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Parasites as drivers of key processes in aquatic ecosystems: Facts and future directions

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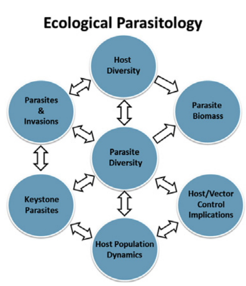
HIGHLIGHTS

- Parasites contribute significantly to species diversity.
- Parasites are seldom considered in ecosystem analyses.
- We need to understand integral and functional roles of parasites in ecosystems.

GRAPHICAL ABSTRACT



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ABSTRACT

Despite the advances in our understanding of the ecological importance of parasites that we have made in recent years, we are still far away from having a complete picture of the ecological implications connected to parasitism. In the present paper we highlight key issues that illustrate (1) important contributions of parasites to biodiversity, (2) their integral role in ecosystems, (3) as well as their ecological effects as keystone species (4) and in biological invasion processes. By using selected examples from aquatic ecosystems we want to provide an insight and generate interest into the topic, and want to show directions for future research in the field of ecological parasitology. This may help to convince more parasitologists and ecologists contributing and advancing our understanding of the complex and fascinating interplay of parasites, hosts and ecosystems.

1. Introduction

Parasites have long been recognized as important pathogens of man and livestock. For a long time, the harm associated with parasites has been the main reason to study them. These efforts resulted in a huge body of knowledge on adverse effects parasites have on their hosts. This in turn has initiated intensive research on parasite life cycles and effective drug treatment options to resolve health problems and to kill parasites, and this has helped to significantly reduce mortality and morbidity in humans and livestock due to parasite infections. However, drug treatment alone often failed to be an effective parasite control measure. During

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medical treatment, the focus is usually on a single parasite stage, for example the adult infecting humans (or livestock), whereas other developmental stages of the parasite are not considered and can quickly lead to re-infections. Schistosomiasis control over the past 100 years across all major schistosomiasis endemic zones, including Africa, Asia and the Americas is an excellent example. It shows that the most successful programs are focused on transmission control instead of treatment (Sokolow et al., 2016). In the case of schistosomiasis transmission, control mainly refers to all kinds of measures against the intermediate snail host and the parasite transmission to the final human host (e.g. molluscicides, engineering interventions, biological control, etc.). This example clearly highlights that understanding a parasite's life cycle including the demands of their hosts from an ecological point of view is a prerequisite for effective and sustainable parasite control programs.

Apart from this anthropogenic view with the goal to control parasite infections, we can expect that ecological implications of parasites and their life cycles are also important for many other aspects. Although the last 20 years have seen a steady advancement of our understanding of parasites as important and integral elements of ecosystems (Hudson et al., 2006; Poulin, 1999; Tompkins et al., 2011; Wood and Johnson, 2015), leading to a new area of research at the junction of ecology and parasitology (Thomas et al., 2009) called ecological parasitology, we are still far away from having a complete picture which connects ecological phenomena to parasites.

We still know only a limited number of examples of parasites that affect the population dynamics or the behaviour of their hosts and we are just at the very beginning of studying how parasites affect energy and biomass flows in ecosystems and food webs. The vast majority of research output connected to the ecological roles and implications of parasites comes from a rather limited number of research groups in North America, New Zealand and Europe and their work on selected freshwater, estuarine and marine ecosystems.

It would therefore be desirable if more parasitologists and ecologists contribute to this field of research and advance our understanding of parasites and ecosystems. Moreover, the recent meeting of the German Society for Parasitology held 2016 in Göttingen, Germany showed that medically oriented parasitology and ecological approaches in parasitology often coexist in parallel with only little interaction. In the present paper we therefore highlight recent studies that address ecological implications of parasites. By using selected examples from aquatic ecosystems we try to indicate directions and generate an insight and interest for future research.

2. Parasite diversity

One of the oldest and most fundamental questions in ecology is how many species there are on our planet. Estimations of experts are ranging between 3 and 100 million species, with recent calculations predicting around 9 million eukaryotic species, 90% of which are still awaiting discovery and description (Mora et al., 2011). It is certainly safe to say that we are a long way from a full inventory of our planet's biodiversity. With every free-living metazoan species serving as host to one or more parasite taxa (Dobson et al., 2005), parasitism can certainly be regarded as the most successful lifestyle on earth (Hechinger and Lafferty, 2005). Consequently, estimations for parasite species range from one third to over half the diversity on the planet, and we are far from a knowledge of the true parasite diversity (Poulin, 2014; Poulin and Morand, 2004). However, recent analyses have also shown that the parasite species discovery rate is decreasing. Additionally, they highlighted the contrast between a high parasite diversity at local scales (up to 40% of a species assemblage) and a much lower diversity on a global level (ca. 5%), indicating a wider distribution of parasites than their hosts (see Costello, 2016 and references therein). This highlights the continuous need to study and address questions of parasite diversity.

The increasing application of molecular tools for species identification and delineation has revealed cryptic parasite species in many major parasite lineages and has shown that parasite species richness has probably long been significantly underestimated (Dobson et al., 2008). Especially in complex groups, such as the Digenea, the largest group of internal metazoan parasites with 18,000 nominal species (Cribb et al., 2001), the use of molecular methods has extensively advanced our understanding of the diversity and phylogenetic relationships (Olson et al., 2003; Olson and Tkach, 2005). For example, the detailed and thorough examination of taxonomically intricate digenean groups, such as the eyeflukes of the genus *Diplostomum* via integrated morphological and molecular approaches has recently brought to light a much higher parasite diversity in North America and Europe than previously assumed, even at small geographical scales (Blasco-Costa et al., 2014; Faltýnková et al., 2014; Georgieva et al., 2013a; Locke et al., 2010, 2015; Pérez-del-Olmo et al., 2014; Selbach et al., 2015). If appropriate tools, i.e. molecular techniques are applied, many parasite species can be detected, as the discovery of cryptic trematode species in snail populations in central European freshwaters revealed (Georgieva et al., 2013a, 2013b; Selbach et al., 2014, 2015).

Likewise, many of the macroinvertebrate groups which are understudied in terms of their relevance as hosts for parasites, such as amphipods and insects show an astonishing diversity of parasites. When studying the ten most abundant species of aquatic insect larvae and two species of *Gammarus* spp. in a low mountain stream in Germany, up to 100% prevalence was found for some parasite taxa (Grabner, 2017). Microsporidians were present in all host species with prevalences between 20% and 100% and also helminths were found in all hosts with high prevalences. In another study focussing on the amphipod and microsporidian diversity in freshwaters in an urban region in Germany, eight amphipod species hosted a total of ten species of microsporidians (Grabner et al., 2015).

Accordingly, high parasite diversity is not only realized in diversity hotspots such as coral reefs or tropical rainforests, but can be uncovered in less obviously diverse systems. Wherever we look closely, we are able to discover new species and lineages, highlighting that our overall understanding of local parasite diversity is still limited and sampling of many parasite groups, especially digeneans, is patchy at best. Therefore, since we are still a long way from a full inventory of parasite diversity, we cannot currently know how many parasite species there are on our planet. Yet, there are other issues and questions we need to address, such as the identification of local parasite diversity and distribution, also with respect to the emergence of zoonotic diseases in the context of changing climate conditions (Poulin, 2014). Another relevant aspect is the deeper understanding of the connection of free-living and parasite diversity to be able to predict the effects of community changes on disease risk (Johnson et al., 2015a). While there are selected ecosystems that are thoroughly studied with regard to the integral role of parasites, the ecology and diversity of parasites in many eco regions is still hardly understood. Furthermore, we need to consider parasite diversity in nature conservation and restoration, because with every free-living species that becomes extinct we potentially lose its parasites (Gómez and Nichols, 2013; Lafferty, 2012; Strona, 2015). Since free-living species become extinct at a much higher rate than we discover new species (see May, 1988), we are losing parasite diversity to a large extent. This often happens