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Article title: Are invasives worse in freshwater than terrestrial ecosystems?

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Abstract

Several lines of evidence suggest that the effects of invasive species may be greater in aquatic freshwaters than in terrestrial ecosystems. We argue that freshwaters are significantly more invasible - from a number of poorly-regulated sources - and also more susceptible to negative biodiversity, physical ecosystem and socioeconomic impacts when invaded, than their terrestrial counterparts. Moreover the nature of freshwaters appears to result in impacts that are wide ranging and severe while being indirect, diffuse and difficult to both detect and predict. For these reasons we conclude that freshwater invasive species represent a special case, when compared with terrestrial invasives, in which the likelihood of negative impacts, and their effects, is disproportionately severe. We suggest that future approaches to research in this area should aim to audit the full array of impacts of a number of representative invasive species, with a view to building an evidence base to support the global implementation of a precautionary approach to the release of aquatic freshwater non-native species.

Keywords: Invasive; non-native; freshwater; terrestrial; ecosystem; impacts.

Introduction

Invasive species are a significant component of human-caused global environmental change¹. Practically every biome, however remote, has been affected by invasive species to some extent^{1,2}. Most countries have recorded several hundred established non-native species - including invertebrates, vertebrates, plants, bacteria, and fungi - and even Antarctica has nearly 200 of them². Invasive species are a major driving force behind species extinctions^{3,4}, have detrimental effects on the biodiversity⁵ and genetic diversity⁶ of native species, and can alter the food web structure⁷ and the physical / abiotic properties^{8,9} of invaded ecosystems. Established non-native species can certainly have positive effects (e.g. the creation of fisheries; see below) but also substantial negative impacts, both on ecosystem services and

human wellbeing¹⁰ and on economies¹¹. For instance in the USA alone, excluding microbes and diseases of humans and livestock, there are 30,000 non-native species, and the small fraction of these considered ‘harmful’ is responsible for associated economic damages totalling over \$72.9 billion per annum¹¹.

The impacts of invasive species are globally ubiquitous, but some biomes and ecosystems are more invasible by, and prone to adverse impacts from, non-native species than others^{2, 12-14}. For example, a model of biodiversity scenarios for the year 2100 for a range of biomes, concluded that biotic exchange (i.e. ecosystem changes resulting from the introduction of non-native species) was likely to be the fourth largest driver of biodiversity change overall, but was relatively more important for freshwater than terrestrial ecosystems¹².

The intention of this opinion piece is to propose, and present the initial arguments supporting, the hypothesis that the negative impacts of invasive species are typically more severe, and more difficult to discern and manage, in freshwater ecosystems than in terrestrial ones. We compare a number of properties of those habitats found on land masses (therefore excluding marine environments), and outline the ways in which the intrinsic nature of aquatic freshwater ecosystems, and the human demands and uses thereof, support our proposition: that in terms of negative ecological and socioeconomic impacts, aquatic freshwater ecosystems are disproportionately at risk from, and affected by, invasion by non-native species than their terrestrial counterparts.

INVASIBILITY

The invasibility of a particular geographical location is a function of a number of factors, but principal determinants are the number of introduced species (‘colonisation pressure’¹⁵, which operates at the community level), and the number of individuals of those species (‘propagule pressure’, operating at the population level), and how well those individuals survive in the new location - which in turn is a function of a species’ intrinsic nature and the environment into which it is introduced². As a general rule, all else being equal, the more species introduced, the more that become established in that area^{2, 15}. It is the comparative ease with which not only single species (commonly from aquarium releases in which large, healthy specimens are released¹⁶) but also relatively intact communities - containing 100s-10,000s of individuals of 10s-1000s of pelagic and benthic aquatic species (e.g. from boat wells) - are transported, and the lack of comparable vectors for terrestrial communities, that make freshwater ecosystems disproportionately at risk of invasion¹⁷. Vectors for the introduction of non-native species into these ecosystems include: ballast water; fish bait buckets; boats, including their live wells, boat trailers and hulls; shipments of fishes, invertebrates, and macrophytes for aquarium hobbyists, aquaculturists, and water gardens¹⁷. Such vectors can be crudely divided into those that introduce non-native species into a new geographic location from a long distance (particularly ballast water - on any given day several thousand of species are moved around the planet in ballast tanks¹⁸ - and aquarium / ornamental trades, which are largely unregulated¹⁶), and those that allow the secondary spread of organisms between lakes and throughout river networks.

Once introduced, secondary spread, or dispersal of invasives from the introduction point, is facilitated by the comparative lack of dispersal barriers in freshwater ecosystems¹⁷, or vectored by a number of agents^{19, 20}. Species can spread from the invasion point through direct water connections²⁰ and the flow of rivers can aid colonisation, in much the same way that the effects of an intravenous injection can spread quickly throughout a body: average dispersal rates of six invasive species in the Rhine have been shown to be between 44–112 km year⁻¹, with substantially shorter time lags in colonisation for species that arrived in upstream sections compared with species initially arriving in downstream areas²¹. Alternately

species may be vectored by larger animals (e.g. water birds, livestock or deer moving between river catchments or ponds²⁰), or by human activities. In the latter case boats are heavily implicated in increasing both the rate and spatial scale of secondary spread, both trailered - when transported overland between water bodies - and through in-water transport. One study predicted 170 dispersal events of zebra mussels (*Dreissena polymorpha*) from boats from one primary public launch location on Lake St. Clair in Michigan, USA, over a summer season¹⁹, and another found a total of 321 individuals comprising at least 15 different species of zooplankton in the standing water in vessels travelling into Lake Simcoe, Canada²².

In addition to the above accidental routes of release, many species have been deliberately introduced. 582 non-native spawning fish and lamprey species are known to have extant populations across 17 countries, and of these 375 were deliberately introduced²³. In the UK the American signal crayfish (*Pacifastacus lenisusculus*) was deliberately introduced to Britain in 1976 to serve as a fishery and had colonised more than 250 British waters by 1988²⁴. (As an aside, despite the colossal numbers of signal crayfish now present in British waters, the vast majority of crayfish consumed in the UK are imported from China²⁵.)

Given the wealth of sources for unintentional and intentional release of non-native species into freshwater ecosystems, the facility with which these invasives may be secondarily spread, and the lack of comparable whole-community vectors for terrestrial ecosystems, we suggest that aquatic habitats are plausibly disproportionately invasible by, and therefore susceptible to, impacts from non-native species¹².

BIODIVERSITY

Aquatic freshwaters are substantially more biodiverse than would be expected from the area that they occupy. Surface freshwater habitats contain only around 0.01% of the world's water and cover 0.8% of the Earth's surface²⁶, but approximately 6% of every species currently described by scientists, 9.5% of all known animal species, and a third of the world's vertebrates (including approximately 40% of global fish diversity), are confined to freshwater^{27, 28}. Moreover freshwater habitats tend to be insular (in that given basins may be hydrologically, and so biotically separate from others), which has led to the evolution of biotas with high endemism and high species turnover between basins²⁹, and this in turn may make them susceptible to invasive species¹². Studies making direct comparisons between extinction rates of terrestrial and freshwater ecosystems are few, but one attempt to construct a model predicting the recent and future extinction rates for a variety of North American terrestrial and aquatic faunal groups, showed that the projected mean future extinction rate for freshwater fauna was approximately five times greater than for terrestrial fauna, and three times the rate for coastal marine mammals³⁰. The authors noted that at least 123 North American freshwater fishes, mollusks, crayfishes, and amphibians have already gone extinct since the beginning of the 20th century, and that this estimate was undoubtedly conservative due to the extinction of species before their discovery. The threats to global freshwater biodiversity underpinning these rates fall into five categories: overexploitation; water pollution; flow modification; destruction or degradation of habitat; and invasion by exotic species^{27, 30}. While invasive species constitute only one of a suite of threats to freshwater biodiversity, the wider point remains that freshwaters are uniquely biodiverse per unit area, relative to their terrestrial surroundings. To quote one author, "Not surprisingly, considering their landscape position and value as a natural resource, freshwaters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems"²⁷, and the impact of invasive species is one primary cause of these uniquely rapid declines.

ECOSYSTEM CHANGES

Invasive species not only have impacts on individual plants and animals but can also transform entire ecosystems by altering resource availability, disturbance regimes, or habitat structure. Examples from terrestrial habitats are many, e.g. a nitrogen-fixing tree, *Myrica faya*, in Hawaii has a dominant influence on the soil chemistry and productivity through its ability to enrich soil at a rate 90 times greater than native plants, and promotes populations of non-native earthworms due to its shading and leaf litter². We suggest that freshwater ecosystems, however, may be more susceptible to such broad environmental alterations simply because they represent the interface between multiple diverse abiotic and biotic components. A perhaps useful concept is that freshwaters represent “ecotonal” habitats, zones of transition between adjacent ecological systems, in this case operating at the terrestrial/aquatic interface, with key roles in regulating the flow of water and materials across the landscape³¹. From a biological perspective freshwater ecotones form sharp transitions and linkages from terrestrial habitats to riparian and aquatic habitats, and between their relevant physical substrates and environments (e.g. from river banks and riverbed to water), and typically occur across a relatively small (often tens of meters or less) distance, while longitudinally (i.e. upstream-downstream) they form continuous features that ramify through the landscape³¹. The ecotonal nature of these ecosystems means that freshwater invasive species are particularly likely to have not only direct effects on other species but also effects on the physical environment that can indirectly affect a broad suite of other aquatic species^{32, 33}. For example, invasive signal crayfish (transported from North America to Britain) have well studied direct negative effects on a large array of native flora and fauna³⁴, but also appear to influence yields of suspended sediment in invaded water courses⁹. Signal crayfish can be extraordinarily numerous in invaded habitats (see “Hidden Problems” below), and a wide range of their activities, including feeding, walking, fighting and burrowing, can mobilise sediments³⁵⁻³⁷ (see Fig. 1). Laboratory experiments have demonstrated direct influence of signal crayfish on mobilisation of pulses of fine sediment through burrowing into banks and fine bed material, particularly around the mid-point of the nocturnal period (when crayfish are most active), and similar patterns of pulsed fine sediment mobilisation, leading to an increase in ambient turbidity levels with a clear nocturnal trend, have been shown under field conditions⁹.

Signal crayfish are just one example of a growing number of invasive species known to alter the aquatic environment³². Zebra mussels, for example, can have the converse effect of substantially increasing water transparency in North American and European lakes, in turn stimulating the growth of benthic algae and macrophytes and altering physical habitat for invertebrates and fishes⁸. Any such widespread alteration in turbidity or clarity may have significant potential to affect the aquatic environment: aggradation of fine sediments can degrade aquatic habitats, reduce survival rates of fish and aquatic invertebrates^{38, 39}, alter community structure⁴⁰ and hamper river restoration efforts⁴¹ as well as reduce flow conveyance, with the potential to increase flood risks⁴². In addition, fine sediments play a significant role in the transport of both nutrients and pollutants within fluvial environments⁴³⁻⁴⁵, with implications for water quality.

SOCIOECONOMIC IMPACTS

The socioeconomic impacts from freshwater aquatic invasive species are vast. By one estimate, the percentage of the accessible global supply of renewable freshwater that is appropriated for human use approximates 30% (24,980 km³ of 82,100 km³), and this

percentage is likely to increase⁴⁶. Human uses for freshwaters include drinking and irrigation, waste disposal, transportation, power production, harvest of plants, fish, game, and minerals, and sites for homes, farms, and industries²⁹, in addition to a number of amenity, recreation and sporting uses. Aside from the huge direct economic value of humans' water use, the ecosystem services provided by freshwater ecosystems have been estimated at \$6.5 trillion USD/y, 20% of the value provided by all of the Earth's ecosystems⁴⁷. All of these uses are made of a resource that, as we state above, covers only 0.8% of the Earth's surface²⁶, therefore providing significant potential for freshwater invasive species to have wide-ranging negative effects, on almost any use and ecosystem service, while invading a comparatively small area. These impacts range from those with fundamental implications for human survival (e.g. those affecting availability of water for drinking and irrigation) to those which are indirect and difficult to foresee, but which nonetheless may have substantial socioeconomic costs. An example in the first category is the "draw down" of water reserves by water hyacinth (*Eichhornia crassipes*), which has an exceptional rate of evapotranspiration, in the Nile region, resulting in one tenth of the average available water (7 billion m³ of water per year) being lost from the river before control efforts were implemented⁴⁸. As an example of an indirect, unforeseen cost, Eurasian watermilfoil (*Myriophyllum spicatum*) invasions of lakes in Wisconsin have been shown to decrease average land values for lakefront properties by 13% on average, in effect meaning that lakefront property owners are willing to pay more than \$28,000 for a property on a lake free of milfoil, all else being equal⁴⁹.

A given invasive species can have impacts that affect a broad-spectrum of human enterprises. Possibly the most (in)famous example of a freshwater invasive with wide ranging negative effect is the zebra mussel in the Northern USA Great Lakes. Among other effects it affects supplies of freshwater by clogging intake pipes, causing \$69,070,780 of management expenses over a six year period to 1995; it affects water purification through filter feeding activities which impart odour in drinking water, with a cost of \$323,000 yr⁻¹ to remove the taste and smell; it affects food sources by changing light conditions and competing with fish for zooplankton, causing \$32.3 million yr⁻¹ in net costs to aquaculture; it threatens tourism and recreation (an industry worth \$4 billion per annum) through covering beaches, boats, docks and piers, causing cyanobacterial blooms, and increasing organochlorine and heavy metal concentrations in some recreational fishes and the ducks that prey on them¹⁰. Similarly, in the UK, floating pennywort (*Hydrocotyle ranunculoides*), introduced in the 1980s from the aquatic plant trade, forms dense vegetative mats that out-compete most native aquatic plants in slow moving channels, resulting in water courses becoming non-navigable and useless for fishing, and total annual costs to tourism and for management are estimated as £25,467,000; current annual estimated costs to the British economy of signal crayfish (which do *not* include any potential costs resulting from their sediment-mobilisation ability, which are not sufficiently quantified but which potentially include costs from biodiversity loss, pollutant mobilisation and flood risk⁹) are estimated as £2,689,000⁵⁰.

HIDDEN PROBLEMS

We propose that one key distinction between freshwater aquatic invasive species and terrestrial invasive species is that the former often have impacts that while certainly substantially damaging and widespread, are particularly difficult to detect. This difficulty may stem from a combination of the nature of the impacts, which are often diffuse in nature, and the observation that events occurring below the water's surface are simply more difficult to detect. As an example of diffuse impacts, Fig. 1 shows a schematic of how local increases

in sediment yield resulting from the behaviour of individual American signal crayfish might be expected to have extensive impacts, with considerable management implications, when multiplied across whole catchments. As an example that to the majority of the human population, many freshwater invasives themselves are simply not as detectable as their terrestrial counterparts, invasive American signal crayfish (*Pacifastacus leniusculus*) populations can reach estimated densities of 0.9 - 20 individuals per square metre⁵¹⁻⁵³, and a recent capture-mark-recapture study of four 100 m lengths of lowland UK rivers made 27,354 captures of 15,793 individual adult crayfish over 64 days of fieldwork (with uncountable juvenile individuals remaining uncaptured)⁵⁴. If these densities were to occur in a given terrestrial UK habitat it seems likely, in our opinion and to paraphrase one colleague, that “People would be out destroying crayfish by any means possible”. And it appears equally likely that considerably greater legislative and management resources would currently be targeted at preventing their introduction and facilitating their removal. While invasive crayfish are certainly the focus of control efforts⁵⁵, the UK public remains largely ignorant of their presence, and current legislation is far from optimised to prevent further invasions⁵⁶.

These observations appear to be part of a wider trend with respect to freshwater communities. Data on the population status or extinction rates of freshwater biota are biased in terms of geography, habitat types and taxonomy, and most populations and habitats in some regions have not been monitored at all²⁷. A comprehensive global analysis of freshwater biodiversity, comparable to those available for terrestrial systems, is lacking - and indeed, for reasons related to the difficulty of studying and quantifying freshwater species, it is not possible accurately to estimate or project extinction rates of the majority of freshwater biodiversity using the approaches applied to terrestrial biota²⁷. Likewise global awareness of the need to conserve freshwater biodiversity appears limited to the extent where a study showed that between 1997 and 2001, only 7% of papers in Conservation Biology was concerned with freshwater species or habitats⁵⁷. To quote the author of that study, “Some specialized journals...feature articles on freshwater biodiversity and conservation...but the paucity of freshwater research in Conservation Biology suggests that the mainstream conservation community has not given this critical issue the attention it requires.”⁵⁷

Conclusion

The intention of this opinion piece was to construct an hypothesis that aquatic freshwater ecosystems are disproportionately likely to suffer negative impacts from invasive species than are terrestrial ecosystems. We approached this by providing initial arguments supporting our hypothesis, but without intending to provide a definitive test of it. Overall, our argument is necessarily one of degree rather than kind. All ecosystems to some extent to suffer biodiversity impacts¹² and socioeconomic impacts^{11, 50} from invasive species, and many terrestrial ecosystems have been physically altered by invasive species, with knock-on consequences for their co-occurring biota¹. We argue, however, that freshwater ecosystems are inherently more invasible, more biodiverse and more at risk of ecosystem-wide changes (due to their ecotonal nature) than their terrestrial counterparts, and, given the vast array of human pressures on, and uses of, freshwater habitats, and their constituent biodiversity, the potential for socioeconomic impacts - including those that threaten lives and livelihoods - resulting from disruption by invasive species is concomitantly vast.

Within this context there is an apparent disconnect between, on one hand, the highly biodiverse nature of freshwaters and the severity of the impacts of freshwater invasive species, and on the other a comparative lack of global research on freshwater biodiversity^{27, 57} and a seemingly passive global attitude towards the prevention of invasions / the implementation of early-stage post-invasion responses by resource managers^{16, 58, 59}. For

example, a principal source of invasions, the ornamental aquarium trade, remains largely unregulated - and notorious invaders such as water hyacinth remain freely available for purchase online, although banned in many countries and states¹⁶ - and there remain “...considerable policy questions as to what constitutes a ‘sufficiently protective’ ballast water discharge standard...” with respect to reducing the likelihood of future invasions⁶⁰. This disconnect is perhaps symptomatic of the final property of freshwater invasive species we identify above: the often hidden and diffuse nature of their presence and impacts.

In short our hypothesis is that a number of factors intrinsic to freshwater ecosystems predispose them to disproportionately severe, and disproportionately difficult to detect, impacts from invasive species (as well as from numerous other anthropogenic sources). A suitable response to this situation might comprise a three-fold approach, incorporating: 1) a renewed research focus, aimed at auditing the full range of all impacts of a selection of freshwater invasive species, to catalogue and understand the full ecological and socioeconomic costs of their presence; 2) using the evidence thus obtained to derive steps for mitigation and solution of the issues identified (where this is possible - many aquatic invasive species are notably resistant to mitigation efforts), and; 3) again using the scientific evidence as a basis, an appeal to the precautionary principle, which here might dictate substantial legislative curbs to the currently ubiquitous sources of introduction for freshwater invasive species, with a view to drastically reducing the rate at which global freshwaters are being invaded.

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Figure captions

Figure 1 Reproduced with permission from Harvey GL et al³⁷. A conceptual model of the impacts of American signal crayfish on the physical structure of river systems, from the micro scale to the catchment scale, demonstrating how the behaviour of individuals might influence the local environment, which in turn may lead to impacts on sediments at the reach and catchment scale. CPOM and FPOM stand for coarse and fine organic particulate matter, respectively.