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## Variations in infection levels and parasite-induced mortality among sympatric cryptic lineages of native amphipods and a congeneric invasive species: Are native hosts always losing?

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## ABSTRACT

Shared parasites can strongly influence the outcome of competition between congeneric, sympatric hosts, and thus host population dynamics. Parasite-mediated competition is commonly hypothesized as an important factor in biological invasion success; invasive species often experience lower infection levels and/or parasite-induced mortality than native congeneric hosts. However, variation in infection levels among sympatric hosts can be due to contrasting abilities to avoid infection or different parasite-induced mortality rates following infection. Low parasite infection levels in a specific host can be due to either factor but have drastically different implications in interaction outcomes between sympatric hosts.

We assessed acanthocephalan infection levels (prevalence and abundance) among cryptic molecular taxonomic units (MOTU) of the native *G. pulex*/*G. fossarum* species complex from multiple populations where they occur in sympatry. We concomitantly estimated the same parameters in the invasive *G. roeselii* commonly found in sympatry with *G. pulex*/*G. fossarum* MOTUs. We then tested for potential differences in parasite-induced mortality among these alternative hosts. As expected, the invasive *G. roeselii* showed relatively low infection level and was not subject to parasite-induced mortality. We also found that both acanthocephalan infection levels and parasite-induced mortality varied greatly among cryptic MOTUs of the native amphipods. Contrary to expectations, some native MOTUs displayed levels of resistance to their local parasites similar to those observed in the invasive *G. roeselii*. Overall, cryptic diversity in native amphipods coupled with high levels of variability in infection levels and parasite-induced mortality documented here may strongly influence inter-MOTU interactions and native population dynamics as well as invasion success and population dynamics of the congeneric invasive *G. roeselii*.

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## 1. Introduction

Parasitism is an important biotic determinant of animal population dynamics and community structure (Hudson and Greenman, 1998). Parasites can influence host numbers within a population by increasing mortality rate (Goater and Ward, 1982; Rousset et al., 1996). For parasites with complex life cycles, intermediate host mortality attributable to parasites can occur through reduction in host survival due to the pathological consequences of parasitic infection, or through host manipulation increasing predation on

infected hosts (Thomas et al., 1995; Latham and Poulin, 2002; Parker et al., 2003; Hansen and Poulin, 2005; Benesh and Valtonen, 2007; Violante-González et al., 2016). However, host species often differ in their susceptibility to infection and/or parasite-induced mortality (Sánchez et al., 2012). For example, invasive species generally suffer less from parasitism than native species (Dunn and Dick, 1998; Torchin et al., 2003; Genner et al., 2008). Native parasites are often less effective at infecting invasive hosts due to the lack of co-evolutionary history between the novel hosts and local parasites (Ebert, 1994; Kaltz and Shyoff, 1998; Emblidge Fromme and Dybdahl, 2006; Genner et al., 2008). Host-parasites interactions proceed in a co-evolutionary context; both species must continually adapt to each other (May and

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E-mail address: [clement.lagrue@gmail.com](mailto:clement.lagrue@gmail.com) (C. Lagrue).<http://dx.doi.org/10.1016/j.ijppaw.2017.04.005>2213-2244/© 2017 Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Anderson, 1983; van Baalen, 1998; Dieckmann et al., 2002; Vale and Little, 2009). Parasites are generally considered to stay ahead of host defenses during co-evolution and are often expected to be adapted to their local hosts (Kaltz and Shykoff, 1998; Morgan et al., 2005). Even if invasive hosts are congeneric species taxonomically close to native hosts, parasites may be so closely adapted to their local host species that they are unable to infect or induce pathogenic effects in the invader (Cornet et al., 2010; Westram et al., 2011a). Local parasites that are able to infect novel, invasive hosts may still reach lower infection levels and pathogenic effects in native than invasive host species (Lagrué et al., 2016). In turn, local, native hosts are also continuously mounting counter-adaptations specifically targeting their local parasites and may be better at dealing with native parasites than a naïve, invasive host (Lagrué et al., 2016). Overall, native and invasive hosts can vary wildly in their vulnerability to infection and local parasites in their host specificity and pathogenic effects (Redón et al., 2015).

Generally, two closely related and sympatric host species infected by the same parasite can exhibit strongly contrasted vulnerability to infection and/or parasite-induced mortality (Thomas et al., 1995; Rousset et al., 1996). Although evidence for parasite-induced host mortality from field data remains difficult to obtain (Anderson and Gordon, 1982), multiple studies have inferred parasite-induced host mortality from distribution of parasite abundances within host populations (Gordon and Rau, 1982; Thomas et al., 1995; Rousset et al., 1996; Médoc et al., 2006). But the direct links between parasite prevalence or abundance and host mortality can be difficult to determine (Benesh, 2011). Differences in parasite prevalence and/or abundance among sympatric host species can be due to one host being more efficient at avoiding the parasite and/or resisting infection following encounter; i.e. lower infection levels result from higher resistance to the parasite. Alternatively or concomitantly, contrasting parasite-induced mortality between co-occurring host species can in turn induce widely different parasite prevalence and/or abundance between hosts. Hosts in which survival is not affected by the infection will tend to accumulate parasites, thus displaying higher prevalence and/or abundance levels than hosts with high parasite-induced mortality, even if their encounter rates and vulnerability to infection are similar. Assessing which of these potential factors affect apparent infection levels among alternative host species in wild host populations remains extremely difficult in the field however.

In France, the native *Gammarus fossarum* and *G. pulex* are often found co-existing with the invasive *Gammarus roeseli*, an established Balkan species (Bauer et al., 2000). These species are also hosts to a variety of acanthocephalan parasites (Bauer et al., 2000, 2005; Westram et al., 2011a). Previous studies have shown that acanthocephalan parasites can induce various behavioural, phenotypic, and physiologic changes in *G. fossarum* and *G. pulex*. These include altered reaction to light (Bauer et al., 2000, 2005; Cézilly et al., 2000; Perrot-Minnot, 2004; Tain et al., 2006), impaired antipredator behaviour (Kaldonski et al., 2007; Dianne et al., 2014), partial castration (Bollache et al., 2002), and lower immune activity (Rigaud and Moret, 2003). No such effects were apparent, or were significantly lower, in the invasive *G. roeseli* (Bauer et al., 2000, 2005; Rigaud and Moret, 2003). Contrasting host manipulation in native compared to invasive amphipod hosts reflected a difference in the ability of the acanthocephalan *Pomphorhynchus laevis* to alter brain serotonergic activity of the two host species (Tain et al., 2007). As a result, predation rates on acanthocephalan-infected *G. fossarum*/*G. pulex* were significantly higher than on infected individuals of the invasive *G. roeseli* (Lagrué et al., 2007; Tain et al., 2007). Consequently, mean parasite abundance relative to host size displayed the characteristic bell-shaped curve supporting a higher mortality in acanthocephalan-infected

*G. fossarum*/*G. pulex* individuals compared to uninfected amphipods (Lagrué et al., 2007). Here, parasite-induced host mortality likely resulted from increased predation on infected amphipods induced by host manipulation (Lafferty, 1999; Outreman et al., 2007; Violante-González et al., 2016). Again, no such pattern was observed in *G. roeseli*; mean parasite abundance simply increased with amphipod host size, indicating an accumulation of acanthocephalan parasites over time by invasive hosts with no apparent induced mortality (Lagrué et al., 2007). Furthermore, although acanthocephalan prevalence is higher in the invasive *G. roeseli* than in the native *G. fossarum*/*G. pulex* in the field, laboratory controlled infections showed that native amphipods were more susceptible to infection by local acanthocephalan (Lagrué et al., 2007; Bauer and Rigaud, 2015). Overall, differences in vulnerability to infection, acanthocephalan prevalence and size distributions of infected individuals suggest a differential parasite-induced mortality between *G. fossarum*/*G. pulex* and the invasive *G. roeseli*. Such pattern of enemy release is commonly observed in a biological invasion context and provides a competitive advantage to the invader (Clay, 2003; Cornet et al., 2010; Arundell et al., 2015). Differential susceptibility to infection by local parasites and parasite-induced mortality are often seen as key factors, among others, for the ability of *G. roeseli* to invade, establish and co-exist with local populations of the native *G. fossarum*/*G. pulex* (Lagrué et al., 2011).

*Gammarus pulex* and *Gammarus fossarum* are widely distributed “morphological” species and are often considered to be single, independent functional taxonomic units (Karaman and Pinkster, 1977; Müller, 1998). However, extensive use of DNA barcoding have recently allowed the detection of high degrees of cryptic diversity (i.e. genetically diverging lineages that differ little or not at all in their morphology) across a variety of taxa (Hebert et al., 2003; Pfenninger and Schwenk, 2007; Fontaneto et al., 2009; Trontelj and Fišer, 2009). Amphipods are no exception with a number of cases of morphologically cryptic lineages reported (Hogg et al., 1998, 2006; Witt and Hebert, 2000; Witt et al., 2006; Lefébure et al., 2007; Sutherland et al., 2010; Grabowski et al., 2012). Several recent studies showed extensive genetic divergence within *G. fossarum* and *G. pulex* (Müller, 1998, 2000; Westram et al., 2011b; Lagrué et al., 2014; Weiss et al., 2014; Weiss and Leese, 2016). Indeed, Lagrué et al. (2014) showed that, in Eastern France, *G. fossarum* and *G. pulex* form a complex of cryptic lineages, or molecular operational taxonomic units (i.e. MOTU; Blaxter et al., 2005), that are morphologically undistinguishable and often co-occur in sympatric populations. Whether these cryptic MOTUs display differential vulnerability to shared parasites remains unclear. For instance, the respective vulnerability to parasites of each *G. fossarum*/*G. pulex* lineage compared to that of the sympatric invasive *G. roeseli* is completely unknown. Many of the studies cited above were conducted on amphipod populations that have proved, in hindsight, to be made of several sympatric MOTUs of *G. fossarum*/*G. pulex* (Bauer et al., 2000, 2005; Lagrué et al., 2007, 2014), thus preventing reliable comparisons of parasitism between native and invasive species (Bauer and Rigaud, 2015).

Morphologically cryptic lineages of amphipod hosts may be physiologically, behaviourally and/or ecologically different and thus not be cryptic to parasites (Cothran et al., 2013a, b). In our study system, whether acanthocephalan parasites are generalists and able to infect any available native amphipod host or are highly specific to particular host MOTUs is yet to be assessed. However, the occurrence of sympatric but genetically divergent native host lineages, coupled with the presence of the invasive *G. roeseli*, has the potential to affect acanthocephalan infection levels, host-parasite interactions and ultimately host-host competition among lineages and/or species (Gandon, 2004; Rigaud et al., 2010; Westram et al., 2011a). In such cases, contrasting parasite-induced mortality

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