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INVASIVE SPECIES

Aquatic invasive species: general trends in the literature and introduction to the special issue

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Abstract Invasion rates are increasing worldwide and most are due to the actions of humans. Deliberate introductions, escapes, and hitchhiking with global commerce transport species to other continents. While most species fail to thrive or have minor impacts on their new ecosystems, the large number of introductions has led to numerous problems. Aquatic invasive species are particularly pervasive and may cause food web disruption, biodiversity loss, and economic harm. Biological invasions appear in an increasing number of publications in the aquatic and general ecology literature. This special issue of *Hydrobiologia* includes 31 papers on aquatic invasive species and the factors that influence their dispersal and success, along with their impacts. Ecosystems include freshwater ponds, lakes and reservoirs, small streams and large rivers, and coastal marine systems. Study regions occur in temperate, as well as less-studied tropical and sub-tropical regions of four different continents. We discuss the dynamics of invasive species research in the current literature and provide a brief overview of the contributions to this issue.

Keywords Invasion biology · Invasive species · Species introductions

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Introduction

Species introduced outside their native ranges have attracted the attention of naturalists and scientists since the 18th century and preeminent scientists like Charles Darwin, Alfred Russel Wallace, and Alphonse de Candolle devoted attention to this problem (Chew, 2011). Despite the early attention to invasive species given by these scientists, invasion biology came to be a field only after a book published in 1958 by Charles Elton, "The Ecology of Invasions by Animals and Plants." The field grew very quickly after 1990 (Ricciardi & MacIsaac, 2008; Richardson & Pyšek, 2008; Davis, 2011), and has currently achieved numerous break-throughs in both theoretical and practical aspects (Simberloff & Vitule, 2014).

Invasion rates are going up due to globalization and increased trade among countries, and the concerns about invasive species come mainly from their impacts at several levels. First, dominant invasive species impact native species to a greater degree than dominant native species do, and this is true with both terrestrial and aquatic ecosystems (Paolucci et al., 2013). Second, impacts may propagate to higher trophic levels and entire communities or even ecosystems may change completely in response to invasions (Strayer, 2012; Simberloff et al., 2013). Third, invasive species can cause tremendous economic impacts (Pimentel et al., 2005; Perrings, 2011) and human health can also be affected (Bol, 2011).

Invasions have likely greater impacts on aquatic than terrestrial ecosystems. For example, biotic exchanges (invasive species) are predicted to be the most important driver of biodiversity decrease in lakes and the third most important driver in streams (after land use and climate) for the year 2100 (Sala et al., 2000). This outcome could be dramatic because freshwater ecosystems have the greatest concentration of species per surface area in the planet (Dudgeon et al., 2006). In general, the biota of aquatic ecosystems has been more affected by humans than their terrestrial counterparts. The Living Planet Index, based on monitoring of animal populations, declined 76% between 1970 and 2010 in freshwater ecosystems, but this decrease was only 39% in marine and terrestrial ecosystems (WWF, 2014). These data suggest an urgency to investigations on aquatic invasive species (AIS) success and their consequences on native communities and ecosystems, especially in freshwater ecosystems.

The present *Hydrobiologia* Special issue (SI) brings 31 papers (not including this preface) dealing with a variety of aquatic invasive species (AIS), from a variety of ecosystems and regions. We include as invasive any species that are alien, have a high capacity to establish and spread, and cause real or potential impacts on native communities, ecosystems, and/or economic losses. In this preface, we first make a general systematic review of the literature about invasions to describe the current state of invasion biology, especially as it applies to aquatic ecosystems. Then, we summarize the contributions of all papers published in this SI. The papers published in this SI will contribute to a better comprehension of the causes of success and impacts of invasive species in aquatic ecosystems, and we hope that these papers serve as a stimulus for new generations of aquatic scientists to investigate this challenging area that embraces the fields of ecology, biogeography, evolution, and management.

Trends in the literature on aquatic invasive species

Methods

We investigated invasion biology as a growing field in aquatic sciences, following the general trend of increasing the number of publications on invasive species over time (e.g., Lowry et al., 2013). To do so, we searched in the Web of Science (WoS) in October 2014 the number of papers published per year in the journals *Hydrobiologia*, *Freshwater Biology*, and *Limnology and Oceanography*, using the combination of words/terms in the WoS topic: invasi* or exotic* or non native* or non-native*. We chose these three journals because they are well established in the field of aquatic sciences, because they fulfill international criteria by publishing papers from a broad range of countries and continents, and because they reach a broad audience. In order to check whether studies on AIS are following the temporal trend observed in studies about invasive species in the general ecology, we compared the number of publications in these aquatic journals over time with the number of studies on invasives published in leading general ecology journals (*Ecology*, *Oikos*, *Oecologia*, *Ecology Letters*, *Trends in Ecology & Evolution*, *Journal of Ecology*, and *Journal of Animal Ecology*). Our search in these ecology journals used the same words/terms in the WoS Topic. The number of papers retrieved using these words/terms were divided by the total number of papers published in the aquatic science and general ecology journals and expressed as percentages.

We also tested whether aquatic scientists studying invasive species are delivering their research in the above-mentioned general ecology journals and investigated the proportion of papers dealing with AIS in these journals, in comparison with their terrestrial counterparts. The percentage of papers about AIS in ecology journals would indicate whether investigations about AIS are currently being conducted in such a way to reach a broad audience in ecology. Because we were interested in the current scenario, we searched for the number of papers published in 2013 using the same terms (invasi* or exotic* or non native* or non-native*).

Finally, we checked whether aquatic scientists working with invasive species are publishing at the same rate as terrestrial scientists in leading journals of the field. To do so, we surveyed all papers published in 2013 in the journals *Biological Invasions* and *Diversity and Distributions*. We chose these journals because they are traditional and have primary focus on invasions (Davis, 2011). Because *Diversity and Distributions* publishes also in other areas, we used only papers that were chosen for the topic that included the words/terms invasi* or exotic* or non native* or non-native* in this journal.

The papers found using the above criteria in the general ecology journals and in the leading invasion biology journals were categorized in freshwater, marine, and terrestrial ecosystems, and in a fourth category including theoretical, meta-analytical, and review papers. The separation was based on the title, abstract, or the entire paper whenever necessary.

Results

Our survey showed a fast increase in the percentage of papers on AIS published after 1990 in both aquatic and general ecology journals (Fig. 1). Few papers were

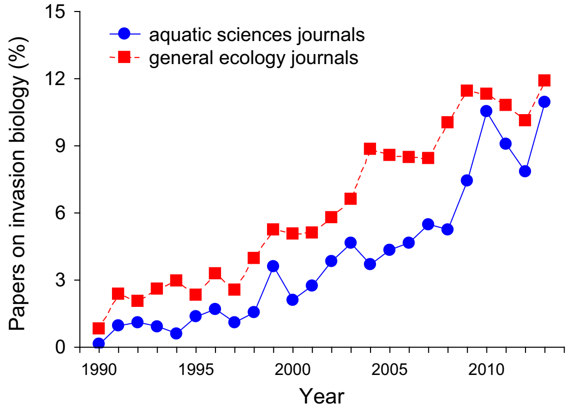

Fig. 1 Temporal trend in the proportion of articles on AIS (of the total number of papers published) in aquatic science (*Hydrobiologia*, *Freshwater Biology*, and *Limnology and Oceanography*) and in general ecology journals (*Ecology*, *Oikos*, *Oecologia*, *Ecology Letters*, *Trends in Ecology & Evolution*, *Journal of Ecology,* and *Journal of Animal Ecology*). Data retrieved from the Web of Science (Thomson Reuters)

published between 1960 and 1989: 34 papers in the general ecology journals and four in the aquatic sciences journals. The highest number of publications were reached for both groups of journals in 2013: 10.9% for aquatic science journals and 11.8% for general ecology journals (Fig. 1).

A total of 169 papers on invasive species were published in leading ecology journals in the year 2013. Terrestrial invaders dominated the survey (59.8% of the total), followed by freshwater (13.0%) and marine (9.5%) organisms. Theoretical, meta-analytical, and review papers were 17.7% of the total.

We found 263 papers published in the leading invasion biology journals (*Biological Invasions* and *Diversity and Distributions*) in 2013. Terrestrial organisms received the most attention (62.1% of the papers), followed by freshwater (19.5%) and marine (14.9%) organisms. Theoretical and review papers represented 3.5% of the total.

Discussion

Our temporal analyses using selected journals in general ecology and in aquatic sciences indicated that aquatic scientists are paralleling the trend found in general ecology journals in regard to the interest in non-native species. We found an increasing number of publications on invasive species after 1990, as has been reported by others (Richardson & Pyšek, 2008; Davis, 2011; Lowry et al., 2013). Interestingly, all these surveys (including ours) show that there was a time lag between the influential book by Elton, in 1958, and the growth of the invasion biology, which started in the mid 1980s. Some of this growth in attention may be related to the increasing prevalence of invasive species (Richardson & Pyšek, 2008) and to two international initiatives: the scientific committee on problems of the environment (SCOPE) (Davis, 2011) and the Convention on Biological Diversity, signed by 150 government leaders at the 1992 Rio Earth Summit. The increasing number of investigations in aquatic ecosystems is related mainly to species that have caused severe ecological and economic damages, such as common carp, brown trout, tilapia, and zebra mussels (MacIsaac et al., 2011).

Our review also showed that studies about freshwater and marine ecosystems and organisms are underrepresented in leading general journals of ecology as well as in leading journals of invasion biology.

This over-representation of terrestrial, compared to aquatic organisms, has also been found in other large systematic literature reviews about invasions (Jeschke et al., 2012; Lowry et al., 2013), and it represents a general trend in several other fields of ecology. For example, the number of articles on the biodiversity-ecosystem functioning research (Caliman et al., 2010) and studies about biodiversity in general (Siqueira et al., 2015) are also higher for terrestrial than for aquatic ecosystems. Thus, it seems that ecologists should still allocate more efforts to comprehend the structure and functioning of aquatic ecosystems (including the causes and consequences of AIS). This "ecosystem bias" may override more general concepts that could be applied for both terrestrial and aquatic ecosystems. At the same time, increasing scientific efforts on AIS would be also important to understand if there are differences in the mechanisms controlling invasions between the two realms, and if so to which extent they differ.

In summary, our literature survey suggests that the number of papers about AIS in aquatic scientific journals is growing at similar rates than those published in general ecology journals; however, the studies about AIS are underrepresented in leading journals of ecology and invasion biology. We contended that the latter findings reflect a current view, since we relied only on articles produced in the year 2013. Even so, this analysis suggests that aquatic ecologists should devote more efforts to put their findings within a broader context and thus, contribute theoretical advances to the field of invasion biology.

Main findings shown in this special issue

The articles of this special issue of *Hydrobiologia* focus on a variety of topics and groups of organisms (Table 1). In addition to reviews encompassing broad aspects on AIS, the primary research papers investigated pathways and vectors of primary introduction and secondary release, dispersal mechanisms, propagule pressure, species invasiveness, ecosystems invasibility, ecological impacts, and management. Some papers investigated more than one topic. Groups of organisms include microbes, macro- and micro-invertebrates, macrophytes, and fish. Most of these investigations were conducted in freshwater ecosystems, while one investigated marine organisms.

Table 1 Main topics and organisms investigated in the 31 papers of this special issue of *Hydrobiologia*

Topics	Organisms	Authors
Review papers		
Invasibility (abiotic and biotic resistance) and impacts	Microbes (bacteria)	Amalfitano et al.
Mechanisms that mediate invasion success	Macrophytes	Fleming & Dibble
Mechanisms that mediate invasion success and impacts caused by invasive species	Macrophytes	Thomaz et al.
Introduction pathways, distribution, and impacts	Macrophytes	Brundu
Impacts	Bivalvia (*Limnoperna fortunei*)	Boltovskoy & Correa
Spread and impacts	Bivalvia (*Dreissena polymorpha* and *D. rostriformis bugensis*)	Karatayev et al.
Primary research papers		
Vectors and dispersal potential	Macrophytes (*Myriophyllum spicatum* and *Potamogeton crispus*)	Bruckerhoff et al.
	Macrophytes (*Cabomba caroliniana*)	Bickel
Dispersal potential	Crustacea (*Procambarus clarkii*)	Ramalho & Anastácio
Introduction pathways	Fish (several species)	Ortega et al.
Effects of abiotic medium on invasion success	Macrophytes (*Alternanthera philoxeroides*)	Fan et al.
	Macrophytes (*Myriophyllum heterophyllum*)	Hussner & Jahns
	Crustacea (*Orconectes rusticus*) and Gastropoda (*Cipangopaludina chinensis* and *Viviparus georgianus*)	Latzka et al.
Effects of biotic interactions on invasion success	Macrophytes (*Ludwigia grandiflora* and *Myriophyllum aquaticum*)	Thiébaut & Martinez
	Fish (several species)	Strictar-Pereira et al.
	Fish (several species)	Ondračková et al.

Table 1 continued

Topics	Organisms	Authors
Effects of biotic interactions and habitat complexity on invasion success	Crustacea (*Pontogammarus robustoides*)	Jermacz et al.
Ecological impacts	Crustacea (*Dikerogammarus villosus*) and Bivalvia (*Dreissena polymorpha*)	Gergs & Rothhaupt
	Crustacea (*Pacifastacus leniusculus*)	Kerby & Sih
	Fish (*Cichla kelberi*)	Pelicice et al.
	Macrophytes (*Hydrilla verticillata*)	Figueiredo et al.
	Fish (*Cyprinus carpio* and *Oreochromis aureus*)	Córdova-Tapia et al.
	Fish (*Cyprinus carpio*)	Bajer & Sorensen
	Amphibian (*Lithobates catesbeiana*) and fish (*Gambusia affinis*)	Hale et al.
	Fish (several species)	Daga et al.
Propagule pressure, vectors, and risk maps	Crustacea (several species)	Crafton
	Invertebrates and fish (several species)	Bobeldyk et al.
Abiotic resistance to invasion and impacts	Gastropoda (*Potamopyrgus antipodarum*)	Bennet et al.
Propagule pressure, abiotic resistance to invasion and ecological impacts	Fish (*Geophagus proximus*)	Gois et al.
Abiotic resistance to invasion and invasive life history	Fish (*Hemiodus orthonops*)	Agostinho et al.
Management	Fish (*Osmerus mordax*)	Gaeta et al.

These articles also represent a variety of ecosystems and geographical regions. The studies presented here addressed rivers, lakes, ponds, floodplains, and streams, and both observational and experimental studies were conducted. Ecosystems studied included those in South and North America, Asia, and Europe. Nine of the studies came from tropical and subtropical regions. Since most studies of invasive species come from temperate ecosystems (Pyšek et al., 2008), this SI will also contribute to reducing the biogeographical bias on our understanding of the ecology of invasions. We summarize below the main findings of the papers published in this SI.

Literature reviews

The environmental factors and ecological mechanisms that mediate invasion, along with potential impacts caused by microorganisms (especially bacteria), are discussed in a review by Amalfitano et al. (2015). Their article presents the main hypotheses in ecology and biological invasions that have been applied to microorganisms. Amalfitano et al. discussed niche *versus* neutral theory, the invasion paradox (i.e., negative relations between invasion success and native diversity at fine scale but the opposite at coarse scales), resource fluctuation, and nutrient availability. The authors conclude that changes made by humans (including pollution) may reduce the resistance of natural communities to invasion, and that invasions by microorganisms could cause important effects on the ecosystem functioning.

Three other review articles focused on exotic invasive macrophytes. The mechanisms that allow an invasive macrophyte to succeed, related to the most influential invasion biology hypotheses, were reviewed by Fleming & Dibble (2015). The role of competition for macrophyte success received support in several examples, and allelopathics (novel weapon hypothesis) seem to play an important role in invasion success of macrophytes. In contrast, the enemy release hypothesis is supported only under certain circumstances and invasional meltdown appears to be a poor predictor of success by invasive macrophytes (Fleming & Dibble, 2015). In their review, data are currently insufficient to test for the importance of phylogenetic relatedness (Darwin's Naturalization Hypothesis). Two other mechanisms that explain invasion potential of macrophytes were propagule pressure and fluctuation in resources. The authors also state that functional diversity and phylogenetic diversity, along with redundancy and species diversity, could help predict invasion success and they suggest potential areas for future research with macrophytes.

Thomaz et al. (2015) also reviewed the literature about non-native invasive macrophytes, but they focused mainly on tropical ecosystems. Propagule pressure explains cases of successful invasion in these ecosystems, and factors related to disturbance, resource availability, and biotic resistance indicate that invasibility of these aquatic ecosystems parallels terrestrial ones. The invasion paradox was also found for non-native macrophytes in some tropical aquatic ecosystems. Impacts were identified at the water medium, in populations and communities of several trophic levels, and they are harsher when macrophytes behave as ecosystem engineers. According to Thomaz et al. (2015), effects of invasive macrophytes on ecosystems and on multiple trophic levels are potential areas for further advance. Combining different scientific paradigms (e.g., state shift) with invasion hypotheses would also produce advances in the invasion biology field.

Brundu (2015) reviewed the literature about the introduction pathways, distribution, and main impacts of the invasive macrophyte species in the European and Mediterranean Plant Protection Organization Zone. The means of introduction have been mainly related to horticultural, ornamental gardens, and aquaria activities, although research and phytoremediation have also contributed to introductions of macrophytes. A list of 21 species of alien macrophytes, along with potential ecological and socio-economic impacts of them in the Mediterranean region, is also provided by Brundu (2015). He suggests prevention, together with management (including habitat restoration) as strategies to avoid threats by these plants.

Boltovskoy & Correa (2015) made an extensive survey on the ecological impacts of the golden mussel *Limnoperna fortunei* in South America. Their survey suggests that this bivalve stimulates growth of periphyton and macrophytes, by changing nutrient concentrations and reducing organic particles in water, and favors the dominance by cyanobacteria. However, *L. fortunei* enhances the abundance and diversity of invertebrates, and their larvae have been used as food by many native fish species. Boltovskoy & Correa (2015) conclude that there are differences between the impacts of *L. fortunei* in South-American and other continent ecosystems and, most importantly, ecosystem-level impacts of this bivalve are still poorly known in South America.

The spread, dynamics, and impacts caused by the bivalves *Dreissena polymorpha* (zebra mussel) and *D. rostriformis bugensis* (quagga mussel) were the focus of the review by Karatayev et al. (2015). The number of water bodies invaded by zebra mussels in the US far exceeds the ones invaded by quagga mussels. Zebra mussels combine rapid colonization of new areas with rapid population increase to damaging levels, giving them the potential to more rapidly impact ecosystems than do quagga mussels. Nevertheless, the overall effects of dreissenids are complex. The impacts of each invasive mussel depend on the lake morphometry and water mixing rates. The diversity and abundance of native invertebrates increase in response to habitat and food provided by these invasive species in the littoral zone, but competition of quagga mussel for space and food reduces native diversity and abundance of macroinvertebrates in the profundal zone (Karatayev et al., 2015).

Primary research papers

Propagule pressure, vectors, and spread

Two studies about invasion vectors investigated the effects of desiccation on survival of macrophyte propagules, simulating the effects of recreational boat movement on macrophyte invasions. In a series of five field experiments conducted in northern Wisconsin USA under mild summer conditions (13–23°C), Bruckerhoff et al. (2015) showed that the widespread nuisance exotics Eurasian water-milfoil (*Myriophyllum spicatum*) and curly leaf pondweed (*Potamogeton crispus*) survive less than a day as single fragments but up to three days as clumps (*M. spicatum*). Typical boaters in this region visit multiple lakes within a couple of days, suggesting that these common weeds can be readily transported and colonize new ecosystems. Furthermore, vegetative buds of *P. crispus* successfully sprout after 28 days of drying, suggesting that these abundant propagules (produced in midsummer) are particularly potent as dispersal stages (Bruckerhoff et al., 2015). In another experimental manipulation, conducted in Australia, Bickel (2015) assessed the effects of air exposure on *Cabomba caroliniana* regeneration and the influence of temperature, shade, clumping, and humidity on this response. He showed that cabomba is resistant to short periods of drying, and that survivorship of propagules decreases mainly with increased wind speed, higher temperature, and low humidity, and survivorship increases when fragments are transported in clumps, when they survive up to 42 h. Increasing fragment mass loss decreased the potential to regenerate healthy plants and thus, it reduces the potential of new invasions. Both studies show that vegetative propagules (fragments) of submersed macrophytes are still able to sprout after relatively long periods of air exposure. Boating activities represent an important target for management actions to prevent spread of invasive macrophytes.

The factors affecting overland dispersal of the crayfish *Procambarus clarkii* were investigated by Ramalho & Anastácio (2015) in Portuguese rice fields. They found a predominance of mature individuals dispersing overland. Dispersal occurred mainly when rice fields became shallow due to drainage. Dispersal rates were positively correlated with rainfall (in afternoon periods) and high humidity, dew, or fog (during sunrise and morning). These findings have great potential in strategies to reduce invasion rates by this invertebrate.

A large-spatial-scale investigation on pathways of fish introductions in Neotropical reservoirs was conducted by Ortega et al. (2015). These authors evaluated the importance of different pathways using data from 57 reservoirs in Brazil. Among the 71 species introduced, cichlids predominated and tilapias were identified in approximately 50% of the reservoirs. Fish farming is the most important pathway of introduction in these Neotropical reservoirs. Fish stocking and the constructions of reservoirs, which eliminate natural barriers, such as waterfalls, are also important pathways. Despite the fact that stocking programs with non-native species should have been abandoned in Brazil, fish farming using non-native species is expanding. The authors recommend efforts to develop safer techniques to avoid accidental releases and more sustainable practices when rearing fish.

Invasibility

The study of invasibility is the area of invasion biology that seeks to comprehend what makes some ecosystems more prone to invasion than the others and is described as the "susceptibility of biological communities to colonization and dominance by introduced organisms" (Fridley, 2011). The degree of invasibility of an ecosystem by AIS is related to several abiotic factors, such as water and sediment physico-chemistry, hydrological regime, and nutrient supply. Herbivores, competitors, predators, and pathogens also play a role as biotic filters to invasions. Eight papers addressed the effects of abiotic and biotic factors on AIS success.

The macrophyte *Alternanthera philoxeroides* is an invasive plant threatening several habitats in China. The survival and growth of this species in response to submergence was tested by Fan et al. (2015). They showed that this species is very resistant to submergence and that this feature may be one of the reasons for its success in habitats heavily disturbed by floods. Another experiment, carried out by Hussner & Jahns (2015) in Germany, evaluated the effects of light, temperature, and carbon availability on the invasive species *Myriophyllum heterophyllum*, and compared it with the European native *M. spicatum*. They showed that the native species attains better use of bicarbonate and has higher growth rates than the invasive species under low CO_2 availability. Thus, the use of bicarbonate cannot explain the invasion success of *M. heterophyllum*. The authors infer that other biological factors, such as remaining evergreen and production of aerial leaves may be involved in the success of this invasive species of European lakes. A third paper about macrophytes investigated survival and colonization of two non-native species (*Ludwigia grandiflora* and *Myriophyllum aquaticum*) in France, and how these invasive species interact (Thiébaut & Martinez, 2015). Two main conclusions emerged from this investigation: (i) the presence of macrophyte beds may reduce the establishment success of *L. grandiflora* fragments; and (ii) *L. grandiflora* facilitates the growth of *M. aquaticum*. This last finding indicates that further invasions by macrophytes may be enhanced by the presence of a previous non-native species of macrophyte. These three investigations on macrophytes show that abiotic and biotic factors, including interactions between invasive species, are important determinants of successful plant invasions in freshwater ecosystems.

The habitat characteristics affecting invasions were also studied for invertebrates. Latzka et al. (2015) modeled the potential of lakes of Wisconsin USA to be invaded by three calcifying AIS: rusty crayfish (*Orconectes rusticus*) and two viviparid snails (*Cipangopaludina chinensis* and *Viviparus georgianus*). Calcification variables were the most important factors to explain distribution of the first two species, whereas the use of saturation state did not improve the predictive models. One very useful conclusion from this study is that measurements of conductivity, which is widely reported, can be used in place of calcium saturation state in distribution models of these AIS.

Jermacz et al. (2015) report on experiments conducted in Poland testing the choice of different types of habitats (including mineral, artificial, and natural plants) by the gammarid amphipod *Pontogammarus robustoides.* Both juveniles and adult gammarids preferred more complex habitats, but the type of preferred substrata varied between them: juveniles chose natural plants over artificial ones and mineral habitats, while adults preferred mineral materials (mainly large particles). These differences in habitat choice were interpreted as a means to reduce competition and cannibalism. These two examples show that water chemistry, along with habitat physical features, may influence the success of invasive aquatic invertebrates.

Two papers report on invasibility of fish communities. Strictar-Pereira et al. (2015) evaluated whether intra-guild predation among native and non-native piscivorous fish may facilitate other fish invasions. Based on the diet of 12 fish species, obtained during eight years sampling 36 sites in a Brazilian floodplain, the authors analyzed whether the consumption of invasive species on their competitors were higher than those of the native species. The authors concluded that the consumption of piscivorous fish by invasive fish species can be considered a mechanism that explains their success and persistence in a new environment. Ondračková et al. (2015) investigated the metazoan parasites of several goby species from Germany. They showed that parasite abundance and richness were lower in the introduced range than in the native range of the gobies. Parasite abundance and richness increased with the increasing time of host introduction, and parasite abundance increased with fish size. They conclude that length of co-occurrence, foraging preferences, host habitat, and the presence of intermediate hosts are important variables to explain parasitism in the new range of these goby species. In addition, the advantage that an invasive species attains with enemy release seems to be higher in the early stages of invasion. Both studies are good examples of the importance of biotic interactions to explain non-native fish success.

Impacts

The impacts of AIS were addressed in eight articles, including invasive invertebrates, fish, and frogs. The impacts of the invasive amphipod *Dikerogammarus villosus* and the zebra mussel *D. polymorpha* on the benthic community were investigated in Lake Constance (Germany) by Gergs & Rothhaupt (2015). These authors showed that the two invasive species (together with macrophyte *Chara* spp. abundance) explained most of the native benthic community composition. While the abundance of most invertebrates increased with zebra mussel, their abundance decreased with increases of the amphipod. Thus, both species change benthic communities but the latter seems to be more detrimental to other benthic invertebrates. Kerby & Sih (2015) examined the effects of an invasive predator (the crayfish *Pacifastacus leniusculus*) and the insecticide carbaryl on native tadpoles of a threatened frog (*Rana boylii*). Curiously, the crayfish ate far more native tadpoles when the pesticide was present than when the pesticide was absent. Independently, the stressors did not cause significant mortality for the tadpoles, but when combined the survival of the tadpoles was greatly reduced.

Pelicice et al. (2015) conducted one of the first studies that investigated the role played by the voracious non-native fish *Cichla kelberi* in disrupting resident fish communities in a Brazilian reservoir. In a previous paper, the authors had described a sudden reduction in fish population size that followed this invasion (Pelicice & Agostinho, 2009), and with the present study they offer evidence supporting the thesis that this predator, and not environmental variation, was the driver behind the collapse. In addition, Pelicice et al. (2015) provide evidence that *C. kelberi* affects the resident fauna by a pulse of young fish during warm months. In an experimental study conducted in Brazil, Figueiredo et al. (2015) investigated whether a native fish prey (*Serrapinnus notomela*) chose a native (*Egeria najas*) or an invasive (*Hydrilla verticillata*) macrophyte as refuge when it faced an invasive voracious predator (the peacock bass *C. kelberi*). Native prey did not show preference for one macrophyte over the other as a refuge, while in the presence of the invasive predator or of its chemical cues. Thus, refuge choice appears to be more affected by habitat structure per se than by the evolutionary history between the fish and macrophytes.

In a study carried out in a Mexican lake, Córdova-Tapia et al. (2015) used carbon and nitrogen stable isotopes to assess the trophic niche overlaps between native and invasive fish species. The trophic niche of two invasive species (*Cyprinus carpio* and *Oreochromis aureus*) had a high overlap with the niche of native fish species, suggesting that competition for food might explain the decline of native species in this lake. The impacts of carp (*C. carpio*) were also studied by Bajer & Sorensen (2015), who examined the effects of carp removal on limnological and biotic variables in a stratified lake in Minnesota (USA). Reduction in carp density led to an increase in vegetation density and water clarity, along with a decline in chlorophyll and suspended solids, although the effects on water clarity were season dependent. Interestingly, carp removal had no effect on total phosphorus concentration in the water column. Thus, carp removal benefited water clarity and macrophyte assemblages in this lake, showing that recovery of a clear, macrophyte dominated ecosystem is possible if this fish is controlled (Bajer & Sorensen, 2015).

The potential of stock ponds and stream pools to be invaded by bullfrogs (*Lithobates catesbeiana*) and mosquitofish (*Gambusia affinis*), and the potential impacts of these invaders on biota were investigated by Hale et al. (2015). They found a reduction of native invertebrate richness and abundance in at least one invaded pond; however, impacts of invaders on aquatic invertebrates seem to be low if the invader populations are kept at low densities. Thus, determining density threshold above which impacts appear is essential in management of these dryland aquatic habitats.

In another study focusing on impacts of AIS on native fish communities, Daga et al. (2015) used a large temporal and spatial scale dataset in Brazil to show that biotic homogenization caused by fish invasions depends on the scale of analysis. Their most interesting finding was that the mechanisms involved in homogenization include both the arrival of non-native species and the extirpation of native fauna. Homogenization of fish assemblages in reservoirs increases over time and the mechanisms underlying the decrease in beta diversity differ among basins and reservoirs. Thus, the homogenization caused by non-native species, already observed at the global scales, also occurs at smaller spatial scales (in river basins).

Mixing approaches

Two primary research papers focused on the interaction of propagule pressure and vectors with environmental suitability to determine the susceptibility of ecosystems to invasions by AIS (invasibility). Crafton (2015) combined the introduction likelihood and environmental suitability in a model to identify susceptibility to invasion in coastal waters. Using five species of marine crabs, his models show a great overlap between proximity to ports (a good proxy for introduction likelihood) and habitat suitability. One important output of this work was the production of invasion risk maps that indicate regions potentially more prone to new invasions. Introduction hotspots for these species, represented by regions with many ports nearby, include China, Europe, and the US Gulf Coast. In another paper, Bobeldyk et al. (2015) used a large database to determine which regions are more invaded (hotspots of invasions) by invertebrates and fish in the US. A clear spatial pattern of invasions was found: freshwater invertebrates invade to a greater extent in the Laurentian Great lakes region, while fish invasions are more concentrated in Florida and the Southwest. The means of introduction also differed: ballast water was the main vector for invertebrates, whereas stocking, aquaculture, and aquarium release were the main pathways for fish. The authors suggest that propagule pressure, associated with vectors, along with ecosystemśs properties (e.g., habitat diversity), are important factors that explain the distribution invasion hotspots in the US.

Bennett et al. (2015) used field observations and laboratory experiments to examine the impacts of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) on native species in California, USA. The mud snail is now invasive on four continents and is of great management concern. Bennett et al. found that the invasive snail impacted native algae and invertebrate communities. The altered algal communities also led to negative impacts on native amphibians. They also found that high stream flow, high temperatures, and drought reduced mud snail densities and that streams with unregulated stream flow will likely see reduced impacts from mud snails.

The invasion of the Amazonian fish *Geophagus proximus* was analyzed by Gois et al. (2015) in the Paraná River basin (Brazil). These authors assessed source of fish stock, habitat features that favor invasion (ecosystem invasibility), and impacts of *G. proximus* on a native, phylogenetically related species. Reservoirs located upstream from the floodplain served as propagule sources, and these reservoirs helped the spread of *G. proximus* by increasing water transparency (the main variable that explained its abundance). The increased abundance of the invasive fish coincided with the decrease of a native species with similar feeding and reproductive habits, suggesting that *G. proximus* had impacted at least one native fish species.

A study by Agostinho et al. (2015) described ecological (habitat features—invasibility) and life history aspects (traits increasing invasiveness) that may have favored the invasion process of a fish species (*Hemiodus orthonops*) and its fast proliferation in the Upper Paraná River (Brazil). These authors compared data obtained in native and invaded ranges and concluded that the invasion success of this fish was related to its dispersal ability, favorable environmental conditions in the new habitat (which are similar to those of its native ranges), ability to explore a food resource with high availability, early maturation, and high somatic growth rates. Thus, combining traits of this fish species with habitat characteristics seems to explain its success in the Upper Paraná basin.

Management

One paper in this SI focused on the potential management of native and invasive fish. A long-term study (32 years) was conducted in a northern Wisconsin lake to test methods for eliminating the invasive rainbow smelt (*Osmerus mordax*) (Gaeta et al., 2015). Their study combined extensive seining of the smelt, along with managing populations of predatory game fish (walleye, *Sander vitreus*), to see if walleye could keep the smelt under control once the smelt numbers had been reduced (Gaeta et al., 2015). Walleye management involved improving stock and reducing allowable catches by anglers. Despite observing a consistent decrease of the rainbow smelt population over time, smelt densities quickly recovered after removal efforts (seining) had ceased. The study showed that walleye had a limited predation impacts on the smelt. Clearly, prevention of rainbow smelt invasion of lakes is the best measure to avoid the damaging impacts of this invasive fish. At the same time, regulatory changes of other fisheries may represent a complementary approach to control rainbow smelt abundances in other lakes.

Final remarks

In general, many of the papers published in this volume highlight significant impacts caused by AIS and point toward difficulties in controlling them. Clearly, additional research is needed for new methods of controlling the exotic species that are causing damage to aquatic ecosystems. Nevertheless, prevention of new invasions is the best long-term strategy for avoiding such disruptions in the future. And avoiding the initial introduction of exotic species into new landscapes is particularly important, because when invasive species spread over large areas, their control becomes much more difficult.

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