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ORIGINAL PAPER

# Invaders are not a random selection of species

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**Abstract** We assembled information on 119 species of freshwater macroinvertebrate invaders in North America and Europe, and compared them to all native freshwater species in North America and Europe. We tested whether the invaders were a random or selected group among taxa (phylum or class), water quality requirements, and feeding habit. We found that freshwater macroinvertebrate invaders are not a random selection of species, and are over-represented by molluscs and crustaceans, while taxa richness of native communities are dominated by insects. Over 35% of native species of aquatic invertebrates in North America are only able to live in areas with excellent or very good water quality, and are intolerant of organic pollution. In contrast, all invaders are tolerant of at least moderate amounts of organic pollution. There was a significant difference in the distribution of feeding habits between native species and invaders: collector-filterers (including suspension feeders) were 2.5–3 times more abundant, and predators were 3–4 times less abundant among invaders than among native invertebrates. The ongoing spread of exotic species affects the biodiversity of selected taxa, shifts communities toward greater tolerance of organic pollution and increases the numbers of suspension feeders, thereby enhancing benthic pelagic coupling in waterbodies with high densities of invaders. Because these processes are very similar in Europe and North America, we suggest that the observed patterns may have a common global effect.

**Keywords** Aquatic exotic species · Freshwater invaders · Pollution · Feeding mode · Suspension feeders

## Introduction

According to community assembly theory, the dynamic structure of communities is due to a continuous process of sequential invasions and extinctions (Fargione et al. 2003). Therefore, past and current invasions, or migration of new species into local

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communities, human mediated or otherwise, are an integral part of community development (e.g., succession, Connell and Slatyer 1977), and are important for community structure and composition (MacArthur and Wilson 1967; Ricklefs and Schluter 1993; Loreau and Mouquet 1999). However, introduction of exotic species is presently one of the most serious challenges for the protection of natural ecosystems and the services they provide. In addition, they are a serious problem for industry and municipalities, which must spend millions of dollars each year to control, eradicate or remove unwanted species, as well as their ecological and environmental impacts (e.g., Pimentel et al. 2005; Keller et al. 2007a). Every year new species are introduced, become established, and become nuisances all over the world. However, we have little ability to predict the future, which is essential for planning and management of resources and habitats, especially in the face of future climate, habitat and population changes. Accurate predictions allow us to direct limited resources to specific taxa that are most likely to cause damage, habitats most likely to suffer, as well as those vectors most likely to transmit the targeted taxa (Karatayev et al. 2007; Keller et al. 2007b).

Before being integrated and flourishing in a community, a species must be able to arrive and establish a population under local conditions. All species face this, including those that undergo range expansion, disperse to new areas, and colonize empty patches; exotic species are no exception. Therefore, a successful invader must possess qualities that will allow invasion in new habitats, and the recipient community must be invasible. Both of these aspects of invasion have been considered by researchers for decades (e.g., Elton 1958; Baker 1965; Mack 1996; Williamson 1996, 1999; Morton 1997; Kolar and Lodge 2001; Fargione et al. 2003). Many scientists have suggested the characteristics of a successful invader, based on general ecological principles and gestalt, which are usually characteristics attributed to early successional species, weedy and ephemeral species (*r*-selected traits) (e.g., Lodge 1993; Rejmanek and Richardson 1996; Reichard 1996; Williamson 1996; Morton 1997).

In order to succeed in a new environment a species should pass through several filters. Several types of filters have been suggested, including biogeographic (physical barriers), physiological (match between invader and recipient environment), and biotic (resistance of the native community) filters (e.g., Carlton 1985; Moyle and Light 1996; Chase 2003; Fargione et al. 2003). However, all filters do not act independently, but rather interact to determine the success of an invasion (Moyle and Light 1996; Wonham 2006). Although many species have the potential to be introduced, only a few pass all filters and establish populations in a new environment and become successful invaders, suggesting that invaders may not be a random selection of species.

To examine the role of species characteristics in invasion, we examined freshwater macroinvertebrate invaders (here defined as species introduced by human action outside of their native range) in North America and Europe, and compared them to all native freshwater species in North America and Europe. We tested whether the invaders were a random or select group among taxa (phylum or class), water quality requirements, and feeding habit.

## Methods

We assembled information on 119 species of freshwater macroinvertebrate invaders found in North and South America, Europe, and Asia based on literature and web-based searches, which included: invasive species databases, primary literature in scientific journals through the Web of Science (1945-present), Zoological Record (1974-present), and searches of books and reports. For each invader we collected data on their water quality requirements (tolerance to organic waste), feeding habit, taxonomy, and their native and invaded range. We used Thorp and Covich (2001) as the source for all native North American macroinvertebrates (22,183 species), and for European species we used Limnofauna Europea (12,728 species; Illies 1978). Because mosquitoes are generally not considered among aquatic invaders (i.e., not included in any aquatic invader databases) or not always considered in native fauna databases, we excluded them from our analysis.

### Water quality

The Hilsenhoff Biotic Index (HBI, Hilsenhoff 1987) was developed to assess water quality for freshwaters in North America. This Index is used to rate fresh water quality as follows: 0.00–3.50, excellent, no apparent organic pollution (pollution that lowers dissolved oxygen); 3.51–4.50, very good, possible slight organic pollution; 4.51–5.50, good, some organic pollution; 5.51–6.50, fair, fairly significant organic pollution; 6.51–7.50, fairly poor, significant organic pollution; 7.51–8.50, poor, very significant organic pollution; 8.51–10.00, very poor, severe organic pollution (Hilsenhoff 1987). Based on this index, species are rated in terms of their tolerance to organic pollution on a scale of 0–10 (0 = species requiring excellent water quality, 10 = species that can survive severe organic pollution). We used tolerance ratings found in Mandaville (2002) for 880 species of North American freshwater invertebrates, 75 species of invaders found in North America and North American-origin species that have invaded elsewhere (Europe, Asia, South America, Australia). If tolerance data were not available for a particular species, we used the index value for the next higher taxon (usually genus), for which values were available; insufficient data were available for 3 species. We compared the distribution of tolerance ratings for native North American species and invaders found in North America, invaders of North American origin found elsewhere (Europe, Asia, South America, Australia), and all freshwater macroinvertebrate invaders. Because insects were such a large portion of the native species pool, and almost absent from the pool of invaders, we then compared these same distributions excluding the insects. Although some non-native macroinvertebrate introductions were deliberate introductions of pollution tolerant species (see Van der Velde et al. 2000 for examples), the majority were not the result of such selection or deliberate introductions. Only organic pollution was considered in our analyses because there are too few data on tolerance to pollutants for the vast majority of taxa (but see Van der Velde et al. 2000 for data on species in the Rhine River).

### Feeding habit

To test whether the feeding mode of most invaders is different from that of native species, we again used data from Mandaville (2002), based on Merritt and Cummins (1996), for 796 species of North American native macroinvertebrates, 76 species of invaders found in North America and invaders of North American origin that are found elsewhere and for 119 found in North and South America, Europe, Asia, and Australia. Feeding habit categories were: collector-gatherer, predator, scraper, collector-filterer (including suspension feeders), and shredder. We also compared these same distributions excluding the insects.

### Taxon diversity

We organized the lists of macroinvertebrate freshwater species native to North America and Europe by phylum, and for the molluscs and arthropods, by class. We then compared the distribution of species that are known to be invaders in Europe or elsewhere of European origin (77 species) with the distribution of all European freshwater species (Illies 1978). For North America, we compared North American invaders or invaders elsewhere of North American origin (76 species) with the distribution of all freshwater species (Thorp and Covich 2001). We also compared these same distributions excluding the insects.

### Statistical analyses

To compare the distributions of native and invasive species grouped by taxon, water quality, and feeding habit, we used a Fisher-Freeman-Halton test (a generalization of the Fishers Exact Test; StatXact-4, version 4.0.1, Cytel Software Corp.) with a Monte Carlo estimate of the *P*-value to test for homogeneity in contingency tables (Freeman and Halton 1951).

## Results

### Water quality

Over 35% of native aquatic invertebrates in North America are able to live only in areas with excellent or very good water quality, and are not found in areas with organic pollution (HBI 0–4; Table 1). In contrast, all invaders are tolerant of at least moderate amounts of organic waste (HBI 5–8). Four percent of native species (34 of a total of 880) are tolerant of waters severely polluted with organic waste (HBI 9–10), while 6% of all invaders (7 of 116) can tolerate severely polluted waters (HBI 9), but none can

**Table 1** Numbers of freshwater invertebrate species, with and without insects included, that are: native to North America (NA), invaders in North America and species of North American origin that have invaded elsewhere in the world, and all freshwater invaders found in North America, South America, Europe, Asia and Australia, independent of origin

| Tolerance | With insects | | | | Without insects | | | |
|---|---|---|---|---|---|---|---|---|
| | Native species | Invaders | | | Native Species | Invaders | | |
| | | NA invaders | Percentage of total NA species | All invaders | | NA invaders | Percentage of total NA species | All invaders |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 | 36 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 85 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 46 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 96 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 5 | 199 | 3 | 1.5 | 4 | 11 | 1 | 8.3 | 2 |
| 6 | 195 | 32 | 14.1 | 54 | 59 | 32 | 35.2 | 54 |
| 7 | 59 | 5 | 7.8 | 7 | 7 | 5 | 41.7 | 6 |
| 8 | 81 | 29 | 26.4 | 44 | 34 | 29 | 46 | 43 |
| 9 | 13 | 6 | 31.6 | 7 | 0 | 6 | 100 | 6 |
| 10 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total | 880 | 75 | 8.5 | 116 | 113 | 73 | 64.6 | 112 |

The percent of the total North American species diversity that is comprised of current invaders is also presented. Water quality tolerance ratings were determined by tolerance to organic waste, based on the Hilsenhoff Biotic Index for water quality (data for species are from Mandaville 2002). Tolerance 0 = requires excellent water quality, 10 = tolerant to severe organic pollution

tolerate the most extremely polluted conditions (HBI 10). Differences between North American native species and North American invaders were significant (Fisher-Freeman-Halton statistic $H = 79.6$, $P \ll 0.001$), as were differences between North American native species and all invaders ($H = 164.0$, $P \ll 0.001$). These differences persisted when insects were removed from the analysis (North American natives vs. North America invaders, $H = 13.5$, $P = 0.012$; North American natives vs. all invaders, $H = 16.6$, $P < 0.003$), indicating that insects alone are not responsible for the observed differences.

## Feeding habit

There was a significant difference in the distribution of feeding habits between native species and invaders in North America ($H = 45.5$, $P < 0.001$, Table 2), as well as differences between North American native species and all invaders ($H = 55.7$, $P \ll 0.001$). In both cases collector-filterers (including suspension feeders) were 2.5–3 times more abundant, and predators were 3–4 times less abundant among invaders than among native invertebrates. These differences persisted when insects were removed from the analysis (North America, $H = 31.2$, $P < 0.001$; North American natives vs. all invaders, $H = 40.5$, $P < 0.001$), indicating that insects alone are not responsible for observed differences.

## Taxon diversity

The distribution of taxa of nonindigenous species differed significantly from the native communities in North America ($P < 0.001$) and Europe ($P < 0.001$), and these differences persisted when insects were removed from the analysis (North America, $P < 0.001$; Europe, $P < 0.001$), indicating that insects alone are not responsible for observed differences. Among native species, insects are by far the most diverse taxon, forming more than 73% of all of the species diversity of freshwater macroinvertebrates in North America, and more than 54% of the species diversity in Europe (Table 3). In contrast, invaders on both continents are dominated by crustaceans (37.8% of all invaders in North America and 52.6% in Europe), and molluscs (50.7% of all invaders in North

**Table 2** Numbers of species, including and excluding insects, grouped by feeding habit for those native to North America, invaders in North America and species of North American origin that have invaded elsewhere in the world, and all freshwater invaders found in North America, South America, Europe, Asia and Australia, independent of origin (based on data from Mandaville 2002)

| Feeding habit | With insects | | | Without insects | | |
|---|---|---|---|---|---|---|
| | Native species | Invaders | | Native species | Invaders | |
| | | NA invaders | All invaders | | NA invaders | All invaders |
| Collector-gatherer | 284 | 29 | 53 | 36 | 29 | 53 |
| Predator | 194 | 4 | 9 | 21 | 4 | 9 |
| Scraper | 121 | 4 | 5 | 33 | 4 | 5 |
| Collector-filterer[a] | 104 | 31 | 41 | 23 | 31 | 39 |
| Shredder | 93 | 8 | 8 | 0 | 6 | 6 |
| Total | 796 | 76 | 116 | 113 | 74 | 112 |

[a] Including suspension feeders

**Table 3** Numbers of native species, numbers of species of invaders, and the percent of all species that are invaders in North America and Europe by major taxon (phylum or class)

| Taxon | North America | | | Europe | | |
|---|---|---|---|---|---|---|
| | All species | Invaders | Invaders percentage of total | All species | Invaders | Invaders percentage of total |
| Porifera | 27 | 0 | 0 | 14 | 1 | 7.1 |
| Cnidaria | 8 | 2 | 25.0 | 17 | 2 | 11.8 |
| Turbellaria | 200 | 1 | 0.5 | 430 | 3 | 0.7 |
| Gastrotricha | 100 | 0 | 0 | 151 | 0 | 0 |
| Rotifera | 610 | 0 | 0 | 1,270 | 0 | 0 |
| Nematoda | 400 | 0 | 0 | 605 | 0 | 0 |
| Mollusca | | | | | | |
| Gastropoda | 659 | 21 | 3.2 | 571 | 9 | 1.6 |
| Bivalvia | 308 | 18 | 5.8 | 49 | 6 | 12.3 |
| Annelida | | | | | | |
| Oligochaeta | 600 | 3 | 0.5 | 197 | 6 | 3.1 |
| Hirudinea | 60 | 0 | 0 | 34 | 2 | 5.0 |
| Polychaeta | 13 | 0 | 0 | 6 | 1 | 16.7 |
| Bryozoa | 24 | 1 | 4.2 | 20 | 1 | 5.0 |
| Arthropoda | | | | | | |
| Hydrachnida | 1,500 | 0 | 0 | 955 | 1 | 0.1 |
| Insecta | 16,226 | 2 | 0.01 | 6,880 | 4 | 0.06 |
| All Crustacea | 1,448 | 29 | 2.0 | 1,529 | 40 | 2.6 |
| Decapoda only | 393 | 13 | 3.3 | 28 | 13 | 46.4 |
| Total | 22,183 | 77 | 0.2 | 12,728 | 76 | 0.6 |

Within the Arthropoda numbers are given for both all Crustacea, and for just the Decapoda

America and 19.7% in Europe). Among native species, however, crustaceans form 6.5% and molluscs represent only 4.4% of the biodiversity in freshwater in North America, and 12.0% and 4.9%, respectively, in Europe (Table 3). Although aquatic insects are the most diverse group among native freshwater invertebrates on both continents, the number of invasive species among freshwater insects was disproportionately low. Only 0.01% of North American and 0.06% of European freshwater insects were listed among invaders, and only 2.6% of freshwater invaders in North America and 5.3% in Europe were insects.

## Discussion

The diversity of invaders in fresh water is clearly different than the diversity of native species in several aspects. Some taxa and groups are over-represented, while others are grossly under-represented relative to their native diversity. Although insects are important invaders in terrestrial systems (e.g., Pellizzari and Dalla Monta 1997; Brockerhoff et al. 2006; Causton et al. 2006), in spite of their dominance in terms of numbers of species, extremely few are aquatic invaders. Certain aspects of habitat quality, habitat type, and life style may act as a barrier for introduction for some taxa, and may provide an opportunity for others.

No freshwater invaders require pristine water quality: all are tolerant of at least some levels of organic pollution (Table 1). Among North American native invertebrates, only insects are the least tolerant of organic pollution. Forty percent (310 species) of all native insects require excellent or very good water quality (no apparent organic pollution HBI = 0–4). Although a small number of invaders are tolerant of low water quality (8% of all invaders), none are tolerant of the lowest water quality rating (HBI = 10). In contrast, 13 species of North American natives tolerate HBI of 9 (7 of which are insects), and 21 species, all insects, tolerate the worst water quality (HBI of 10). With moderate levels of pollution, a waterbody will be unsuitable for more than one third of the native species. However, this waterbody would still be a good environment for all invaders. Thus, pollution can dramatically reduce abundances of or eliminate native species, allowing more tolerant invaders to colonize (Den Hartog et al. 1992; Rajagopal et al. 2006). Alternatively, improving water quality in previously severely polluted waters can facilitate invasion.

Although tolerance to pollution has been suggested as a trait of a successful invader for certain species (Den Hartog et al. 1992; Çinar et al. 2005; Vila-Gispert et al. 2005; Boltovskoy et al. 2006; Piola and Johnston 2006; Rajagopal et al. 2006; Villar et al. 1999; Grabowski et al. 2007; and see Van der Velde et al. 2000 for examples of pollution tolerance of some freshwater taxa), prior to our study there were no quantitative data testing and supporting this hypothesis for the wide taxonomic range of aquatic invaders included here. Disturbed communities have been hypothesized to be more invasible than pristine communities (Elton 1958; Moyle and Light 1996; Williamson 1996; Lozon and MacIsaac 1997), and pollution could be considered a form of disturbance. Low to moderate pollution could eliminate native species making resources available for more tolerant invasive species. However, most of invaders do not tolerate severe pollution (Table 1).

Collector-filterers, including suspension feeders (40.8%), and collector-gatherers (38.2%) are the two dominant feeding modes of freshwater macroinvertebrate invaders in North America. This sharply contrasts with the native assemblage, where collector-gatherers (35.7%) are the most abundant feeding group, followed by predators (24.4%), and scrapers (15.2%). For North American assemblages the collector-filterers (13.1%) are only the fifth most abundant group. When insects are excluded from the native assemblage, none of the remaining species are shredders, and the rest of the taxa are divided among the remaining 4 feeding groups (Fig. 1).

Collector-filterers are disproportionately over-represented among the freshwater invaders in North America (and around the World), and predators are disproportionately under-represented compared to the native fauna (Table 2). This may indicate that suspension feeders are much more likely to become established in new waterbodies than predators or representatives of other feeding types. Olenin and Daunys (2005) found that suspension-feeders comprise 61–72% of invaders in European brackish and marine environments in the Baltic, Black, Caspian and North Seas. Species with broad, generalized diets such as suspension feeders, which feed on a wide range of microalgae, suspended organic matter and even small zooplankton, are more likely to be successful in new environments, and may even be facilitated by low to moderate levels of eutrophication, which increase local production but do not result in oxygen depletion.

Although freshwater macroinvertebrates in Europe and North America are dominated by insects, there

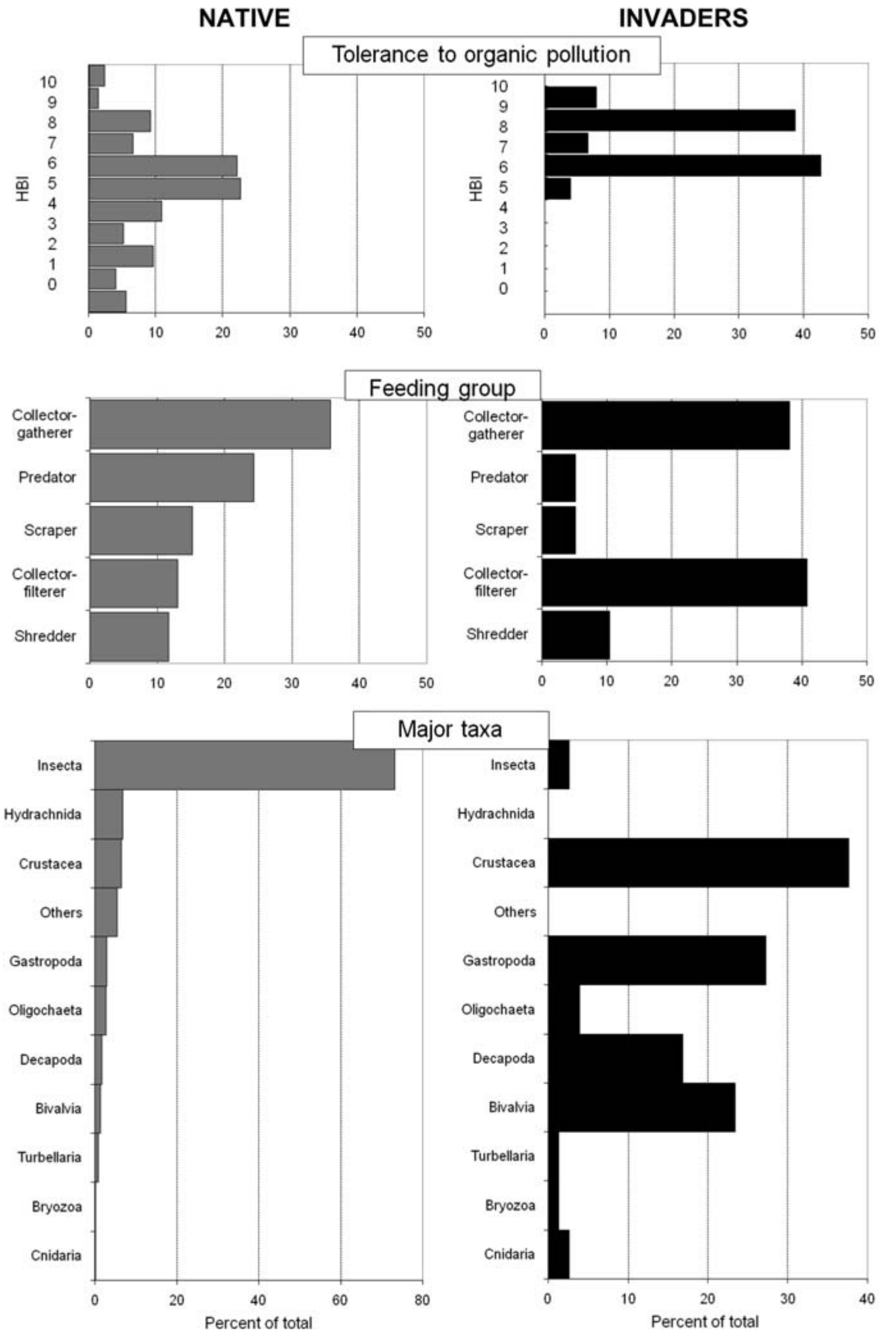

**Fig. 1** The frequency distributions of native species and invaders in North America by sensitivity to pollution (*upper graphs*), feeding groups (*middle*) and major taxa (*lower graphs*). Species are rated in terms of their tolerance to organic pollution based on the Hilsenhoff Biotic Index (Hilsenhoff 1987) on a scale of 0–10 (0 = species requiring excellent water quality, 10 = species that can survive severe organic pollution); tolerance ratings are from Mandaville (2002). Feeding groups are based on Merritt and Cummins (1996) (Mandaville 2002). Most species of freshwater macroinvertebrates are grouped by phylum, except for the molluscs, annelids and arthropods, which are grouped by class. Several phyla that do not have freshwater invaders in North America (e.g., Nematoda, Rotifera, Porifera, Polychaeta, Gastrotricha) are lumped in "Others". Data are presented for both all Crustacea (including the Decapoda) and separately for just the Decapoda

are extremely few aquatic insect invaders. This is especially surprising because aquatic insects often have an aerial adult stage that disperses, and are among the first to recolonize disturbed waterbodies (reviewed in Hershey and Lamberti 2001). Moreover, introduced insects are very common in terrestrial systems (e.g., Pellizzari and Dalla Monta 1997; Brockerhoff et al. 2006; Causton et al. 2006). Also, many species of insects are capable of living in very poor water quality and, therefore, pollution alone can not be responsible for the lack of insects among freshwater invaders.

Several hypotheses could be invoked to explain the paucity of insects among freshwater invaders, including: (1) saturated niches due to the high diversity of insects in native communities, (2) the need to match both the aquatic and terrestrial environments for completion of their life history, (3) reproductive limitations due to an aerial adult stage, 4) vector limitations.

Many of the most notable aquatic invaders are those that occupy relatively novel ecological niches (Karatayev et al. 2007). Byssate bivalves are extremely uncommon in freshwaters, except for the invaders *Dreissena polymorpha* and *D. rostriformis bugensis.* Similarly tube-dwelling amphipods, like the invader *Chelicorophium curvispinum*, are rare. Thus, these species that represent novel ecological types will compete with relatively few native species, and may escape from specialized predators or parasites. A typical lake or a stream may have over a hundred species of insects of all types (Hershey and Lamberti 2001), leaving relatively few unoccupied niches. If a new species of insect is introduced into a waterbody, it will have to compete with many similar native species, and most niches may already be saturated. In addition, any introduced insect is likely to face local predators. The biotic resistance hypothesis by Elton (1958) indicates that communities with high diversity are likely to be less susceptible to invasion because all resources (and thus niches) in such communities are utilized to a much greater extent than in systems with low species diversity. However, recent studies testing this hypothesis provide contradictory results, with some showing positive correlations between native community diversity and invasion success, while others showing negative correlations (reviewed in Moyle and Light 1996; Williamson 1996; Levine and D'Antonio 1999; Mack et al. 2000; Wonham 2006; Zaiko et al. 2007). An important factor for community invasiveness might be not simply the total amount of species present, but the amount of functionally similar species (Fargione et al. 2003) or same genera in the recipient community (Ricciardi and Atkinson 2004).

Most aquatic invaders complete their lifecycle in the water and do not have a terrestrial or aerial phase, as is common for insects (Thorp and Covich 2001). For an aquatic insect to be a successful invader, it will need to occupy not only a suitable aquatic environment, but also a suitable terrestrial one. This may pose a constraint on some potential insect invaders. In addition, those species that emerge as adults from the aquatic habitat must fly to find a mate. This requires synchronized emergence and densities high enough to ensure adequate reproduction to sustain a population. In contrast, organisms that spend their entire life in the water may require smaller inoculation sizes for successful colonization. For example, the invasive bivalve *Corbicula fluminea* reproduces parthenogeneticaly, and therefore a single individual can start a new population (Lee et al. 2005).

The typical vectors for spreading freshwater invaders include: ballast water for large freshwater ports such as the Great Lakes, ship and barge fouling in commercial waterways, pet, aquarium and ornamental trade, freshwater aquaculture, live food, trailered boat traffic, and scientific research. These vectors may be less likely to transport insects than other taxa. At present there is no commercial food, aquaculture, pet, aquarium or ornamental trade in insects. However, insects could be moved incidentally with some of these vectors. Although some insects could be in the sediments of ballast tanks, insect larvae would not be able to reproduce within these tanks. Also, few insects have long-term resting stages, as are seen in copepods and cladocerans, and thus may be unlikely to be transported in large numbers with sediment. Bailey et al. (2005) found resting stages solely for rotifers and cladocerans when they sampled the residual sediments from the ballast tanks of 39 transoceanic ships entering the Great Lakes. To date, no insects have been found among active invertebrates inhabiting ballast tank residual sediments or ballast water (Duggan et al. 2006). We do not know which factor or, more likely, combinations of factors are responsible for the lack of insects among freshwater invaders. However, this surprising result clearly calls for future study.

Contrasting with the disproportionately low number of insect invaders, some taxa are disproportionately over-represented, including some species poor taxa, such as Cnidaria (Table 3; Fig. 1). Bivalves and gastropods are also over-represented relative to their native diversity, comprising over 50% of the invaders in North America and 20% in Europe. At present, 46% of all decapods in Europe are introduced species. The ongoing spread of introduced species is likely to continue to have a very different effect on different taxonomic and feeding groups, and, thus, may cause a serious shift in the biodiversity of selected taxa and impact ecosystem functions.

As has been suggested in the past, there is a series of barriers that a species needs to pass to become a successful invader, including geographic and physiological barriers as well as biotic resistance in the recipient community. Our data indicate that water quality, feeding habit, and taxon diversity are particularly important barriers for freshwater macroinvertebrates (Fig. 1). Declines in water quality may make a habitat more vulnerable to invaders while decreasing local diversity, but invaders will not colonize the most polluted waters. Feeding habit requirements may promote the invasion of invertebrate suspension feeders and limit predators (Fig. 1). This result is opposite to findings for freshwater fish invaders, which are dominated by predators and omnivore/detritivores (Moyle and Light 1996). This difference could result from the fact that most of the invertebrate invaders were unintentionally introduced, while many fish invaders were deliberately introduced, especially for aquaculture and fisheries (Casal 2006).

## Conclusion

Freshwater macroinvertebrate invaders are not a random selection of species, and are over-represented by molluscs and crustaceans. Freshwater macroinvertebrate invaders are tolerant of at least moderate levels of organic pollution, and are dominated by species with feeding modes different than those of most native species. Native freshwater macroinvertebrate communities are dominated by insects, have different major feeding modes than invaders, and include species intolerant to even low organic pollution and require excellent or very good water quality. The ongoing spread of invaders could be facilitated by moderate water pollution, which may reduce freshwater biodiversity due to the extirpation of local species that require high water quality. The high percentage of suspension feeders among nonindigenous species, many of which are usually found in extremely high densities (e.g. Karatayev et al. 2007), can shift the trophic structure of native invertebrates and increase the benthic-pelagic coupling, resulting in dramatic impacts on the entire ecosystems they invade. Because these processes are very similar in Europe and North America, we suggest that the observed patterns may have a common global effect. Predicting future invaders and determining the characteristics of good invaders remains a major focus of invasion biology. The results of our study reveal important patterns about the types of organisms that have been the most successful invaders, and thus are likely to be the groups of most successful future invaders. Understanding the mechanisms driving these patterns among invaders is essential for developing a predictive science.

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