Influence of biogeographic origin and taxonomic relatedness on the impacts of introduced aquatic species

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Abstract

Rates of species invasion are rising globally, particularly in freshwater ecosystems. The impacts of only a small fraction of these invasions have been studied, and some have been found to cause substantial ecological and socio-economic damage. Nevertheless, there have been recent claims that the impacts of non-native species have been exaggerated, that native species have an equal propensity to cause damage, and therefore the biogeographic origins of species should not be considered in management decisions. Here, I address these claims by comparing the socio-economic impacts of native and non-native species in freshwater systems. Using data from North American and European watersheds, I find that non-native species are five times more likely than natives to become pests.

Another major issue concerning the impacts of non-native species is that managers lack predictive tools for prioritizing invasion threats, because very few general correlates of impact have been identified. The functional distinctiveness of a non-native species within the invaded assemblage has been proposed as a predictor of its impact on native species populations. Using a global dataset of non-native freshwater molluscs and taxonomic relatedness as a proxy for functional similarity, I find that novel taxa comprise disproportionately large numbers of high-impact invaders. Moreover, more taxonomically distant taxa have the highest proportions of high-impact species. These results support the use of taxonomy and biogeographic origin in invasion risk assessment.

Résumé

Les taux d’invasions d’espèces sont en hausse dans le monde, et particulièrement dans les écosystèmes d’eau douce. Seuls les impacts d’une petite fraction de ces invasions ont été étudiés. Il a été démontré que certaines d’entre elles peuvent causer des dommages environnementaux et socioéconomiques considérables. Toutefois, certains écologistes suggèrent que l’impact des espèces non indigènes pourrait avoir été exagéré. Selon eux, les espèces indigènes auraient la même propension à causer des dommages environnementaux et socioéconomiques. L’origine biogéographique d’une espèce ne devrait alors pas être considérée lors d’une prise de décision. Je tente ici de vérifier la validité de ces affirmations en faisant la comparaison des impacts socioéconomiques des espèces indigènes et non indigènes dans les écosystèmes d’eau douce. En analysant des données provenant de bassins d’eau douce nord-américains et européens, il s’avère que les espèces non indigènes ont cinq fois plus de chances de devenir nuisibles.

Un problème majeur relié à l’impact des espèces invasives est que les preneurs de décisions manquent d’outils de prédiction leur permettant de prioriser les menaces d’invasion. Le caractère distinctif de la fonction écologique d’une espèce non indigènes au sein de la communauté envahie à été proposé comme prédicteur de son impact sur la population indigène. En construisant un ensemble de données mondial sur les mollusques non indigènes et en utilisant la parenté phylogénique comme indicateur de la similarité fonctionnelle des espèces, il ressort que les taxons nouveaux sont plus susceptibles de devenir des envahisseurs à haut impact. De plus, les taxons les plus distants phylogéniquement ont la plus haute proportion d’espèces envahissantes à haut impact. Ces résultats soutiennent l’utilisation de la phylogénie et de l’origine biogéographique pour l’évaluation des risques associés à une invasion par une espèce non indigène.

Preface

This thesis has been written in the manuscript-based format as permitted by McGill University regulations. This thesis is a product of my own independent research conducted under the supervision of Professor Anthony Ricciardi at McGill University. Dr. Ricciardi provided guidance, helped develop research ideas, and edited written work.

Contribution of authors

Chapter 1, *Are non-native species more likely to become pests? Influence of biogeographic origin on the socioeconomic impact of freshwater organisms,* was accepted by the peer reviewed journal Frontiers in Ecology and the Environment, and is currently in press. I developed the methods for this project, performed the literature search and statistical analyses, and prepared the manuscript. My coauthor, Dr. Anthony Ricciardi, aided in the conception of the research project and provided editorial and critical feedback on the manuscript.

Chapter 2, *Influence of taxonomic relatedness on the ecological impact of freshwater molluscs,* is being prepared for submission to Diversity and Distributions. I developed the methods for this project, performed the literature search, statistical analyses, and prepared the manuscript. My coauthor, Dr. Anthony Ricciardi, aided in the conception of the research project, development of methods, and provided editorial and critical feedback on the manuscript.

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(WP), North Africa and Middle East (ME), Afrotropics (AF), Oceania (OC).

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Figure 3. Numbers of high- and low-impact non-native molluscs that belong to a novel or shared (A) genus, (B) family, and (C) order. Percentages above bars indicate proportion of high-impact species. Asterisk indicates significant difference in the proportion of high and low impact species between taxonomic relatedness categories ($p<0.05$).

General introduction

Extent and impact of biological invasions

A *biological invasion* is the introduction and establishment of a species beyond its historic native range (Williamson 1996). Owing to natural mechanisms of organismal dispersal, such events have occurred throughout the history of life; but over the past several centuries, natural biogeographic barriers to dispersal have been compromised by human travel, trade, and landscape alterations (Vitousek *et al.* 1997, Rahel 2007). Consequently, invasions now occur at rates that are orders of magnitude greater than prehistoric rates (Ricciardi 2007). Even seemingly remote areas of the planet are vulnerable to invasion (e.g., Usher 1988, Frenot *et al.* 2005), and most countries report 10^3 to 10^4 established non-native species (Vitousek *et al.* 1997). As the world's economies continue to expand and globalize, so too will vectors of invasion (Cohen and Carlton 1998, Meyerson and Mooney 2007, Hulme 2009, Essl *et al.* 2011). Given the unprecedented rate and spatial scale of the phenomenon, modern invasions are considered to be a form of anthropogenic global change (NRC 2000, MEA 2005, Ricciardi 2007).

A variety of vectors permit the inadvertent transport of species beyond their native range (Carlton 2003), but species introductions are not exclusively accidental byproducts of transportation systems. Humans place economic value on many non-native species, and thus have intentionally moved and cultivated them in new regions for economical or aesthetic purposes (e.g., agriculture, livestock, aquaculture, pet trade, ornamental trade, and biological control; Carlton

2003). There have also been recent proposals to move species beyond their native range in order to enhance resources in a target region (Briggs 2008) or for conserving particular taxa deemed to be threatened by climate change (Hoegh-Guldberg *et al.* 2008), in spite of abundant evidence that even well-planned introductions often have unintended consequences (e.g., Spencer *et al.* 1991, Simberloff and Stiling 1996, Knapp *et al.* 2001, Ricciardi and Simberloff 2009).

The impacts of most species introductions – intentional or unintentional – have not been documented (Parker *et al.* 1999, Ricciardi *et al.* 2013). Some effects are considered to be highly positive to some stakeholders (Schlaepfer *et al.* 2011). However, a burgeoning number of cases demonstrate that non-native species can cause local and global extinctions of native species, alter habitat structure and ecosystem function, enhance disease transmission, create new pathways of contaminant cycling, and damage ecosystem services associated with agriculture, forests, fisheries and water quality (Mack *et al.* 2000, Clavero and Garcia-Berthou 2005, Pimentel *et al.* 2005, Ricciardi and MacIsaac 2011). A severe case is the introduction of the Eurasian zebra mussel, *Dreissena polymorpha* to the Great Lakes in the mid-1980s. Within a few years of its discovery, it had caused significant ecological and economic damage by fouling hydroelectric and water supply systems (Ram *et al.* 1992) and reducing native mussel populations (Schloesser *et al.* 1996, Ricciardi *et al.* 1998). Several non-native crayfish species have transformed invaded freshwater systems, outcompeting native crayfish species (Capelli and Munjal 1982) and altering zoobenthic and littoral community structure (Lodge *et al.* 1994, Gherardi 2007).

Initially introduced for aquaculture purposes, North American crayfish species have transmitted the crayfish plague (*Aphanomyces astaci*) to commercially important European crayfish populations, resulting in massive population declines and economic loss throughout Europe (Westman 2002). As these examples illustrate, non-native species can have far-reaching and irreversible consequences.

Predicting the impacts of invaders: a priority for effective management

The majority of species that are introduced to a region do not establish self-sustaining populations; of those that do so, only a fraction appears to cause damage (Williamson and Fitter 1996, Ricciardi and Kipp 2008). From a management perspective, it is crucial to identify those species that pose the greatest risk to recipient regions, allowing more efficient allocation of resources for prevention and mitigation of undesirable impacts (Byers *et al.* 2002). There has been substantial progress in forecasting establishment success (Kolar and Lodge 2001, Holle and Simberloff 2005, Lockwood *et al.* 2005). However, the invasiveness (colonization ability) of a species is not necessarily correlated with its ecological impact potential (Ricciardi and Cohen 2007); therefore, models that explicitly predict impact are also needed for risk assessment. The impact of an invader can vary greatly across its invaded range, owing to context dependent factors such as local biotic and abiotic conditions (Ricciardi *et al.* 2013). Consequently, there exist very few methods for predicting impact (Simberloff *et al.* 2013). Although invasion history of a species, if sufficiently documented, can be used to develop specific predictive models (Ricciardi 2003), general models of impact – even “rules of thumb” –are rare (Ricciardi *et al.* 2013). One promising approach to identifying and testing predictable patterns is to statistically relate impact to traits of both the invader and the recipient community in combination (e.g., Ricciardi and Atkinson 2004, Strauss *et al.* 2006). This approach is applied to a hypothesis in Chapter 2.

Given the current paucity and practical limitations of predictive tools, precautionary approaches have been advocated as the most effective strategy for managing non-native species impact; indeed, prevention or intervention at early stages of the invasion process is more economically viable than managing the chronic costs of an invasion (Leung *et al.* 2002, Simberloff *et al.* 2013). Prevention, eradication, and control of non-native species have been integrated into numerous legislative and conservation agendas, making non-native species a focal point of many research and management programs (e.g., U.S. National Invasive Species Act; EU Biodiversity Strategy; Canadian Aquatic Invasive Species Network).

Do non-native species cause greater impacts than natives? An emerging controversy

Reacting to this apparent management prejudice against non-native species, some ecologists and philosophers have argued that their impacts are overstated (Sagoff 1999, Davis *et al.* 2011) and, moreover, native species are just as likely to be invasive pests; so the biogeographic origin of a species should have no bearing on management decisions (Davis *et al.* 2011, Valéry *et al.* 2013).

Widespread acceptance of this argument would force reconsideration of current legislation and alter management practices that employ a precautionary approach to invasions in order to protect biodiversity and biosecurity. The argument is apparently bolstered by criticisms of the native/non-native dichotomy (Sagoff 1999, Davis *et al.* 2011, Valéry *et al.* 2013). Of course, the "nativeness" of a species is more accurately a continuous variable that depends on temporal and spatial scope (Usher 2000, Carthey and Banks 2012); however, this simple dichotomy is still usefully informative. Recent quantitative studies suggest that non-native species pose a higher risk to ecosystem function and inflict greater damage to native populations than do their native counterparts (Simberloff *et al.* 2012, Paolucci *et al.* 2013). The disparity in frequency and severity of ecological impacts between native and non-native species was attributed to the recipient community's lack of co-evolutionary experience with the invader (Paolucci *et al.* 2013), which may promote naïve prey communities and reduced predation and parasitism of the invader (Diamond and Case 1986). Expanding such quantitative native/non-native comparisons is necessary for addressing Davis *et al.* (2011) claim that biogeographic origin (and, by implication, evolutionary experience) has no useful basis in management.

Evolutionary naïveté as a mediator of invasion impact

Even among invaders, the degree of "alienness" of a species within its invaded region may also mediate effects. Here, the term can be used to denote the degree of evolutionary divergence between the invader and the recipient community. Communities lacking native species that are functionally similar to the invader are hypothesized to be subjected to more severe impacts (Diamond and Case 1986). This hypothesis, termed evolutionary naïveté has been almost exclusively explored in terms of impacts on biodiversity. Numerous examples exist for cases involving introduced pathogens and parasites (Reynolds 1988, Tompkins *et al.* 2002, Rosenkranz *et al.* 2010). Insular habitats are perhaps the best model systems to study naïveté. For example, introduced rats have decimated native avifauna on oceanic islands worldwide (Long 2003, Blackburn *et al.* 2004), because native species on these islands have no adaptation to deal with them; however, such impacts have not been observed on islands where native rats or land crabs (the functional equivalent of scavenging rats) are present (Atkinson 1985), presumably because of selection for defenses to reduce nest predation (Diamond and Case 1986). A burgeoning number of cases have been documented from freshwater lakes and river basins – insular systems where evolutionary naïveté also appears to operate strongly, especially with respect to introduced predators (Ricciardi and Atkinson 2004, Cox and Lima 2006, Ricciardi and MacIsaac 2011). Indeed, the bulk of evidence on evolutionary naïveté from these ecosystems involves direct consumptive effects (i.e., predation, herbivory). Genetic interference (i.e., hybridization, introgression) is a clear exception to this hypothesis (Ricciardi and Atkinson 2004); however, it is not obvious how other mechanisms of impact would be influenced by the absence or presence of functionally similar species. Competition, for example, may be influenced in a variety of ways. Direct competition would presumably be greater among functionally similar species (e.g., aggression and territoriality among crayfish; Capelli and Munjal 1982), but is this also true for exploitative or apparent competition? A functionally distinct invader may utilize resources in a novel manner thereby indirectly competing with native species.

The evolutionary naïveté hypothesis has explanatory power, but has not been employed for predictive purposes in risk assessment. This is because quantifying functional similarity would involve comparison of multiple life history parameters, and as such, has not been extensively tested. An alternative approach uses taxonomic or phylogenetic relatedness as a proxy for functional similarity; this was first used to predict impacts of aquatic invasions (Ricciardi and Atkinson 2004) and subsequently to predict the pest status of nonindigenous plants in California (Strauss *et al.* 2006). The rationale for using taxonomic or phylogenetic relatedness is based on evidence that closely related species tend to be more functionally similar (Harvey and Pagel 1991, Burns and Strauss 2011) and that genetic divergence increases with phylogenetic distance (Thorpe 1982). It is difficult to identify an ecological function that is lacking in a community until the effects of the invader becomes apparent. Novel taxa, on the other hand, can be identified before the introduction event occurs; for example, a risk assessment could consult a list of native species in the region and compare probable future, or recently established invaders.

Thesis objectives

This study examines the influence of biogeography and taxonomic relationships on the ecological and socio-economic impacts of freshwater flora and fauna. Freshwater systems experience exceptionally high rates of invasion (Ricciardi 2006, Jackson and Grey 2013), yet there exist very few predictors of impact (but see Ricciardi and Atkinson 2004, Keller *et al.* 2007). This is a cause for concern because freshwater systems are experiencing rapid rates of biodiversity loss (Ricciardi and Rasmussen 1999) and are disproportionately affected by high-impact invaders (compared to marine systems; Ricciardi and MacIsaac 2011). Moreover, freshwater systems provide essential ecosystem services (Postel and Carpenter 1997) and support socioeconomic activities that are vulnerable to being impacted by invasive pests (Dudgeon *et al.* 2006). Thus, there is theoretical and applied value for using freshwater systems as model systems for testing hypotheses regarding invasion impact.

In Chapter 1, I evaluate the claim by Davis *et al.* (2011) that there is no difference in the propensity for native and non-native species to cause harmful effects. Here, data on socio-economic pests of North American and European freshwater habitats are used to test whether pest status is independent of biogeographic origin. I hypothesize that non-native species, especially those from other biogeographic regions, will have a greater probability of reaching nuisance proportions.

Chapter 2 explores predictive applications of the evolutionary naïveté hypothesis. The relationship between taxonomic relatedness and ecological impact is tested using freshwater molluscs – a well-documented and globalized taxon. This study is the first to examine the predictive power of taxonomic relatedness at a large spatial scale using multiple levels of taxonomic resolution (genus, family, order). I predict that taxonomically novel invaders will be more likely to cause conspicuous population-level impacts, and further, this pattern will be more pronounced among species more taxonomically distant from native species in the recipient assemblage.

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Chapter 1

Are non-native species more likely to become pests? Influence of biogeographic origin on the socioeconomic impact of freshwater organisms

Abstract

Some ecologists have claimed that non-native species are no more likely than native species to cause ecological or economic harm. We evaluated this claim by testing whether the pest status of a species is independent of its origin, using data on freshwater plants and animals established in North America and Europe. Pests were defined as those whose presence resulted in socioeconomic damage. All species were classified on the basis of whether they are native to the continent, transplanted beyond their native range within the continent (transplant invaders), or non-native to the continent (foreign invaders). Non-native species comprised the majority (60%) of aquatic pests in North America and Europe and were 6 times more likely than native species to be pests. The incidence of pests was greatest among foreign invaders. These results counter the assertion that the potential for a species to cause socioeconomic damage is independent of its biogeographic origin.

Introduction

Rates of biological invasion are apparently increasing on a planetary scale (Ricciardi 2007), and many countries have recorded several hundreds to several thousands of non-native species established within their borders (Vitousek *et al.* 1997). Although the effects of most of these invasions have not been studied (Parker *et al.* 1999), it has been suggested that only a small fraction of them have strong negative impacts (Williamson and Fitter 1996). However, a burgeoning number of non-native species are deemed responsible for local and global extinctions of native species, disruptions to ecosystem functioning, enhanced disease transmission, and substantial damages to natural resources and ecosystem services associated with agriculture, forests, fisheries and water quality (Mack *et al.* 2000, Clavero and Garcia-Berthou 2005, Pimentel *et al.* 2005, Ricciardi and MacIsaac 2011). Nevertheless, some ecologists claim that non-native species have been unfairly targeted by scientists and managers, because such species may have positive effects that are often overlooked and, moreover, natives can also become invasive (Goodenough 2010, Davis *et al.* 2011, Schlaepfer *et al.* 2011). Specifically, critics have argued that non-native species are no more likely than natives to cause ecological or economic harm and, therefore, the biogeographic origin of a species does not merit consideration in management decisions (Davis *et al.* 2011, Valéry *et al.* 2013).

Researchers have begun to address these criticisms quantitatively. Simberloff *et al.* (2012) showed that non-native plants are 40 times more likely than native plants to be invasive –i.e. to spread aggressively and cause ecological or economic harm. In a meta-analysis, Paolucci *et al.* (2013) compared the impacts of native and non-native consumers (predators and herbivores) and revealed that non-native consumers caused more than twice as much damage to native prey populations. However, to our knowledge, no previous study has made a broad statistical comparison of the socioeconomic damage of native and non-native species.

Here, we compare the likelihood of native and non-native freshwater species to become socioeconomic pests. Using data on freshwater plants and animals in North America and Europe, we tested if the pest status of a species is independent of its biogeographic origin – i.e., whether it is native to the continent, transplanted beyond its native range within the continent, or non-native to the continent. We hypothesize that non-native species have a greater likelihood of becoming a pest and that the proportion of pests will be greatest among species foreign to continents, based on the following assumptions: 1) release from biotic constraints (e.g. adapted predators and parasites) can cause introduced species to achieve nuisance-level abundances (Cappuccino and Carpenter 2005, Hill and Kotanen 2009); and 2) species native to more distant regions are more likely to be ecologically novel and thus potentially more disruptive in their resource use in the invaded region (cf. Ricciardi and Atkinson 2004, Strauss *et al.* 2006).

Methods

Data Collection

Separate literature searches were conducted for North America and Europe using Web of Science spanning the years 1900 to 2010, inclusively. We used the following combination of search terms: (*pest* OR *nuisance* OR *harmful* OR *outbreak* OR *weed* OR *range expansion* OR *inva** OR *foul**) AND (**water** OR *aquatic*). Our search was limited to freshwater species – namely fish, vascular plants, and macroinvertebrates (excluding insects). To clarify impact details of species identified through the above sources, data obtained from the literature search were supplemented with those from specialized volumes or gray literature.

Owing to difficulties in assessing the socioeconomic costs of introduced species (Pimentel *et al.* 2000, 2005, Lovell *et al.* 2006), our study used a simple binary metric (pest/ benign) to categorize socioeconomic impact. Here, *pest* is defined as a species that interferes with human activities (e.g., recreation), negatively affects human health, or causes negative impacts to industry (Figure 1). This definition explicitly excludes the economic costs of management and eradication efforts. Any species that did not meet the above criteria was deemed *benign* by default, even if it had negative ecological or economic impacts in regions outside our study area.

All species, pest or benign, were then organized on the basis of their origin: *Foreign* invaders are species that are non-indigenous to the continent and have self-sustaining populations; *transplant* invaders are species that are indigenous to the continent, but have a self-sustaining population in an intracontinental region outside of their historical range; and *natives* are species that have occurred in a region historically and are thought to have evolved there. Total numbers of native, foreign, and transplanted species in North America and

Europe were obtained using online databases and published volumes (Table 1 & 2). The number of benign species for each taxon was determined by subtracting the number of pests from the total number of species in a given origin category.

Our study excludes pest organisms that were not identified to a taxonomic level sufficient to differentiate their origin. In some cases, it is unknown whether the species is native or exotic in all parts of its range. This is particularly true for certain bryozoans, whose native and introduced ranges are conflated owing to a poorly documented biogeography (Wood 2002). To err on the side of caution, we treated such cryptogenic species as natives in this study.

Analyses were conducted for North America and Europe separately, such that a species that occurs in both continents could potentially be listed as a pest in one and benign in another. Given that transplants are a subset of native species within a continent, these species are considered twice in our analysis: their pest status is evaluated in both their native and non-native (transplanted) ranges. The final data set included the total number of species in each continent organized by origin and pest status, arranged into 2x2 contingency tables and analyzed using Pearson's chi-square test without Yate's continuity correction (Haviland 1990). Pearson's residuals were observed to determine the direction and strength of relationships within each table.

Results

Our literature search located 2484 papers (1819 for North America, 665 for Europe). In total, 96 species were implicated in 113 accounts of pest occurrence (Table 3 & 4). The majority (60%) of pests were non-native in origin (i.e., transplant and foreign). After pooling data for North America and Europe, 5% of non-native species and 0.9% of native species were found to be socioeconomic pests. The relationship between pest status and species origin was statistically significant ($p<0.0001$; Figure 2).

In both North America and Europe, foreign species contain the highest proportion of pests, followed by transplants, and then natives (Figure 3a, b). Native species have significantly lower pest proportions than foreign species ($p<0.0001$) and transplanted species ($p<0.05$). In both regions, foreign species contain a higher proportion of pests than do transplants; however, this relationship is significant for North America ($p<0.0001$) but not for Europe ($p>0.51$).

Plants and animals exhibit a similar trend in which the proportion of pests is highest among species non-native to the continent, followed by transplants, and then natives (Figure 4a, b). Proportions of foreign, transplant, and native animal pests differ significantly from one another ($p<0.001$ for all comparisons; Fig. 4b). Among plants, foreign species are more likely than native species to be pests ($p<0.0001$); however, there are no significant differences between foreign and transplant invaders, nor between transplant invaders and natives (Fig. 4a).

Discussion

Our study counters the claim that the propensity of a species to cause undesirable impacts is unrelated to its biogeographic origin. In freshwater systems, non-native species are significantly more likely than native species to be socioeconomic pests – a pattern that is confirmed in both North America and Europe. These results are probably conservative, as our analysis ignored the ecological impacts of species and the costs associated with their management. In addition, economically important diseases may be transmitted through intentional species transfers (Gozlan *et al.* 2005, Peeler *et al.* 2011), but many such cases were excluded from our analysis owing to a dearth of definitive information on the species and regions through which diseases were spread.

Numbers of non-native species are increasing rapidly in many aquatic systems (Ricciardi 2006, Leuven *et al.* 2009, Marsden and Hauser 2009, Jackson and Grey 2012). It seems likely that the non-native species already established within North America and Europe will continue to expand their range at a greater rate than native species (cf. Simberloff *et al.* 2012), potentially adding further to the number of pests; the more widely distributed a non-native species, the more likely it will cause undesirable economic or ecological effects in at least some areas (Ricciardi and Kipp 2008). Moreover, currently benign species, native or non-native, will not necessarily remain so (Crooks 2005). Given that the invasiveness of native species appears to be linked to disturbance events (at least for plants; Cook 1990, Simberloff *et al.* 2012), continued habitat alteration and climate change may cause formerly-benign species to become problematic, although this may pertain to native and non-native species alike.

In North America, the highest frequency of pests is observed among non-native species that have been introduced from geographically distant regions. In Europe, however, the pest proportions that occur within foreign and transplanted species pools are not significantly different. Perhaps the distinction between foreign and transplant is not as relevant in Europe, because Europe is not isolated from other continents to the same extent as North America. Alternatively, this discrepancy may be attributable to a majority of European pests being plants (67%, compared to 57% in North America). Among animals, the relationship between pest status and native/non-native origin is magnified, and pest status is also dependent on the geographic scale of the introduction event (foreign/transplant). By contrast, the relationship is tenuous for plants, and this could be explained by differences in the nature of the economic impacts of plants and animals. The economic impacts of animals in North America and Europe appear to be derived primarily from consequences of ecological interactions (e.g., declines in sport fish populations, spread of pathogens); whereas, for plants, they relate to excessive growth (e.g., blocking waterways and impeding recreation). Native plants may become invasive owing to changes in human land use, nutrient pollution, or other disturbances that promote increased productivity (Cook 1990, Davis *et al.* 2000, Simberloff *et al.* 2012). Davis *et al.* (2000) hypothesized that plant invasions are limited by the availability of unused resources, which can be enhanced by disturbance. In contrast, the range expansion of introduced animals is far less dependent on disturbance events (Lozon and MacIsaac 1997).

Caveats

We endeavored to employ a method of data collection that would generate an unbiased sample of socioeconomic pest species. In our literature review, we used search terms that explicitly excluded any reference to origin; we consulted alien species databases only to confirm details on species already identified as pests through our initial search. Given these methods, our data set does not capture all problematic freshwater species, but rather a large subset of pests that occur in North America and Europe. The percentage of pests for all origin categories are equally conservative, therefore the observed differences in pest proportions illuminates real discrepancies in pest rates among origin categories.

A potential bias of this study is that non-native species are perhaps more likely to be discovered when they exhibit impacts, thus exaggerating their pest proportion. In recognition of this possibility, we restricted our study to conspicuous species groups (fish, vascular plants, and macroinvertebrates) that are well recognized in North America and Europe. When taxonomically problematic species (i.e., bryozoans, cnidarians, nematodes) are removed from the analysis, foreign and transplanted species still comprise the majority of socio-economic pests (64%) and remain significantly more likely to be a pest than are native species.

Another potential bias may be generated by increased attention to non-native species in recent decades. However, our study encompasses literature published over the past century, and we also included species that were historically pests but are not currently problematic (e.g., owing to effective management). Further, there is no reason to believe that the pest characteristics of native species are more likely to be overlooked than those of non-native species. For example, a major impact of some aquatic nuisance species is the fouling of anthropogenic structures such as pipes, intake screens, net cages, and boats. However, fouling species are usually studied without explicit consideration of their biogeographic origin (e.g., Callow 1993, Dubost *et al.* 1996, Wood 2005), presumably because their impacts alone were sufficient motivation to examine them. The same conclusion applies to the nuisance effects of aquatic weeds (e.g., Cook 1990).

Reasons for the pattern

In order for a species to become established outside its native range, it must overcome a series of biotic and abiotic barriers (Blackburn *et al.* 2011), which operate as a form of artificial selection that determines the non-native species composition in a region. As some key traits of successful invaders – e.g., high fecundity, asexual modes of reproduction, ability to colonize disturbed habitats (Rejmánek and Richardson 1996, Kolar and Lodge 2001, Drake and Lodge 2006) – are also common in aquatic pests (Pieterse and Murphy 1990, Keller *et al.* 2007), this selection regime may promote a higher frequency of nuisance species in freshwater systems. Furthermore, non-native species – particularly those from other biogeographic realms – are likely to encounter naïve recipient communities (Cox and Lima 2006) and, consequently, less effective predation and competition (cf. Hill and Kotanen 2009), which might explain why invaders belonging to taxa that have no native analogue in the invaded community tend to be more disruptive (Ricciardi and Atkinson 2004, Strauss *et al.* 2006).

Regardless of the reason for the observed pattern, this study complements one that examined invasive plants in the United States (Simberloff *et al.* 2012), and it counters claims that the native/non-native dichotomy is unjustified and that species should be targeted for management based solely on their observed impacts (Davis *et al.* 2011, Head 2012, Valéry *et al.* 2013). Another consideration is that the impacts of non-native species may change through time such that seemingly benign species may become problematic later (Crooks 2005, Strayer *et al.* 2006). This being the case, researchers (e.g., Blossey *et al.* 2001) have argued that a lack of impact studies should not prevent management action to stem the spread of non-native species, and such action is likely to be more beneficial if applied early in an invasion (Leung *et al.* 2002, Lodge *et al.* 2006).

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Table 1. Pest and benign species in North America.

	Foreign		Transplant		Native		References for total number of species per origin category
	Pest	Benign	Pest	Benign	Pest	Benign	
Macrophytes	17	190	3	81	17	627	Chambers *et al.* 2008; USDA 2012
Fishes	5	76	3	327	0	1061	Fuller *et al*. 1999; Leveque *et al*. 2005
Molluscs	6	35	0	23	0	813	Leveque *et al*. 2005; USGS 2012
Crustaceans	3	37	2	48	1	870	Leveque *et al*. 2005; USGS 2012
Bryozoans	2	1	0	2	5	22	Leveque *et al*. 2005; USGS 2012
Cnidarians	1	1	0	0	0	22	Leveque *et al*. 2005; USGS 2012
Total	**34**	**340**	**8**	**481**	**23**	**3415**	

Table 2. Pest and benign species in Europe.

	Foreign		Transplant		Native		References for total number of species per origin category
	Pest	Benign	Pest	Benign	Pest	Benign	
Macrophytes	12	84	2	20	18	479	Chambers *et al*. 2008; Hussner, 2012
Fishes	1	95	1	57	0	360	Leveque *et al*. 2005; Gherardi *et al*. 2009
Molluscs	2	31	1	13	1	176	Leveque *et al*. 2005; Gherardi *et al*. 2009
Crustaceans	4	101	1	44	0	445	Leveque *et al*. 2005; Gherardi *et al*. 2009
Bryozoans	0	14*	0	1*	3	19	Massard and Geimer, 2008; Gherardi *et al*. 2009
Cnidarians	0		1		0	15	Leveque *et al*. 2005; Gherardi *et al*. 2009
Nematodes	1		0		0	84	Leveque *et al*. 2005; Gherardi *et al*. 2009
Total	**20**	**325**	**6**	**133**	**22**	**1494**	

* refers to species counts of "other macroinvertebrates" in Gherardi, 2009.

Table 3. List of pest species in North American freshwaters. F= foreign invader; T= transplant invader; N= native.

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
Fredericella indica	bryozoan	N	Fouling of water supply systems	T.S. Wood, pers. comm.
Lophopodella carteri	bryozoan	F	Fouling of fish hatcheries, potential toxic threat	Tenney and Woolcott 1964; Collins *et al*. 1966
Paludicella articulata	bryozoan	N	Fouling of water supply systems	Smith *et al.* 2005
Pectinatella magnifica	bryozoan	N	Fouling of water supply systems	Wood 2010
Plumatella casmiana	bryozoan	N	Fouling of water supply systems	Wood 2005
Plumatella rugosa	bryozoan	N	Fouling of water supply systems	Wood 2005
Plumatella vaihiriae	bryozoan	F	Fouling of water supply systems	Wood and Marsh 1999; T.S. Wood, pers. comm.
Cordylophora caspia	cnidarian	F	Fouling of water supply systems	Folino-Rorem and Indelicato 2005
Bythotrephes longimanus	crustacean	F	Fouling of fishing lines	Boudreau and Yan 2004
Cercopagis pengoi	crustacean	F	Fouling of commercial fishing gear	MacIsaac *et al.* 1999
Eriocheir sinensis	crustacean	F	Damage to irrigation systems	Dittel and Epifanio 2009
Fallicambarus devastator	crustacean	N	Damage to livestock and farm equipment	Hobbs and Whiteman 1991
Orconectes virilis	crustacean	T	Damage to rice fields and irrigation systems	Grigarick and Way 1982
Procambarus clarkii	crustacean	T	Damage to rice fields and irrigation systems	Grigarick and Way 1982
Bithynia tentaculata	mollusc	F	Fouling of water supply systems	Keller *et al.* 2007
Corbicula fluminea	mollusc	F	Fouling of power plants	McMahon 1983
Dreissena bugensis	mollusc	F	Fouling of water supply systems	Benson *et al.* 2013
Dreissena polymorpha	mollusc	F	Fouling of water supply systems	Ram *et al.* 1992
Melanoides tuberculatus	mollusc	F	Pathogen, damage to pet-trade fish production	Mitchell *et al.* 2005
Pomacea canaliculata	mollusc	F	Damage to rice fields	Grigarick and Way 1982
Alosa pseudoharengus	fish	T	Sport fish declines	Couillard *et al*. 2008, Fuller *et al*. 2013b
Ctenopharyngodon idella	fish	F	Damage to fisheries	GSMFC 2003; Cudmore and Mandrak 2004
Gymnocephalus cernua	fish	F	Damage to fisheries	McLean 1993; Lovell *et al*. 2006
Hypophthalmichthys	fish	F	Hazard to recreational boating	USFWS 2007

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
molitrix				
Neogobius melanostomus	fish	F	Damage to fisheries	Fuller *et al.* 2013a
Petromyzon marinus	fish	T	Damage to fisheries	Waldman *et al.* 2004
Salmo trutta	fish	F	Damage to fisheries	Crawford 2001
Salvelinus namaycush	fish	T	Damage to fisheries	Varley and Schullery 1995
Alisma gramineum	macrophyte	N	Interference with irrigation systems	Anderson 1990
Alternanthera philoxeroides	macrophyte	F	Crowding of recreational waterways	Pan *et al.* 2007
Butomus umbellatus	macrophyte	F	Boating hazard	Cao *et al.* 2013
Cabomba caroliniana	macrophyte	T	Crowding of recreational waterways	Wilson *et al.* 2007
Ceratophyllum demersum	macrophyte	N	Interference with irrigation systems	Anderson 1990
Egeria densa	macrophyte	F	Crowding of recreational waterways	WSDE 2003
Eichhornia crassipes	macrophyte	F	Interference with irrigation systems, reduction of property value	Ding *et al.* 2006
Elodea canadensis	macrophyte	N	Interference with irrigation systems	Anderson 1990
Hippuris vulgaris	macrophyte	N	Interference with irrigation systems	Royer and Dickinson 1999
Hydrilla verticillata	macrophyte	F	Interference with irrigation systems, crowding of recreational waterways	Chilton *et al.* 2008
Hydrocharis morsus-ranae	macrophyte	F	Interference with irrigation systems, crowding of recreational waterways	Catling *et al.* 2003
Iris pseudacorus	macrophyte	F	Interference with irrigation systems, contact may result in skin irritation	Jacobs *et al.* 2010
Lemna trisulca	macrophyte	N	Crowding of recreational waterways	Royer and Dickinson 1999
Ludwigia repens	macrophtye	N	Interference with irrigation systems	Anderson 1990
Lythrum salicaria	macrophtye	F	Crowding of recreational waterways	Duncan *et al.* 2004
Myriophyllum aquaticum	macrophyte	F	Interference with irrigation systems	Anderson 1990
Myriophyllum heterophyllum	macrophyte	T	Crowding of recreational waterways, reduction of property value	Bailey and Calhoun 2008
Myriophyllum sibiricum	macrophyte	N	Interference with irrigation systems	Anderson 1990

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
Myriophyllum spicatum	macrophyte	F	Interference with irrigation systems, reduction of property value	Anderson 1990
Najas guadalupensis	macrophyte	N	Interference with irrigation systems	Blackburn and Weldon 1964
Nuphar luteum	macrophyte	F	Crowding of recreational waterways	Steward 1990
Nymphoides peltata	macrophyte	F	Crowding of recreational waterways	Darbyshire and Francis 2008
Pistia stratiotes	macrophyte	F	Crowding of recreational waterways	Dray and Center 2002
Phalaris arundinacea	macrophyte	F	Interference with irrigation systems	Kilbride and Paveglio 1999
Potamogeton crispus	macrophyte	F	Crowding of recreational waterways	Anderson 1990
Potamogeton foliosus	macrophyte	N	Interference with irrigation systems	Anderson 1990
Potamogeton nodosus	macrophyte	N	Interference with irrigation systems	Anderson 1990
Potamogeton pusillus	macrophyte	N	Interference with irrigation systems	Anderson 1990
Potamogeton richardsonii	macrophyte	N	Interference with irrigation systems	Anderson 1990
Ranunculus longirostris	macrophyte	N	Interference with irrigation systems	Anderson 1990
Salvinia molesta	macrophyte	F	Crowding of recreational waterways	Everitt *et al*. 2002
Stuckenia pectinata	macrophyte	N	Interference with irrigation systems and reservoirs	Slade *et al.* 2008
Stuckenia vaginata	macrophyte	N	Interference with irrigation systems, crowding of recreational waterways	Anderson 1990
Trapa natans	macrophyte	F	Crowding of recreational waterways	Hummel and Kiviat 2004
Typha angustifolia	macrophyte	T	Interference with irrigation systems	Anderson 1990
Typha latifolia	macrophyte	N	Interference with irrigation systems	Anderson 1990
Vallisneria americana	macrophyte	N	Crowding of recreational waterways	Catling *et al.* 1994

Table 4. List of pest species in European freshwaters. F= foreign invader; T= transplant invader; N= native.

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
Plumatella fungosa	bryozoan	N	Fouling of water supply systems	Khalanski 1997
Plumatella repens	bryozoan	N	Fouling of aquaculture systems	Dubost *et al.* 1996
Fredericella sultana	bryozoan	N	Fouling of water supply systems	Khalanski 1997
Cordylophora caspia	cnidarian	T	Fouling of water supply systems	Folino-Rorem and Indelicato 2005
Cercopagis pengoi	crustacean	T	Fouling of fishing lines	Krylov *et al.* 1999
Eriocheir sinensis	crustacean	F	Fouling of water supply systems; damage of irrigation systems	Wagley *et al.* 2009
Orconectes limosus	crustacean	F	Pathogen transfer causing damage to crayfish aquaculture	Holdich *et al.* 2009
Pacifastacus leniusculus	crustacean	F	Pathogen transfer causing damage to crayfish aquaculture	Holdich *et al.* 2009
Procambarus clarkii	crustacean	F	Pathogen transfer causing damage to crayfish aquaculture; damage to rice fields	Holdich *et al.* 2009
Bithynia tentaculata	mollusc	N	Fouling of water supply systems	Khalanski 1997
Corbicula fluminalis	mollusc	F	Fouling of water supply systems	Khalanski 1997
Corbicula fluminea	mollusc	F	Fouling of water supply systems	Khalanski 1997
Dreissena polymorpha	mollusc	T	Fouling of water supply systems	Karatayev *et al.* 1997; Khalanski 1997
Anguillicola crassus	nematode	F	Parasitic, damage to fisheries	Ashworth and Blanc 1997
Pseudorasbora parva	fish	F	Pathogen transfer causing damage to fisheries	Gozlan *et al.* 2005; Witkowski 2011
Salmo salar	fish	T	Pathogen transfer causing damage to fisheries	Johnsen and Jensen 1986
Alisma plantago-aquatica	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
Azolla filiculoides	macrophyte	F	Interference with irrigation systems	Ferreira *et al.* 1998
Ceratophyllum demersum	macrophyte	F	Interference with irrigation systems	Murphy *et al.* 1990
Crassula helmsii	macrophyte	F	Interference with irrigation systems	Sheppard *et al.* 2006
Eichhornia crassipes	macrophyte	F	Interference with irrigation systems	Murphy *et al.* 1990
Elodea canadensis	macrophyte	F	Fouling of water supply systems; crowding of recreational waterways	Sheppard *et al.* 2006
Elodea nuttallii	macrophyte	F	Interference with irrigation systems	Murphy *et al.* 1990
Equisetum fluviatile	macrophyte	N	Tainting of distillery reservoirs	Murphy *et al.* 1990
Glyceria maxima	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Heteranthera reniformis	macrophyte	F	Damage to rice fields	Cook 1990
Hydrocotyle ranunculoides	macrophyte	F	Crowding of waterways	Van De Wiel *et al.* 2009
Juncus bulbosus	macrophyte	N	Fouling of water supply systems; crowding of recreational waterways	Murphy *et al.* 1990; Brandrud and Roelofs 1995
Lemna gibba	macrophyte	N	Interference with irrigation systems	Ferreira *et al.* 1998
Lemna minor	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Ludwigia grandiflora	macrophyte	F	Interference with irrigation systems; crowding of recreational waterways	Sheppard *et al.* 2006
Ludwigia peploides	macrophyte	F	Interference with irrigation systems; crowding of recreational waterways	Sheppard *et al.* 2006
Menyanthes trifoliata	macrophyte	N	Tainting of distillery reservoirs	Murphy *et al.* 1990
Myriophyllum aquaticum	macrophyte	F	Interference with irrigation systems and water supply systems, crowding of recreational waterways	Sheppard *et al.* 2006
Myriophyllum spicatum	macrophyte	N	Interference with irrigation systems	Ferreira *et al.* 1998

Species	**Taxa**	**Origin**	**Socio-economic Impact**	**Reference**
Nymphaea alba	macrophyte	N	Boating hazard	Murphy *et al.* 1990
Nymphoides peltata	macrophyte	T	Interference with irrigation systems	Kelly and Maguire 2009
Phragmites australis	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Pistia stratiotes	macrophyte	F	Interference with irrigation systems	Sajna *et al.* 2007
Potamogeton natans	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Ranunculus fluitans	macrophyte	N, T	Fouling of water supply systems; crowding of recreational waterways	Murphy *et al.* 1990; Laughton *et al.* 2008
Ranunculus penicillatus	macrophyte	N	Damage to fisheries; increased flooding risk	Murphy *et al.* 1990
Rorippa amphibia	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Salvinia natans	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Stratiotes aloides	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Stuckenia pectinata	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990
Zannichellia palustris	macrophyte	N	Interference with irrigation systems	Murphy *et al.* 1990

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Figure 1. Examples of freshwater pest species: (a) The Eurasian quagga mussel (*Dreissena rostriformis bugensis*), a fouling pest in the Great Lakes and, more recently, in the western United States. (b) Water hyacinth (*Eichhornia crassipes*), a globally invasive pest of waterways. (c) Silver carp (*Hypophthalmichthys molitrix*), a hazard to recreational water users in the Illinois River (USFWS). (d) The bryozoan *Plumatella rugosa*, a native fouling pest in North America, shown here encrusting a submersible pump.

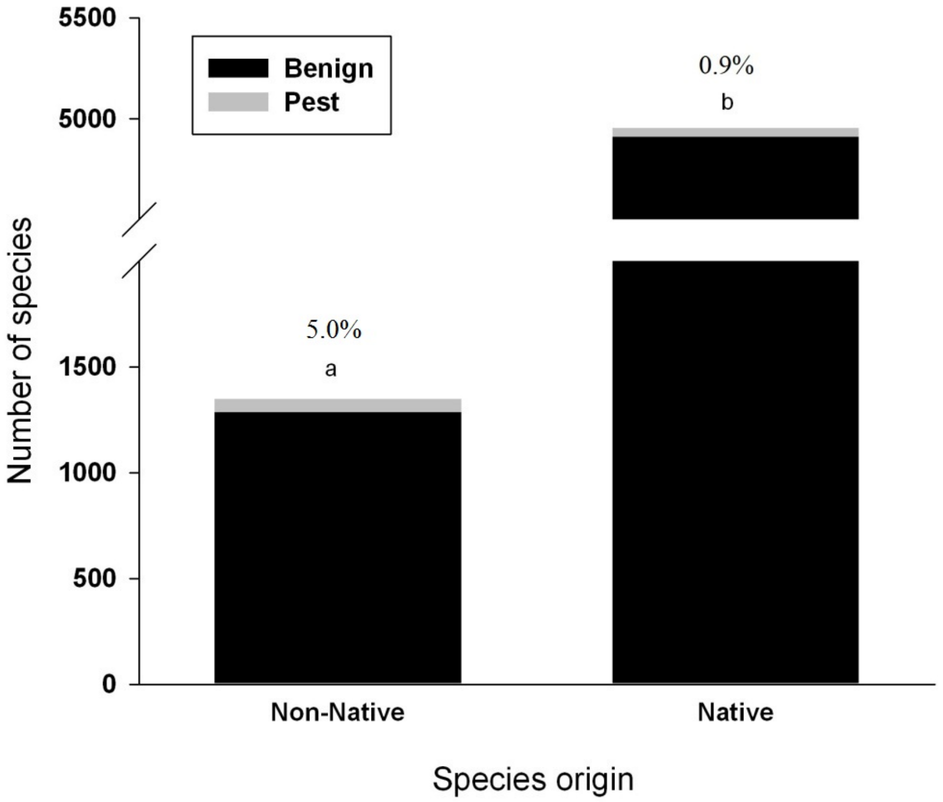

Figure 2. Number of freshwater pest and benign species organized by origin. Percentages above bars indicate proportion of pest species per origin category. Different letters above bars indicate significant differences in proportions ($p < 2.2E-16$).

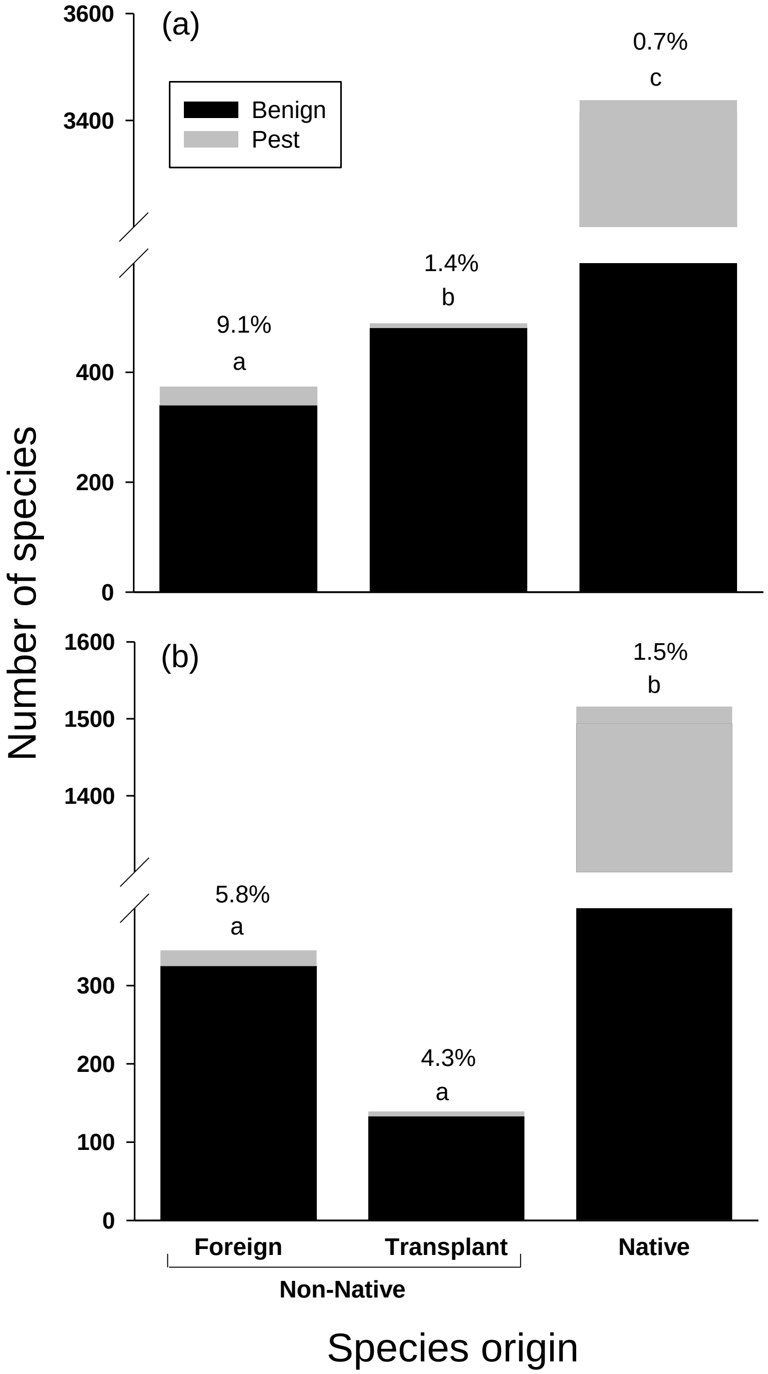

Figure 3. Number of freshwater pest and benign species in Europe (A) and North America (B). Percentages above bars indicate proportion of pest species per origin category. Different letters above bars indicate significant differences in proportions (p<0.05).

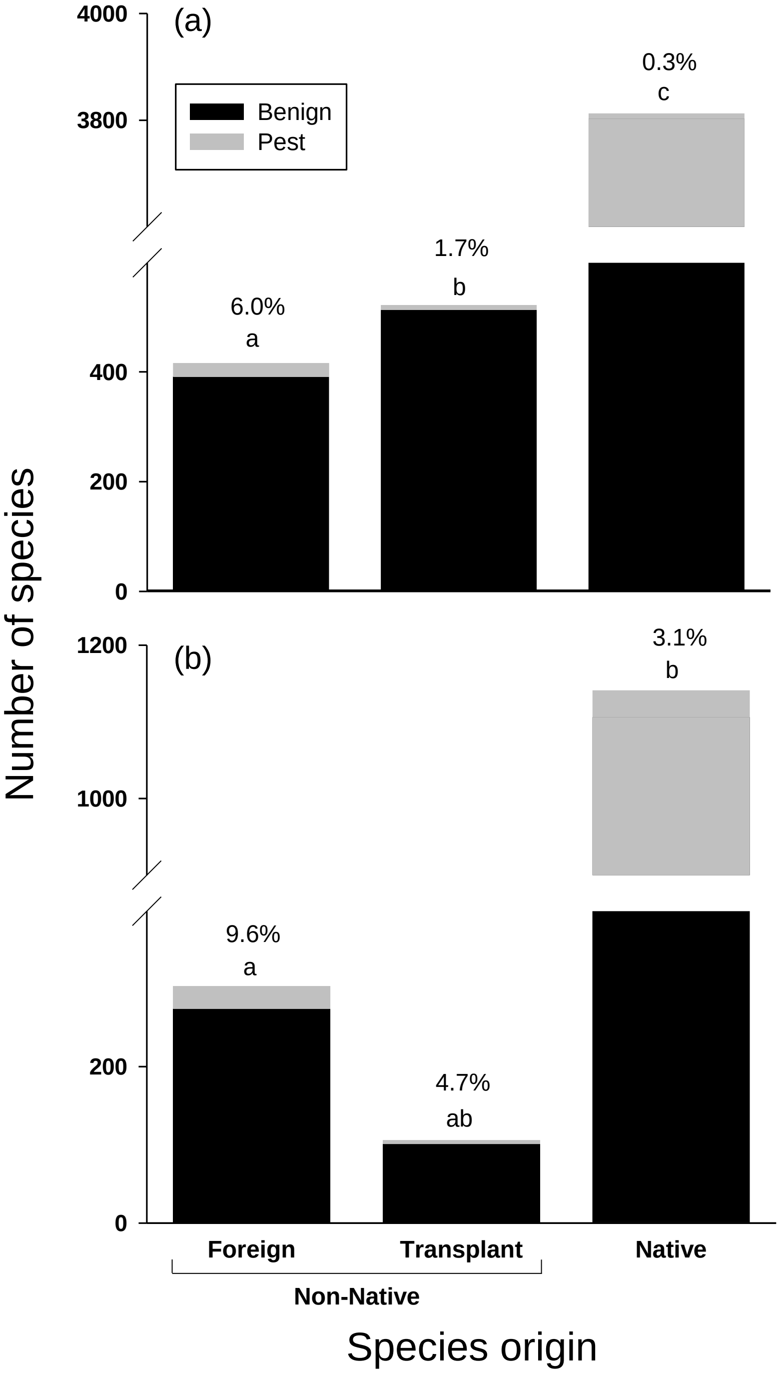

Figure 4. Number of freshwater animal (A) and plant (B) pest and benign species in North America and Europe combined. Percentages above bars indicate proportion of pest species per origin category. Different letters above bars indicate significant differences in proportions (p<0.001).

Connecting Statement

In the previous chapter, I showed that non-native species have a greater propensity than native species to be socio-economic pests in freshwater systems. This propensity is greatest among species originating from another biogeographic region. Assuming that this discrepancy is at least partly attributable to differential biotic regulation – that is, non-native species from distant regions likely experience less predation, parasitism and competition – these results suggest that the evolutionary experience of a recipient assemblage may regulate the capacity for an invader to be disruptive or to reach nuisance levels. Chapter 2 tests the hypothesis that non-native species have greater ecological impacts in areas where functionally similar natives are absent. Using taxonomic relatedness as a proxy for functional similarity, I examine its strength as a predictor of the impacts of non-native freshwater molluscs on native species populations.

Chapter 2

Influence of taxonomic relatedness on the ecological impact of introduced freshwater molluscs

Abstract

Non-native species are hypothesized to have greater ecological impacts in areas where functionally similar natives are absent, owing to differential resource use and a lack of evolutionary experience in the invaded assemblage. Using freshwater molluscs as model organisms and taxonomic relatedness as a proxy for functional similarity, we test whether taxonomically novel invaders have a greater tendency to a cause a severe ecological impact – here defined as a >50% decline in a native species population. In a global-scale analysis, the relationship between the impact of non-native molluscs and their distinctiveness in the invaded biogeographic region was assessed at multiple levels of taxonomic organization (genus, family, order). Our results show that ecological impact is dependent on taxonomic relatedness, where novel taxa comprise disproportionately large numbers of high-impact invaders – a discrepancy that is most pronounced at the family level. This study is the first to test the influence of multiple scales of taxonomic relatedness on the ecological impact of introduced animals, and demonstrates the value of incorporating taxonomic logic into invasion risk assessments.

Introduction

The impacts of the vast majority of biological invasions have not been studied (Parker *et al*. 1999). Although it appears that many invasions have relatively weak impacts (Williamson and Fitter 1996), some non-native species cause ecological and economic harm that may be extremely costly and difficult to reverse (Vitousek *et al*. 1997, Pimentel *et al*. 2000, 2005, Clavero and Garcia-Berthou 2005). Although the identification of high-impact invasion threats is a priority for management (Pyšek and Richardson 2010), predictive models and broad generalizations are rare, owing largely to the highly context-dependent nature of impact (Ricciardi *et al*. 2013). Few reliable predictors have been identified, particularly for animals (e.g., Ricciardi 2003, Keller *et al*. 2007). One underused, but promising, approach to identifying and testing predictable patterns is to consider the traits of the invader and the recipient community in combination (e.g., Ricciardi and Atkinson 2004, Strauss *et al*. 2006). Variation in an invader's success has been related to the recipient assemblage’s evolutionary experience with functionally similar species. For example, Darwin’s naturalization hypothesis proposes that non-native species will be most successful when introduced to regions which lack native congeners (Daehler 2001). Similarly, but with respect to impact, it has been suggested that absence of functionally similar organisms in native species assemblages contributes to the evolutionarily naïveté of the system, resulting in reduced adaptive capabilities and greater susceptibility to ecological harm (Cox and Lima 2006); an example is the strong effect of mammalian predators and herbivores introduced to islands (Diamond and Case 1986, Ebenhard 1988).

Quantifying functional similarity would involve comparisons of multiple life history parameters, and as such, has not been integrated into risk assessment frameworks. An alternative approach uses taxonomic or phylogenetic relatedness as a proxy for functional similarity, based on the observation that closely related species tend to be more functionally similar (Harvey and Pagel 1991, Burns and Strauss 2011) and genetic divergence increases with phylogenetic distance (Thorpe 1982). This technique has been used to predict the impact of non-native species in aquatic ecosystems (Ricciardi and Atkinson 2004), and to predict the pest status of non-native terrestrial plants in California (Strauss *et al*. 2006). These studies, conducted at small regional scales, find that the impact of invaders is magnified in assemblages in which closely-related species are historically absent. Given the potential predictive value of this hypothesis, there is a need to explore its generality at a larger (biogeographic) spatial scale and across multiple taxonomic resolutions.

Our objective is to determine whether taxonomic relatedness can predict variation in the ecological field impacts of freshwater molluscs. Molluscs are used as our study organisms because 1) they are among the most globalized and well documented freshwater fauna, and 2) their taxonomic relationships are well studied, allowing us to categorize them with reasonable taxonomic resolution (Bogan 2008, Strong *et al*. 2008). We test the relationship between an invader’s impact and relatedness at multiple taxonomic levels (genus, family, order) at the scale of biogeographic realms. We hypothesize that introduced molluscs belonging to novel taxa are more likely to contribute to a significant local decline in a native species population. Alternatively, if direct competitive interactions, genetic interference or hybridization (Rhymer and Simberloff 1996) are of primary ecological importance, then the presence of a native congener may result in the opposite pattern.

Methods

A global list of introduced freshwater molluscs was compiled from non-native species databases (e.g., USGS, ISSG, DAISIE), published volumes, and a literature search (Web of Science, 1900-2012) using the following combination of search terms: (inva* OR non-native OR nonnative OR non-indigenous OR nonindigenous OR introduc* OR exotic OR alien) AND (mollus* OR bivalve* or gastropod*) AND (freshwater OR lake OR river OR stream). All accounts of self-sustaining non-native mollusc populations were included, where they have been established for more than 10 years (allowing us to account for a potential lag time between establishment and impact; Strayer *et al*. 2006). Only species introduced to a region beyond their historic natural range were considered.

We used a binary measure of impact (high/low), following the approach of other studies that synthesized impact data that are often heterogeneous in quality and difficult to ordinate (e.g., Ricciardi and Atkinson 2004, Keller *et al*. 2007, Ricciardi and Kipp 2008). Impact was documented as “high” if there was evidence that the invader caused a severe (> 50% decline) in the abundance of at least one native species population in the field. By default, this classification assigns a “low” impact ranking even for species whose impact may not have been studied, and is thus highly conservative. Furthermore, our strict definition excludes socio-economic impacts, despite their potentially costly consequences (e.g., Madsen and Frandsen 1989, Karatayev *et al*. 2012).

Ten distinct regions considered in this analysis were differentiated based on boundaries of evolutionary significance – a modification of Wallace’s biogeographic realms (Wallace 1876): Australasia, Nearctic, Central America and the Caribbean, Neotropics, Indo-Malay, Eastern Palearctic, Western Palearctic, North Africa and the Middle East, Afrotropics, and Oceania (Fig. 1). All known established non-native mollusc species in each biogeographic realm were examined and, for each invasion event (species per biogeographic region), the maximum population-level impact was recorded.

Quantifying taxonomic relatedness

We categorized all invaders based on whether they belong to taxa shared by natives in the region, or alternatively belong to novel (unshared) taxa, at multiple levels or organization (genus, family, and order). When determining shared/unshared taxonomic affiliations, only native species – those that have occurred historically in the region – were used for comparison. This includes extinct species, to allow for the best approximation of the native community’s breadth of evolutionary experience. Various sources were used to determine the native faunal composition of the biogeographic realm (e.g., Brown 1980, 1994, Bogan 2008, Strong *et al*. 2008, Thompson 2011). Taxonomic information for all molluscs identified through our literature search was obtained using the Integrated Taxonomic Information System (ITIS), which permitted us to reduce pseudoreplication by aggregating synonyms in species lists, and provided consistency in our taxonomic classifications.

Statistical treatment

A non-parametric statistical approach was employed in this analysis. The final data set includes the total number of invasion events (species per biogeographic realm), organized by impact and taxonomic relatedness. Data were arranged into 2x2 contingency tables and analyzed using Pearson's chi-square test without Yate's continuity correction. Pearson's residuals were observed to determine the direction and strength of relationships within each table.

Results

72 species of freshwater molluscs (belonging to 38 genera, 17 families, and 7 orders) were found to have non-native distributions (Appendix A). These were involved in 131 invasions, 25 of which have demonstrable high impacts (Table 1; Appendix B). Proportions of high-impact species vary along a gradient of taxonomic relatedness (Fig. 2). Consistent with our hypothesis, non-native molluscs that share genera with resident natives have the lowest proportion of high-impact species (6%) and are significantly less likely to comprise high-impact species compared to novel taxa ($p<0.02$ for all comparisons; Fig. 2). The proportion of high-impact species does not differ significantly between species of novel genera and novel order, nor between species of novel family and novel

order; however, those from novel families comprise the greatest proportion of high-impact species (57%) and are more likely to have strong impacts than species from a novel genus/shared family ($p<0.02$; Fig. 2).

Comparisons of the proportions of high-impact species belonging to shared and unshared taxa show a significant relationship at the genus and family levels ($p<0.001$ for both comparisons; Fig 3a, b), but not at the order level ($p>0.3$; Fig. 3c).

Discussion

This study is the first to test the relationship between taxonomic relatedness and ecological impact of non-native species at biogeographic scales and across multiple levels of taxonomic organization. The greatest proportion of high-impact invaders occurred among novel taxa, supporting the Taxonomic Distinctiveness Hypothesis proposed by Ricciardi and Atkinson (2004). The mechanisms driving this pattern remain to be determined, but we suggest that they involve, at least in part, the evolutionary experience of the recipient assemblage (Diamond and Case 1986, Cox and Lima 2006). Given that novel taxa are more likely to be functionally distinct within the recipient community (Burns and Strauss 2011), they may encounter naïve residents and, consequently, less effective predation and parasitism (cf. Hill and Kotanen 2009). They are also more likely to use limiting resources differently from natives, a trait that is characteristic of high-impact invaders (Vitousek 1990).

The mechanisms linked to the native species declines recorded in our dataset were rarely tested or even hypothesized. Much of the attention to evolutionary naïveté in aquatic systems has centered on novel predators (Cox and Lima 2006, Ricciardi and MacIsaac 2011), but these are not represented among freshwater molluscs. The majority of impacts in our dataset involve declines of native mollusc populations (Appendix B). Mechanisms that were examined or inferred in these cases included interference and resource competition (Harman 1968a, 1968b, Ricciardi 2003, Moore *et al*. 2012), whereas plant-herbivore interactions were rarely identified as a direct cause of impact (but see Cowie 2002, Carlsson and Lacoursiere 2005, Hidaka *et al*. 2007).

Distinctiveness at both the family- and genus- level are useful tools for risk assessment at large (biogeographic) scales (Fig. 3). Order-level distinctiveness does not appear to be a useful indicator of freshwater mollusc impact (Fig. 3); however, this may be an artifact of small sample size (i.e., very few species belong to an unshared order within our dataset).

We expect the relationship between taxonomic resolution and impact to vary with spatial scale, reflecting different levels of geographic isolation. Boundaries of evolutionary significance occur on smaller (subcontinental) scales for freshwater species than for terrestrial ones (Cox and Lima 2006, Ricciardi and Simberloff 2009); hence, distinctiveness at the genus level might be a more accurate predictor of impact for freshwater taxa (see Ricciardi and Atkinson 2004, Ricciardi and MacIsaac 2011). We attempted to perform a watershed-scale analysis for comparison, but very few systems have a sufficient number of mollusc invaders with well documented impacts (Table 2).

Our study distinguished transplant invaders – i.e. species established in an intracontinental region outside of their historical range, but within the biogeographic realm to which they are indigenous; these species, by definition, share genera with native residents of the realm. They permitted us to test our hypothesis without conflating it with hypotheses concerning the biogeographic scale of an introduction event (see Ricciardi and Simberloff 2009). Although many transplanted invaders have low impacts, we do not believe their inclusion biased our results. In fact, within our study, the majority of all high-impact invaders that belong to shared taxa are transplant invaders (e.g., *Corbicula fluminea* in Eastern Palearctic, *Physa acuta* in Western Palearctic, *Biomphalaria straminea* in the Neotropics); therefore, excluding them would underestimate the number of high-impact invaders from taxonomically related groups.

The timing of impact studies may lead to false assignment of low-impact rankings, as the impact of an invader varies temporally (Strayer *et al*. 2006). Even where changes to community structure have been observed, lack of consistent monitoring or experimental evidence precludes a causal link between the invader and the observed change. For example, Dobson (2004) reports a shift in dominance where the native *Bulinus africanus* group appears to have been displaced by the introduced *Physa acuta*, but the cause of this replacement is inferred only from field surveys conducted nearly fifty years apart. Moreover, the impacts of most invaders have not been recorded (Simberloff *et al*. 2013), and in cases where impact data are absent were categorized these as low-impact invasions. As such, we suggest that the significant patterns revealed in our study are robust.

A variety of non-exclusive factors can generate spatial and temporal variation in impact (Ricciardi *et al*. 2013). Species can establish in habitats with suboptimal conditions, where they may perform poorly and achieve lower abundance – and thus exert lower impacts – compared to populations in optimal conditions (e.g. Kestrup and Ricciardi 2009). In cases where habitat conditions (e.g. temperature, chemical factors) are highly limiting to the invader, we expect that functional distinctiveness will have less predictive power.

From a management perspective, it is crucial to identify those species that pose the greatest risk to recipient regions, allowing more efficient allocation of resources for prevention and mitigation of undesirable impacts (Byers *et al*. 2002). The use of taxonomy as a proxy for ecological distinctiveness appears to be a feasible standardized method to predict the evolutionary experience of a recipient community to a variety of invaders. It is otherwise difficult to identify an ecological function that is lacking in a community until the effects of the invader become apparent. Novel taxa, on the other hand, can be identified before the introduction event occurs; risk assessments need only consult a list of native species historically present in the region. The generality of this hypothesis, which has heretofore been tested positively for freshwater taxa and terrestrial weeds, remains to be explored for a broad range of taxa in different environments.

Acknowledgements

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Table 1. Non-native distributions of freshwater mollusc species. The taxonomic relationship between the mollusc and invaded region is indicated as shared (S) or unshared (U) genus, family, and order (Genus/Family/Order). "H" indicates a high-impact species (causing >50% decline in a native population). Nearctic (NA), Central America and Caribbean (CR), Neotropics (NEO), Western Palearctic (WP), North Africa and Middle East (NAF), Afrotropics (AF),Indo-Malay (IM), Eastern Palearctic (EP), Australasia (AU), Oceania (OC). Superscripts indicate source references for region.

Species	**NA**[1]	**CR**[2]	**NEO**[3]	**WP**[4]	**NAF**[5]	**AF**[6]	**EP**[7]	**IM**[8]	**AU**[9]	**OC**[10]
Alasmidonta marginata	S/S/S									
Amerianna carinata		U/S/S				U/S/S	U/S/S	U/S/S		
Anodonta woodiana		S/S/S		S/S/S				S/S/S		
Aplexa hypnorum							S/S/S			
Bellamya heudi guangdungensis									U/S/S	
Biomphalaria glabrata	S/S/S	S/S/S			S/S/S					
Biomphalaria pfeifferi						S/S/S				
Biomphalaria straminea		S/S/S	S/S/S-H					U/S/S		
Biomphalaria tenagophila						S/S/S				
Bithynia tentaculata	U/U/S-H									
Cipangopaludina chinensis	U/S/S									U/U/U
Cipangopaludina	U/S/S									

Species	**NA**[1]	**CR**[2]	**NEO**[3]	**WP**[4]	**NAF**[5]	**AF**[6]	**EP**[7]	**IM**[8]	**AU**[9]	**OC**[10]
japonica										
Corbicula fluminalis				U/U/S						
Corbicula fluminea	U/U/S-H		U/U/S	U/U/S-H			S/S/S-H			
Dreissena bugensis	U/U/S-H									
Dreissena polymorpha	U/U/S-H			U/U/U-H						
Drepanotrema aeruginosis	U/S/S									
Drepanotrema cimex	U/S/S									
Drepanotrema kermatoides	U/S/S									
Elimia virginica	S/S/S									
Eupera cubensis	S/S/S									
Ferrissia fragilis				U/S/S				U/S/S		
Fusconaia flava	S/S/S									
Gillia altilis	S/S/S									
Gyraulus chinensis				S/S/S					S/S/S	
Gyraulus parvus				S/S/S						
Helisoma duryi			U/S/S	S/S/S	U/S/S	U/S/S				U/S/S
Helisoma nigricans				S/S/S						
Helisoma trivolvis							U/S/S			
Indoplanorbis exustus		U/S/S				U/S/S		S/S/S		

Species	**NA**[1]	**CR**[2]	**NEO**[3]	**WP**[4]	**NAF**[5]	**AF**[6]	**EP**[7]	**IM**[8]	**AU**[9]	**OC**[10]
Lasmigona subvirdis	S/S/S									
Limnoperna fortunei			U/U/U-H				U/U/U	S/S/S		
Lithoglyphus naticoides				U/S/S						
Lymnaea a. auricularia	S/S/S								S/S/S	
Lymnaea a. rubiginosa									S/S/S	
Lymnaea columella			S/S/S	S/S/S	S/S/S	S/S/S			S/S/S	S/S/S
Lymnaea stagnalis									S/S/S	
Lymnaea truncatula									S/S/S	
Lymnaea viridis									S/S/S	S/S/S
Marisa cornuarietis	U/S/S	U/S/S-H		U/S/S-H						
Melanoides amabilis		U/S/S								
Melanoides tuberculata	U/U/S-H	U/S/S-H	U/S/S-H	U/S/S	U/S/S	S/S/S	S/S/S		U/S/S	
Melanoides turriculus	U/U/S									
Menetus dilatatus				U/S/S						
Musculium partumeium										U/U/U
Musculium				S/S/S						

Species	NA[1]	CR[2]	NEO[3]	WP[4]	NAF[5]	AF[6]	EP[7]	IM[8]	AU[9]	OC[10]
transversum										
Physa acuta				S/S/S-H	U/U/S	U/S/S	S/S/S	U/U/S	U/U/S-H	U/U/S
Physa fontinalis							U/S/S			
Physa gyrina				S/S/S						
Physa venustula			U/S/S							
Pila conica										U/U/U
Pisidium amnicum	S/S/S									
Pisidium casertanum										U/U/U
Pisidium henslowanum	S/S/S									
Pisidium moitessierianum	S/S/S									
Pisidium punctiferum	S/S/S									
Pisidium supinum	S/S/S									
Pomacea bridgesii	S/S/S									U/U/U
Pomacea canaliculata	S/S/S						U/S/S-H	U/S/S-H		U/U/U-H
Pomacea diffusa	S/S/S									
Pomacea haustrum	S/S/S									
Pomacea insularum	S/S/S-H							U/S/S		
Pomacea paludosa	S/S/S									U/U/U
Potamopyrgus antipodarum	U/S/S-H			U/S/S-H			U/S/S		S/S/S	
Sphaerium	S/S/S									

Species	**NA**[1]	**CR**[2]	**NEO**[3]	**WP**[4]	**NAF**[5]	**AF**[6]	**EP**[7]	**IM**[8]	**AU**[9]	**OC**[10]
corneum										
Stenophysa marmorata	S/S/S					U/S/S				
Stenophysa maugeriae	S/S/S									
Tarebia granifera	U/U/S-H	U/S/S-H	U/S/S-H			U/S/S				
Thiara scabra							S/S/S			
Valvata piscinalis	S/S/S									
Viviparus georgianus	S/S/S									
Viviparus viviparus				S/S/S						

[1] Murray 1971, Gardner *et al.* 1976, Jokinen 1992, Strayer 1999, Grigorovich *et al.* 2000, Howells *et al.* 2006, Schloesser *et al.* 2006, Keller *et al.* 2007, Rawlings *et al.* 2007, Solomon *et al.* 2010, Moore *et al.* 2012, USGS 2012.

[2] Oliver-González *et al.* 1956, Pointier 1993,1999, 2001, Watters 1997, Pointier and Augustin 1999, Pointier *et al.* 2005.

[3] Duarte and Diefenbach 1994, Darrigran *et al.* 1998, Pointier 1999, Martin 2001, Appleton 2003, Pointier *et al.* 2005, Santos *et al.* 2007, Boltovskoy *et al.* 2009, Fernandez *et al.* 2010.

[4] Doby *et al.* 1966, Anderson 1996, Karatayev *et al.* 1997, Watters 1997, Beran and Horsak 2002, Van der Velde *et al.* 2002, Bernauer and Jansen 2006, Walther *et al.* 2006, Cianfanelli *et al.* 2007, Gherardi 2007, Sousa *et al*. 2011.

[5] Demian and Kamel 1973, Brown 1980, Brown 1994, Pointier *et al.* 2005.

[6] Brown 1980, Appleton 2003, Pointier *et al*. 2005.

[7] Ishibashi and Komaru 2003, Mito and Uesugi 2004; Hidaka *et al.* 2007.

[8] Madsen and Frandsen 1989, Watters 1997, Ricciardi 1998, Carlsson and Lacoursiere 2005, Pointier *et al*. 2005, Walther *et al.* 2006, Rawlings *et al.* 2007.

[9] Climo and Pullan 1972, Boray 1978, Charleston and Climo 1979, Winterbourn 1980, Shea 1994, Brown 2001, Duggan 2002, Schreiber *et al.* 2002, Appleton 2003.

[10] Cowie 1998, 2002, Burky *et al.* 2000.

Table 2. Number of high- and low-impact non-native mollusc species in freshwater systems. Superscripts indicate source references for system.

	Genus-level				Family-level*			
	High Impact		Low Impact		High Impact		Low Impact	
	Shared	Unshared	Shared	Unshared	Shared	Unshared	Shared	Unshared
[1]Great Lakes- St. Lawrence	0	3	9	6	0	3	14	1
[2]Hudson River	0	2	9	6	0	2	15	0

*$p<0.01$ for both the Great Lakes-St. Lawrence and Hudson River at the family level.

[1] Ricciardi 2006, USGS 2012.

[2] Mills *et al.* 1996, Strayer 1999, USGS 2012.

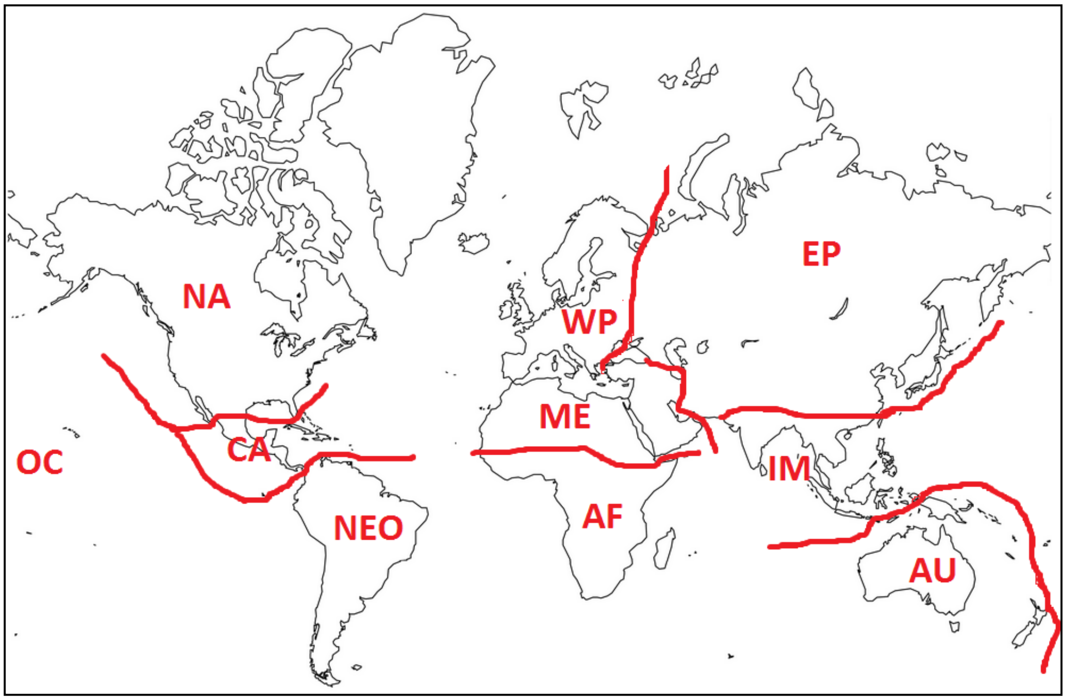

Figure 1. Biogeographic realms used in global-scale analysis. Australasia (AU), Nearctic (NA), Central America and Caribbean (CA), Neotropics (NEO), Indo-Malay (IM), Eastern Palearctic (EP), Western Palearctic (WP), North Africa and Middle East (ME), Afrotropics (AF), Oceania (OC).

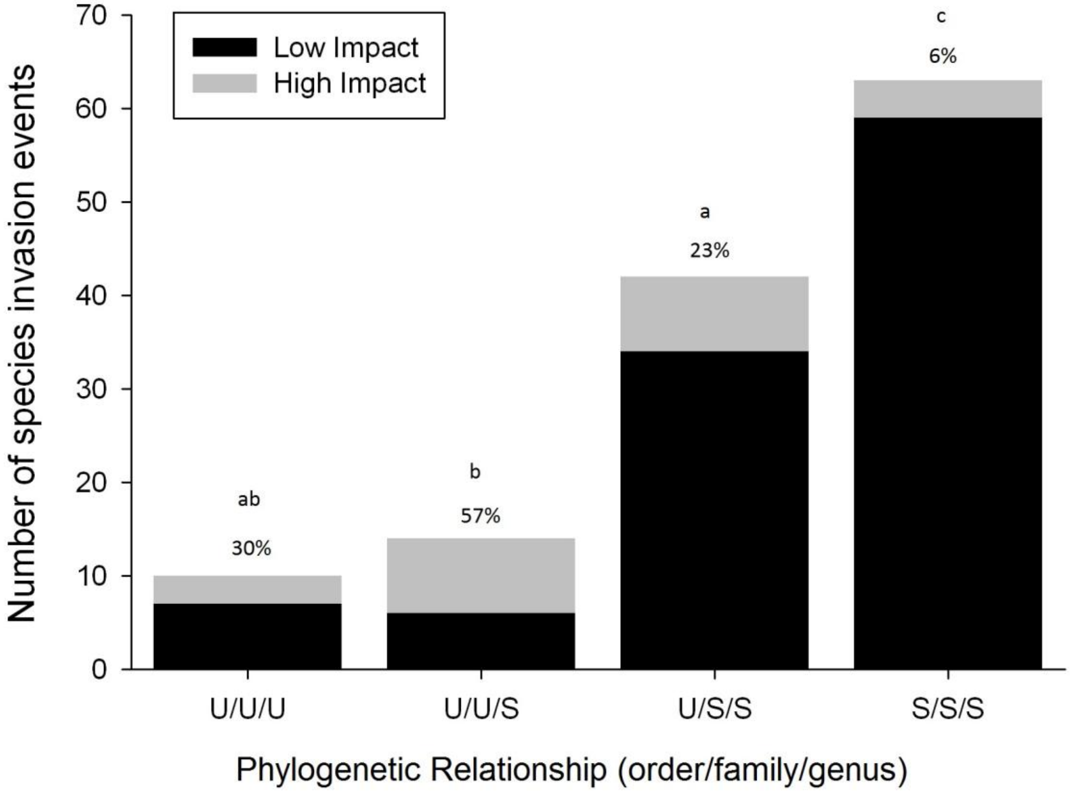

Figure 2. Numbers of high- and low-impact non-native molluscs along a gradient of taxonomic relatedness. Percentages above bars indicate proportion of high-impact species. Taxonomic relationship between the mollusc and invaded community is indicated as shared (S) or unshared (U) genus, family, and order (Genus/Family/Order). Different letters indicate significant differences in the proportion of high and low impact species between taxonomic relatedness categories ($p<0.05$).

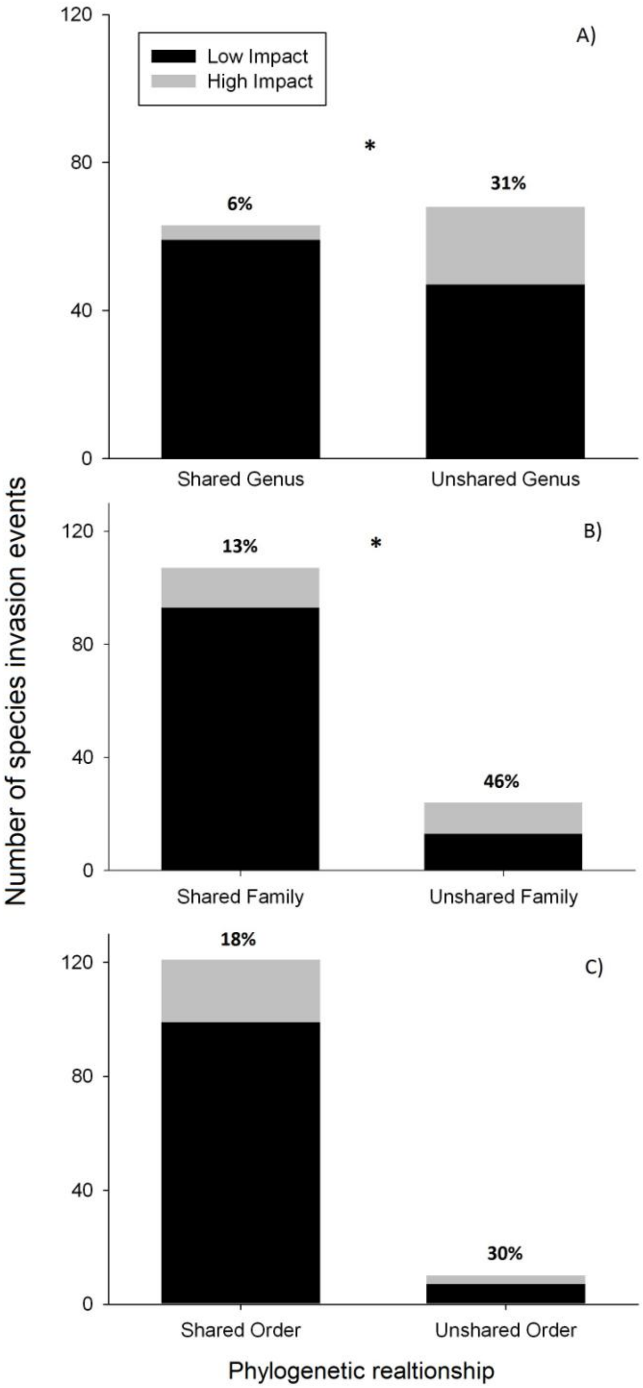

Figure 3. Numbers of high- and low-impact non-native molluscs that belong to a novel or shared (A) genus, (B) family, and (C) order. Percentages above bars indicate proportion of high-impact species. Asterisk indicates significant difference in the proportion of high and low impact species between taxonomic relatedness categories ($p<0.05$).

General conclusion

Variation in the biogeographic origin of non-native species and their taxonomic relatedness to the invaded native assemblage was correlated with differential frequencies of strong impact. This is the first study to compare the frequency of socioeconomic pests among native and non-native species (Chapter 1). Non-native aquatic species are significantly more likely to cause socioeconomic damage, and the likelihood increases for species introduced from other biogeographic regions. These findings refute the claim (e.g., Davis *et al.* 2011, Valéry *et al.* 2013) that a species' propensity to cause undesirable impacts is independent of its biogeographic origin. They also add support to criticisms of proposals to intentionally moving species beyond their native range for purposes of conservation or resource enhancement (i.e., assisted colonization; Ricciardi and Simberloff 2009).

This study is also the first to explore the relationship between taxonomy and ecological impact at biogeographic scales and across multiple levels of taxonomic organization (Chapter 2). Results show that the impacts of a non-native mollusc are mediated by its taxonomic relatedness to the native species assemblage, such that a larger proportion of high-impact invaders occur among novel taxa.

Thus, this study has identified correlates of impact that are potentially useful for risk assessment. The generality of these impact correlates should be further tested across multiple spatial scales, taxonomic groups, and habitat types.

As published syntheses of the impacts of non-native species continue to become available (e.g., Gherardi 2007, Kraus 2009), taxa that currently lack sufficient data may be tested with respect to impact in the near future. Risk assessment might need to be taxon or habitat specific; for example, Cox and Lima (2006) observe that terrestrial systems are less naïve to the impacts of novel predators compared to freshwater systems.

Owing to data scarcity, our study of socio-economic impacts was limited to freshwater regions in developed countries. It would be of interest to extend this analysis to other regions of the world allowing comparison between developed and developing countries. One might hypothesize that the socio-economic impacts of non-native species is more pronounced in developing countries, where less economic investment is directed toward mitigation of non-native species impacts.

As demonstrated here and elsewhere (Diamond and Case 1986, Ricciardi and Atkinson 2004, Paolucci *et al.* 2013), the evolutionary experience of an invaded community regulates severity of non-native species' impact, but there are a variety of other factors that can also mediate impact (Ricciardi *et al.* 2013). For example, species can establish in habitats with suboptimal conditions, where they may perform poorly and achieve lower abundance – and thus exert lower impacts – compared to populations in optimal conditions (Kestrup and Ricciardi 2009). Research should continue to identify factors relevant to risk assessment and seek to integrate them into predictive models.

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Appendix A. Taxonomic classification of all non-native freshwater mollusc species identified in Chapter 2.

Order	**Family**	**Species**
Architaenioglossa	Ampullariidae	*Marisa cornuarietis*
Achitaenioglossa	Ampullariidae	*Pila conica*
Architaenioglossa	Ampullariidae	*Pomacea bridgesii*
Architaenioglossa	Ampullariidae	*Pomacea canaliculata*
Architaenioglossa	Ampullariidae	*Pomacea diffusa*
Architaenioglossa	Ampullariidae	*Pomacea haustrum*
Architaenioglossa	Ampullariidae	*Pomacea insularum*
Architaenioglossa	Ampullariidae	*Pomacea paludosa*
Architaenioglossa	Viviparidae	*Bellamya heudi guangdungensis*
Architaenioglossa	Viviparidae	*Cipangopaludina chinensis*
Architaenioglossa	Viviparidae	*Cipangopaludina japonica*
Architaenioglossa	Viviparidae	*Viviparus georgianus*
Architaenioglossa	Viviparidae	*Viviparus viviparus*
Basommatophora	Ancylidae	*Ferrissia fragilis*
Basommatophora	Lymnaeidae	*Lymnaea viridis*
Basommatophora	Lymnaeidae	*Lymnaea columella*
Basommatophora	Lymnaeidae	*Lymnaea a. auricularia*
Basommatophora	Lymnaeidae	*Lymnaea a. rubiginosa*
Basommatophora	Lymnaeidae	*Lymnaea stagnalis*
Basommatophora	Lymnaeidae	*Lymnaea truncatula*
Basommatophora	Physidae	*Aplexa hypnorum*
Basommatophora	Physidae	*Physa acuta*
Basommatophora	Physidae	*Physa fontinalis*
Basommatophora	Physidae	*Physa gyrina*
Basommatophora	Physidae	*Physa venustula*
Basommatophora	Physidae	*Stenophysa marmorata*
Basommatophora	Physidae	*Stenophysa maugeriae*
Basommatophora	Planorbidae	*Amerianna carinata*
Basommatophora	Planorbidae	*Biomphalaria glabrata*
Basommatophora	Planorbidae	*Biomphalaria pfeifferi*
Basommatophora	Planorbidae	*Biomphalaria straminea*
Basommatophora	Planorbidae	*Biomphalaria tenagophila*
Basommatophora	Planorbidae	*Drepanotrema aeruginosis*
Basommatophora	Planorbidae	*Drepanotrema cimex*
Basommatophora	Planorbidae	*Drepanotrema kermatoides*
Basommatophora	Planorbidae	*Gyraulus chinensis*
Basommatophora	Planorbidae	*Gyraulus parvus*
Basommatophora	Planorbidae	*Helisoma duryi*
Basommatophora	Planorbidae	*Helisoma nigricans*
Basommatophora	Planorbidae	*Helisoma trivolvis*
Basommatophora	Planorbidae	*Indoplanorbis exustus*
Basommatophora	Planorbidae	*Menetus dilatatus*
Heterostropha	Valvatidae	*Valvata piscinalis*
Mytiloida	Mytilidae	*Limnoperna fortunei*

Order	**Family**	**Species**
Neotaenioglossa	Bithyniidae	*Bithynia tentaculata*
Neotaenioglossa	Hydrobiidae	*Gillia altilis*
Neotaenioglossa	Hydrobidae	*Lithoglyphus naticoides*
Neotaenioglossa	Hydrobiidae	*Potamopyrgus antipodarum*
Neotaenioglossa	Pleuroceridae	*Elimia virginica*
Neotaenioglossa	Thiaridae	*Melanoides tuberculata*
Neotaenioglossa	Thiaridae	*Melanoides amabilis*
Neotaenioglossa	Thiaridae	*Melanoides turriculus*
Neotaenioglossa	Thiaridae	*Tarebia granifera*
Neotaenioglossa	Thiaridae	*Thiara scabra*
Unioniformes	Unionidae	*Alasmidonta marginata*
Unioniformes	Unionidae	*Anodonta woodiana*
Unioniformes	Unionidae	*Fusconaia flava*
Unioniformes	Unionidae	*Lasmigona subvirdis*
Veneroida	Corbiculidae	*Corbicula fluminalis*
Veneroida	Corbiculidae	*Corbicula fluminea*
Veneroida	Dreissenidae	*Dreissena bugensis*
Veneroida	Dreissenidae	*Dreissena polymorpha*
Veneroida	Sphaeriidae	*Musculium partumeium*
Veneroida	Sphaeriidae	*Musculium transversum*
Veneroida	Sphaeriidae	*Pisidium amnicum*
Veneroida	Sphaeriidae	*Pisidium casertanum*
Veneroida	Sphaeriidae	*Pisidium henslowanum*
Veneroida	Sphaeriidae	*Pisidium moitessierianum*
Veneroida	Sphaeriidae	*Pisidium punctiferum*
Veneroida	Sphaeriidae	*Pisidium supinum*
Veneroida	Sphaeriidae	*Sphaerium corneum*
Veneroida	Pisidiidae	*Eupera cubensis*

Appendix B. Impact details for all high-impact species identified in Chapter 2.

Species	**Introduced Region**	**Impact**	**Reference**
Biomphalaria straminea	Neotropical	Exclusion of *Biomphalaria glabrata*	Pointier *et al.* 2005
Bithynia tentaculata	Nearctic	Exclusion of pleurocerid species	Jokinen 1992
Corbicula fluminea	E. Palearctic	Disappearance of *Corbicula leana*	Ishibashi and Komaru 2003
Corbicula fluminea	Nearctic	Reduction of native sphaeriids	Gardner *et al.* 1976
Corbicula fluminea	W. Palearctic	Disappearance of native peaclam	Sousa *et al.* 2011
Dreissena bugensis	Nearctic	Extirpation of native unionids	Schloesser *et al.* 2006
Dreissena polymorpha	Nearctic	Extirpation of native unionids	Schloesser *et al.* 2006
Dreissena polymorpha	W. Palearctic	Ecosystem changes (phytoplankton)	Karatayev *et al.* 1997
Limnoperna fortunei	Neotropical	Exclusion of native mollusc species; ecosystem changes (chlorophyll a, primary production)	Darrigran *et al.* 1998; Boltovskoy *et al.* 2009
Marisa cornuarietis	Central America/ Caribbean	Exclusion of *Austratorbis glabratus* and *Biomphalaria glabrata*	Oliver-González *et al.* 1956; Pointier and Augustin 1999
Marisa cornuarietis	N. Africa/ Middle East	Exclusion of *Bulinus truncatus*	Demian and Kamel 1973
Melanoides tuberculata	Central America/ Caribbean	Exclusion of *Biomphalaria glabrata*	Pointier 1999
Melanoides tuberculata	Neotropical	Exclusion of native mollusc species	Santos *et al.* 2007
Melanoides tuberculatus	Nearctic	Exclusion of native *Gonibasis comalensis*	Murray 1971
Physa acuta	Australasia	Exclusion of *Physastra variabilis*	Winterbourn 1980
Physa acuta	W. Palearctic	Exclusion of *Physa fontinalis*	Cianfanelli *et al.* 2007
Pomacea canaliculata	E. Palearctic	Reduction of native crops	Hidaka and Tokuoka 2007
Pomacea canaliculata	Indo-Malay	Excludes native macrophytes and	Carlsson and Lacoursiere 2005; Wood *et*

Species	**Introduced Region**	**Impact**	**Reference**
		bryozoans	*al*. 2005
Pomacea canaliculata	Oceania	Reduction of native crops	Cowie 2002
Pomacea insularum	Nearctic	Replacement of native molluscs	Rawlings *et al*. 2007
Potamopyrgus antipodarum	Nearctic	Population crash of native snails at high densities	Moore *et al*. 2012
Potamopyrgus antipodarum	W. Palearctic	Extirpation of native molluscs	Cianfanelli *et al*. 2007
Tarebia granifera	Central America/ Caribbean	Replaces native *Biomphalaria glabrata*, *Pachychilus violaceus*	Pointier 1999
Tarebia granifera	Nearctic	Exclusion of native *Gonibasis comalensis*	Murray 1971
Tarebia granifera	Neotropical	Replaces native *Biomphalaria glabrata*	Pointier 1999

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