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Parasites and marine invasions: Ecological and evolutionary perspectives

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ABSTRACT

Worldwide, marine and coastal ecosystems are heavily invaded by introduced species and the potential role of parasites in the success and impact of marine invasions has been increasingly recognized. In this review, we link recent theoretical developments in invasion ecology with empirical studies from marine ecosystems in order to provide a conceptual framework for studying the role of parasites and their hosts in marine invasions. Based on an extensive literature search, we identified six mechanisms in which invaders directly or indirectly affect parasite and host populations and communities: I) invaders can lose some or all of their parasites during the invasion process (parasite release or reduction), often causing a competitive advantage over native species; II) invaders can also act as a host for native parasites, which may indirectly amplify the parasite load of native hosts (parasite spillback); III) invaders can also be parasites themselves and be introduced without needing co-introduction of the host (introduction of free-living infective stages); IV) alternatively, parasites may be introduced together with their hosts (parasite co-introduction with host); V) consequently, these co-introduced parasites can sometimes also infect native hosts (parasite spillover); and VI) invasive species may be neither a host nor a parasite, but nevertheless affect native parasite host interactions by interfering with parasite transmission (transmission interference). We discuss the ecological and evolutionary implications of each of these mechanisms and generally note several substantial effects on natural communities and ecosystems via i) mass mortalities of native populations creating strong selection gradients, ii) indirect changes in species interactions within communities and iii) trophic cascading and knock-on effects in food webs that may affect ecosystem function and services. Our review demonstrates a wide range of ecological and evolutionary implications of marine invasions for parasite–host interactions and suggests that parasite-mediated impacts should be integrated in assessing the risks and consequences of biological invasions.

1. Introduction

The increase in marine aquaculture activities and global shipping during the last decades has resulted in the worldwide distribution of a multitude of invasive species (Bax et al., 2003). As a result, marine coastal systems are among the most heavily invaded ecosystems of the world (Grosholz, 2002). A potential role of parasites in the success and impact of marine invasions has been recognized and gained mainly attention in the form of the enemy release hypothesis, which refers to a loss of parasites in the invasion process, leading to potential competitive advantages for invasive species (see reviews by Blakeslee et al., 2013; Torchin et al., 2002). However, recent empirical studies and new conceptual frameworks beyond the marine realm have identified various additional ways of how parasites and their hosts can be involved in species invasions (e.g. Dunn, 2009; Tompkins et al., 2011). Here we review these recent theoretical developments in invasion ecology and link them with empirical studies from marine ecosystems in order to provide a conceptual framework for studying the role of parasites and their hosts in marine invasions.

We firstly summarize the different ways in which marine invaders directly or indirectly affect parasite and host populations and communities (Section 2). Then we explain each mechanism, its direct ecological effects on the host and indirect effects on the surrounding community in more detail, including mechanisms where invasive species act as host (Sections 3.1 and 3.2), mechanisms in which parasites are introduced (Sections 3.3–3.5) and a mechanism where invaders are neither parasite nor host, but nevertheless affect parasite–host interactions (Section 3.6). We do so based on an extensive literature search using Google Scholar and Web of Science with the key words parasit*, parasit* AND spill*, invas* AND parasit*, parasit* AND "dilution effect", introduce* AND parasit*, "enemy release". To this initial literature database, we added further studies by searching reference lists of publications and our own literature collections. This resulted in a comprehensive

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and up to date (December 2014) database of our current knowledge on parasites and marine invasions. In Section 4, we discuss the evolutionary implications of all six ecological mechanisms highlighted in Section 3. Finally, we provide a summary and outlook for future studies on ecological and evolutionary perspectives of parasites and marine invasions in Section 5.

Throughout this review we use the term *parasite* for an organism that is living in or on another organism (the host), feeding on it and causing some degree of harm (*sensu* Poulin, 2006) and thereby refer to all microparasites, macroparasites and pathogens. In addition, we will use the term *introduction* when an organism is directly or indirectly moved by human activities beyond the limits of its native geographical range into an area in which it does not naturally occur (Falk-Petersen et al., 2006). Such introduced organisms we will call introduced or invasive species (*sensu* Blackburn et al., 2011; Lymbery et al., 2014) as most introduced hosts or parasites reported in the literature are in the state of spreading in invaded ecosystems.

2. Six mechanisms by which marine invaders affect parasite–host interactions

There are at least six mechanisms by which invaders directly or indirectly affect interactions between invasive and native parasite and host populations and communities. They differ in the invasive/native status of the host and/or the parasite and in their respective ecological implications (Fig. 1): I) the competitive ability of invasive species relative to native species in invaded ecosystems may be increased if an invasive species loses (some of) its native parasites in the process of introduction (*parasite release* or *parasite reduction*; Colautti et al., 2004; Keane and Crawley, 2002; Torchin et al., 2001, 2003; Torchin and Mitchell, 2004); II) invasive species can act as a competent host for native parasites (*parasite acquisition*; Tompkins et al., 2011), thereby increasing host diversity and amplifying transmission dynamics of native parasite populations that can ultimately lead to increased infection levels in native hosts (*parasite spillback*; Kelly et al., 2009); III) invasive parasites can be introduced into a new habitat via a vector (e.g. ballast water, Ruiz et al., 2000) and infect native hosts, without needing the co-introduction of an invasive host species (*introduction of free-living infective stages*); IV) invasive parasites can be introduced together with the introduction of a host and only infect the invasive host in the introduced range (*parasite co-introduction with host*), potentially giving native species a potential competitive advantage relative to the invader in the invaded range (Daszak et al., 2000; Taraschewski, 2006); V) invasive parasites can be co-introduced with their invasive host and spill over to naive native species (*parasite spillover*; Prenter et al., 2004; Kelly et al., 2009), potentially causing deleterious infections (*emerging disease*); and VI) invasive species may be neither a host nor a parasite but can nevertheless potentially reduce the parasite burden in a system if an invader interferes with parasite transmission between native hosts (*parasite transmission interference*), e.g. by preying on free-living infective stages of parasites (Johnson et al., 2010).

It is important to realize that these six mechanisms are not mutually exclusive for a single invasive parasite or host species, but can act synergistically during an invasion process. For example, an invading host may be released from one species of parasite (parasite release), but at the same time co-introduce an invasive parasite (parasite co-introduction with host) that spills over to native species (parasite spillover).

3. Ecological implications

There are varying amount of empirical data supporting each of the six mechanisms. This includes mechanisms where invasive species act as host (Sections 3.1 and 3.2), mechanisms in which parasites are introduced (Sections 3.3–3.5) and a mechanism where invaders are neither parasite nor host, but nevertheless affect local parasite–host dynamics (Section 3.6).

3.1. Parasite release or reduction

When an invasive host species is introduced to a new ecosystem, it often leaves all or some of its co-evolved parasites behind in its native range (Fig. 1, *parasite release or reduction*), because introduced species must overcome barriers to introduction, establishment and spread before they become invasive (Colautti et al., 2004; Kolar and Lodge, 2001). Such barriers also act on parasites — either before, during or after the translocation phase. First, native parasites of introduced hosts are likely to be lost before or during translocation, because many introduced species arrive as larvae in the new environment and are therefore free of parasite species infecting juvenile or adult stages (Lafferty and Kuris, 1996; Torchin et al., 2002, but see Arzul et al., 2011). Moreover, parasites and/or infected hosts might die during transportation, reducing the likelihood of establishment. In addition, introduced aquaculture organisms can be treated with an anti-parasite treatment (e.g., copper sulphate to eliminate monogeneans of fish, Vignon et al., 2009a) before translocation to the new environments (Mitchell and Power, 2003) and translocations of stocks usually select only healthy individuals, reducing the possibility of translocating parasites (Colautti et al., 2004). Second, once infected hosts are translocated, their parasites may not find

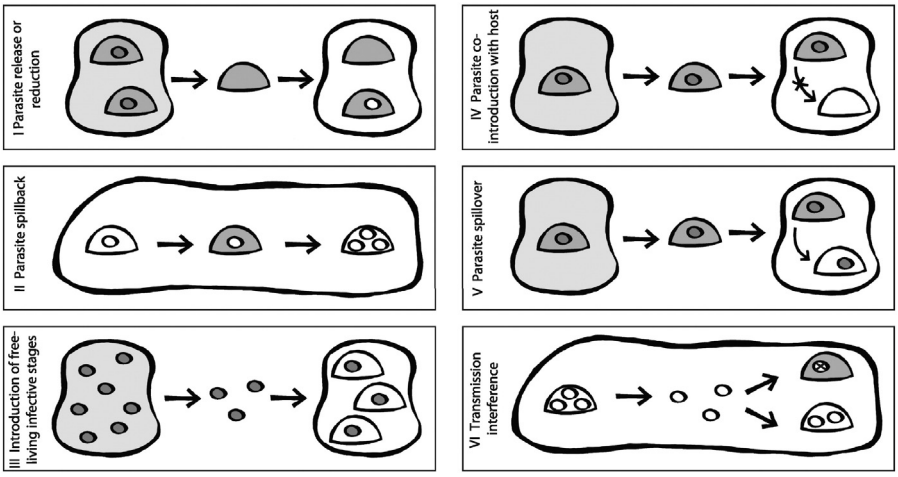

Fig. 1. Conceptual overview of the six mechanisms of how invaders can directly or indirectly affect parasite–host interactions. Grey semicircle = invasive host species, white semicircle = native host species, dark grey dot = invasive parasite species, white dot = native parasite species, grey environment = native range of invader, white environment = introduced range of the invader. For detailed explanation of the mechanisms see text.

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