

Aquatic invasive species: challenges for the future

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Abstract Humans have effectively transported thousands of species around the globe and, with accelerated trade; the rate of introductions has increased over time. Aquatic ecosystems seem at particular risk from invasive species because of threats to biodiversity and human needs for water resources. Here, we review some known aspects of aquatic invasive species (AIS) and explore several new questions. We describe impacts of AIS, factors limiting their dispersal, and the role that humans play

in transporting AIS. We also review the characteristics of species that should be the greatest threat for future invasions, including those that pave the way for invasions by other species (“invasional meltdown”). Susceptible aquatic communities, such as reservoirs, may serve as stepping stones for invasions of new landscapes. Some microbes disperse long distance, infect new hosts and grow in the external aquatic medium, a process that has consequences for human health. We also discuss the interaction between species invasions and other human impacts (climate change, landscape conversion), as well as the possible connection of invasions with regime shifts in lakes. Since many invaders become permanent features of the environment, we discuss how humans live with invasive species, and conclude with questions for future research.

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Introduction

Humans have had enormous impacts on Earth and its biodiversity and many of these effects are global. Lakes and streams are particularly prone to species loss (Ricciardi & Rasmussen, 1999), with the greatest

threats coming from land use changes and exotic invasive species (“biotic exchange”, Sala et al., 2000). Humans have been particularly effective in breaking down biogeographic barriers through long-distance trade, intentionally introducing some species and carrying others as hitchhikers (Kolar & Lodge, 2000). The result has been a translocation of numerous freshwater species (Hulme, 2009). Although most introduced species fail to establish and spread (Williamson, 1996), many freshwater species have become invasive (see definition in Box 1) and some have caused widespread environmental effects and economic harm (Pimentel et al., 2005).

Freshwater ecosystems have greater biodiversity per surface area than marine and terrestrial ecosystems (Dudgeon et al., 2006; Balian et al., 2008). Freshwater ecosystems also play an active role in nutrient and water cycling (Wetzel, 2001), which translate into goods and services for human societies. At the same time, freshwater ecosystems have been deeply transformed by invasive species from a wide variety of taxonomic groups (Strayer, 2010; Simberloff et al., 2013). It is thus vital to understand the factors that govern the introduction, spread, and subsequent impacts of invasive species in these ecosystems.

Among several important syntheses relevant to the topic of invasive species in aquatic environments are reviews of climate change (Rahel & Olden, 2008), epidemiology and control (Mack et al., 2000), assessments of invasion potential (Ibanez et al., 2014), invader traits and impacts (Strayer, 2010; Pyšek & Richardson, 2010), vectors (Carlton, 1992), and functional homogenization (Olden et al., 2004). The purpose of this paper is to explore and review the little-studied interactions of aquatic invasive species (AIS) with natural and anthropogenic environmental changes in freshwater ecosystems and the challenges they present to humans in the 21st century. In particular, we examine impacts of invasive species;

the role of humans in accelerating transport of aquatic invasive species beyond ordinary dispersal barriers; the characteristics of successful invaders; the susceptibility of communities to invasion and the positive feedbacks for future invasion (“invasional meltdown”); microbial invasions and their hosts; the interaction of invasion with other human impacts; and living with invasive species as a permanent fixture of the environment.

Impacts of invasive species

Biological invasions of freshwater ecosystems have a large number of known and potential impacts on community structure and ecosystem function. The establishment rates of AIS are also high, as has been shown for several types of aquatic organisms and ecosystems (Ricciardi, 2001; García-Berthou et al., 2005; Bobeldyk et al., 2015). Even though biotic interchanges and paleo-invasions contributed to biodiversity as we know it (Pascal & Lorvelec, 2005; Gillson et al., 2008), the pace of current invasions far exceeds that of the previous events that took place over geologic time scales (Ricciardi, 2007). In view of the great biodiversity and vulnerability of freshwater communities to biotic exchange (Sala et al., 2000), impacts caused by invasions are certainly a cause of concern. Furthermore, the change itself is often perceived as undesirable even if an invasion is a delayed response to previous climatic events (Gillson et al., 2008) or has seemingly minor effects on the overall ecosystem function.

Although some invasive species have had little or no detectable effects (e.g., *Daphnia lumholtzi*, Havel et al., 2005a, b), many AIS have had damaging effects on the environment and on human interests. Case histories of their effects are widely reported in primary literature (e.g., Zaret & Paine, 1973; Goldschmidt

Box 1 Some key terms for invasion biology

Exotic A species transported by humans from far outside its natural range, often from other continents, and is introduced into a new environment (Also called *alien species* or *non-native species*.) Some exotic species are deliberately introduced, some escape, and others “hitchhike” with human goods

Invasive species An exotic species that persists in its new environment, reproduces, and spreads greatly in its distribution. Some, but not all, invasive species have detectable impacts on their environment or cause harm to human interests

Native species Species that evolved in the local environment or dispersed there by natural means

et al., 1993), the popular press (Zinsser, 1934; Bright, 1998), and scholarly books (Elton, 1958; Simberloff, 2013). Here we focus on the impacts of AIS on communities and ecosystems, since perturbations to these levels cause other unsuspected effects (Simberloff et al., 2013). For example, when invasive species behave as ecosystem engineers they may rapidly transform entire ecosystems (Strayer, 2012). An illustration of this scenario is the transformation of the Hudson River following zebra mussel invasion, from a pelagic-based food web to a littoral-based food web (Strayer, 2010). The high densities of zebra mussels in places like Lake Erie and the Hudson River can filter most of the algae from the water column, leaving little food for pelagic zooplankton (Strayer, 2010) and increasing light for vascular plants. Increased growth of these plants, in turn, increases habitat structure and has numerous other effects (Scheffler, 2009). Another example of an ecosystem transformation is the effect of invasive plants in Australia, where high densities of African Poaceae altered stream hydrology by trapping sediments in the channel (Bunn et al., 1998). Hydrologic changes, in turn, have large impacts on nutrient dynamics (Allan & Castillo, 2007). Overall, ecosystem effects of AIS are still greatly under-studied and a challenge for future research.

Invasive species are well known to restructure freshwater food webs (Vander Zanden et al., 1999). Because predatory fish often control community structure of lakes and streams (Brooks & Dodson, 1965; Power, 1990) and game fish have been widely introduced by fisheries agencies, much attention has been placed on exploring the community impacts of fish. Some impacts have been huge. The introduction of Nile Perch (*Lates niloticus*) to Lake Victoria, East Africa, annihilated the native community of haplochromine cichlid fishes, driving many species to extinction (Goldschmidt et al., 1993). The introduction of Peacock Bass (*Cichla* spp.) to Lake Gatun, Panama, greatly simplified the food web, extending to zooplankton and insects (Zaret & Paine, 1973). By reducing mosquitofish (*Gambusia affinis*), this introduction had the further effect of increasing mosquito populations and mosquito-borne illness (Zaret & Paine, 1973). Omnivores can also have large impacts on aquatic communities. Lodge et al. (2000) describe how non-native rusty crayfish (*Orconectes rusticus*) not only consume macroinvertebrates, but also

aggressively out-compete native crayfishes and destroy macrophyte cover, indirectly affecting the fish community.

Invasive plants have community level effects as well. For example, Eurasian water-milfoil (*Myriophyllum spicatum*) forms dense surface mats, and reduces light and diversity of native aquatic plants (Madsen et al., 1991). The simplified plant community is a poorer food resource for macroinvertebrates and higher-level consumers. Similarly, experiments conducted in ponds showed that dense monotypic stands of hydrilla (*Hydrilla verticillata*) changed the taxa composition of invertebrate assemblages compared with macrophyte multi-species treatments, although both treatments did not differ in regard to invertebrate taxa richness (Theel et al., 2008). Hydrilla likely impacts microbes as well, with shifts of metabolic profiles and phylogenetic structure of bacterial communities as density of hydrilla increases (Gordon-Bradley et al., 2015).

Although a half century of research has provided a wealth of knowledge about the spread and impacts of particular invasive species, aquatic ecologists still have a number of unanswered questions about the general nature of invasive species impacts on communities and ecosystems.

At what densities do invasive species begin to impact native communities? This question has to do with density dependence of impacts from invasive species, which increase with their abundance. Some studies have failed to identify impacts from invasive species that were in low or similar abundance to native species (Douglas & ÓConnor, 2003; Aday, 2007). For example, surveys in the River Paraná showed that fish species richness was no different in the invasive hydrilla than in native *Egeria najas*, and this finding was attributed in part to similar biomass of both macrophytes (Cunha et al., 2011). Investigation of impacts along a gradient of invasive density is necessary to identify abundance thresholds above which impacts would occur.

Do invasive species differ in their impacts from that of native species if they were to achieve similar densities? This question deals with the comparison of the change in an ecological property caused by the invasive species with the change of the same property caused by a native one. In this case, the characteristics of the native species should be as similar as possible to the invasive and the changes caused by the native

would be considered the “control” (e.g., Mormul et al., 2010). For instance, the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) reaches very high densities in streams of the western United States, where it dominates nutrient cycling (Hall et al., 2003). If native hydrobiid snails achieved a similar density, would they also dominate nutrient cycling?

What environmental factors contribute to time lags in impacts from invasions? In several ecosystems, spread, and/or impacts of non-native species occur several years or even decades following their introduction (Pelicice & Agostinho, 2009; Downing et al., 2013). Such time lags create difficulties for predicting their impacts. “Legacy effects” are effects of invasive species that persist after their removal (Corbin & D’Antonio, 2012). Such lagged impacts are mediated via changes in resource pools, habitat structure, or persistent feedback loops. Legacy effects are virtually unstudied in aquatic systems, but have been demonstrated to have lasting effects in some terrestrial ecosystems (Yelenik & D’Antonio, 2013). Invasional Meltdown may also lead to lags in impacts caused by invasive species, because a given non-native species may have its spread and impacts enhanced after it has been facilitated by the arrival of other non-native species (*Invasional meltdown* section below).

Dispersal and colonization are accelerated by human behavior

Although all species disperse to some degree, the rate of moving species across the planet has been greatly accelerated by humans (Kolar & Lodge, 2000). Once established in a new habitat, most invasive species are nearly impossible to eradicate and some of the major pests are extremely expensive to control (Pimentel et al., 2005). For these reasons, human-mediated colonization is generally best avoided in the first place. One key to understanding the process of invasion is the different ways in which humans transport species.

Invasion of an exotic species involves long-distance transport to a suitable habitat and establishment (colonization), followed by spread into other suitable habitats in the region (Fig. 1). Propagule pressure has an important role in the first steps of invasion and in latter spread. It is related to the number of individuals and/or propagules (e.g., seeds) arriving in a region and the number of release events (Duncan, 2011). Colonization

of each new population requires tolerance of the physical and chemical conditions of the new habitat, food acquisition, predator avoidance, and reproduction within the new habitat. AIS must find another water body in the “terrestrial matrix”. A crayfish that is dumped on land will quickly dry out and fail to survive more than a day. Introduced to a lake too low in dissolved calcium, the crayfish may live for a while but fail to molt. Introduced to a lake with sufficient calcium but lacking habitat structure as protection, the crayfish may succumb to predation by fish. Finally, a single crayfish that has passed through these “physiological and biotic filters” (Rahel, 2002) may fail to reproduce if only a single gender of a bisexual species is introduced or if potential mates are too rare to find (Allee effect). The widespread occurrence of asexual reproduction (Bell, 1982) provides many species with the capability to establish a population from a single colonist. In this respect, macrophytes and cladocerans have an advantage over crayfish.

Once established in one lake, AIS can more-easily spread to other nearby lakes. The chance of colonization is much greater for nearby populations than those far away. (This invasion probability-with-distance function is called a “dispersal kernel”.) For instance, logistic regression models using multiple years of *Daphnia lumholtzi* distributions, together with environmental data for ca. 100 reservoirs, revealed that the chance of new invasions declined rapidly for reservoirs more than 20 km away from source populations (Havel et al., 2002). Such spread within a region is important for longer-term invasion success. Metapopulation theory predicts that the chance of regional persistence is greatly enhanced by increasing the number of populations (greater “patch occupancy”, Hanski, 1999). For instance, invading crayfish that have successfully colonized one lake and subsequently spread to several other lakes in the region will be more likely to persist in the region than will a single population, because a single population is more prone to become extinct by some localized catastrophe (e.g., pollution event, invasion of largemouth bass, etc.).

Passive dispersal by natural and human vectors

Many freshwater species have adaptations that allow persistence in temporary environments and these characteristics are also useful for remaining viable during overland dispersal. Examples include seeds of

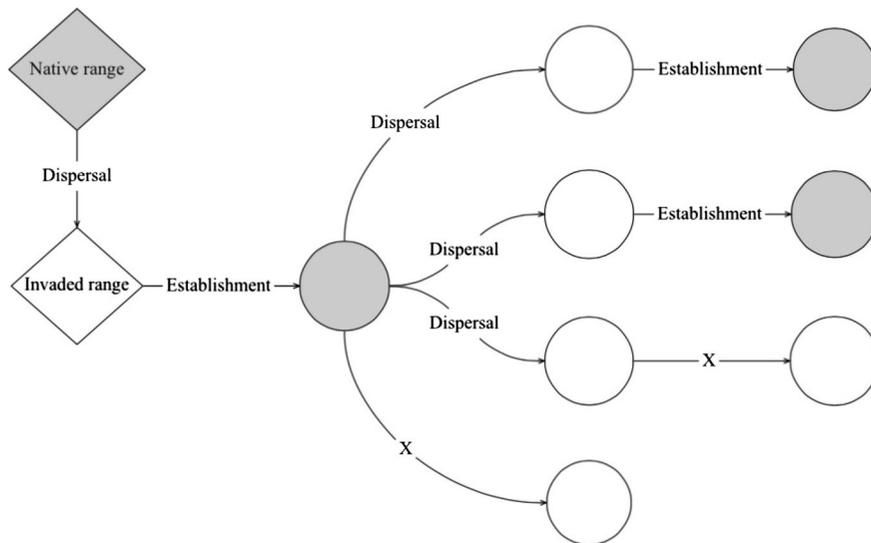


Fig. 1 Biological invasion of a water body (site) requires both dispersal and establishment. In this illustration, *closed symbols* represent populations, *open circles* by sites open to invasion, and a failure to disperse or establish is indicated by an X. For most species, dispersal requires a vector that moves between invaded and open sites. Establishment requires that individuals

are physiologically matched to the physical–chemical environment, find adequate food, avoid predators, and can reproduce. Initial establishment in the new range allows further spatial spread into other nearby open sites. In this example, 2 out of 4 new populations developed from the initial colonizing population

aquatic plants and their counterpart (resting eggs) in zooplankton (Hairston & Cáceres, 1996), cryptobiosis of rotifers (Wallace & Snell, 2001), resistance of freshwater snails to extended periods of drying (Havel et al., 2015), and dormant stages and spores of prokaryotes (Fazi et al., 2008). Survival is only half of the story; the propagule must move from one habitat to the other.

With the exception of flying insects and mobile vertebrates, most aquatic species lack the means for active dispersal into isolated drainages and instead use a variety of transport vectors for passive dispersal (Havel & Shurin, 2004). Numerous vascular plants produce wind-dispersed seeds, using a variety of different structures to increase drag and remain aloft (Vogel, 1994; Raven et al., 1999). Despite its apparent potential for long-distance movement, wind transports the dried eggs of freshwater invertebrates to colonize water bodies for only short distances from the source (Jenkins & Buikema, 1998; Brendonck & Riddock, 1999). Transport by birds and other vertebrates is made possible by attachment to fur and feathers and viable germination or hatching after passing through the digestive tract (Bilton et al., 2001). Nevertheless, the fact that most plant and animal species are not

cosmopolitan (Brown & Lomolino, 1998) implies that dispersal rate is limited at larger geographic scales. The increase in global travel and commerce has provided many more avenues for human-mediated transport of exotic species across great distances (Kolar & Lodge, 2000; Padilla & Williams, 2004), and the increased speed and efficiency of travel should increase the chance that individuals arrive to their new habitats alive.

Humans move aquatic species by intentional stocking, accidental releases, and through hitchhiking with other carriers (vectors). Resource agencies deliberately translocate and stock game fish in lakes worldwide (Kolar & Lodge, 2000; Rahel 2002; Pelicice et al., 2014). Anglers introduce other species by dumping bait. The aquarium and ornamentals trades import a stunning variety of fishes, invertebrates, and aquatic plants (Padilla & Williams, 2004), with very little regulatory oversight. Aquarium releases, either on purpose by naïve (though well-meaning) people or by accident, are commonplace events. Worldwide, these releases have led to establishment of over 150 species, many on the “worst invasive species” list (Padilla & Williams, 2004).

Hitchhiking plants and small animals are carried by a variety of human vectors (Carlton, 1992; Havel & Shurin, 2004). Large ships carrying ballast water have been documented to carry hundreds of species (Carlton & Geller, 1993), and such ships are the likely source for 75% of the species introduced to the Laurentian Great Lakes since 1970 (Ricciardi & MacIsaac, 2000). These ballast-vector species include zebra mussels (*Dreissena polymorpha*), which had been previously released from the Ponto-Caspian region through European shipping canals (Bij de Vaate et al., 2002), allowing their transport to North America from the Baltic Sea (Ricciardi & MacIsaac, 2000). Similarly, ballast water has been the source of Asian bivalves (*Corbicula fluminea*) that invaded South American freshwater ecosystems in the last two decades (Boltovskoy et al., 2006), as well as free-living microorganisms, including pathogenic bacteria, viruses, and toxic algae (Drake et al., 2007).

Water transported for fish stocking carries exotic plants and invertebrates, and is the likely source for introducing Eurasian water-milfoil to North America (Couch & Nelson, 1985). Subsequent spread of invasive plants and invertebrates into new drainages have been linked to recreational boats (Johnstone et al., 1985; Johnson et al., 2006). The importance of these vectors provides a clue for how regulatory agencies and volunteers can help reduce the rate of spread.

Interrupting the chain of transmission

Although some invasions that are quickly recognized and contained may be eradicated (see *Living with aquatic invasive species* below), many AIS achieve high population sizes before they are detected. This is particularly true for invasive plants that reproduce by fragmentation and plants and invertebrates that form resting eggs and seeds. Avoiding introduction in the first place seems particularly important. Understanding the vectors for transmitting invasive species (above) allows the chance to control their spread through influencing human behavior.

Some methods seem more feasible than others. For instance, rules on ballast water release from large ships have been legislated in a number of countries (e.g., United States: Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990) and invasion models predict that mid-ocean exchange of water

should reduce the load of propagules by a factor of 10^3 – 10^4 (MacIsaac et al., 2002). On a regional scale, recreational boats are a target for control. The spread of nuisance aquatic plants and the invertebrates may be reduced by state laws, public education (e.g., signs at boat landings and information brochures), and coordinated volunteer groups (e.g., Wisconsin: Clean Boats, Clean Waters; <http://www.dnr.wi.gov/lakes/cbcw/>). In such lake-rich regions where tourism is a billion-dollar industry, many people are motivated by a common goal of preserving lakes. Nevertheless, protecting lakes visited by many boaters is a challenge, since most boaters visit multiple lakes over short periods of time (Buchan & Padilla, 1999; Bossenbroek et al., 2001; B. Beardmore, University of Wisconsin, pers. com., December 22, 2013).

More problematic is the aquarium and water garden industry, where the business relies on demand of people for exotic plants and animals (Padilla & Williams, 2004). This industry successfully lobbies against regulation and people are able to easily circumvent specific outlawed species (e.g., water hyacinth, *Eichhornia crassipes*) through purchases over the internet. Similarly, the live bait industry resists efforts to restrict selling live crayfish in many states, despite the problem of widespread bait dumping. In both the aquarium and bait industries, public education through signs and brochures could reduce the rate of dumping, despite the natural instincts of most people to treat animals humanely.

Only a small percentage of those AIS that arrive in a place will establish successfully. Establishment success is explained both by differences in species traits (below), as well as by differences in the recipient communities (*Invasibility* section below).

Species traits that enhance their ability to invade

Like many ecological phenomena, early studies on invasive species consisted primarily of elegant descriptions of the successful invaders. These studies described in detail how non-native species arrived and their detrimental effects on local communities (Elton, 1958). More recently, ecologists have analyzed common features that separate successful invaders from those that fail (Ehrlich, 1986; Simberloff, 2013). Although each successful invasion has some unique properties, generalizations on invasion traits allow

better prediction of species that are most likely to invade. Invasion success actually depends upon two groups of characteristics. The first includes traits that allow non-native species to reach new habitats (*Dispersal* section above). The second suite of characteristics applies to the ability of a colonizing species to succeed in its new aquatic habitat (Ehrlich, 1986).

A variety of life history characteristics can be used to predict invasion success. One of the most important is asexual reproduction, common in many aquatic plants and invertebrates. Vegetative reproduction allows single viable macrophyte fragments to give rise to an entire population. Similarly, resistant resting eggs of rotifers and cladocerans, after overland dispersal and hatching, can initiate new populations or clonal lineages through asexual reproduction (apomictic parthenogenesis) (Dodson & Frey, 2001). Among terrestrial plants, species that are invasive tend to be larger and have higher growth rate and shoot allocation than do species that are not invasive (van Kleunen et al., 2010). We expect that similar traits would increase invasive potential of aquatic plants. For fish, a study from the Colorado River basin found that invasive species were more likely to be characterized by early maturation and production of smaller eggs (Olden et al., 2006). Yet many successful invaders are large-bodied fishes with large eggs and/or parental care (e.g., Nile perch; peacock bass; brown trout, *Salmo trutta*). In the Laurentian Great Lakes, fast growth was associated with establishment success in non-native fish, but not with the rate of spread, demonstrating the importance of different traits at different stages of invasion (Kolar & Lodge, 2002).

Trophic interactions are also an important feature for predicting invaders. Invasive species are often represented by different ratios of functional feeding groups than native species. In freshwater macroinvertebrates, invaders were much more frequently represented by collector-filterers and less likely to be collector-gatherers, predators, and scrapers, than were members of the native assemblage (Karatayev et al., 2009). Invasive fish were more likely to be represented by piscivores, planktivores, and omnivores than were native fish (Moyle & Light, 1996; Olden et al., 2006). In simulated food webs, models combining both network structure and non-linear population dynamics demonstrated that being a trophic generalist was one of the best predictors of invasion success (Romanuk et al., 2009). The greater prevalence of generalist

traits, shifts to different functional feeding groups, and increasing dominance of invaders are likely to accelerate the loss of functional diversity in native communities (Olden et al., 2004).

Geographic range and environmental tolerance are also useful predictors of invasion success. For freshwater and marine invertebrates and fish, species with greater geographic range tend to be over-represented among invasive species, relative to those not invading (Kolar & Lodge, 2002; Bates et al., 2013). Furthermore, species with greater heat tolerance tend to also be over-represented in the invaders (Bates et al., 2013), a trend that has important implications for interactions between invasive species and climate change (*Interaction with other processes* section below). Increased pollution tolerance has also been noted in some invaders as compared to native species (e.g., Karatayev et al., 2009; Fröh et al., 2012b). Some invasive mollusks use rapid growth and reproduction for rapid population recovery following disturbance (McMahon, 2002), which enhances their role as colonizers.

In summary, we would predict that the most common successful invaders will include those that are both likely to be carried into new freshwater environments and also those that have some combination of asexual breeding, high reproductive output, generalist feeding, and broad environmental tolerance. Using information about species biogeography and ecology, the Australian Weed Risk Assessment was shown to be effective in classifying plant invaders across several islands and continents (Gordon et al., 2008). This example shows that increasing our understanding of species traits as predictors of future invasions, likely specific for each assemblage, may also hold promise for aquatic invasions as well (see also Kolar & Lodge, 2002). Nevertheless, predicting invasions also depends on characteristics of the community at risk.

Invasibility: susceptibility of aquatic communities to invasion

Biotic resistance, together with abiotic environmental factors, can often explain the failure of non-native species to invade a novel ecosystem (Catford et al., 2009). The biotic resistance hypothesis was proposed by Elton (1958), who considered that the species

diversity of the recipient community is the main determinant of invasion success. In its essence, resistance of a native community to invasion by non-native species is related to competition, predation, and parasitism (Elton, 1958; Simberloff, 2011). The intensity of these negative interactions generally increases with the number of native species. Thus, tests on the role of biotic resistance often use diversity as a surrogate for the resistance of native (e.g., Fridley et al., 2007; Jeschke et al., 2012 and references therein). However, a meta-analysis showed that although such biotic resistance reduces invader establishment and performance, it does not completely repel plant invasions (Levine et al., 2004).

The role of biotic resistance to invasions has been widely investigated in freshwater ecosystems. The importance of competition in biotic resistance has been shown for macrophytes, whose growth is reduced with increasing density and diversity of native species (Peter and Burdick, 2010; Michelan et al., 2013). Herbivory also plays a role in reducing invasive macrophytes abundance, as evidenced by the impacts of beavers on one species of invasive macrophyte in wetlands (Parker et al., 2007). Native predators can impact invasive species as well. Crabs and other predators increase the mortality of zebra mussels in rivers (Carlsson et al., 2011) and native fish depress non-native crayfish abundance in lakes (Tetzlaff et al., 2011). Predators such as crayfish, fish, and turtles resist invasion by apple snails in rivers (Yamanishi et al., 2012).

Although less studied, parasitism also reduces invasion success. For example, an oomycete parasite reduced the abundance of an invasive amphipod and allowed coexistence with another native species of amphipod in a Canadian river (Kestrup et al., 2009). Most of these studies support the role of biotic resistance in reducing, and sometimes excluding, invasive species in their novel habitats. This decrease may be important if an invader is thus unable to reach a critical density necessary for maintaining a viable population. Furthermore, higher native diversity can make a freshwater community more resilient to invasion, by increasing the threshold to community collapse (Downing et al., 2012).

Biotic resistance depends on spatial scale. Invasion success is usually negatively related to native diversity on fine scales (at the scale of plots or experimental units; Xu et al., 2004; Michelan et al., 2013), but

positively related to diversity at coarse scales (plant patches or entire ecosystems) (Stohlgren et al., 2006; Capers et al., 2007). This pattern became known as the “invasion paradox” (Fridley et al., 2007), and it may be explained by the more important role of biotic interactions (e.g., competition and predation) on fine scales and of abiotic influence (e.g., resources availability and habitat heterogeneity) on coarse scales (Fridley et al., 2007). As an example from field studies of aquatic communities, positive associations between invasive establishment and native macrophyte diversity have been shown at coarse scales in both natural lakes (Capers et al., 2007) and reservoirs (Thomaz et al., 2009, 2012). In contrast, experiments conducted at fine spatial scales showed an opposite pattern, with a negative association between growth rates of invasive species and native diversity (Xu et al., 2004; Michelan et al., 2013). Because different factors likely influence invasions at different spatial scales, aquatic ecologists should carry out more studies that encompass different scales simultaneously (e.g., see Pintor & Sih, 2011).

Invasional meltdown

Invasional meltdown (IM) can be defined as a “community-level phenomenon in which the net effect of facilitations would lead to an increasing rate of establishment of introduced species and/or an accelerating impact” (Simberloff, 2006). The “meltdown” implies a positive feedback among invasions over time, leading to an increase in the cumulative number of successful invaders. Unless native species are replaced by invaders, the IM hypothesis predicts an increase in species richness. The IM hypothesis thus appears to contradict the biotic resistance hypothesis, which predicts enhanced resistance to invasion with increased species richness (Ricciardi, 2001). In a recent review of the guiding principles of invasion biology, IM was one of the few hypotheses with good empirical support (Jeschki et al., 2012). However, most of this support consists of descriptive case studies of facilitation between non-native species. However, the IM prediction that precedent invasions result in increasing rates of invasions and of impact caused by invasive species has not yet been conclusively demonstrated (Simberloff, 2006). This conclusion by Simberloff also applies to freshwater ecosystems. While a variety of observational and experimental investigations have demonstrated facilitation between

non-native species (Adams et al., 2003; Devin et al., 2003; Cucherousset et al., 2006; Chucholl, 2013; Michelan et al., 2014; Thiébaud & Martinez, 2015), the data are insufficient to show the existence of a true meltdown through increasing invasion rates and/or impacts over time.

One of the best examples for the possible occurrence of IM in freshwater ecosystems is the case of the Laurentian Great Lakes, for which a good history of multiple invasions and their consequences are known (Mills et al., 1993). In these lakes, both direct and indirect facilitation between non-native species was more common than negative interactions and invasions increased over time, results consistent with the IM model (Ricciardi, 2001). Nevertheless, this conclusion is based primarily on correlative observations from field surveys (Simberloff, 2006), which may be influenced by other confounding variables. For example, increased propagule pressure (from increased vector traffic) has also increased the opportunities for new invasions over time (Ricciardi, 2001). Indeed, the conclusion about the occurrence of a true IM in the Great Lakes has been questioned by De Vanna et al. (2011), who stated that indiscriminate facilitation of both native and non-native species by the ecosystem engineer *Dreissena* (zebra mussels and quagga mussels) is a better explanation for what is occurring in those lakes.

Future research to demonstrate IM would benefit from carefully designed experiments involving multiple species. Such experiments require a test of two questions. First, are invasive species facilitating each other? And, second, does facilitation between non-natives propagate in such a way as to impact the community level and enhance invasion rates? These kinds of experiments require careful attention to controls and understanding what exactly are the response variables (e.g., invasion rate) and treatments (e.g., presence or absence of prior invader). To conclude about a true meltdown, both the individual performance of non-natives and their impacts would have to be greater when they interact than when they are alone.

In summary, based on the evidence to date, we cannot conclude whether IM in freshwater ecosystems is common but poorly documented or if IM is rare in nature. The challenge for future research is to refine experiments, using a variety of different aquatic communities, which produce clear-cut conclusions about the impact of invasion on future invasion rates.

The role of reservoirs

Reservoirs are now a significant proportion of freshwater ecosystems (Rosenberg et al., 2000), and their representation is increasing with the rapid hydroelectric development in South America and Asia (Dudgeon et al., 2006). Reservoirs act as stepping stones for establishing invaders in new watersheds (Havel et al., 2005a, b). Reservoirs serve this role by providing a propagule source close to uninvaded water bodies and simultaneously altering the habitat, making it more prone to invasions. Recent studies suggest that reservoirs are indeed more susceptible to invasion than natural systems (Johnson et al., 2008; Banks & Duggan, 2009). The high invasibility of reservoirs was first noted in dammed mountain streams (Moyle & Light, 1996) and was later supported in a comparison of reservoirs with natural lakes in northern Wisconsin (Johnson et al., 2008). The latter study demonstrated that a number of AIS (Eurasian water-milfoil, zebra mussels, spiny water fleas [*Bythotrephes longimanus*], rainbow smelt [*Osmerus mordax*], and rusty crayfish) are much more likely to occur in reservoirs than in natural lentic systems, and this effect was robust to inclusion of potentially confounding environmental factors (Johnson et al., 2008). This study has also clearly shown the role of reservoirs in increasing connectivity by reducing the distance to other aquatic ecosystems and facilitating further spread of invasive species (Johnson et al., 2008). Nevertheless, the relative importance of biotic resistance and disturbance or habitat degradation in reservoirs has not yet been elucidated.

As young, early successional and often species-poor systems, reservoirs are likely to have decreased biotic resistance to invasion. A recent study in Mediterranean reservoirs demonstrated that richness of non-native fish was negatively related to richness of the native fish community, indicating the importance of biotic resistance, whereas native fish were mostly affected by the abiotic factors (Clavero et al., 2013). The role of biotic resistance on invasibility of constructed systems has also been demonstrated with zooplankton (Shurin, 2000; Taylor & Duggan, 2012). For instance, in a mesocosm experiment (viewed as a model of a reservoir in its earlier phase), seeding newly constructed tanks with native species eggs decreased establishment success of invasive zooplankton one year later, relative to

tanks without a native assemblage (Taylor & Duggan, 2012).

Abiotic conditions could also play an important role in colonization of reservoirs by invasive species. Such abiotic factors include water quality degradation and increased variability in water levels from regulation for flood control and hydropower, which reduces macrophytes and creates sub-optimal habitats for native species (Havel et al., 2005a, b). Mainstem reservoirs lack the riffle-pool structure characteristic of the streams they impound. Reservoirs also lack the flood pulses characteristic of large rivers and their floodplains, and dams reduce the migratory opportunities of fish (Agostinho et al., 2004, 2008). Many shallow water reservoirs are exceedingly prone to sediment resuspension and eutrophication (Thomaz et al., 2014). Physically and chemically degraded habitats are more likely to harbor invasive species (Früh et al., 2012a). Reservoirs create conditions more suitable for the invasive and more heat-tolerant species (Bates et al., 2013), as well as fauna tolerant of degraded ecosystems (Karatayev et al., 2009; Früh et al., 2012b). Therefore, reservoirs can promote establishment of invasive species via habitat degradation and also allow for the selection for taxa different from the native assemblage in functional attributes.

The large-scale environmental changes due to reservoir construction have important consequences to freshwater ecosystems. Reservoirs greatly contribute to worldwide homogenization of freshwater faunas as endemic riverine species are replaced by cosmopolitan lake taxa by removing biogeographic barriers and causing habitat alteration (Rahel, 2002; Gido et al., 2009; Vitule et al., 2012). Native species declines in response to invasion in reservoirs have been shown for a number of assemblages (e.g., fish: Agostinho et al., 2008; macrophytes: Michelan et al., 2010). With that, it is important to understand how taxonomic changes and homogenization translate into shifting balance among functional groups and ecosystem-level changes. Invaders are not a random collection of species and can be functionally distinct from the native assemblage (Karatayev et al., 2009; Gido et al., 2009). The resulting functional homogenization can in turn lead to further food web disruption, decrease in resilience to anthropogenic disturbance and increase in invasibility (Olden et al., 2004). In-depth comparisons of invasive and native species

functional attributes in impoundments vs. natural similar-sized lentic systems in the same geographic area are needed to understand the role of reservoirs in functional homogenization of freshwater faunas.

Aquatic microbial communities and host susceptibility

The aquatic microbes comprise microscopic eukaryotes, two prokaryotic domains (Bacteria and Archaea), and viruses. Most of those also retain a high potential for long-range dispersal given their minute sizes, high densities of individuals, and ability to rapidly form resting stages (Fontaneto, 2011; Lennon & Jones, 2011). Using many molecular tools, microbial ecologists can now describe the great genetic and metabolic diversity of eukaryotic and prokaryotic microorganisms in their natural environments, allowing comparisons of species and genotypes across the globe. A large body of research demonstrates that aquatic microorganisms can exhibit distinctive biogeographic patterns (Fontaneto, 2011; Incagnone et al., 2014, and references therein). Such distributions of microbial assemblages suggest that some microbial taxa disperse globally (e.g., in oceans; Pommier et al. 2007; Schauer et al., 2009; Ladau et al., 2013), while others disperse only over short distances (Green & Bohannan, 2006; Martiny et al., 2006; Ramette & Tiedje, 2007; Lindstrom & Langenheder, 2011). Although such conclusions are tentative at this time (Jenkins et al., 2007; Fontaneto, 2011), the biogeographic patterns of freshwater microbes offer the potential for future range expansion and invasion.

Microbial population traits (e.g., individual density, genotypic diversity) and community characteristics (e.g., taxonomic richness, interspecific interactions, community evenness, functional redundancy) may affect the capability of native microbial communities to resist or accept microbial invaders (Shade et al., 2012). Though important, such features of microbial communities have not yet been clearly linked to invasion mechanisms. Climate-related changes in the environment (e.g., increases in atmospheric temperature, changes in precipitation patterns) will likely affect both the dispersal of microbes (e.g., through flooding) and the conditions of lakes and streams that favor particular species and their hosts.

We have much to learn about whether microbial invasions follow patterns and processes that are already known for plants and animals (Ehrlich, 1986; Amalfitano et al., 2015). To date, there have been few comparative studies based on a set of samples of aquatic micro- and macro-organisms from the same set of sites, which would enable a direct comparison of the relative dispersal and colonization mechanisms. In one example, Beisner et al. (2006) evaluated the community composition of bacteria, phytoplankton, crustacean zooplankton, and fish in Canadian lakes and reported that larger and less motile species (zooplankton and fish) were more strongly influenced by spatial factors than by local environmental factors.

From the perspective of this review on biological invasion, we have two primary questions about microbes, both based on the idea that freshwaters could represent a “melting pot” for microbial invasive species. In particular, does the freshwater medium offer an environment where infectious microbes can meet and interact prior to colonizing their hosts? Second, do natural and human-assisted movements of waters and organisms transport microbes to new environments?

Clearly, freshwater provides a medium for infectious microbes. A large body of literature is dedicated to waterborne diseases and invasive microbial pathogens transmitted through contact with infected waters or infected hosts having aquatic phases in their life cycles. Reported cases include a long list of microbial eukaryotes (e.g., *Entamoeba histolytica*, *Cryptosporidium parvum*, *Cyclospora cayetanensis*, *Giardia lamblia*, *Microsporidia*), bacteria (e.g., *Vibrio cholera*, *Escherichia coli*, *Campylobacter jejuni*, *Legionella* spp., *Salmonella* spp., *Leptospira* spp.), and viruses (e.g., *Coronavirus*, *Hepatitis A virus*, *Poliovirus*, *Polyomavirus*, *Norovirus*) (see Leclerc et al., 2002 for a review). Thus, aquatic microbes may infect an introduced host species, with the aquatic environment acting itself as a reservoir. The aquatic environment can also mediate polymicrobial interactions, particularly within the context of infections. In the case of fecal bacteria, *E. coli* and enterococci are known to acquire new determinants of virulence and resistance by gene transfer mechanisms during their stay in the secondary habitat (the freshwater environment outside the host) (Luna et al., 2010).

Movement of non-native plants and animals also transports aquatic pathogens. For example, endozoic

and epizoic microbes find new opportunities to proliferate within or on individual plants and animals of native communities. Guts and teguments of fishes and crustaceans are important pathogen transmission routes in aquatic systems (Blokesch & Schoolnik, 2007; De Schryver & Vadstein, 2014). Considering that opportunistic pathogens preferentially infect young and stressed individuals (Skjermo & Vadstein, 1999; Hajek, 2004), host-associated invaders may play a role so far underestimated within the ecological interactions of invaded systems.

Although controlling contamination and proliferation of potential pathogens in freshwater is extremely challenging (Cabral, 2010), their control could be achieved partly at the level of the host, such as by infection tracking in human populations. For example, Gatto et al. (2013) observed that hydrological network, human mobility, and landscape complexity mediate the spread of diarrheal infections from *Vibrio cholera* that could be potentially modeled to predict which communities will be hit hardest during the epidemic.

So far, studies exploring microbial AIS and emerging infectious threats in freshwaters have oriented research efforts toward relevant human health issues and ecosystem services (e.g., Morens et al., 2004; Conn, 2014). While less attention has been placed on the invasion of aquatic non-pathogenic microbes (“invisible invaders”, Litchman, 2010), these microbes offer an interesting challenge for distinguishing native from non-native microbial species. Such studies require a greater understanding of bacterial taxonomy and historical patterns of microbial community composition. For bacteria, such historical studies are few, but offer interesting possibilities using methods from paleolimnology (Romero et al., 2006; Smol, 2008). Such studies require easily detectable microscopic, biochemical, and genetic traits.

Invasion of non-native cyanobacteria into freshwater has several important consequences for native food webs and human uses of water. In a summary of recently published records on the invasion of cyanobacteria into subtropical and temperate lakes and reservoirs, Sukenik et al. (2012) analyzed the dynamics of two genera of invasive *Nostocales* (*Cylindrospermopsis* and *Aphanizomenon*). The immediate threat of the invasion by cyanobacteria is that numerous strains, belonging to a variety of genera (e.g.,

Microcystis, *Nostocales*, *Oscillatoria*, *Anabaena*), produce harmful substances toxic to humans, animals, and other eukaryotes (Codd et al., 2005). Such secondary metabolites function as allelochemicals that may inhibit the growth of other phytoplankton species and grazers, thus affecting the entire food web (Ger et al., 2014; Paerl & Paul, 2011). Moreover, invasive cyanobacteria can potentially alter the nitrogen budgets in invaded aquatic systems by nitrogen-fixation (Litchman, 2010). To our knowledge, there are no published examples on the global impact of invasive microbes on major biogeochemical cycles. Thus, this topic is a fertile area for future research.

Microbial invasion ecology has been tested experimentally using artificially assembled microbial communities. Hornak and Corno (2012) reported the effects of the invasion by the opportunistic bacterium *Limnohabitans planktonicus* on growth of pure cultures and mixtures of freshwater bacteria (*Arthrobacter agilis*, *Aeromonas hydrophila*, *Brevundimonas* sp., *Flavobacterium* sp.). In most experimental conditions, the invader had a strong detrimental effect on the abundance of the dominant species, owing to competition for nutrients and possibly by allelopathic interactions.

As obligate intracellular life forms, viruses deserve further consideration as an important component of microbial communities. Since many viruses are transported by aquatic animals and plants (Kurath & Winton, 2011; Roossinck, 2011), they also may play an important role in biological invasions of freshwater communities. On the one hand, introduced hosts commonly convey viruses from their native ranges, which may allow the hosts to achieve greater fitness in their introduced ranges. On the other hand, viruses that do infect introduced hosts may reduce the fitness of invasive hosts (Rua et al., 2011). However, methodological limitations and a paucity of environmental data prevent us from describing the distribution of most viruses and hence differentiating native and non-native viruses. Now that we are able to survey viral diversity in the environment using metagenomic tools (Fierer, 2008), we can begin to investigate the spatial structure and dynamics of viruses and their transport vectors.

In conclusion, we have much to learn about microbial communities and the mechanisms that control microbial invasions. First, information is needed on the geographic distribution of species and

factors related to their spatial structure. Such knowledge will allow distinguishing native from non-native species. Second, experiments on the ecological mechanisms that control microbial assembly in aquatic systems would provide the understanding necessary for identifying and managing the effects of disturbed conditions, including anthropogenic impacts, on natural microbial communities.

Interaction of invasion with other processes

Because of the important role that humans play in spreading invasive species, agencies have begun to develop procedures and policies that attempt to prevent further introductions (Hulme, 2011). Nevertheless, humans may affect non-native species distributions and impacts in the future by other indirect means, including global climate change, land use conversion, and pollution (Dullinger et al., 2013).

Invasive species and climate change

As climate and global environmental conditions continue to change in response to anthropogenic disturbances, many non-native aquatic species are expected to flourish (Rahel & Olden, 2008; Sorte et al., 2013). Since many non-native species are tolerant to a wide range of environmental conditions (Kolar & Lodge, 2002; Bates et al., 2013; Sorte et al., 2013), we expect changing climate should facilitate the establishment of non-native species. In contrast, many native species seem less likely to adapt to their changing environment (Sorte et al., 2013). Thus, native aquatic species may be buffeted by both changing environmental conditions and rapidly expanding invasive species (Dukes, 2011).

As an example of what changes may happen in aquatic habitats, Loyola et al. (2012) modeled the range for one of the most widespread non-native aquatic vertebrates, the American bullfrog (*Lithobates catesbeianus*) and how it may spread in the future. Taking into account the current distribution of *L. catesbeianus*, its known ability to tolerate wide environmental conditions, and current climate models, the authors predict that the American bullfrog will invade reserves associated with the Atlantic Forest Biodiversity Hotspot (Brazil). This could very well be the pattern we see for many successfully introduced

aquatic species. In addition, climate change may facilitate the dispersal of potential invaders that were previously held in place by past environmental conditions.

Changes in weather patterns may also modify species interactions in favor of the non-native species. Increasingly, biologists are reporting that historic weather patterns are promoting coexistence between invasive and native species, with certain weather extremes limiting the negative effects of invasive species. Luja and Rodriguez-Estrella (2010) found that tropical cyclones produce enough heavy rainfall to wash invasive American bullfrogs downstream. Native Baja California treefrogs (*Pseudacris hypochondriaca curta*), which would otherwise be eliminated with rising bullfrog populations, are well adapted to the cyclones and persist through the heavy rainfalls. Similarly, Kats et al. (2013) reported that invasive crayfish (*Procambarus clarkii*) and native amphibians likely coexist because of periodic heavy rainfall that washes crayfish from streams. *Procambarus clarkii* is not well adapted to the rapid flows of post-storm Southern California mountain streams. Native frogs (*Pseudacris regilla* and *P. hypochondriaca*) and newts (*Taricha torosa*) persist through the periodic spates. During a 20-year study, newts had significantly more reproduction in years with above average rainfall than in years with average or lower rainfall. In both of these instances, if climate change results in decreased rainfall, which is predicted for parts of Western North America, then conditions will become increasingly favorable for such invasive species. As a result, local amphibians are in danger to becoming extirpated.

A different potential consequence of climate change is the increase in humic substances in aquatic ecosystems in response to rainfall, and consequent reduction in light transmission through the stained water column (“brownification”). Such circumstances favor species that thrive in low light environments. For example, Mormul et al. (2012) showed that increases in humic substances in freshwater north-temperate ecosystems allows the invasive macrophyte *Elodea nuttalli* to out-compete native macrophytes, facilitating its spread and potential impacts in European freshwater ecosystems. This example highlights that an indirect outcome from global warming (in this case, brownification) may be more important than temperature itself to magnify impacts caused by invasive

species. Increases of disturbances (e.g., extreme drought and rainy periods) are also predicted to occur in response to global changes in some regions. The effects of these disturbances on AIS success are still to be identified.

An indirect, but nonetheless, important consequence of climate change could be human activities that attempt to counteract drying conditions accompanying climate change. Rahel and Olden (2008) suggest that as humans experience increasingly dry conditions, more water reservoirs will be built. In addition to the reservoirs, ditches, aqueducts, and canals will likely be constructed to transport water to areas where it is needed. These new water bodies have the potential to facilitate the spread of AIS (Bij de Vaat et al., 2002; Havel et al., 2005a, b), as well as provide them permanent habitat.

Land use and invasive species

Land use intensification affects freshwater communities via increased sedimentation, altered hydrology, pollution, and nearshore habitat destruction (Allan, 2004). By altering aquatic habitats, such disturbance reduces species richness and hence biotic resistance to invasion. Watershed development and urbanization cause non-linear changes in fish, macroinvertebrate, and diatom assemblages (Hilderbrand et al., 2010; King et al., 2011; Kovalenko et al., 2014), which are also correlated with the presence of invasive species (Riley et al., 2005). Notably, increasing anthropogenic development resulted in simultaneous non-linear decreases in abundance of sensitive native species and increases in invasive species (Riley et al., 2005). Several invasive macrophytes were associated with increase in watershed agriculture, which was in turn correlated with increased turbidity and nutrient levels (Trebitz & Taylor, 2007). Similarly, both development and agriculture were important predictors of invasive fish species richness in California watersheds (Marchetti et al., 2004). Analysis of a large number of European streams (Früh et al., 2012a) revealed that habitats that were physically and chemically degraded were also more prone to invasion by a variety of macroinvertebrates. Decreased dissolved oxygen and increased temperature and chloride concentrations were the most important predictors of the presence of invasive amphipods, isopods, and mollusks, and invasive species displayed greater tolerance of

degraded conditions than their native counterparts (Früh et al., 2012b). However, this association between disturbed landscapes and increased prevalence of invasive species is difficult to interpret, since increased boater traffic, and thus propagule pressure, is also expected in the more developed areas. This problem with confounding factors may explain why the mostly intuitive assumption that invasive species would interact with eutrophication, habitat destruction, and other anthropogenic stressors has only been tested in a handful of studies (*reviewed in* Strayer, 2010). Invasive species are likely to complicate management of other issues facing freshwater ecosystems (Strayer, 2010), so understanding the interaction between the effects of invaders and landscape change on the native assemblages is of great interest for identifying vulnerable ecosystems and applying adaptive management to address a variety of stressors (Thomas et al., 2008).

Regime shifts and invasive species

Regime shifts, or large changes in the state of the system in response to a small change in the driver, are a common phenomenon, particularly in shallow lakes. Regime shifts have an intriguing connection with invasive species. Invasive floating plants are a classic example of an alternative stable state: a shift from submerged to floating plants is induced by nutrient enrichment and maintained by floating plants shading out the submerged (Scheffer, 2009). Invasive species can induce a regime shift via several, often complementary, pathways. The shift can be triggered directly by changes in assemblage composition or water quality due to invader dominance (Witte et al., 1992; Strayer et al., 2008). Regime shifts can also be triggered by invasive species increasing the system's vulnerability to other stressors, such as eutrophication, which shifts or widens the basin of attraction of an alternative stable state. Invasive species may also cause a regime shift by tipping the state of the system via self-reinforcing mechanisms, such as alteration of fire regimes in terrestrial systems (D'Antonio et al., 2000) or light attenuation by floating macrophytes (Scheffer et al., 2003).

Invasive species that directly affect the state of the system are often species that have functional traits distinctive from those present in the native community. Classic examples of this effect are herbivores

(Carlsson et al., 2004; Strayer et al., 2008; Nicholls et al., 2011) and predators (Zaret & Paine, 1973; Witte et al., 1992) that invade communities with low herbivore or predator biomass and cause considerable shifts in the native assemblages via direct consumption. New growth forms of aquatic plants are another example of such distinctive traits (Yarrow et al., 2009). However, even invaders that are similar in their traits to members of the native community can contribute to a regime shift via indirect mechanisms. For example, invasive species often cause decreased diversity at all trophic levels, and decreased diversity has been shown to reduce reticulation (number of food web pathways) and decrease food web stability, pushing the system away from equilibrium and increasing the amplitude of oscillations in abundance (Rooney & McCann, 2012). Even small declines in native species abundance, such as those commonly occurring with increasing invader dominance, could lead to functional extinctions and result in food web reorganization (Säterberg et al., 2013). Furthermore, spatially heterogeneous systems (e.g., species-rich littoral zones) are more likely to exhibit a gradual response to stress due to decreased spatial coupling between nearby patches (Van Nes & Scheffer, 2005). Monocultures of invasive plants often result in decreased heterogeneity in habitat structure, assemblage composition and environmental conditions compared with diverse native assemblages, thus potentially unraveling the role of greater heterogeneity in preventing abrupt regime shifts. Invasive species may also be playing a large role in the so-called slow regime shifts with transitions that are more gradual but even more difficult to reverse (Hughes et al., 2013).

Based on a recent meta-analysis of terrestrial invasive plants, Gaertner et al. (2014) showed that invasive species that are most likely to cause regime shifts are those that can enhance their own persistence by changing internal feedback mechanisms. The most common reinforcing feedbacks identified in this study were associated with the ability of invasive species to produce large numbers of seeds and litter, changing the fire frequency or intensity, accumulating soil nitrogen, and altering soil biota (Gaertner et al., 2014). A comparable meta-analysis and overview has not been attempted for aquatic invasive plants; however, potential pathways for disruption by invasive aquatic plants include their ability to increase sediment loads (Bunn et al., 1998), reduce sediment resuspension, and

uptake nutrients from water (Yarrow et al., 2009), and reduce underwater light (Farrel et al., 2009). A systematic analysis of regime shift-associated traits of aquatic species may be increasingly important, given the high susceptibility of aquatic ecosystems to negative impacts from invasive species and to regime shifts and possibly unique mechanisms of self-reinforcement by aquatic invaders.

Living with aquatic invasive species

The vast number of AIS has resulted in freshwater communities that are quite different in composition from those that existed before human introductions began. Impacts caused by non-native species depend a bit on human perception. Although an impact occurs when an invasive species causes a net change of any ecological property (Pyšek et al., 2012; Simberloff et al., 2013), interpretation of these impacts depends on the type of ecological attribute measured (Pyšek et al., 2012). A given invasive species may cause a neutral or positive effect on one ecological property but a negative effect on another. For example, the invasive macrophyte *Hydrilla verticillata* did not significantly impact the native invertebrate richness but did impact invertebrate assemblage composition (Theel et al., 2008; Mormul et al., 2010). How the effects caused by invasive species on native communities and ecosystems are interpreted (“good” or “bad”) depends on human values. For example, introduction of generalist herbivores such as sterile triploid grass carp requires careful attention to density, in order to avoid destroying all the vegetation and creating a turbid, algae-choked lake (McComas, 1993, Dibble & Kovalenko, 2009). The reduction of macrophytes biomass is perceived by lake managers and society as a positive impact of this procedure; however, its side effects (elimination of native vegetation and increasing turbidity by resuspending sediments) are understood as negative impacts. A tradeoff between these two types of effects and on their perception by managers and ecosystem users will determine whether or not carp are introduced.

Quantifying the cost of impacts

Biological invasions can cause tremendous economic impacts. An estimate carried out for aquatic

ecosystems of the US showed an approximate annual cost of 7.7 billion USD associated with damages caused by alien species and their control (Pimentel et al., 2005). These costs are associated mainly with introduced fish (ca. 5.4 billion), mollusks (2.2 billion), and aquatic weeds (0.1 billion). As reviewed in Pimentel et al. (2005), these cost estimates are based both on direct losses and damage and on control costs to prevent a variety of impacts. Introduced fish cause extinctions of native species and, for some species like carp, a reduction of water quality. Invasive mussels, such as *Dreissena* sp., reduce food and oxygen for native fauna and they clog pipes and filters for humans (drinking water, industry). Invasive aquatic plants block light to native plants, choke waterways, alter nutrient cycles, and reduce recreational use of rivers and lakes. Control of invasive aquatic weeds involves spending considerable time and effort each year on reducing densities to levels that are tolerable to recreation, navigation, and other uses of lakes and streams. A secondary effect of nuisance plant control may be restoration of a more diverse native plant community (Pedlow et al., 2006). Similar efforts are required for control of biofouling animals, such as *Dreissena* sp., which overgrow natural and man-made structures.

Further estimates of the economic cost from invasive species are a challenge for the future. Better metrics to quantify impacts are required by cost-benefit analyses for management and risk assessment (Simberloff et al., 2013). There is a need to shift focus from exclusively biodiversity-related impacts to assessment of functional changes, as the biodiversity loss is a poor and inconsistent metric to reflect the dramatic turnover and reorganization experienced by many biological communities (Dornelas et al., 2014; Pandolfi & Lovelock, 2014). Biodiversity alone often does not reflect the more consequential underlying functional changes (Säterberg et al., 2013). Nevertheless, additional work is needed to quantify and interpret such functional changes in freshwater ecosystems.

One reflection of human values is the perspective on invasive versus native species. There is currently a debate about whether invasive species should be treated in the same way as natives, and even a call for the end of invasion biology has been proposed (Valéry et al., 2013). Countering this idea, Simberloff & Vitule (2014) provide compelling argument that invasive

species are fundamentally different from most natives. Invasive species may create impacts only after time lags (Simberloff et al., 2013) and impacts caused by invasive species have been shown to be more severe and more frequent than those caused by excessive growth of natives (Simberloff et al., 2012; Hassan & Ricciardi, 2014).

Is extirpation of aquatic invasive species possible?

Since non-native species have invaded many aquatic habitats, natural resource managers must deal with them now and in the future. Some have suggested that we need to focus increasing efforts on the early detection and rapid eradication response toward invasive species (Westbrooks and Eplee, 2011). This approach has proven effective with some terrestrial and aquatic plants (Westbrooks, 2004). We are seeing an increasing emphasis placed on eradication and restoration of habitats to conditions they were in before the non-native species invaded. For instance, a combination of flooding and removal of two invasive plants allowed quick reestablishment of native plants and enhanced richness of native fishes in a tropical Australian floodplain (Perna et al., 2012). Where restoration proves difficult or impossible, ecologists, and managers have focused on strategies that minimize the potential impacts of the invader.

Eradication of non-native invasive species has occasionally been successful in both terrestrial and aquatic communities (Simberloff, 2013). In such locations, the invasive species could be isolated and the habitat either treated chemically or drained. In streams or more open waterways, such approaches will likely fail. Physical removal, such as by exhaustive trapping (e.g., crayfish: Hansen et al., 2013) or hand pulling (e.g., nuisance plant control), can greatly reduce densities but fail to completely eradicate the population. A few studies have reported successful transitions back to native species dominance after non-native species removal (e.g., aquatic macrophytes: Perna & Burrows, 2005; Perna et al., 2012), although recovery may take a longer time in other ecosystems. Other studies (e.g., fish: Gaeta et al., 2015) indicate greater resilience of the invasive species to return again to higher population densities once control efforts stop, particularly when top-down control from native predators is weak.

Some native populations recover following extirpation of introduced species. Knapp et al. (2007)

found that a small population of rare native frogs began to recover quickly after introduced trout (*Oncorhynchus* spp. and *Salvelinus fontinalis*) were removed from high elevation mountain lakes. Zooplankton recovery was slower; some species of zooplankton did not recolonize lakes at all if trout had been present for more than 50 years (Knapp & Sarnelle, 2008). Just as there is frequently a time lag between the colonization of an introduced species and the subsequent impacts on the aquatic community, there evidently is also a time lag in native species recovery after the successful removal of an invasive species.

A comprehensive review of successful invasive eradications in Europe showed that the majority of projects involved either mammal removals or removal of specific terrestrial species from islands (Genovesi, 2005). There has not been an in-depth overview of eradication effort success for AIS. Even when there has been a well-coordinated and systematic strategy to remove a high profile invasive mammal, the task has been daunting (Bryce et al., 2011). For example, in order to protect native small mammal populations in North East Scotland, teams of volunteers were trained to trap American mink in a systematic approach beginning in high mountain lakes and continuing down rivers. Scientists and project managers are confident that mink can be eradicated from northern Scotland, but this will be a multi-year, volunteer-based effort taking tremendous effort (Bryce et al., 2011). This example reminds us that policies surrounding invasion ecology should focus on prevention given that restoration can be difficult if not impossible.

Concluding remarks: challenges of invasive species and directions for future research

Invasive species provide challenges to management, as well as an opportunity to explore basic ecological questions. How are communities assembled and how do these communities respond when new species come in? How commonly do niche shifts occur (Guisan et al., 2014)? What processes regulate dispersal and what is the relative importance of such regional processes with local community interactions? How does community succession proceed following disturbance? How redundant are biological communities across the planet? What are the main impacts of

invasive species and how do these impacts change ecosystem goods and services?

This review touches upon some persistent challenges in aquatic invasive species, such as the limited ability to predict establishment success and generalize invasive species impacts across systems. This review also considers the role of invasional meltdown in invasibility and the complex interactions of invasive species with other stressors affecting aquatic ecosystems. These areas, as well as our limited knowledge of the density-dependence, time lags, and legacy effects of invasive species, suggest several emerging issues and fruitful avenues for future research.

In addition, our current review of literature on AIS points out some important biases in the amount of research conducted in different ecosystems. First, freshwater ecosystems have received much less attention than terrestrial ecosystems. For instance, prospective studies of invasions in progress have many examples from terrestrial communities (reviewed in Elton, 1958; Jeschke et al., 2012), whereas such studies are rather few in freshwater (e.g., zebra mussels: Johnson & Padilla, 1996; *Daphnia lumholtzi*: Havel et al., 2002). Second, far more research has been conducted in temperate regions (North America, Europe, and Australia) than in the tropics (Hulme et al., 2013). Part of this bias is a consequence of our poorer understanding of species ranges in the tropics. Nevertheless, because of the higher diversity in the tropics, particularly of plants and fishes (Brown & Lomolino, 1998), tropical freshwater communities are threatened to lose a higher number of species in response to invasions than are temperate systems. Invasion biologists thus have numerous opportunities for important contributions from research investigated in the tropics.

Another challenge to aquatic biologists studying AIS is to examine the combined impacts of multiple invasive species on freshwater communities. Multiple species invasions are common in lakes (e.g., Mills et al., 1993). Are their effects additive, synergistic, or antagonistic? Such interaction effects can be explored with factorial design experiments, conducted at a large enough scale to capture the key responses.

Finally, we see a great challenge in management strategies to reduce introductions, such as through better legislation over the transportation of species across countries and between basins. Management and eradication actions are poorly coordinated for

freshwater ecosystems. In addition, there is a need of adequate distributional databases to track invasive species and help prioritize management actions (Bobeldyk et al., 2015). If predictions about climate change and invasive species are correct, aquatic systems will experience increasing pressures from invasive species. Countries and regions will need to redouble efforts toward the prevention of invasive species and toward eradication of newly invaded species. Historic “wait and see” approaches toward invasive species will not be viable and a more aggressive approach toward prevention and eradication will be necessary to preserve current ecosystems.

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