International Journal for Parasitology: Parasites and Wildlife 4 (2015) 442–451

Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Host manipulation in the face of environmental changes: Ecological consequences

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A R T I C L E I N F O

Article history:
Received 29 June 2015
Received in revised form
30 July 2015
Accepted 3 August 2015

Keywords:
Ecosystems
Environment
Global changes
Host manipulation
Host–parasite interactions

A B S T R A C T

Several parasite species, particularly those having complex life-cycles, are known to induce phenotypic alterations in their hosts. Most often, such alterations appear to increase the fitness of the parasites at the expense of that of their hosts, a phenomenon known as “host manipulation”. Host manipulation can have important consequences, ranging from host population dynamics to ecosystem engineering. So far, the importance of environmental changes for host manipulation has received little attention. However, because manipulative parasites are embedded in complex systems, with many interacting components, changes in the environment are likely to affect those systems in various ways. Here, after reviewing the ecological importance of manipulative parasites, we consider potential causes and consequences of changes in host manipulation by parasites driven by environmental modifications. We show that such consequences can extend to trophic networks and population dynamics within communities, and alter the ecological role of manipulative parasites such as their ecosystem engineering. We suggest that taking them into account could improve the accuracy of predictions regarding the effects of global change. We also propose several directions for future studies.

1. Introduction

Understanding the consequences of environmental changes has become a major challenge in recent years in many fields of science. Parasitology is among the most sensitive topics regarding the effects of global changes, since accurate predictions about the expansion of parasites and their hosts might be essential to take appropriate measures to prevent epidemic diseases. Moreover, an increasing number of reviews have highlighted the potential impact of climate change on parasitism (e.g. MacLeod and Poulin, 2012; Marcogliese, 2001; Morley and Lewis, 2014). As a result, the number of theoretical models providing simulations about the future geographical range of parasites and their vectors is increasing too. However, most predictive parasitological studies have been limited to vector-borne diseases affecting either humans, livestock, or domestic animals (Genchi et al., 2009; Giles et al., 2014; Moore et al., 2012; Mordecai et al., 2013; Paaijmans et al., 2010; Stensgaard et al., 2013; Sternberg and Thomas, 2014; White et al., 2003), with noticeable exceptions such as blood parasites in wild birds (Fuller et al., 2012; Loiseau et al., 2013).

Parasitic organisms altogether might represent close to half of all biodiversity (Dobson et al., 2008; Poulin and Morand, 2000). Apart from causing diseases, there is increasing evidence that they can play pivotal roles in ecosystems (Thomas et al., 1997; Hatcher et al., 2012). In particular, many parasites are able to alter their hosts' phenotypes, with far-reaching consequences for, for instance, population dynamics or the persistence of species in ecosystems (Lefèvre et al., 2009).

Parasites that are able to manipulate their hosts are very diverse, ranging from viruses (Ingwell et al., 2012) and bacteria (Werren et al., 2008) to many eukaryote organisms, including animals such as cestodes, trematodes, or acanthocephalans (Poulin and Thomas, 1999). The number of hosts susceptible to be manipulated by parasites is also wide, including both vertebrate and invertebrate species (Poulin and Thomas, 1999), and even plants (Ingwell et al., 2012). Interestingly, the inventory of manipulative parasites also includes medically and veterinary important species that are already well studied (Hurd, 2003; Lagrue and Poulin, 2010), such as parasites causing malaria (Koella et al., 1998), toxoplasmosis (Berdoy et al., 2000), or rabies (Klein, 2003). However, even though the manipulative abilities of those parasites could have implications for epidemiology and pathology (Lagrue and Poulin, 2010), epidemiologic models tend to completely ignore them.

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http://dx.doi.org/10.1016/j.ijppaw.2015.08.001

Similarly, despite the importance of host manipulation by parasites for ecosystems and health, the effects of environmental changes on their ecological roles are largely ignored. After emphasizing the ecological importance of manipulative parasites, we show here that environmental changes can interact with them in many different ways, leading to consequences that deserve more attention, especially in the area of conservation, in order to make accurate predictions regarding the effects of global change.

2. Ecological importance of host manipulation by parasites

Parasites are widely recognized to have numerous effects on communities and ecosystems, in particular through density-dependent pathogenic effects on their hosts (Hatcher et al., 2012). For instance, differential host susceptibility and tolerance can reverse the outcome of competition, when the fitness of the superior competitor is more impaired by parasitic infection than that of other host species. The presence of parasites might then lead to the coexistence of several species that would otherwise exclude each other. Moreover, parasites influence the organization of communities and, through that, play such an important role in the stability of ecosystems that they have been proposed to serve as a proxy of their quality (Hudson et al., 2006). On the other hand, parasites can also have negative effects on biodiversity, such as causing local extinctions (McCallum and Dobson, 1995).

An important aspect is that all parasites are embedded in large food webs. In particular, parasites with complex life-cycles have the potential to impact several host species in succession, making their global impact (see below) even more consequent. Some of those parasites are able to induce phenotypic modifications in their intermediate hosts, which are believed to be more than simple pathological effects. Through host manipulation, parasites are thought to enhance their own fitness, in particular by increasing their probability of transmission from one host to another, at the expense of that of their hosts (Thomas et al., 2005). Many theoretical as well as empirical studies have highlighted that this phenomenon, along with more classic pathogenic effects, can have profound ecological impacts on a large scale, ranging from host populations to ecosystems (Lefèvre et al., 2009). Although manipulative parasites can affect ecosystems in diverse ways, three major effects can be distinguished: the impact of parasites on food webs, their influence on the population dynamics of host species, and their impact on habitats.

2.1. Impact on food webs

Trophically-transmitted parasites often manipulate their intermediate hosts in ways that increase their probability of being predated by definitive hosts. For instance, killifish (*Fundulus parvipinnis*) parasitized by the trematode *Euhaplorchis californiensis* are up to 31 times more susceptible to predation than uninfected individuals (Lafferty and Morris, 1996). The effect on the energy flow is even more substantial considering that the increased vulnerability to predation induced by parasites is often not restricted to suitable hosts (Kaldonski et al., 2008; Seppälä et al., 2008b), leading to a higher predation by other species, as illustrated by cockles (*Austrovenus stutchburyi*) being exploited as intermediate hosts by trematode parasites. Infected cockles typically remain lying on the sediment surface (Thomas and Poulin, 1998), where they are more conspicuous to birds that serve as a definitive host for trematodes. However doing so, infected cockles also become more vulnerable to predation by fish which constitute 'dead-end' predators for parasites (Mouritsen and Poulin, 2003).

Manipulative parasites can also create new trophic interactions. One of the most spectacular examples comes from nematomorph parasites (*Gordionus* spp.), which induce their terrestrial insect hosts into jumping in the water (a crucial stage in the life cycle of the parasite; Sato et al., 2011). Empirical evidence shows that manipulated insects represent a new and substantial energy intake for fish (Sato et al., 2011), with the interesting consequence of decreasing fish predation on benthic invertebrate communities, thus leading to subsequent decrease in algae biomass, and, ultimately, to a reorganization of the whole ecosystem (Sato et al., 2012).

Another impact of parasites on food webs, though not necessarily restricted to manipulative ones, lies in the alteration of the functional role of their hosts. For instance, several acanthocephalan parasites are known to alter the feeding ecology of their intermediate hosts, decreasing predation rate in amphipods (Fielding et al., 2003) or reducing the consumption of detritus in isopods (Hernandez and Sukhdeo, 2008). Such alterations can have substantial effects within ecosystems, especially when modified host species play important functional roles (Hernandez and Sukhdeo, 2008).

2.2. Impact on population dynamics

Host modifications induced by manipulative parasites are likely to alter hosts population dynamics and structure. For instance, the trematode *Gynaecotyla adunca* alters the vertical distribution of its snail host on sandbars (Curtis, 1987). Several gammarid species infected by acanthocephalan parasites present altered geotactic or phototactic preferences (Bauer et al., 2005, 2000; Haine et al., 2005), supposed to drive them to areas where they are more exposed to predators. By altering both the behavior and morphology of their hosts, parasites can then lead them to occupy new ecological niches (Miura et al., 2006; Ponton et al., 2005). Along with effects on individual distribution, other phenotypic alterations induced by manipulative parasites are likely to induce ecological segregation, through dividing the host population into two sub-units consisting of infected vs. uninfected individuals, each of them having its own properties (Lefèvre et al., 2009).

Manipulative parasites are also likely to modify predator-prey dynamics. Evidence from mathematical modelling (Fenton and Rands, 2006) suggests that manipulation can influence both predators' and prey's abundance, and induce oscillations in their population densities that are likely to have consequences on the dynamics of other species within the ecosystem. Accordingly, Lafferty and Kuris (2012) suggested that the parasite *Echinococcus granulosus* might be responsible for the persistence of moose and wolves on Isle Royale. Indeed, recordings suggest that infection with *E. granulosus* increases moose vulnerability to wolves (Joly and Messier, 2004). As suggested by another mathematical model (Hadeler and Freedman, 1989), the parasite might be essential for wolves to be able to feed on moose, and to persist in the ecosystem. The presence of the parasite and its interaction with moose and wolves might actually prevent the demographic explosion of moose populations, which would lead to over-grazing followed by starvation, as was observed before colonization by wolves (Lafferty and Kuris, 2012).

Similarly, manipulative parasites can drive competition between hosts. In the same way that non-manipulative parasites can affect closely-related host species with different susceptibility and tolerance to infection, host species can also present different susceptibility to manipulation. Hatcher et al. (2014) used a mathematical model to show that parasite manipulation can change the outcome of the competition between two hosts showing mutual predation, and determine whether the two host species can coexist or not. In addition, some studies have shown that parasites do not always manipulate closely-related host species to the same extent