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INVASIVE SPECIES II

Preface

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Introduction

This special issue of *Hydrobiologia* commemorates the 60th anniversary of the 1958 publication of Charles Elton's book, "The Ecology of Invasions by Animals and Plants." In a brilliant synthesis, Elton described the devastating effects of epidemic diseases, crop and forest pests, and outbreaks of other species that impact natural communities. He focused on invaders from other continents and placed invasions in both biogeographical and ecological contexts. Elton pointed out that the rate of introductions has increased with time and he related that trend to increased transport of people and goods around the world. Indeed, the rate of discovery of exotic species has continued to rise in the years since (Seebens et al., 2015; van Kleunen et al., 2015).

Elton used the analogy of an explosion to describe the sudden outbreak in numbers and described numerous examples of geographic spread, from plague and malaria to starlings and muskrats. He also recognized that, following introduction, a number of invaders simmered for a long time before showing

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rapid increase and spread. Examples of lag between arrival of organisms and their successful spread and establishment, first recognized by Elton, abound in aquatic communities (e.g., Brundu et al., 2013; Yanygina, 2017). Elton was curious about the ecological factors that kept these invaders in check. Ecologists are still curious about these factors. Elton suggested that communities that are disturbed or have lower species richness may be less stable and are at an increased risk of invasion, and we now know that invasion risk can be explained by propagule load (Colautti et al., 2006). Locations that are disturbed often have more visits by humans and greater exposure to the things we carry (Lonsdale, 1999).

Since Elton's time, we have seen numerous new invaders that have drawn the attention of the public. In aquatic environments, zebra mussels and invasive aquatic plants cost billions of dollars in direct damage and control efforts (Pimentel et al., 2005). Ecologists took notice as well. Besides recognizing the importance of applied ecology for understanding and controlling pests, ecologists also realized that invasive species offer an opportunity for studying fundamental ecological questions, such as processes regulating colonization and community assembly (Sax et al., 2011). Elton's (1958) book continues to be a source of inspiration for many of the key questions explored in invasion biology, including those tested in papers of this special issue.

Invasion Biology accelerated as a topic in the scientific literature in the early 1990s, following the launch of the SCOPE Programme on biological invasions and the widespread interest in invasions during this period (Richardson & Pyšek, 2008). *Hydrobiologia* published a small number of papers on aquatic invasive species during the 1990s and early 2000s. [Here, we define invasive species as exotic (non-native) species that persist, reproduce, and spread in the new environment, Havel et al., 2015]. More recently, the number of papers on aquatic invasive species published by *Hydrobiologia* has greatly increased. During the past 10 years (2008–2017), 10.7% of the 4162 published papers in *Hydrobiologia* dealt with them. We co-edited the first special volume on aquatic invasive species published by *Hydrobiologia* in 2015. Since interest has remained high, we invited submissions for this new special issue, Aquatic Invasive Species II.

A total of 36 papers were accepted for publication in this volume and are listed in Table 1, with brief summaries below. We thank the authors for their prompt contributions and all the reviewers for their insightful suggestions for improvements to the papers.

Dispersal and factors regulating introduction

Dispersal and introduction of non-native species outside their native range may be associated with several human activities, and they may be accidental or on purpose. Five papers in the present volume investigated this first step of invasions.

In order to assess the risk of establishing invaders from ballast discharge, Aliff et al. (2018) used the planktonic diatom *Melosira varians* in mesocosm trials, along with logistic growth models, to show an inoculation density of 12 cells/mL would lead to establishing a viable population. They recommend that this risk-release relationship be explored with other model organisms. Avoiding introductions is the best line of defense against aquatic invasive species, and understanding the past introductions gives perspective on how they might be best avoided in the future. Examining several combinations of introduction pathway intensities for aquatic invasive species in the Laurentian Great Lakes, O'Malia et al. (2018) identified city population size as the best predictor of their presence, and this pathway's importance increased over time. Clearly, most invaders are transmitted with and by people.

Unauthorized introductions of non-native fishes are a continuing problem for fisheries managers. Rahel and Smith (2018) reviewed Wyoming, USA agency records over a 57-year period to show that the greatest source of introductions was deliberate illegal release of fish by the public, and pointed to the importance of public education and enforcement to curtail these introductions. Using a literature survey, Gubiani et al. (2018) showed that unauthorized introductions also dominate in Neotropical ecosystems. Most invasive fish species in this region originated from other Neotropical basins, and were introduced through creation of impoundments and stocking of sport fish. Fish from outside the ecoregion were illegally introduced through the aquarium trade and aquaculture. In Brazil, for example, a literature survey from 70 reservoirs recorded 91 non-native species, of which

Table 1 Topics, organisms, and aquatic ecosystems studied in the 36 papers included in this special issue of Hydrobiologia

Topic	Organism	Ecosystem	Author
Dispersal and factors regulating introduction			
Ballast water release risk	Diatom	Mesocosm	Aliff et al.
Relative importance of various introduction vectors	All taxa	Lake (Great Lakes)	O'Malia et al.
Unauthorized releases (and management)	Fish	Freshwaters (any)	Rahel and Smith
Sources of invaders	Fish	Freshwaters (any)	Gubiani et al.
Distribution of non-native species	All taxa	Reservoirs	Pereira et al.
Rapid assessment methods for detecting non-native species	Fish	Lakes and reservoirs	Latini and Petrere
Genetic methods for detecting introduced species			
DNA barcoding to identify cryptic invaders	Bivalves	Estuarine	Fernandes et al.
DNA barcoding to identify cryptic invaders	Fish (larvae)	River	Almeida et al.
Factors influencing colonization and persistence			
The invasion paradox: scale affects association with native species	Fish	River	dos Santos et al.
Ecological niche modeling and invasion resistance	Fish	Reservoir	Cassemiro et al.
Ecological niche modeling and invasion resistance	Fish	Reservoir	Franco et al.
Ecological niche modeling and invasion resistance	Fish	Reservoirs	Ortega et al.
Physical features limiting persistence: light and DOC	Jellyfish	Lab (mimic lake)	Caputo et al.
Physical features limiting persistence: salinity	Macrophyte	Lab (mimic marine)	Thouvenot and Thiébaut
Physical features limiting persistence: nutrients	Macrophyte	Lab	Xie et al.
Invasiveness of exotic plants: effects of DOC and nutrients	Macrophyte	Lab	Xu et al.
Competition with native and effects of nutrient (DIC) levels	Macrophyte	Mesocosm (mimic lake)	Fasoli et al.
Food resources (diet breadth)	Fish	River	Tonella et al.
Population dynamics and parasitism	Snail and trematode	Stream	Gerard et al.
Population dynamics and parasitism	Frog and chytrid fungus	Lab (mimic pond)	Urbina et al.
Predation (including herbivory)	Fish	River	Rodrigues et al.
Predation: turbidity and risk	Fish	Lab (mimic floodplain)	Santos et al.
Predation: trophic cascade (insect parasitoids and herbivores)	Insects and macrophyte	Lab (mimic reservoir)	Martin et al.
Predation: experimental herbivory	Macrophytes	Lab	You et al.
Trophic niche overlap with native species	Fish	River	Lombard et al.
Allelopathic effects of native frog on invasive snail	Amphibians on snails	Lab and stream mesocosm	Ota et al.
Multiple abiotic and biotic factors	Macrophytes	Reservoir mesocosms	Strange et al.
Multiple abiotic and biotic factors	Fish	Stream	Hill and Tuckett
Impacts of invaders			
Community and ecosystem effects (literature review and model)	Fish on macrophytes	Lakes	Bajer et al.
Community and ecosystem effects	Fish on macrophytes	Reservoir mesocosms	Vasconcelos et al.
Effects of Asian carp on population dynamics of gizzard shad	Fish on native fish	River	Love et al.
Community and ecosystem effects: multimetric index	Fish on ecosystem	Streams	Ruaro et al.

Table 1 continued

Topic	Organism	Ecosystem	Author
Community and ecosystem effects	Bivalve on benthic diver	River	Duchini et al.
Community and ecosystem effects	Fish on amphibians	Stream	Velasco et al.
Community and ecosystem impacts (literature review)	Fish	Marine	Arndt et al.
Impacts of invasive species and drought on food web	Fish	Reservoir (tropical, semi-arid)	Bezerra et al.

Ecosystems: lakes (natural lakes and ponds), reservoir, river (includes floodplains and delta), stream (smaller than named rivers), freshwaters (any lake, reservoir, or stream), marine (includes salt marshes and estuaries), lab (laboratory experiment), mesocosm (any in situ enclosure, scaled to size of the organism)

59% were fish (Pereira et al., 2018). Since the number of non-native species is likely underestimated, there is an urgent need to develop more precise approaches for early detection. Latini and Petrere (2018) addressed this sampling issue using a dataset of Neotropical lakes, and showed that rapid assessment protocols can provide accurate estimates of the number of invasive fish species in lakes. They recommend that this cost-effective method be widely employed to quickly detect colonization and spread of non-native fish.

Genetic analysis for detecting introduced species

Accurate species identification is one important step for monitoring invasive species and implementing prevention programs. Molecular tools allow detection of cryptic species. Fernandes et al. (2018) analyzed mtDNA COI gene sequences, together with phylogenetic analyses, to determine genetic distances among estuarine populations from the Brazilian coast of the dreissenid mussel *Mytilopsis*. Interpreting their data with a barcode program suggested discovery of three species, rather than the single species previously reported. Such data can also provide information on possible source regions. Precise and quick detection of aquatic invasive species at all developmental stages and in low numbers is a challenging problem. Almeida et al. (2018) applied a similar DNA barcoding approach to successfully identify non-native species of freshwater ichthyoplankton (fish larvae) in a set of cascading reservoirs.

Factors influencing colonization and persistence

The "invasion paradox" refers to the positive correlation between native and invasive species richness at coarse spatial scales, and the opposite trend at fine spatial scales (Stohlgren et al., 2006; Fridley et al., 2007). This paradox was investigated by dos Santos et al. (2018) with 146 fish communities sampled over 13 years in the Upper Paraná River in Brazil. They showed that non-native fish richness was positively correlated with native richness, and this trend was independent of the spatial scale analyzed. The authors explained their contrary result as influenced by fish mobility and habitat disturbance.

The majority of papers published in this special issue employed field or experimental approaches to explore how invasion success is associated with abiotic and biotic features. Species interactions included predation, parasitism, competition, and allelopathy.

A study conducted in Brazilian reservoirs found that peacock bass abundance was higher in reservoirs that were warmer, less turbid, and with lower water residence time, whereas habitat structure, fish species richness, and time since introduction did not explain much of their abundance (Franco et al., 2018). In a compilation of data for Brazilian reservoirs, Ortega et al. (2018) found that the richness of both native and non-native fish species was positively correlated with temperature and total fish abundance. Interestingly, native fish species richness was negatively correlated with reservoir age, suggesting that as reservoirs age, they gradually lose native fauna. Using ecological niche modeling, Cassemiro et al. (2018) predicted that

Central and South America are more susceptible to invasion by tilapias than is North America. Because the first two areas are more subject to impacts caused by tilapias, management efforts should differ between them and North America.

Combining laboratory and field experiments in Chilean Patagonian lakes, Caputo et al. (2018) assessed the effects of natural solar and artificial UV radiation on the free-living medusae of *Craspedacusta sowerbii*. Because of their high susceptibility to damage from solar radiation, the authors predicted increased invasion success by this freshwater jellyfish with increasing levels of DOC (i.e., lake brownification) in subtropical and temperate lakes.

The effects of abiotic factors and species interactions on invasive macrophyte performance were examined in several papers. A mesocosm experiment by Fasoli et al. (2018) demonstrated that the invasive macrophyte *Hydrilla verticillata* (L.f.) Royle exhibited higher relative growth rates and greater number of branches in response to elevated dissolved inorganic carbon than the native *Egeria najas* Planchon. Such plasticity in growth may contribute to the high competitiveness of *H. verticillata* and ultimately its status as one of the world's most notorious invasive species. Experiments conducted in microcosms with two submerged invasive macrophytes (*Elodea canadensis* Michaux and *Elodea nutallii* (Planch.) H. St. John) showed that they differ in tolerance of salinity changes, though the effects of salinity also depended on season (Thouvenot & Thiébaut, 2018). An important implication of this study is that salt marshes and brackish waters have the potential to be invaded by these two species. Experiments with the invasive *Myriophyllum aquaticum* (Vell.) Verdc. demonstrated that increased nutrients enhanced plant regeneration, which was higher in emergent than in amphibious fragments (Xie et al., 2018). The authors concluded that this difference in fragment regeneration should be taken into account when managing this species. An experiment by Xu et al. (2018) showed that competitive ability of the invasive *Elodea nuttallii* over the Chinese native *H. verticillata* was not enhanced by eutrophication and increased DOC (brownification).

The host–pathogen interaction between the invasive bullfrog *Lithobates catesbeianus* in the western U.S. and the fungal pathogen *Batrachochytrium dendrobatidis* was investigated by Urbina et al. (2018), who found that wild-caught bullfrogs were differentially susceptible to two regionally distinct strains of fungus. These results suggest that the ability of invasive frogs to reduce their infection levels with the time of interaction might increase the magnitude of their ecological impacts, especially if different non-native bullfrog populations continue to be spread.

Experiments on macrophyte–herbivore–parasitoid interactions in South Africa by Martin et al. (2018) showed that the relative competitive abilities of the native macrophyte *Lagarosiphon major* (Ridley) Moss and the invasive macrophyte *Myriophyllum spicatum* L. changed in response to the presence of herbivores or parasitoids. An important implication of these results is that competitive interactions depend on other members of the community. Another study of multi-trophic interactions showed that herbivory on the invasive free-floating *Pistia stratiotes* L. increased the success of the invasive submerged *Egeria densa* Planch, but reduced the success of the native submerged *L. major* (Strange et al., 2018). Thus, biological control employing herbivores may contribute to unintended impacts on other members of the community. Effects of herbivory were studied by You et al. (2018), who simulated different degrees of defoliation in terrestrial and aquatic forms of the invasive macrophyte *Alternanthera philoxeroides* (Mart.) Griseb. Clonal integration reduced the effects of herbivory to a higher degree in the terrestrial than in the aquatic plant form, which explains the low efficacy of biological control in terrestrial habitats.

Factors explaining invasion success of fish were investigated in five papers in the current issue. In a large dataset from 30 years of study in the Upper Paraná basin, Tonella et al. (2018) compared feeding strategies of fishes in the introduced range with their native range. These authors showed that the most successful invaders were either omnivorous ("high trophic plasticity"), piscivorous, and consuming a wide diversity of fish, or else detritivorous with access to abundant food resources. Lombard et al. (2018) studied trophic overlap between invasive largemouth bass (*Micropterus salmoides*) and native omnivorous fish, demonstrating that the invader occupied a subset of the niche space occupied by the native species in South African reservoirs. Rodrigues et al. (2018) used a 26-year dataset to compare one native and one invasive species of piranha in the Upper Paraná River (Brazil) and showed that, despite decreased abundances of the native species, its persistence in the long term is possible because of differences in resource use. Experiments with the invasive peacock bass, tilapia, and channel catfish by Santos et al. (2018) showed that predation from native predators on juveniles of these alien species increased with lower water clarity. The paper suggests that construction of reservoirs and subsequent increase in water clarity may decrease biotic resistance of native predators and serve to enhance invasion success of alien fish. Assessing the effects of temperature, habitat features, and potential control by the native black bass over non-native and indigenous fish species in Florida streams, Hill and Tuckett (2018) found that richness and abundance of non-native ornamental fish species decreased markedly with the distance from aquaculture facilities, while habitat features and biotic resistance of native predators had limited effects on their distribution.

Two papers of this special issue examined dynamics and interactions of the highly invasive New Zealand mud snail (*Potamopyrgus antipodarum* Grey 1853), which has invaded and spread in multiple continents. Using data on abundance and parasite prevalence over a 14-year period in a French stream, Gerard et al. (2018) showed *P. antipodarum* to dominate the mollusk assemblage in most years and to have a low but stable association with a trematode (*Aporocotylid* sp. I) native to this snail's native range. Ota et al. (2018) conducted an experiment in California, where *P. antipodarum* is also invasive. In treatments with tetrodotoxin (a neurotoxin released by the native salamander, *Taricha torosa* Stebbins & McGinnis 2012), *P. antipodarum* moved less than in the control. This result suggests that allelochemicals from the native salamander may offer biotic resistance to this invasive snail.

Impacts of invaders

Impacts of invasive species on native communities and ecosystems have been widely recognized (e.g., Zaret & Paine, 1973; Gallardo et al., 2016; Koester et al., 2016; Ortiz-Sandoval et al., 2017). Eight papers in this special volume examined impacts of aquatic invasive fish species. Bajer et al. (2018) compared density-dependent impacts of invasive common carp (*Cyprinus carpio* Linnaeus, 1758) with a functionally equivalent native species (black bullhead, *Ameiurus melas* Rafinesque, 1820) and showed that the invader had stronger negative effects on macrophyte richness than did the native fish. The planktivorous Asian carps (*Hypophthalmichthys nobilis* Richardson and *H. molitrix* Valenciennes) have reached high densities in the Illinois River, USA, where they compete with native planktivorous fish. Local natural resource agencies have recently encouraged commercial harvest, and Love et al. (2018) showed, using 26 years of population estimates, that gizzard shad (*Dorosoma cepedianum* Lesueur) densities declined after Asian carps were numerous and then rebounded following harvest of the Asian carps. Using surveys conducted in 148 sites in a Patagonian stream, Velasco et al. (2018) found that the occupancy of the amphibians *Pleurodema somuncurense* (Cei, 1969) and *Rhinella arenarum* (Hensel, 1867) was best explained when the presence of invasive trout was included in the models. The negative impact of trout on *P. somuncurense* is of special concern because it is an IUCN Critically Endangered species in Argentina.

As shown by the seminal paper of Zaret and Paine (1973), invasive fish can have far-reaching effects at the community level. Ruaro et al. (2018) investigated impacts of invasive fish in Neotropical streams and found that the abundance of native fish species was explained to a higher degree by abundance of invasive fishes than by urbanization. They proposed including invasive fishes in multimetric indices used to estimate environmental impacts. Two other papers revealed impacts of tilapias in semi-arid Brazilian reservoirs. Using mesocosms, Vasconcelos et al. (2018) showed that the tilapia *Oreochromis niloticus* Linnaeus, 1757, negatively affected zooplankton and algae. However, the effects were dependant on the dynamics of algae, with the strongest impacts on rotifers and microalgae during an algal bloom and strongest effects on cladocerans and copepods and on large algae after the algal bloom. In another investigation using food web modeling, Bezerra et al. (2018) showed that drought and increase of invasive detritivores (mainly tilapias) caused a reduction in native species abundances along with changes in nutrient cycling. Thus, in future climate change scenarios, drought may interact with invasive species to worsen aquatic diversity and ecosystem properties.

The bivalve mollusc *Limnoperna fortunei* (Dunker, 1857) is invasive in South America (Boltovskoy et al., 2006). The impacts of *L. fortunei* on benthic communities were investigated experimentally by Duchini et al. (2018), who showed that its presence increases the number and biomass of invertebrates, and that this facilitation is enhanced in treatments subject to predation. Interestingly, comparisons with an experiment conducted a decade ago (Sylvester et al., 2007a, b) suggest that the facilitation has increased over time.

Historically, there has been limited cross-disciplinary exchange between invasion biologists working in freshwater and marine ecosystems. As an exception, Arndt et al. (2018) reviewed numerous studies on the impacts of invasive marine fishes, comparing them with what is known for freshwater ecosystems, and emphasized an urgent need to understand ecological effects of marine fish invaders.

Recent advances since the last volume

Papers in this issue of *Hydrobiologia* advance our understanding of aquatic invasive species, including factors regulating their introduction, methods for identifying cryptic invaders, factors that influence their success at colonizing new populations, and impacts of invaders on native communities. Since many of the papers in this volume were produced with data from tropical regions, this special volume contributes to reducing existing biogeographic bias in the literature. Furthermore, a number of the papers in this issue use long-term datasets, which allow a broader perspective than typical research using short experiments or few years of sampling.

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