, close to its place of origin, and North America. Comparisons of parasites in both the round goby and native hosts on these two continents yield interesting and illuminating differences (table 2). The round goby is native to south-eastern Europe and found naturally in the Ponto-Caspian region, including the Black Sea (Kornis *et al.*, 2012). Along with some other goby species, this fish has expanded its range throughout Europe via both ballast water transport and canal systems (Kornis *et al.*, 2012; Kvach & Ondračková, 2020). The fish has spread throughout large river systems. To the east, the fish colonized south-eastern Europe and Russia via the Don and Volga Rivers in the 1960s. It spread into central and northern

Table 2. Comparison of characteristics of helminth parasitological communities in invasive round gobies (*Neogobius melanostomus*) between North America and European fresh waters.

| Parasites | North America | Europe |
|--|--------------------|-------------------------------------|
| Parasite loss (support for enemy release hypothesis) | Yes | No |
| Parasite species richness vs. native range | Lower | Higher, but decreases with distance |
| Parasite species richness with time | Increases | Increases |
| Co-invasive parasites | No | Yes |
| Spillover | No | Yes |
| Acquired parasites in invaded range | Yes | Yes |
| Type of acquired parasites | Larval generalists | Larval generalists |
| Spillback with amplification | No | Yes |
| Dilution (encounter reduction) | Yes | No |

Europe via the Dnieper and Vistula Rivers in the 1980s and 1990s. Westward expansion followed the Danube and Rhine River corridors in the 1990s to present day (Kvach & Ondračková, 2020). Numerous studies in European waters show that invasive round gobies are infected with both acquired parasites in the invaded range and co-invasive parasites at similar levels of species richness to their native range (Ondračková *et al.*, 2005, 2010; Molnár, 2006; Mühlegger *et al.*, 2010). In contrast to predictions of the ERH, parasite infracommunity richness was higher in invasive round gobies compared to that in its native range in the Bulgarian portion of the Danube River (Ondračková *et al.*, 2010). This was attributed to the fact that the round goby is native to the southern part of the Danube River and was considered susceptible to parasites in the invasive range (Ondračková *et al.*, 2010). Studies of round gobies in recently-invaded habitats further away from their native range yield results more in line with the ERH. Parasite abundance and species richness were lower in recently-introduced round gobies collected from the Rhine and Elbe Rivers, compared to its native range (Ondračková *et al.*, 2015). Most acquired parasites were larvae or subadults with low host specificity in both systems. Round gobies may be involved at least partially in spillback of the nematode *Raphidascaris acus* in German rivers (Hohenadler *et al.*, 2019). Abundance of this parasite has increased since the invasion of the round goby and other gobies. A longitudinal study of parasites of both native and invasive round gobies along the Danube River revealed that 29 metazoan parasite species, 24 of which were helminths, infected the round goby in the river, 12 of which occurred in both the native and non-native fish. With eight species restricted to the native range in Bulgaria and nine to the invasive range in Slovakia and Austria, losses of parasites and parasite acquisition in the invaded range were not considered significant (Francová *et al.*, 2011). Curiously, parasite species diversity was higher at the invaded sites compared to the native sites (Francová *et al.*, 2011). A comprehensive study examined which parasites were shared between five invasive goby species and native fishes in three European river basins, including the Vistula, Morava and Rhine Rivers. Invasive gobies in general acquired about half the parasites found in local host fishes, all of which were larval/subadult generalists (Ondračková *et al.*, 2021). Species richness of infracommunities and component communities was lower in the invasive gobies compared to native fishes. Shared local hosts were phylogenetically or ecologically similar to the gobies, and parasite community composition was strongly related to regional affiliation (Ondračková *et al.*, 2021). Among helminths, trematode metacercariae occurred at the highest prevalence, suggesting that invasive gobies may play important roles in their transmission (Ondračková *et al.*, 2021). In addition, mean parasite abundance and species richness were positively related to the time since a host species was introduced among four species of goby, including the round goby, in the Danube River (Ondračková *et al.*, 2015).

The pattern of parasitization of invasive round gobies in North America is very different from that observed in Europe (table 2). Round gobies were introduced into the Great Lakes and associated waters via ships' ballast, being first observed in 1990 (Kornis *et al.*, 2012). Early parasitological studies in these waters indicated that the round gobies were infected by relatively few parasites, with no co-invasive helminths (Muzzall *et al.*, 1995; Pronin *et al.*, 1997; Camp *et al.*, 1999; Kvach & Stepien, 2008). Kvach & Stepien (2008) noted some parallels with the situation in Europe, as all the helminths found but one were larvae, with trematodes being

the most common. They also observed no increase in infections of round gobies in the decade following their introduction. There were far fewer parasite species compared to the round goby's native range, supporting the ERH (Kvach & Stepien, 2008). First seen in the upstream section of the St Lawrence River in 2004, the round goby was parasitized by relatively few species in 2007–2009, also supporting the ERH (Gendron *et al.*, 2012). All species were larval and generalists, common to native fishes, and species richness was much lower than in sympatric native fishes and in round gobies from their native range. However, Gendron *et al.* (2012) also examined round gobies from Lake St Clair, the site of its original introduction and first parasitological study (Muzzall *et al.*, 1995). Interestingly, parasite abundance and species richness in the round goby have more than doubled and infracommunity species richness has increased to levels similar to native fishes within 15 years. These results suggest that any advantages posed to invasive species such as the round goby due to the ERH may be lost over time (Gendron *et al.*, 2012). Further studies in this system provided support for dilution or encounter reduction, due to the presence of the round goby. Round gobies in the St Lawrence River were commonly infected with cystacanths of *Neoechinorhynchus tenellus*, a parasite of piscivorous fish whose larvae are commonly found in assorted prey species. However, over half the cystacanths in the livers of round gobies were degraded and dead, compared to very few in native fishes (Gendron & Marcogliese, 2016). In addition, levels of infection in a native fish, the johnny darter (*Etheostoma nigrum*), were low when sympatric with the round goby and much higher at a goby-free site, supporting possible encounter reduction due to the presence of the round goby. However, the rate of cystacanth degradation was negatively correlated with time since colonization across several sites, including Lake St Clair, lead to the suggestion that a dilution effect caused by an invasive species due to parasite–host incompatibility might also wane over time (Gendron & Marcogliese, 2016). Prior to the round goby invasion, *Diplostomum* spp. was the most common and abundant parasite in fishes in the St Lawrence River (Marcogliese *et al.*, 2006). However, since the appearance of the round goby, its mean abundance has plummeted drastically to extremely low levels at all sites where the round goby also was found in spottail shiners (*Notropis hudsonius*), golden shiners (*Notemigonus crysoleucas*) and yellow perch (*Perca flavescens*), but not at those where the goby was absent (Gendron & Marcogliese, 2017). These authors examined different hypotheses for the puzzling decline, including: (a) reduced abundance of snail intermediate hosts due to goby predation; (b) possible hydrological changes impacting transmission of free-living stages; (c) gobies acting as decoys for cercariae; (d) poor parasite survival in the invasive host; (f) potential decline in abundance of the final gull host; and (g) a diet shift in the definitive host towards less-parasitized gobies. Note that these are not necessarily mutually exclusive. Published information and their own data on other fish parasites that require snail intermediate hosts led to the conclusion that hypotheses a, b, f and g were not well supported (Gendron & Marcogliese, 2017). Efficiency of transmission of cercariae to round gobies may be low and interfere with transmission to native fishes, or survival and proper development of metacercariae in the goby may be reduced (Gendron & Marcogliese, 2017). Nevertheless, as round gobies carry infections and are prey for the definitive host gulls, they may still help maintain *Diplostomum* spp. in the system at a low level, a form of spillback (Marcogliese & Locke, 2021).

A final case study examines parasite–host relationships in invasive and native hosts across an ongoing invasion front, providing interesting insights into both co-invasive and native parasites in invasive and native hosts. Cane toads (*Rhinella marina*), which are distributed from the southern United States to South America, were introduced from Hawai'i into Queensland, Australia, in 1935 and continue to spread through northern tropical and subtropical regions there (Selechnik *et al.*, 2017). Like many invasive species, they left most of their parasites behind and are infected with fewer species than in their native range presumably due to the low number of introduced toads in the founding population (Selechnik *et al.*, 2017). For example, in Australia, they are infected with five local species of larval spirurid nematodes, while more than 30 species have been found in their native range (Kelehear & Jones, 2010). Cane toads experimentally exposed to eight Australian species became infected by all eight. However, most of the parasites were encapsulated and subsequently destroyed by the host response, unlike native frogs (Kelehear & Jones, 2010). This host response in an invasive species is similar to that observed in invasive round gobies in North America (see above). Cane toads also brought with them an invasive lungworm, *Rhabdias pseudosphaerocephala* (Selechnik *et al.*, 2017). Experimental infections of this nematode in cane toads and three species of native frogs yielded higher infections in the cane toad than in the frogs. However, few worms managed to migrate to the lungs in the native frogs and infections led to inflammatory reactions (Pizzatto *et al.*, 2010). Cane toads and native frogs maintain separate but common lungworm faunas, the cane toad being infected with the co-invader *R. pseudosphaerocephala* and local frogs hosting four species of the *Rhabdias hylae* complex, despite over 75 years of co-existence (Pizzatto *et al.*, 2012; Selechnik *et al.*, 2017). There is no spillover or spillback from the invasive toads (Selechnik *et al.*, 2017). Distribution of the invasive lungworms varies across the range of the cane toad in Australia. Toads on the invasion front are uninfected, as *R. pseudosphaerocephala* lag behind the expanding cane toad range by one to three years (Phillips *et al.*, 2010). There are large populations of the lungworm in cane toads from a slowly spreading invasion front but not at a fast-spreading invasion front. Further laboratory studies demonstrated that *R. pseudosphaerocephala* from toads at the invasion front colonized within the last five years had higher infectivity and establishment in the lungs than those from the core part of the range, inhabited for over 80 years. Yet toads from the invasion front were more resistant to lungworm infection than were those from the core distribution (Mayer *et al.*, 2021). Furthermore, populations of lungworms of any species were smaller in native frogs sympatric with invasive toads compared to those from areas yet to be colonized (Lettoof *et al.*, 2013). Thus, neither spillover nor spillback seem to occur in the invaded areas. The native nematodes may experience dilution due to the invasive cane toad's immune response (Lettoof *et al.*, 2013). Laboratory experiments confirmed that while native lungworms can infect cane toads, they do not reach the lungs and do not survive in the invasive host (Nelson *et al.*, 2015). Results suggest that the immune response of the cane toad varies along its invasive range (see Becker *et al.*, 2020).

At the same time, a parallel study revealed novel interactions between the invasive cane toad and another invasive parasite, the tongue-worm or pentastome *Raillietiella frenata*. Despite their common name, these worms are not really helminths, but related to arthropods. This parasite colonized Australia approximately 30 years ago in its invasive host, the Asian house

gecko (*Hemidactylus frenatus*). The tongue worm uses a cockroach as intermediate host and both host and parasite are currently limited to urbanized areas around Darwin (Kelehear *et al.*, 2013). Cane toads near Darwin are also infected, and laboratory experiments confirmed that they are competent hosts. Thus, cane toads may facilitate the spread of another invasive parasite that entered Australia independently (Kelehear *et al.*, 2013).

The three case studies share some common ground, but also provide interesting contrasts. Two of these invasive species are colonized by generalist larval helminths; they all tend to show resistance to some native helminths; and two invasive hosts co-introduced host-specific helminths, with no spillover. There appears to be a dilution or encounter reduction effect in two cases. However, in one of these (the round goby), the effect is observed in North America but not in Europe. Indeed, in the cases presented here, the immune response to native parasites appears to be more effective in invasive species far from their native range.

Pollution

The effects of pollution on parasitism have been the subject of numerous reviews (e.g. Khan & Thulin, 1991; Poulin, 1992; Overstreet, 1993; MacKenzie *et al.*, 1995; Lafferty, 1997; MacKenzie, 1999; Williams & MacKenzie, 2003; Sures, 2004, 2008; Marcogliese, 2005; Sures *et al.*, 2017; Sures & Nachev, 2022). Indeed, the question has been examined analytically through the use of meta-analysis (Lafferty, 1997; Blanar *et al.*, 2009; Vidal-Martínez *et al.*, 2010; Gilbert & Avenant-Oldewage, 2021), although the latter only considered monogeneans. A comparison of the contemporary analyses of Blanar *et al.* (2009) and Vidal-Martínez *et al.* (2010) yields some interesting patterns. Both studies examined effects of various types of pollutants on different groups of parasites, but there are some interesting differences between them. Unlike Blanar *et al.* (2009), Vidal-Martínez *et al.* (2010) not only looked at helminths and microparasites, but also crustacean and terrestrial parasites. Furthermore, the latter also considered trematode cercariae in laboratory studies as a separate group, along with the bioaccumulation of contaminants by parasites as a category of bioindicator. Aside from these and some other procedural differences, these two studies also posed very different questions. Vidal-Martínez *et al.* (2010) concerned themselves with methodological issues, while Blanar *et al.* (2009) tested biological questions. Both studies demonstrated effects of some contaminants on specific groups of parasites. However, effects of contaminants not only varied among parasite groups in both studies, but were highly variable within groups (Blanar *et al.*, 2009). Vidal-Martínez *et al.* (2010) found that field and laboratory studies generated results differently. Furthermore, each group of parasites provided distinct information on effects of contaminants, such that these authors suggested that groups should not be pooled, except for eutrophication effects on communities. Blanar *et al.* (2009) examined effects of contaminants on parasites based on their level of organization (populations vs. communities), life cycle complexity (direct vs. complex), the type of exposure (indirect, for endoparasites vs. direct, for ectoparasites and free-living stages) and habitat (marine vs. freshwater). Effects of contaminants on parasites were negative for both populations and communities, negative for ectoparasites but not endoparasites and negative for freshwater parasites but not marine ones (Blanar *et al.*, 2009).

Sures *et al.* (2017) provided the most recent comprehensive review of effects of pollution on parasites, an aspect of a broader area of study they refer to as ‘environmental parasitology.’ Generally, effects of contaminants on parasites are often negative and can be direct, as on ectoparasites and free-living stages, or indirect, acting on the intermediate and definitive hosts of endoparasites (Sures *et al.*, 2017; Sures & Nachev, 2022). There have been several studies on pollution and parasites since that review, and a few are deserving of special mention. While most studies of effects of pollution on parasites examine a limited number of stages, Monte *et al.* (2016) examined effects of glyphosate on multiple stages in the life cycle of *Echinostoma paraensei*. Three different realistic concentrations of the commercial formulation Roundup® were tested experimentally on eggs, miracidia, cercariae, metacercariae and adults of different ages. A 24 hr exposure of eggs to the herbicide significantly reduced miracidial hatching rate only for newly embryonated eggs, but not developing or fully developed miracidia within eggs (Monte *et al.*, 2016). Sensitivity of both miracidial and cercarial mortality increased with herbicide concentration, although miracidia were more sensitive than cercariae. Metacercarial excystment of parasites raised *in vitro* from the first intermediate host, the gastropod *Biomphalaria glabrata*, was negatively related to herbicide concentration. The number of adult parasites removed from experimentally infected hamsters (*Mesocricetus auratus*) and *in vitro* egg production were not affected by herbicide exposure of metacercariae. (Monte *et al.*, 2016). From these sorts of experiments, vulnerable points in a parasite’s life cycle may be determined, that in turn may be used to explain results from field studies that would be hard to interpret otherwise (Marcogliese, 2005).

Comprehensive, holistic approaches such as the one described above yield much better understanding of the relationship between parasite abundance and pollution. Rohr *et al.* (2008a) experimentally exposed different stages of the trematode *Echinostoma trivolvis* and its intermediate hosts (the snail *Planorbella trivolvis* and tadpoles of the green frog, *Lithobates clamitans*) to four different pesticides, including atrazine, glyphosate, carbaryl and malathion, at four concentrations each. They examined effects of pesticide exposure on snail survival, snail growth and fecundity, cercarial infectivity, cercarial survival, tadpole

survival and tadpole susceptibility (fig. 3). Pesticides in general reduced cercarial survival, but only atrazine at the highest concentration did so significantly. None of the pesticides affected snail survival, growth or fecundity, or tadpole survival. Cercarial infectivity was not affected by pesticides, but pesticide exposure of tadpoles increased their susceptibility to infection (Rohr *et al.*, 2008a). The result was that the reduction in exposure due to pesticide-induced cercarial mortality was less than the pesticide-induced increase in tadpole susceptibility, leading to the conclusion that the net effect of exposure of both hosts and *E. trivolvis* to pesticides would be an increase in the infection levels (Rohr *et al.*, 2008a). Another mesocosm experiment where snails and tadpoles were exposed to atrazine demonstrated that not only did atrazine suppress the immune response in tadpoles, but it led to an increase in periphyton, snail egg masses and numbers (Rohr *et al.*, 2008b). The result was an increase in numbers of plagioid trematode metacercariae in green frogs, due to direct ecotoxicological and indirect ecological effects.

A series of multidisciplinary experimental and analytical studies investigated the direct and indirect ecological effects of agrochemicals on risk of infection by *Schistosoma* spp. These studies were not directly examining the effects of contaminants on parasites, but searching for agrochemical applications in agricultural landscapes that would reduce the risk of schistosomiasis. Nevertheless, the results are intuitively useful and could be applied to other trematode systems. Halstead *et al.* (2018) tested the indirect ecological effects of an herbicide (atrazine), an insecticide (chlorpyrifos), a fertilizer and their mixtures on gastropod intermediate hosts. Herbicides and fertilizer have the potential to increase infection risk by promoting the growth of periphyton, which serves as food for the snails (a bottom-up effect). Insecticides may eliminate insects and crayfish, which can be snail predators (a top-down effect). As expected, the insecticide reduced predator densities, indirectly increasing snail density. Ultimately, combined factor and path analysis revealed that top-down effects were greater than bottom-up effects (Halstead *et al.*, 2018). In sum, exposure to these agrochemicals all served to increase snail density and infection risk by *Schistosoma* spp. (Halstead *et al.*, 2018) and presumably other trematodes as well. In a follow-up study, indirect effects of a fertilizer, six insecticides

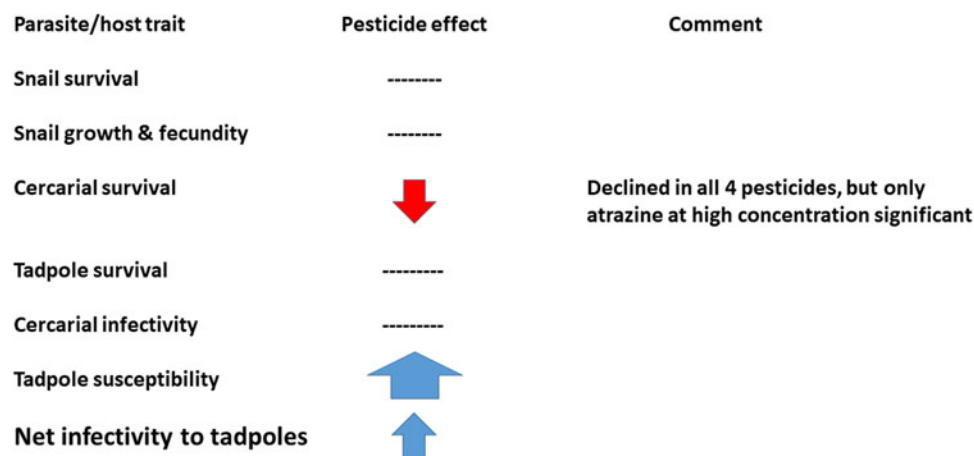


Fig. 3. Effects of four pesticides (atrazine, glyphosate, carbaryl and malathion) on life history traits of the trematode *Echinostoma trivolvis* and its first intermediate host, the snail *Planorbella trivolvis*, and the green frog tadpole, *Lithobates clamitans*. The width of the arrows indicates relative magnitude of the effect. The net effect is that exposure of this host–parasite system to pesticides would increase infection levels in the tadpoles. Dotted lines indicate no effect. Based on results from Rohr *et al.* (2008a).

and six herbicides were examined on snails belonging to two genera primarily responsible for transmitting *Schistosoma* spp. (Haggerty *et al.*, 2022). Four of six of the insecticides increased snail biomass by reducing snail predators. This top-down effect overshadowed any effects of herbicides as there were so few snails remaining after application. In the absence of predators, herbicides had negative effects on snails through reduction in submergent vegetation that serves as snail habitat, although atrazine and acetochlor increased infected snail biomass and total snail biomass, respectively. Fertilizer treatment led to increased submerged vegetation and periphyton, which serves as snail food, increasing snail population growth (Haggerty *et al.*, 2022). This in turn was associated with greater infected snail biomass and cercarial production, and thus, risk of *Schistosoma* spp. infection. Haggerty *et al.* (2022) concluded that fertilizers and insecticides would promote schistosomiasis more than do herbicides.

Hoover *et al.* (2020) used mathematical models of dose-response relationships between life cycle components and agrochemical concentration to estimate transmission risk and exposure of humans to *Schistosoma haematobium* (fig. 4). Modelling results showed that herbicides increase parasite transmission through bottom-up effects on the snail intermediate hosts (see above), but decrease transmission through effects on miracidial survival, snail reproduction and snail survival. Insecticides increase transmission through top-down effects on snail predators (see above) and may decrease infection via effects on survival of miracidia and cercariae and snail reproduction and survival (Hoover *et al.*, 2020). Results vary among the pesticides. Even accounting for treatment and intervention regimes, results indicated that agrochemicals increase human mortality due to *S. haematobium*. In general, the direct negative effects of pesticides on parasites and snails are more than compensated for by the indirect effects on snail predators and snail resources that serve to increase intermediate host densities (Hoover *et al.*, 2020).

As in studies of effects of climate change on parasites, interesting and useful information is derived from experimental laboratory and mesocosm studies on effects of pollution on different host and parasite life history traits. Such studies then permit the determination of net effects of exposure on parasite transmission. They also permit an evaluation of indirect ecological effects on parasite transmission. Nevertheless, they must be interpreted cautiously as they represent a simplification of natural ecosystems.

Parasites as indicators

Parasites with complex life cycles found in a host rely on the presence in the ecosystem of a variety of different organisms that serve as intermediate and definitive hosts, as well as trophic interactions required for transmission. Free-living transmission stages and those found on the external surface of a host are directly exposed to environmental conditions. For these reasons, parasites may be affected directly or indirectly by environmental conditions and have been proposed as good bioindicators of pollution and environmental stress (Overstreet, 1993; MacKenzie *et al.*, 1995; Lafferty, 1997; MacKenzie, 1999; Marcogliese, 2005; Sures *et al.*, 2017). Indeed, it has been suggested that healthy ecosystems are rich in parasites and that parasites may be good indicators of overall environmental health (Marcogliese, 2005; Hudson *et al.*, 2006). Advances and developments in the field were reviewed most recently and comprehensively by Sures *et al.* (2017) and herein emphasis is placed on novel developments since that review or those relatively neglected up until now.

It is imperative to choose any parasite indicator wisely, depending on the biology of the system in question (Marcogliese, 2005; Blonar *et al.*, 2009). Appropriate targets in a host can be parasite communities or particular components of those communities, such as parasite populations, higher taxa, or functional groups based on life history characteristics (Marcogliese, 2005; Blonar *et al.*, 2009; Sures *et al.*, 2017). However, while functional traits have been used to explain several ecological questions and mechanisms related to diversity, their application in parasitology is rare (Llopis-Belenguer *et al.*, 2019). To that end, these authors proposed a list of seven functional traits that are related to parasite dispersal, establishment and persistence that should be applied in parasitology.

Parasite communities were examined from numerous sites on the Yucatan shelf in relation to 46 environmental variables, including hydrocarbons, heavy metals and physicochemical variables (Vidal-Martinez *et al.*, 2022). Using functional groups based on biological characteristics of 48 species of parasite, parasite communities of the dusky flounder (*Syacium papillosum*) were condensed into 15 functional groups. In this case, the functional traits used were adapted from Llopis-Belenguer *et al.* (2019), including body tegument, life cycle, transmission, feeding mode, reproductive mode, specificity and attachment (Vidal-Martinez

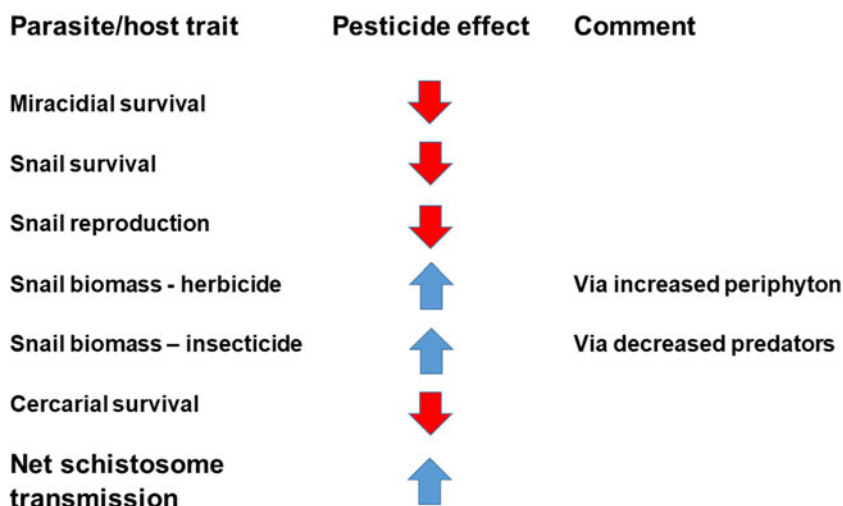


Fig. 4. Generalized overall effects of agrochemicals (insecticides and herbicides) on gastropod intermediate host and parasite life history traits and net risk of infection to humans by *Schistosoma haematobium*. Results varied among individual pesticides. Information tabulated and summarized in Hoover *et al.* (2020).

et al., 2022). These results were compared to those of a previous study on the same system that utilized infracommunity abundance, diversity and richness metrics (Vidal-Martínez *et al.*, 2019). The most important functional groups turned out to be both larval and adult trematodes and tetraphyllidean larvae. Notably, analysis of functional groups explained a similar level of variation in parasite community structure as did species level analyses, but at a much lower cost in terms of labour and financial cost (Vidal-Martínez *et al.*, 2022). Nevertheless, these authors caution that any analysis using functional traits should be validated for the system in question with species-level data for the proper interpretation of ecological patterns.

Numerous authors have called for the integration of multiple techniques in environmental evaluations (Marcogliese, 2005; Vidal-Martínez, 2007; Sures *et al.*, 2017). To that end, Erasmus *et al.* (2022) employed a relatively unique approach to examine impacts of anthropogenic activities on the klipfish (*Clinus superciliosus*) along the South African coast. Fish were examined for ectoparasites and endoparasites and host tissues were analysed for metals. Sites included those receiving anthropogenic inputs and those exposed to natural contamination from geochemical weathering. Infection with certain parasites was associated with concentrations of specific metals in the same host. The most significant finding was that these authors could use parasites to discriminate anthropogenic from natural contamination, which they attributed to the evolution of tolerance in the parasites exposed to natural contamination over long periods of time (Erasmus *et al.*, 2022). While this approach is not novel (see Landsberg *et al.*, 1998; Vidal-Martínez *et al.*, 2003, 2006), this type of multidisciplinary research is far too rare.

One area relatively neglected until recently, but receiving more attention, is the use of parasites as indicators of environmental restoration in ecosystems (Sures *et al.*, 2017). Indeed, parasite communities in American eels were shown to recover after streams suffering from acidification were artificially limed to restore pH (Cone *et al.*, 1993; Marcogliese, 2005). These results were considered to be due to recovery in the populations of molluscs that serve as intermediate hosts for trematodes and are pH-sensitive (Cone *et al.*, 1993). Similarly, parasite communities of roach (*Rutilus rutilus*) and perch (*P. fluviatilis*) appeared to recover and resemble those from more pristine lakes following a reduction in pollution loading from a pulp mill in a lake in Finland (Valtonen *et al.*, 2003). Specifically, *Rhipidocotyle* spp. showed signs of recovery. These parasites use anodontid mussels as their first intermediate host. Trematode parasites were monitored in the California horn snail (*Cerithidea californica*) prior to and for six years following a restoration project in Carpinteria Salt Marsh, in California, United States. Trematode prevalence increased almost four-fold and species richness doubled over the study, with significant differences seen within two years (Huspeni & Lafferty, 2004). These authors attributed the rise in trematodes to the increased bird use with habitat improvement. Taken together, these studies suggest that trematodes are good indicators of recovery because of the sensitivity of their molluscan first intermediate hosts.

An experimental study of parasites of killifish (*Fundulus heteroclitus*) in four salt marshes experiencing different degrees of restoration demonstrated the importance of time since restoration for the recovery of parasite communities. Following anthelmintic treatment, killifish were placed in cages in the four marshes and their parasite communities monitored for several weeks. Sites that were restored ten and 20 years earlier had similar mean parasite species richness as an unrestored site, while the richness was

significantly lower in a newly restored marsh, where only directly-transmitted parasites were found (Anderson & Sukhdeo, 2013). Yet, overall animal diversity was high at the sites restored ten and 20 years earlier, but low at the unrestored site. The longer time since restoration was considered important in establishing stability in the system, similar to the unrestored site, allowing the persistence of parasites with complex life cycles that rely on stable predator–prey relationships for transmission, independent of parasite species richness (Anderson & Sukhdeo, 2013).

A series of studies over time proved enlightening. By comparing parasite communities before and after an environmental disaster, Pérez-del Olmo *et al.* (2007) detected alterations in community structure in the bogue (*Boops boops*) in 2004–2005, two and three years after the *Prestige* oil spill off the coast of Spain in November 2002. Overall species richness, infracommunity species richness, the numbers of monoxenous species and individuals and the numbers of heteroxenous species and individuals all increased following the oil spill. The monogenean *Microcotyle erythrini* was identified as a key contributor to the differences pre-oil spill and post-oil spill, possibly resulting from immunosuppression in the fish due to exposure to polycyclic aromatic hydrocarbons (Pérez-del Olmo *et al.*, 2007). The unexpected increase in heteroxenous parasites, largely due to hemiurid and lepecreadid trematodes, may have been due to organic enrichment of the sediments, thus enhancing benthic intermediate host populations. A follow-up study in 2005–2006 yielded similar results, although a trend in community structure towards pre-oil spill parasite abundance and richness was detected (Pérez-del Olmo *et al.*, 2009). More recently, parasite community structure in the bogue 12–13 years after the oil spill in 2014–2015 was significantly different from that in 2005–2006, but less so from pre-spill times (Pérez-del Olmo *et al.*, 2022). Results show that recovery from an environmental disaster such as an oil spill can take over a decade.

Other examples of parasites used as indicators of recovery from a variety of different natural and anthropogenic disturbances are provided in table 3. From these studies and the ones described above, it appears that: mollusc–trematode systems provide good indicators of recovery; that time to recovery varies among ecosystems and perturbations; and that restoration failures may be detected, which can then lead to revised and improved management strategies. Essentially, parasites are also excellent tools that inform on numerous threats to animal conservation (Gagne *et al.*, 2022).

Summary and conclusions

The major threats to biodiversity worldwide (habitat change, overexploitation, climate change, invasive species and pollution) all have major consequences for helminth populations and communities. In general, effects on parasite communities are negative, but difficult to predict. Each of these stressors has differential impacts on parasites, their hosts, and their interactions that vary among species, between life cycle stages, and among ecosystems. Those parasites with complex life cycles that are trophically transmitted often experience declines, although larval generalist parasites with a wide host spectrum and directly transmitted ectoparasites may display population increases in disturbed situations. Excellent insight has been gained from comprehensive laboratory and mesocosm experiments that test effects on the various parasite stages in different hosts in a life cycle that ultimately calculate the net effect of the stressor in question on parasite abundance

Table 3. Selected examples of helminth parasites used as indicators of recovery from various natural and anthropogenic perturbations to ecosystems.

| Environmental perturbation | Location | Host species | Time since perturbation or restoration | Main results | Reference |
|---|---|---|---|--|-------------------------------------|
| Canal closure in 1949 (disrepair and neglect) | Basingstoke Canal, United Kingdom | Molluscs | Restoration 1973–1991; canal re-opened 1991 | Prevalence and diversity of trematodes decreased during restoration; modest recovery by 2003 | Morley & Lewis (2006) |
| Fire in 1992 | Serra Calderona Natural Park, Spain | Wood mouse (<i>Apodemus sylvaticus</i>) | Post-fire regeneration started in 1994; sampling 2–5 years post-fire | Higher prevalence and abundance in burned area compared to control area, especially for parasites with free larval stages; possibly due to aggregation of hosts in burned area | Fuentes <i>et al.</i> (2007) |
| Fire in 1992 | Serra Calderona Natural Park, Spain | Wood mouse (<i>Apodemus sylvaticus</i>) | Post-fire regeneration started in 1994; sampling 2–10 years post-fire | Results similar to above, with tendency towards similarity with control area, due to post-fire regeneration process | Fuentes <i>et al.</i> (2010) |
| Fire in 1992 | Serra Calderona Natural Park, Spain | Wood mouse (<i>Apodemus sylvaticus</i>) | Post-fire regeneration started in 1994; sampling 2–10 years post-fire | After 10 years, more similarity in populations of certain helminths between burned and control areas. Authors conclude that wood mouse and parasites are good indicators | Sáez-Durán <i>et al.</i> (2018) |
| Fire in 1992 | Serra Calderona Natural Park, Spain | Wood mouse (<i>Apodemus sylvaticus</i>) | Post-fire regeneration started in 1994; sampling 2–18 years post-fire | After 18 years, differences between communities in burned and control areas related to climate effects on post-regeneration process | Sáez-Durán <i>et al.</i> (2021) |
| Oil spill in 2007 | Campeche Sound, Gulf of Mexico | Flatfish (<i>Cyclopsetta chittendeni</i>) | Sampling five and nine months afterwards, in 2008 | Parasite prevalence, abundance declined near spill but recovered within five months, due to rescue effect from non-impacted areas | Centeno-Chalé <i>et al.</i> (2015) |
| Hurricane Isidore in 2002 | Celestún Lagoon, Yucatán, Mexico | Horn snail (<i>Cerithidea pliculosa</i>) | Monthly sampling 20 months before (2001–2002) and 87 months after (2002–2009) hurricane | No snails observed for six months after storm; no trematodes for 14 months. Recovery took 4–5 years | Aguirre-Macedo <i>et al.</i> (2011) |
| Earthquake tsunami in 2011 | Sendai Bay, Tohoku, Japan | Mud snail (<i>Batillaria attramentaria</i>) | Sampling before (2005–2006) and after (2012–2019) tsunami | Trematode parasitism increased following tsunami, but not fully recovered after 8 years. Recovery requires more time | Miura <i>et al.</i> (2019) |
| Oyster reef habitat decline | Rachel Carson National Estuarine Research Reserve, North Carolina | Mud snails, crustaceans, benthic fishes | Sampling 3–5 months prior and twelve months after artificial reef restoration | Parasite richness increased post-restoration. Abundance of trematodes, nematodes and cestodes increased over time. Response varied between restoration techniques, but was rapid overall | Moore <i>et al.</i> (2020) |
| Mangrove destruction | Terminos Lagoon, Yucatán, Gulf of Mexico | Sailfin molly (<i>Poecilia velifera</i>) | Sampling five years after restoration in 2010 | No difference in parasite prevalence, abundance or communities between degraded and conserved sites | Morales-Serna <i>et al.</i> (2019) |

and pathology in any specific host, although results still should be interpreted cautiously. Use of natural history collections may prove a useful approach to examine long-term changes in parasite abundance and species composition as a result of climate change, pollution, species introductions or other environmental factors (Wood & Vanhove, 2023). While the use of parasites as indicators may still be somewhat contentious, trematodes often are useful due to the sensitivity of their molluscan intermediate hosts. An oft-neglected, but potentially useful component of habitat

remediation is the use of parasites as indicators to assist habitat restoration efforts.

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