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Biological invasions and host–parasite coevolution: different coevolutionary trajectories along separate parasite invasion fronts

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ABSTRACT

Host–parasite coevolution has rarely been observed in natural systems. Its study often relies on microparasitic infections introducing a potential bias in the estimation of the evolutionary change of host and parasite traits. Using biological invasions as a tool to study host–parasite coevolution in nature can overcome these biases. We demonstrate this with a cross-infection experiment in the invasive macroparasite *Mytilicola intestinalis* and its bivalve host, the blue mussel *Mytilus edulis*. The invasion history of the parasite is well known for the southeastern North Sea and is characterised by two separate invasion fronts that reached opposite ends of the Wadden Sea (i.e. Texel, The Netherlands and Sylt, Germany) in a similar time frame. The species' natural history thus makes this invasion an ideal natural experiment to study host–parasite coevolution in nature. We infected hosts from Texel, Sylt and Kiel (Baltic Sea, where the parasite is absent) with parasites from Texel and Sylt, to form sympatric, allopatric and naïve infestation combinations, respectively. We measured infection rate, host condition and parasite growth to show that sympatric host–parasite combinations diverged in terms of pre- and post-infection traits within <100 generations since their introduction. Texel parasites were more infective and more efficient at exploiting the host's resources. Hosts on Texel, on the other hand, evolved resistance to infection, whereas hosts on Sylt may have evolved tolerance. This illustrates that different coevolutionary trajectories can evolve along separate invasion fronts of the parasite, highlighting the use of biological invasions in studies of host–parasite coevolution in nature.

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1. Introduction

Theoretical predictions of the dynamics underlying host–parasite coevolution (Van Valen, 1973; Hamilton et al., 1990; Sasaki, 2000) have been confirmed in study systems that employ experimental evolution (Schulte et al., 2010; Berenos et al., 2011; Gomez and Buckling, 2011; Joop and Vilcinskis, 2016, this issue). However, evidence from natural systems supporting these proof-of-principle observations is limited, although some natural systems (e.g., the water flea *Daphnia magna* and its castrating bacterial parasite *Pasteuria ramosa*) offer the opportunity to cross-infect different generations of hosts and parasites sam-

pled directly from the environment, confirming that negative frequency-dependent selection can also act in natural populations (Decaestecker et al., 2007).

The above-mentioned studies use hosts with short generation times that are infected by microparasites. It is likely to observe coevolution in these systems, because often microparasites tend to be virulent, favouring host responses. Furthermore, short host generation times facilitate evolutionary responses. In contrast to host–microparasite interactions, host–macroparasite combinations have been investigated far less often and experimental studies are scarce (but see the study on *Potamopyrgus antipodarum* and its castrating trematode *Microphallus* sp.; Dybdahl and Lively, 1998; Koskella and Lively, 2007, 2009). More support for host–macroparasite interactions comes from local adaptation experiments (reviewed in Kaltz and Shykoff, 1998; Greischar and Koskella, 2007; Hoeksema and Forde, 2008) that represent proxies

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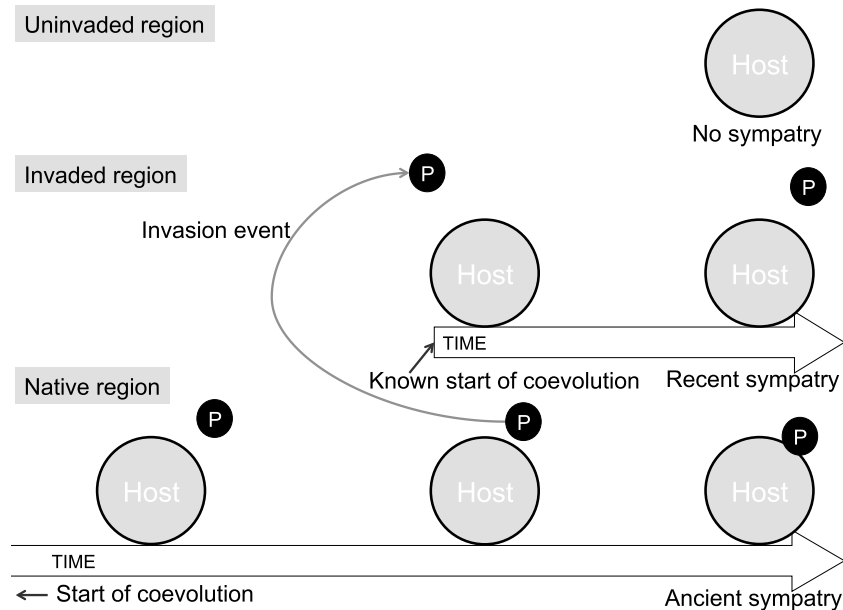


Fig. 1. Coevolution in biological parasite invasions. While in native regions host–parasite coevolution occurred over long and usually unknown time spans (ancient sympatry), invasions of parasites clearly define the onset of new coevolutionary interactions with new hosts (recent sympatry). In the uninvaded region there is no sympatry with naïve hosts. “P” symbolizes the parasite and the distance of the parasite to the host represents the coevolutionary relation between host and parasite. Reciprocal infection experiments with hosts and parasites of different levels of sympatry, covering a range from ancient sympatry over recent sympatry to no sympatry, can thus be used to estimate the rate of evolutionary change.

for coevolution, but often fail to capture the temporal dimension of coevolution.

It thus becomes clear that our empirical understanding of host–parasite coevolution is based on phylogenetic and experimental biases that fail to encompass the phylogenetic variety of host–parasite interactions, as well as the variety of their underlying dynamics that are present in nature.

Biological invasions can overcome several of these biases and therefore represent excellent opportunities to study the ecological and evolutionary effects of parasites and pathogens (Goedknecht et al., 2015), and thus, coevolutionary processes. Invasions are natural experiments with phylogenetically diverse combinations of hosts and parasites (Goedknecht et al., 2015). Additionally, the time frame of evolutionary changes is often known since it coincides with the time of invasion. It is therefore possible to estimate a rate of change by comparing native, invasive and naïve combinations of hosts and parasites after the invasion event (Fig. 1). In this way, biological invasions can add a time frame to local adaptation experiments. Finally, several invasion scenarios in which only the host or the parasite invade, or in which both host and parasite co-invade, lead to different predictions regarding the underlying evolutionary dynamics (reviewed in Goedknecht et al., 2015).

The invasive parasite *Mytilicola intestinalis* (Copepoda: Cyclopoida) offers a compelling natural history background to test several predictions of host–parasite coevolution in the wild. Originating from the Mediterranean Sea (Steuer, 1902, 1905) where it infests the Mediterranean mussel *Mytilus galloprovincialis*, the parasite invaded the North Sea and spread southwest and north in two fronts (see Fig. 2). The direct life cycle of this parasite limits coevolution to one principal host, the blue mussel *Mytilus edulis*, in its invaded range, and controlled infections (Hepper, 1953; Gee and Davey, 1986) can be applied to previously treated mussels (Blateau et al., 1992) to generate experimental combinations of host and parasite populations. Since *M. intestinalis* creates lesions in the epithelium of the intestinal walls of its host, especially at higher infection intensities (Couteaux-Bargeton, 1953; Watermann et al., 2008), and has been associated with mass

mortalities (Korringa, 1950; Meyer and Mann, 1950; Blateau et al., 1992), selection for host resistance seems likely.

Pre- and post-infection traits of hosts and parasites can be separated within the mussel–*Mytilicola* system. The pre-infection traits are parasite infectivity, which is the ability to infect the host, and host resistance, i.e. the host’s ability to prevent infections. Once infected, coevolution can occur for post-infection traits, i.e. host tolerance, which is the capability of the host to deal with infection, and parasite virulence, which is the harm inflicted on the host that should correlate with the ability to exploit the host. Both pre- and post-infection traits of hosts and parasites are tightly coupled and are therefore difficult to disentangle. While the proportion of successful infections resulting from exposure to a defined number of infective stages is a precise estimator of infectivity and resistance, tolerance and virulence can only be derived indirectly from host body condition in relation to parasite load. Nevertheless, pre- and post-infection traits can be separated in this system, offering the opportunity to investigate the evolutionary trajectories involving these traits.

Here, we describe these coevolutionary trajectories for the host *M. edulis* and the parasite *M. intestinalis* after its invasion in relation to naïve hosts lacking coevolutionary interactions. In particular, we answer how invasive parasites affect naïve hosts, and if similar host–parasite interaction patterns were found at the two different invasion fronts in the Wadden Sea.

2. Materials and methods

2.1. Field collection of mussels and treatment against previous infestations

Mussels in the size category of 3.5–5.0 cm shell length were collected from mixed mussel and oyster beds at the tidal flats of Vlakte van Kerken on the island of Texel, Netherlands (53°09′17.7″N, 04°53′36.1″E) and on the island of Sylt, Germany (55°02′17″N, 08°26′32″E) in June/July 2014 (Fig. 2). Naïve hosts were collected from a mussel bed in Kiel Harbour, Germany (Baltic Sea,

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