

## POSITIVE ECOLOGICAL ROLES OF PARASITES

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The traditional assessment of parasites by veterinarians and medical professionals is unequivocally negative. In this minireview, we focus on the positive aspects of the presence of parasites in the environment. Most notably, the host-parasite system is a long-term interaction because parasites, despite their negative impact on the host, rarely lead to its death. We analysed three important aspects of the presence of parasites in the environment: (i) participation in the regulation community balance leading to changes in the dominance structure, the formation of trophic chains as well as the inclusion of new energy sources into the ecosystem, (ii) control of invasions of alien species to new areas through the impact on the adaptive abilities of invaders and (iii) efficient accumulation of heavy metals resulting from the physiological properties of parasite tissues, and thus providing the additional environmental pollution index. The presented examples show that parasites play an important role as ecosystem engineers, affecting the dynamic balance of ecosystems. The present review aims to challenge the stereotype of parasitism as an unambiguously negative interaction and show evidence of the significant impact of parasites on healthy functioning communities and environmental safety.

Key words: parasite, food webs, biological invasions, ecosystem engineering, heavy metal accumulation.

### INTRODUCTION

By definition, parasites impose a fitness cost for their hosts that exerts a selection pressure on them to evolve a series of morphological, physiological and behavioural adaptations, including defence mechanisms (SORCI & GARNIER 2008). The parasite-induced reductions in host fitness enhance selection for host resistance mechanisms, which confer an advantage in the interaction and rapidly spread through the population (PAPKOU *et al.* 2016). According to LAFFERTY *et al.* (2008), parasitism is one of the most common trophic strategies used by organisms. One of the most important features of this interaction is longevity, both at the population and the individual level (POJMAŃSKA 2005). Despite their negative impact on the hosts, parasites rarely lead to their death. The host tolerance to parasitic infestations is a rarely highlighted phenomenon in host-parasite interaction. According to KUTZER and ARMITAGE (2016), it is essential for reducing the negative fitness effects of given parasites. This means that the established host-parasite systems gain an advantage over ran-

domly emerging new ones. Unfortunately, the traditional approach to parasitic organisms as the etiological factors of diseases makes them of primary interest in medicine and veterinary practice (BANETH *et al.* 2012). They constitute a highly diverse group of ubiquitous organisms, which is limited only by the scarcity of susceptible hosts. Parasites are widespread in all ecosystems, and they exert significant effects at different levels of biological organisation in parallel with each other (HATCHER *et al.* 2012). Many researchers emphasise the important role of parasites in shaping and functioning of ecosystems, and more specifically, their positive impact on biodiversity, food webs and energy flow. Some authors suggest that parasite conservation paradigms should align with the 20th-century paradigm shift around predator conservation (DOUGHERTY *et al.* 2016). However, this perspective concerning parasite conservation remains based chiefly on theory, without clear goals and priorities (CARLSON *et al.* 2020). This review aims to challenge the stereotype of parasitism as an unambiguously negative interaction and show evidence of the significant impact of parasites on the community and the environment.

## THE ECOLOGICAL ROLES OF PARASITES

Firstly, we focus on the role of parasites in creating the structure and functions of the ecosystem. By definition, parasitic organisms usually have a negative effect on their hosts, potentially also causing pathological changes that may lead to death and, consequently, reduce the size of the host population (KESSING *et al.* 2010). However, it is worth noting that parasites can also affect the form and stability of food webs, as well as energy flow and biodiversity, positively modifying the functioning of the ecosystem (HATCHER *et al.* 2012). The authors emphasise the influence of parasites on the susceptibility of hosts to predators (e.g. through behavioural manipulations) and their regulatory role in intraspecific and interspecific competition. This regulating function can be of considerable importance in shaping the dominance structure among competing predators. Studies carried out on *Gammarus pulex* infected with *Polymorphus minutus* showed that predatory fish more often attack infected hosts than uninfected ones (MARRIOTT *et al.* 1989). This means that the presence of the parasite may cause an increase in the predator population and, consequently, change the structure of predator domination in the ecosystem.

Parasites may influence the host behaviour to reduce the risk of being eaten by predators that do not belong to the parasites' life cycle. Contrarily, when the predator is part of the life cycle, they may increase the chance of being eaten (MINCHELLA & SCOTT 1991). This means that parasitic organisms can play an essential role in the host's survival, which may be important for species with low population sizes. Parasites can also act as the prey of predators (JOHNSON *et al.* 2010). Furthermore, they may become accidental victims

eaten together with their host. This is important because an infected host can be beneficial to the predator. When the biomass of the parasite constitutes a significant part of the host biomass, it becomes a highly energetic food. Such food types are e.g. snails infected with flukes or nematodes living in the intestines of mammals (JOHNSON *et al.* 2010, LAMBDEN & JOHNSON 2013). When analysing the role of parasitic organisms in the formation of food webs, it is worth paying attention to the changes in the energy value resulting from parasitic invasion concerning host biomass as the food. Individuals of *Artemia parthenogenetica*, infected by different species of tapeworms, show twice the level of triglycerides in tissues than non-infected specimens (SANCHEZ *et al.* 2009). Also, a central but underestimated element of food chains may be the free-living stages of parasites, characterised by a high content of glycogen and fat in their tissues (JOHNSON *et al.* 2010). In the ecosystem, these free-living stages are a very abundant source of energy for non-host organisms. They constitute an important resource of food for predators and reducers (JOHNSON *et al.* 2010, SOLDÁNOVÁ *et al.* 2016). Predation on the free-living stages of the parasites is evident when the number of free-living *Schistosoma mansoni* cercariae is reduced by about 70–90% in the presence of non-host organisms of the genera *Daphnia*, *Cyclops*, *Cypria* and *Lebistes* (CHRISTENSEN 1979).

Due to the significant role of parasites in building and/or shaping food chains, it is worth emphasising that parasites with a long life cycle greatly influence the value of biomass in the ecosystem (KURIS *et al.* 2008). Authors indicate that the biomass of parasitic organisms exceeds that of predators located at the end of food chains, which, as underlined by LAFFERTY *et al.* (2008), fundamentally changes the traditional energy flow pyramid. One of the determinants of these changes is the influence of parasites on host behaviour. This phenomenon is visible in the case of the acanthocephalan species infecting crustaceans. Infected organisms show positive phototaxis, and swim toward the surface of the water, where they become easier prey for birds – the final hosts of Acanthocephala (MACNEIL *et al.* 2003). A similar situation can be observed with *Fundulus parvipinnis* fish infected by *Euhaplorchis californiensis* fluke. Specimens infected with the parasite are more active, leading to increased visibility in the water and, therefore, a greater chance of being eaten by birds (LAFFERTY & MORRIS 1996). Non-host birds become double beneficiaries of parasitic infection in their host victims. They (i) acquire prey more efficiently, and (ii) the infected prey presents the increased energy value, which obviously has a positive effect on the growth and reproduction of non-host predators (JOHNSON *et al.* 2010).

Another aspect of parasites' influence on food webs concerns the energy flow between two types of ecosystems (SATO *et al.* 2011). The authors point to Nematomorpha, which alter the behaviour of orthopteran hosts. Infected terrestrial insects jump into the water, allowing the parasite to continue its

life cycle. This phenomenon is so common that in Japanese rivers and land streams, orthopterans have been incorporated into the diet of many species of fish. One example is the endangered species of trout, *Salvelinus leucomaenis*, in whose case insects infected with the parasite cover near 60% of the annual trophic needs (SATO *et al.* 2011). Consequently, Nematomorpha has emerged as a new food source for many fish species, including *Salvelinus leucomaenis*, which may increase their chances of survival.

## PARASITES IN BIOLOGICAL INVASIONS

Biological invasions are natural phenomena, though often strongly affected by human activity, that refer to range expansions of species into a new area. During invasions, alien populations may reach stabilisation gain the ability to grow. They affect changes in biodiversity and the interactions in new ecosystems (DUNN *et al.* 2012). The effect of biological invasions can be negative as well as positive. Depending on the specificity, an invasive species may threaten biodiversity by disturbing the balance between elements of the native community.

On the other hand, the appearance of an alien species can exert pressure on the native species, which can be beneficial to the ecosystem. Invasive species interact with native species by competition and/or predation. Parasitism plays a vital role in the course of invasion since parasites significantly influence the adaptation of hosts to the environment. They can modify the relationship of the hosts with other native and alien species and thus determine the success of the invasion (DUNN 2009, TOMPKINS *et al.* 2011). The effects of parasites can be considered in two ways: (i) ensuring the success of the invasion, i.e. positive for invasive species and having a negative impact on native species, and (ii) preventing invasion and ensuring the survival of native species.

The success of the invasion of the hosts in a new area may be influenced by parasites introduced with them (PRENTER *et al.* 2004). Authors point out that native species infected by the introduced parasites become their hosts, and the introduced host species more easily inhabit a new area. The reasons include the lack of adequate immune mechanisms between native host and introduced parasite (PRENTER *et al.* 2004). An example is the extinction of *Austropotamobius pallipes* crayfish population in Europe due to infection with *Aphanomyces astaci* transmitted with the North American *Pastifastacus leniusculus* (HOLDICH *et al.* 1991). *Austropotamobius pallipes* was the main freshwater species in the UK aquatic environments, but its range was limited to central and northern England (DUNN 2009). This species has been replaced by an invasive crustacean, due to the imported parasites. Thus, the invader has achieved undisputed success in the new territory.

Considering the positive role of parasites in biological invasions, one cannot ignore the aspect of the difficult acquisition of parasites by newcomers due to the lack of appropriate ways of transmission. Critical is the specialisation in the host-parasite system that can help the alien species to settle in the new area. This phenomenon is visible in the case of two snail species: *Cerithidea californica* and *Batillaria attramentaria*. The first species naturally inhabits the southwestern coast of the United States and the northwest coast of Mexico. *Batillaria attramentaria* is an invasive species from Japan, whose range covers the northern part of the area inhabited by *C. californica* (BYERS 2000). Both species show similarities in development and morphology, including (i) a similar maximum body size, (ii) a similar lifespan, (iii) a similar period of reproduction, and (iv) the same food resources (WHITLACH & OBREBSKI 1980, RACE 1982, BYERS 2000). Competition for food resources had a significant impact on the interaction between the populations of both species, which resulted in a significant reduction in the abundance of *C. californica* and, in some locations, even its extinction (BYERS 2000). The success of *B. attramentaria* was determined by several species of flukes that used *C. californica* as an intermediate host (TORCHIN *et al.* 2002). Despite many similarities between the snail species, the prevalence of flukes in the *B. attramentaria* populations was very low, which gave the snail species a significant advantage in the competition for food resources and allowed for successful invasion. DUNN *et al.* (2012) suggest the limited genetic pool of the introduced population or the absence of properly developed immune mechanisms between the newcomer and native parasites are factors that can affect the success of the invasion.

#### PARASITES AND HEAVY METAL ACQUISITION BY TISSUES OF AQUATIC ORGANISMS

The presence of pollutants in the aquatic environment is the cause of numerous pathological changes in aquatic organisms, e.g. changes in the (i) level of stress and sex hormones (WENDELAAR BONGA 1997), (ii) immune response (ARKOOSH *et al.* 1998), (iii) DNA damage, (iv) production of heat shock proteins or (v) activity of detoxifying enzymes (SURES 2008). One type of contamination is heavy metals entering the aquatic animals through the gills, the digestive tract, or absorbed by the body surface (BRYAN 1971). Heavy metals accumulate in the tissues and exert significant systemic changes (SURES 2008).

Years of research have shown strong dependencies between the accumulation of heavy metals in tissues of aquatic organisms and the presence of parasites inside them (SURES *et al.* 1999, ZIMMERMANN *et al.* 1999, SCHEEF *et al.* 2000, SURES 2003). The hosts infected with specific parasites show lower levels of heavy metals in their tissues than uninfected individuals. This phenom-

enon was observed in hosts of *Pomphorhynchus laevis*, *Acanthocephalus lucii* or *Paratenuisentis ambiguus* (acanthocephalans) (SURES 2001). Lead content in the intestinal wall of host fish *Squalius cephalus* infected with *P. laevis* was lower than in non-infected fish (SURES & SIDDALL 1999). Additionally, the lead content in adult parasites isolated from the intestine of the host was several times higher than in fish tissue. According to these authors, the host bile is likely to be the important factor affecting the acquisition of heavy metals by parasitic *P. laevis*. A higher concentration of lead in *A. lucii* than in host tissue was also observed by SURES *et al.* (1994).

Similar results were obtained by SURES (2003) in the case of parasitic nematodes and tapeworms. Additionally, HASSAN *et al.* (2016) studied the level of various metals (including lead) in infected and uninfected fish muscles. The authors analysed several species of nematodes inhabiting the intestine, stomach, liver and gonads of the host fish (*Epinephelus summana*). They observed significant differences in metal concentrations between fish infected and non-infected with intestinal nematodes. A slightly greater difference in the bioaccumulation by parasite tissue was observed between two tapeworms: *Bothriocephalus scorpii* and *Monobothrium wageneri* (SURES *et al.* 1999). These species develop in different hosts living in different environments: *B. scorpii*, hosted by turbot (*Scophthalmus maximus*), occurs in saltwater, while *M. wageneri* is hosted by freshwater tench (*Tinca tinca*) (SURES *et al.* 1997). The results differed both for the species of parasites and for the tested metals. The differences were especially visible in the level of lead in the tissues of tapeworms and their hosts, which suggests that these parasites show different ability to uptake and accumulate heavy metals. According to the authors, it may result from different bioavailability of metals, which depends on the physicochemical properties of water, and in this case, on the degree of its salinity. Sea fishes are hypoosmotic in relation to the environment, and that causes the loss of water compensated by increased consumption. This means that the parasite living in the sea fish intestine is exposed mainly to the inorganic, ionic form of metals – characterised by lower bioavailability. On the other hand, in the case of freshwater fish, metal ions are absorbed mainly by the gills, transported with the blood to the liver in the form of organometallic complexes that are easier to uptake for the parasite (SURES & SIDDALL 1999).

The studies presented above indicate an increase of scientific interest in the bioaccumulation of heavy metals by aquatic organisms and the influence of various species of parasites on this phenomenon. Especially results of the study concerning the fish infection by acanthocephalans indicate that parasites could be the excellent bioindicators of water pollution with heavy metals (SURES 2003). However, further research is needed on the mechanisms leading to heavy metal accumulation by parasites.



## ECOSYSTEM ENGINEERING

“Ecosystem engineers” are organisms that directly or indirectly alter the biotic and abiotic environment to a great extent, modifying the availability of environmental resources to other organisms and influencing the formation of new habitats (JONES *et al.* 1994). This happens as a result of the self-modification of organism structure (i.e. by their growth and development, such as corals) as well as by the transformation of environmental properties (ALPER 1998). The effect of these transformations is a change in conditions of species living in the ecosystem (JONES *et al.* 1997). Various groups of organisms, including parasites, are involved in this process (THOMAS *et al.* 1999). The changes affected by parasites usually concern the phenotype of the host, which can influence ecosystem properties (LEFÉVRE *et al.* 2009, HATCHER *et al.* 2012). One example is the pathological change caused by parasites or adaptive changes related to transmission and reproduction of the parasite by shaping the size of the host or affecting its activity (THOMAS *et al.* 1999). The authors studied *Austrovenus stutchburyi* bivalve molluscs infected with *Curtuteria australis*. The clam of this species – the second intermediate host of parasite – affects the sludge bioturbation, enabling the release of stored nutrients into the water. Heavy infection by the flukes’ metacercariae reduces host mobility, causing their subsidence in the sediment. The change of the clam behaviour has a significant impact on the ecosystem, as the shell of the immobilised mollusc becomes easier to colonise for many small organisms living on the surface. This change leads to an increase in the number of specimens and the diversity of species. On the other hand, when the bioturbation process is inhibited, primary production decreases, impacting the ecosystem negatively (HATCHER *et al.* 2012).

Another example of the influence of fluke larvae on molluscan hosts is shell gigantism. This phenomenon was described by JOOSSE and VAN ELK (1986) in *Lymnaea stagnalis* infected by *Trichobilharzia ocellata*, and in the same snail species infected by *Echinoparyphium aconiatum* or *Diplostomum pseudospathaceum* (ŻBIKOWSKA 2011). As a result, a bigger shell surface can be inhabited by a greater number of benthic species, affecting biodiversity in the ecosystem (THOMAS *et al.* 1999). Another example concerns nematode *Streptopharagus pigmentatus* and its intermediate host, dung beetle (BOZE *et al.* 2012). The dung beetle strongly affects the natural and agricultural ecosystem due to removing faeces from the soil surface. The parasite affects insect feeding behaviour and has a potentially strong impact on the agriculture ecosystem.

The next example when parasites act as “ecosystem engineers” is the emergence of new host features due to infections (LEFÉVRE *et al.* 2009). *Microphallus papillorobustus* and *Maritrema subdolum* flukes have a similar life cycle and use

the same intermediate (*Gammarus insensibilis*) and final (different birds) host species (THOMAS *et al.* 1997). *Microphallus papillorobustus* modifies the behaviour of the intermediate hosts towards positive phototaxis, negative geotaxis and suicidal behaviour (HELLUY 1984). This increases the chance of *G. insensibilis* being eaten by the aquatic bird species. *Maritrema subdolum* has no effect on the intermediate host phenotype but prefers to infect animals previously infected with *M. papillorobustus*. Due to the presence of the parasite, *Gammarus insensibilis* gained new features and becomes easier habitat for the *M. subdolum*.

Also, *Polymorphus minutus* infecting *Gammarus roeseli* affects changes in host feature that have an important influence on the transmission of some microsporidia into the same host (HAINE *et al.* 2005). Acanthocephalid species influence the host's behaviour and thereby increase the likelihood of the crustacean being eaten by birds (BETHEL & HOLMES 1977). The microsporidia, the second parasites of *G. roeseli*, undergo vertical transmission, and they have no way of avoiding hosts infected with *P. minutus*. However, they have developed the accelerated reproduction when an intermediate host is infected with acanthocephalans (HAINE *et al.* 2005). Additionally, microsporidia weaken the impact of *P. minutus* on *G. roeseli*, and reduce the likelihood of its predation by birds (RIGAUD & HAINE 2005). Therefore, it can be concluded that parasitic microsporidia co-infecting gammarid host induce positive changes in defence mechanisms of pre-adult crustaceans against acanthocephalan parasites, causing them to reach sexual maturity undisturbed by acanthocephalans.

## CONCLUSIONS

Parasites are undoubtedly essential elements in ecosystems. Their huge share in the biomass and biodiversity of communities and their common occurrence in ecosystems are not accidental. The niches occupied by the host-adapted parasite species guarantee the host populations' stability and fitness. It seems that the traditional negative assessment of the influence of parasites on communities requires a critical reconsideration. Published data indicate the complexity of the interaction between parasites and the external and internal environment, which eludes the unequivocal classification of parasites as purely etiological factors. It is essential to recognise the positive ecological roles of parasites in ecosystems and even to consider their biological protection, if necessary.

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