

Parasites of exotic species in invaded areas: does lower diversity mean lower epizootic impact?

Sergey E. Mastitsky^{1*}, Alexander Y. Karatayev¹, Lyubov E. Burlakova¹ and Daniel P. Molloy²

¹Great Lakes Center, Research Foundation of SUNY, Buffalo State College, 1300 Elmwood Avenue, Buffalo, NY 14222, USA, ²Division of Research and Collections, New York State Museum, Albany, NY 12230, USA

ABSTRACT

Aim Exotic species may serve as vectors for the introduction of parasites from their native range and may also become infected by parasites already present in invaded areas, but the total number of parasites infecting such exotic species in their invaded areas is typically less than that in their native range. We tested whether the diversity of parasites associated with exotic species in the native and invaded areas is related to the epizootic impact these parasites cause.

Location Global.

Methods We examined the diversity and epizootic impact of 384 parasite taxa associated with 22 exotic freshwater invertebrate species. The epizootic impact of each parasite was rated based on whether it had been documented to cause a major pathological impact on a large proportion of an infected host population (other than the invader under consideration).

Results The total number of parasites associated with an exotic host in its native range was about twice that of all parasites associated with it in its entire invaded range. This was mainly because of the loss in the invaded areas of low impact parasites, whereas the average number of high impact parasites per host in these areas did not differ statistically from that in the native range.

Main conclusions Our study suggests similar levels of adverse impact of parasites of exotic species in both their native and invaded areas. In addition to the introduction of highly pathogenic exotic parasites, other mechanisms that may be involved include (1) acquisition by the invaders of new high impact parasites in the invaded ranges, (2) high abundance of the invaders in their new ranges and (3) susceptibility of novel hosts to exotic parasites because of the 'naive host syndrome'.

Keywords

Biological invasions, epizootic impact, naive host, parasite spillback, parasite spillover.

*Correspondence: Sergey E. Mastitsky, Great Lakes Center, Research Foundation of SUNY, Buffalo State College, 1300 Elmwood Avenue, Buffalo, NY 14222, USA.
E-mail: aliensinbelarus@gmail.com

INTRODUCTION

The past several decades have been characterized by the emergence of a number of pathogenic diseases in populations of humans, domesticated species and wildlife (Daszak *et al.*, 2000; Dobson & Foufopoulos, 2001). The impact of diseases on host populations is expected to continue to increase, facilitated by factors such as global climate change (Harvell *et al.*, 2002), rapid fragmentation of natural habitats and pollution-mediated suppression of the host immune system (Holmes, 1996).

In addition, outbreaks of severe diseases may be promoted by the spread of exotic species that serve as vectors of introduction for their parasites and can also become hosts for aboriginal disease agents (Torchin *et al.*, 2002, 2003; Prenter *et al.*, 2004; Taraschewski, 2006; Kelly *et al.*, 2009). In contrast to other facilitating factors, the spread of parasitic diseases along with non-indigenous species has received less attention from invasion ecologists, parasitologists and environmental managers. Perhaps, this has been because of the typically reduced diversity of parasitic organisms associated with

invaders in introduced regions (Torchin *et al.*, 2002, 2003; Colautti *et al.*, 2004; Prenter *et al.*, 2004; Kelly *et al.*, 2009), which may create an impression of an insignificant epizootic role of these parasites. However, the parasites of exotic species may pose serious threats to recipient ecosystems, including the risk of extinction of endangered species (Dobson & Foufopoulos, 2001; Mitchell *et al.*, 2005), mass mortalities of novel hosts (Alderman *et al.*, 1987; Burrenson *et al.*, 2000; Taraschewski, 2006), and, as a result, major modifications in food webs and the functioning of invaded ecosystems. Also, exotic species can vector parasites that threaten public health (Pointier, 1999). Parasites of exotic species can also render considerable economic damage, especially when commercially valuable hosts are threatened (Burrenson *et al.*, 2000).

We conducted a range-wide examination to test whether the diversity of parasites associated with exotic species is related to the epizootic impact these parasites cause. In general, epizootics can occur after the introduction of exotic species due either to 'parasite spillover' (exotic parasites infecting novel hosts in invaded areas) or 'parasite spillback' (increase of the native parasites' impact because of their amplification in exotic hosts) (Kelly *et al.*, 2009). We also discuss the biological mechanisms that may underlie these two types of disease outbreaks.

METHODS

A list of 47 major benthic and planktonic exotic freshwater invertebrates was generated from online invasive species databases and the primary scientific literature. To this list, we added information on the parasites of these invaders from primary papers in scientific journals available through the Web of Science, JSTOR, BioOne, ScienceDirect, EBSCO Academic Search Premier and Academic OneFile, online invasive species databases, and searches of books, reports, and conference abstracts. Web-based searches were conducted using the Latin species name and 'parasit*' or 'infect*' or 'pathogen*' as keywords. Analogous keywords were used when searching for foreign language literature.

In a strict sense, parasitism implies an intimate coexistence of heterospecific organisms, with the parasite obtaining benefits at the expense of the host (Kinne, 1980). Nevertheless, for a comprehensive treatment of the 'parasites' of invaders, we included commensals and the many symbionts whose relationships with their hosts remain unclear.

However, information on parasites from the native and/or invaded range was lacking for 25 of the species screened, so our final database covered only 22 of the initially selected 47 host species (nine gastropods, five bivalves, four amphipods, four decapods; see Appendix S1 in Supporting Information).

We considered only those parasites documented as infecting invaders under natural, not experimental conditions. The group of trematodes '*Cercaria helvetica*' found in the snail *Bithynia tentaculata* is composed of several species whose taxonomic position is ambiguous (Bychovskaya-Pavlovskaya & Kulakova, 1971), and thus was treated as a single taxon.

We rated all parasites documented from the 22 invader species as having either 'low', 'high', or 'unknown' epizootic impact. The 'high impact' category included those documented as causing a distinct pathological effect in a large proportion of an infected host population (e.g., life threatening histopathologies, mortality). However, the quality of the reports on parasite impacts varied substantially across studies, often providing no quantitative information on the affected proportion of a host population. Therefore, to apply a standardized approach, we categorized a parasite as having a high impact only if a report's author(s) used one or more of the following terms to describe the impact of the parasite in the study area: 'epizootic', 'mass mortality', 'large-scale mortality', 'heavy mortality', 'outbreak', 'die-off'. Analogous terms were searched for in foreign language literature. Parasites not documented to cause such epizootic-like events and all organisms considered as commensals were categorized as 'low impact'. The 'unknown impact' category included parasites whose taxonomic identity as reported in the literature examined was insufficient for categorization using the above criteria.

Threatened hosts included all the reported wildlife and/or domesticated hosts of a parasite under assessment, but not the exotic host of the parasite. Reports of human infections were also excluded because of the possible confounding effects of cultural, dietary and behavioural differences between the native and invaded regions.

We examined how the average numbers of parasites with different epizootic impact changed after establishment of an invader in its new geographical range. Similarly, we calculated how many parasites of each category an invader acquired on average in its introduced range. The category of 'acquired parasites' was mainly composed of the species that were encountered by the invader for the first time (i.e., they had never been documented to infect the invader in its native range). In respect to cosmopolitan parasites, however, it was difficult to assess their status as 'acquired' or 'introduced'. If no other evidence was available, we considered such cosmopolitan parasites as 'acquired'. This approach was in agreement with previous investigations (Torchin *et al.*, 2002, 2003; Prenter *et al.*, 2004; Kelly *et al.*, 2009), which indicated that it was much more likely that an invader re-encountered such parasites in an invaded area than that it introduced them from its native range. This was particularly reasonable for invaders that often spread in their larval stages (e.g. zebra mussel and quagga mussel), the parasite assemblages of which are typically less diverse than they are in the adults. Although this approach could introduce a bias into our classification of the parasites as 'introduced' or 'acquired', cosmopolitan parasites were reported in almost all of the species examined, suggesting similar levels of the bias among them.

We tested the null hypothesis of no difference in diversity of parasites of a particular category between the native and invaded ranges and assessed the proportional numbers of exotic parasites differing in their epizootic potential using the

generic functions of the software package R 2.10.1 (R Development Core Team 2009).

RESULTS

In total, we recorded 384 parasite species infecting the 22 exotic freshwater invertebrate species examined. Most of these parasites (317, 82%) have never been reported as causing epizootics and so were categorized as low impact. Parasites reported to cause epizootics in native and/or invaded ranges (22, 6%) were overwhelmingly dominated by trematodes; other epizootically important taxa were viruses and oomycetes (see Appendices S2 and S3). The remaining 45 (12%) were categorized as of unknown impact.

The number of parasite species infecting the exotic invertebrates in their native ranges varied from 3 to 75 (mean 17.1 ± 3.8 species/invader; \pm SE here and below). The average number of parasites introduced with invaders into the new regions (2.2 ± 0.5) was significantly lower ($P < 0.001$, Wilcoxon matched pair test) (Fig. 1). The parasite loss following invasion was on average $78 \pm 6\%$.

In the native range, each exotic invertebrate hosted an average of 14.5 ± 3.0 parasite species with low epizootic impact, 0.7 ± 0.3 high impact species and 1.9 ± 0.6 species with unknown impact. Of the 22 invader species, eight (36%) were not interpreted as having introduced any parasites to the new regions (i.e., the snails *Cipangopaludina chinensis*, *Lymnaea auricularia*, *Physella acuta*, *Pomacea canaliculata*, *Potamopyrgus antipodarum*, and the bivalves *Corbicula fluminea*, *Pisidium amnicum* and *Sphaerium corneum*). The remaining 14 species introduced a total of 39 parasites. Of these parasite species, only 5% were documented as causing disease outbreaks in their native ranges. However, some of the introduced parasites previously classified as low impact species

in their native range caused mass mortalities in the invaded range, and thus were classified as 'high impact'. The high impact parasites were introduced with 7 of the 22 invaders (32%) (the molluscs *B. tentaculata*, *Dreissena polymorpha*, *Lithoglyphus naticoides*, *Melanoides tuberculata*, and the crayfish *Orconectes limosus*, *Pacifastacus leniusculus* and *Procambarus clarkii*), a proportion that did not differ significantly from the proportion of invaders that acquired high impact parasites in invaded areas (five species, 23%; $P = 0.736$, Fisher's exact test; see also Appendix S3). Although the percentage of high impact species among the introduced parasites was more than four times that in the parasites in their native ranges (21% vs. 5%), the overall proportions of the three categories of parasite epizootic potential did not differ significantly between their native and introduced ranges ($P = 0.161$, Fisher's exact test).

Our data suggest that 19 of the 22 invaders were susceptible to infection with novel parasites in the introduced regions. When the numbers of parasites associated with an invader in all of its introduced areas were combined, the average number of acquired parasites (5.7 ± 1.7 species/invader) was higher than the number of introduced ones (2.2 ± 0.5 species/invader), although this difference was not significant statistically ($P = 0.067$, Wilcoxon matched pair test; Fig. 1). Also, in 6 of the 22 invaders, the total number of parasites (introduced and acquired) was more diverse in the introduced range (i.e., in the amphipods *Dikerogammarus villosus* and *Gammarus tigrinus*; the snails *L. naticoides* and *P. acuta*; the zebra mussel, *D. polymorpha*, and the spiny-cheek crayfish, *O. limosus*). It should be stressed, however, that this is a generalization made by pooling all data on each of these six species, and there are some examples, such as *D. polymorpha* in North America, in which the total number of parasites is far less than in the host's native range.

Of the acquired parasites, on average 4.5 ± 1.6 species were categorized as low impact, 0.2 ± 0.1 species as high impact and 1.0 ± 0.4 species as unknown impact (Fig. 1). The average number of acquired high impact parasites did not differ statistically from the number of introduced high impact parasites (0.2 ± 0.1 vs. 0.5 ± 0.2 parasite species/invader; $P = 0.294$, Wilcoxon matched pairs test).

After pooling the numbers of introduced and acquired 'high impact' parasites, each invader in its new range hosted an average of 0.7 ± 0.2 species, which did not differ statistically from the number of high impact parasites hosted in the native range (0.7 ± 0.3 species/invader; Fig. 1). There was also no significant difference between ranges in the number of parasites with unknown epizootic impact (native range: 1.9 ± 0.6 species/invader, invaded range: 1.1 ± 0.4 species/invader; $P = 0.209$, Wilcoxon matched pairs test) but the number of low impact parasites in the native ranges was significantly higher than in the invaded ones (14.5 ± 3.0 vs. 6.1 ± 1.6 ; $P = 0.011$, Wilcoxon matched pair test; Fig. 1).

DISCUSSION

This study provides the first quantitative evidence that despite the typically reduced overall diversity of the parasites

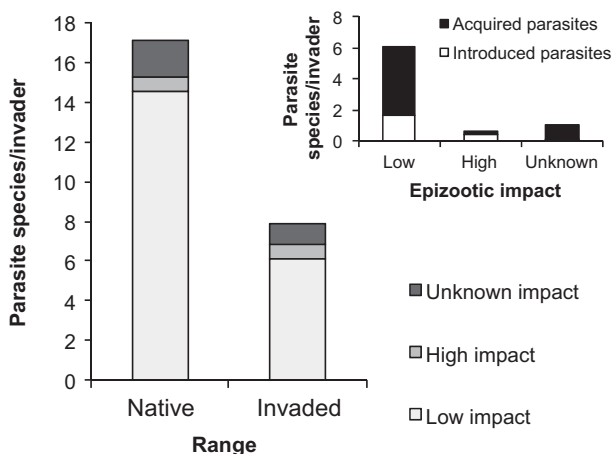


Figure 1 Diversity of parasites associated with the 22 freshwater exotic invertebrates in their native and invaded ranges, categorized by the parasite epizootic impact. Inset: composition of parasites in invaded areas, categorized by the parasite origin. Bar heights correspond to the average numbers of parasite species in a certain category per invader.

associated with exotic species in invaded areas, the number of epizootically significant species among these parasite assemblages does not differ from that in the native areas. This finding suggests that there is a similar level of adverse impact caused by parasites of exotic species in both their native and invaded areas. We emphasize, however, that our quantitative analysis of epizootic impact was unavoidably based on subjective estimates of impact in the original publications we examined (see Methods). Thus, our study should not be considered as a definitive investigation of this topic, but rather an invitation for further exploration to advance our understanding of this dynamic process in invasion biology.

The average number of parasite species associated with the exotic invertebrates in their native areas was over twice as high as that in the invaded areas (Fig. 1), a pattern in line with similar studies involving other host taxonomic groups (Torchin *et al.*, 2002, 2003; Prenter *et al.*, 2004; Kelly *et al.*, 2009). Of the invertebrates examined, 36% did not successfully introduce any of their coevolved parasites into the invaded areas. This finding may be explained by the complexity of the process of biological invasion, in which all potential invaders progress through a series of stages. At each of these stages, an invader faces a number of abiotic and/or biotic conditions ('filters') that may prevent its successful transportation to and establishment in the new environment. As species vary tremendously in many characteristics, only some potential invaders pass through the entire chain of 'filters' and become established in a recipient ecosystem (Colautti & MacIsaac, 2004; Karatayev *et al.*, 2009). Similarly to the free-living invaders, exotic parasites are also subject to a variety of conditions that hamper their invasion into new areas. Moreover, simultaneous action of the parasite-specific and host-specific 'filters' is likely to make the invasion of exotic parasites even more complicated. As a result, most exotic free-living species establish in new regions with significantly reduced numbers of their coevolved parasites (Torchin *et al.*, 2002, 2003; Prenter *et al.*, 2004; Kelly *et al.*, 2009).

The reduction of parasite diversity in invaded areas occurred mainly as a result of the loss of low impact species, whereas the number of high impact species did not differ statistically between the native and invaded ranges (Fig. 1). We hypothesize that the similar average numbers of high impact parasites in the native and recipient ecosystems may be because of the action, either individually or in combination, of the following three mechanisms.

Acquisition of novel high impact parasites

The majority (19, 86%) of the 22 invertebrates examined acquired parasites in the invaded regions, including ones previously documented to cause epizootics in these regions. Moreover, six species (27%) of the invaders harboured more parasites in their invaded than their native range. As others have found, parasites acquired by invaders in their new regions are typically represented by generalist species which, in contrast to highly host-specific, coevolved parasites, are far more likely to successfully infect new hosts (Prenter *et al.*,

2004; Kelly *et al.*, 2009). In our study, the numbers of acquired and introduced high impact parasites did not differ significantly (0.2 ± 0.1 and 0.5 ± 0.2 species/invader, respectively); neither did the proportion of invaders that acquired high impact parasites (23%) differ significantly from the proportion that co-introduced high impact parasites from the native areas (32%). Thus, our findings suggest that exotic species may co-introduce and acquire similar numbers of epizootically important parasites in the invaded regions and thus 'compensate' for the loss of such parasites during the invasion process.

Although acquisition of new parasites by invaders is probably taking place in nature, it is often difficult to conclude with confidence whether such an inference was not caused by sampling bias. Because of the impacts they cause, some exotic species attract more attention in the invaded areas, so that higher numbers of parasites are reported. Or in contrast, the reduced numbers of parasites in invaded ranges of exotic species might be an artefact of more extensive research work historically having been conducted in the native regions and/or the larger sizes of those regions (Torchin *et al.*, 2003; Colautti *et al.*, 2004). There is a need for equal-effort parasitological studies in the native and invaded areas of major exotic species. These studies would help in obtaining comparable data on species richness and abundance of the parasites of invaders that further could be used for robust tests of hypotheses regarding the role parasites play in the process of invasion of their hosts (e.g., the 'enemy release hypothesis') and in emergence of new diseases in the invaded areas.

Positive effect of the invader's population density

Truly parasitic organisms are by definition detrimental to their hosts. For evolutionary reasons, however, outbreaks of parasitic diseases are rather rare and occur in host populations only under appropriate local conditions. In particular, the host population density is theoretically one of the major biotic factors promoting the transmission and persistence of parasitic diseases (Anderson & May, 1981). Epizootics caused by exotic parasites in their novel hosts ('spillovers') may often be facilitated by the high population densities that many invaders-transmitters achieve in the new areas. For example, the snail *L. naticoides*, an intermediate host of the highly pathogenic trematode *Apophallus muehlingi*, formed an unusually dense population (up to 8800 individuals per m²) soon after its invasion of the Volga River Delta (Biserova, 1990). This, in combination with the high prevalence of infection with *A. muehlingi*, could have led to production and release by the snails of enormous numbers of the parasite's cercariae, resulting in the documented 80% mortality rate among young cyprinid fishes (Biserova, 1990). Similarly, the European snail *B. tentaculata* and its three specific trematode parasites (*Cyathocotyle bushiensis*, *Leyogonimus polyoon* and *Sphaeridiotrema globulus*) have been blamed for mass mortalities of aquatic birds in North America (Cole & Franson, 2006).

Outbreaks of native parasitic diseases can also be positively correlated with the abundance of their novel exotic hosts (Kelly

et al., 2009). For instance, the metacercarial stage of the native trematode *Echinoparyphium recurvatum* in invasive zebra mussels has become substantially more abundant than that of other echinostomatid trematodes in native molluscs in Lake Naroch, Belarus, probably because of the disproportionately high density of the mussels, suggesting an increased load ('spillback') of *E. recurvatum* on the native waterfowl that serve as its final hosts (Mastitsky & Veres, 2010).

Many exotic species are thought to be successful and able to achieve abundant populations in invaded areas because of release from their natural enemies, including parasites (Torchin *et al.*, 2002, 2003; Prenter *et al.*, 2004). If this is true (Colautti *et al.*, 2004), the loss of some parasites during the invasion process may promote amplification of the remaining parasites via positive feedback on the invader's abundance. Further research is needed to test this hypothesis.

Naive host syndrome (NHS)

In their native ranges, only 5% of the exotic parasites we examined were high impact species. In the introduced range, however, some of the exotic parasites, previously considered non-pathogenic, caused mass mortalities in their novel hosts (Appendices S2 and S3). This might in part be a result of what we refer to as 'naive host syndrome'. Hosts and the parasites with which they have a long-established relationship are usually co-adapted, so that the parasites rarely seriously harm their hosts (May & Anderson, 1983; Taraschewski, 2006), unless death or prostration of the host is an integral part of the parasite life cycle required to increase the transmission rate (May & Anderson, 1983; Ebert & Herre, 1996). In the invaded areas, however, exotic parasites can meet new, naive hosts that lack historically evolved resistance; they may therefore severely impact these novel hosts, often resulting in large-scale mortality (Alderman *et al.*, 1987; Bureson *et al.*, 2000; Taraschewski, 2006). Thus, even though there is reduced parasite diversity in the invaders, some exotic parasites may actually have a stronger adverse impact in their introduced range, perhaps due in certain instances to NHS.

In some cases, e.g. the crayfish plague *Aphanomyces astaci* (Alderman *et al.*, 1987), the naivety of hosts in the new range to exotic disease agents has been demonstrated experimentally. In other cases, however, the reasons for mass mortality among hosts infected with exotic parasites are not as clear and perhaps do not involve NHS. In our study, the majority of parasites with high epizootic potential were trematodes. However, NHS is most likely to occur among microparasite (e.g. bacterial, fungal, viral), not helminth infections (Alderman *et al.*, 1987; Bureson *et al.*, 2000). Helminths have evolved a variety of strategies for modulating the protective action of their hosts' immune systems, resulting in the lack of effective long-lasting parasite-specific immunity (Maizels *et al.*, 2004). Nonetheless, the well-known example of the nematode *Anguillicola crassus*, which causes mass mortality in its immunologically naive eel hosts in Europe (Taraschewski, 2006), indicates that NHS can be just as applicable to helminthes as to microparasites.

The concept of NHS can equally be applied to the parasites that invaders acquire in their new regions: in addition to the above-mentioned wide host specificity of such parasites, some of them may switch more easily to an exotic host if it is susceptible to new infections. Amplification of parasites native to the recipient ecosystems in such highly susceptible exotic hosts can also have serious negative impacts (Kelly *et al.*, 2009). Further research is needed to better understand the underlying reasons for NHS, and the role this mechanism plays in the emergence of novel parasitic diseases transmitted by exotic species.

In conclusion, our study demonstrates that the spread of non-indigenous species is an important yet underestimated and insufficiently studied factor in the emergence of disease outbreaks. The number of introductions of exotic species globally is growing exponentially and probably so does the risk of epizootics that may be caused by the parasites of invaders, due either to parasite 'spillover' or 'spillback'. The problem gets especially complicated because of the inability to predict which native species will be susceptible to the introduced parasites or which native parasites will readily use exotic hosts for amplification. Therefore, the parasitological consequences of the introduction of exotic species should be an integral part of the assessment of the ecological risks these species pose and thus should attract more attention from invasion biologists, parasitologists and environmental managers.

ACKNOWLEDGEMENTS

S.E.M. and L.E.B. were supported by the Research Foundation of SUNY; S.E.M. was also partly supported by the EU Framework 6th Integrated Project ALARM 'Assessing large-scale environmental risks with tested methods' (contract GOCE-CT-2003-506675).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The freshwater invertebrate invaders screened, with the references used to compile the lists of their parasites in native and invaded ranges.

Appendix S2 Invaders documented to host the parasites of high epizootic impact in their native ranges.

Appendix S3 Invaders documented to host the parasites of high epizootic impact in their invaded ranges.

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BIOSKETCH

Sergey E. Mastitsky is a Research Scientist with the Great Lakes Center at Buffalo State College, New York, USA. He received his undergraduate degree from Belarusian State University, and PhD degree in Hydrobiology from Zoological Institute of the National Academy of Sciences of Belarus. His primary research interests include patterns of spread of exotic species and their role in aquatic ecosystems.

Authors contributions: A.Y.K., S.E.M., L.E.B. and D.P.M. conceived the ideas; S.E.M. and D.P.M. collected the data; S.E.M. conducted statistical analyses; S.E.M., A.Y.K., L.E.B. and D.P.M. led the writing. This study is part of a more extensive project that the authors conduct as members of the International Research Consortium on Molluscan Symbionts (<http://www.nysm.nysed.gov/ircoms>).

Editor: Robert Cowie