

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

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Some ecologists have claimed that non-native species are no more likely to cause ecological or economic harm than native species. 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 were 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 six times as likely to be pests as compared with native species. The incidence of pest species 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.

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Rates of biological invasion are increasing worldwide, and many countries have recorded several hundred to several thousand non-native species established within their borders (Vitousek *et al.* 1997). Although the effects of most 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 damage to natural resources and ecosystem services associated with agriculture, forests, fisheries, and water quality (Vitousek *et al.* 1997; Lovell *et al.* 2006; 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 (Davis *et al.* 2011; Schlaepfer *et al.* 2011). Specifically, critics have argued that non-native species are no more likely than native species to cause ecological or economic harm and, therefore, the biogeographic origin of a species does not warrant 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 in the US are 40 times as likely to be invasive – ie to spread aggressively and cause ecological or economic harm – as native plants. 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 geographical comparison of the relative likelihood for native and non-native species to cause socioeconomic damage.

Here, we compare the incidence of socioeconomic pests among native and non-native aquatic species. Using data on freshwater plants and animals in North America and Europe, we tested whether the pest status of a species is independent of its biogeographic origin – that is, if it was native to the continent, transplanted beyond its native range within the continent, or non-native to the continent. We hypothesized that (1) non-native species have a greater likelihood of becoming pests, and (2) the proportion of pests will be greatest among species foreign to continents. The rationale for these hypotheses is that release from biotic constraints (eg imposed by adapted predators and parasites) can cause introduced species to achieve nuisance-level abundances (Cappuccino and Carpenter 2005; Hill and Kotanen 2009). Moreover, species native to more distant regions are more likely to be ecologically novel and thus potentially more disruptive in their resource use within 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 via 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**

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OR *foul**) AND (**water** OR *aquatic*). Our search was limited to freshwater species – namely fish, macroinvertebrates (excluding insects), and vascular plants. To clarify impact-related details of species identified through the above sources, we supplemented data obtained from the literature search with those from specialized volumes or gray literature.

Owing to difficulties in assessing the socioeconomic costs of introduced species (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 (eg 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

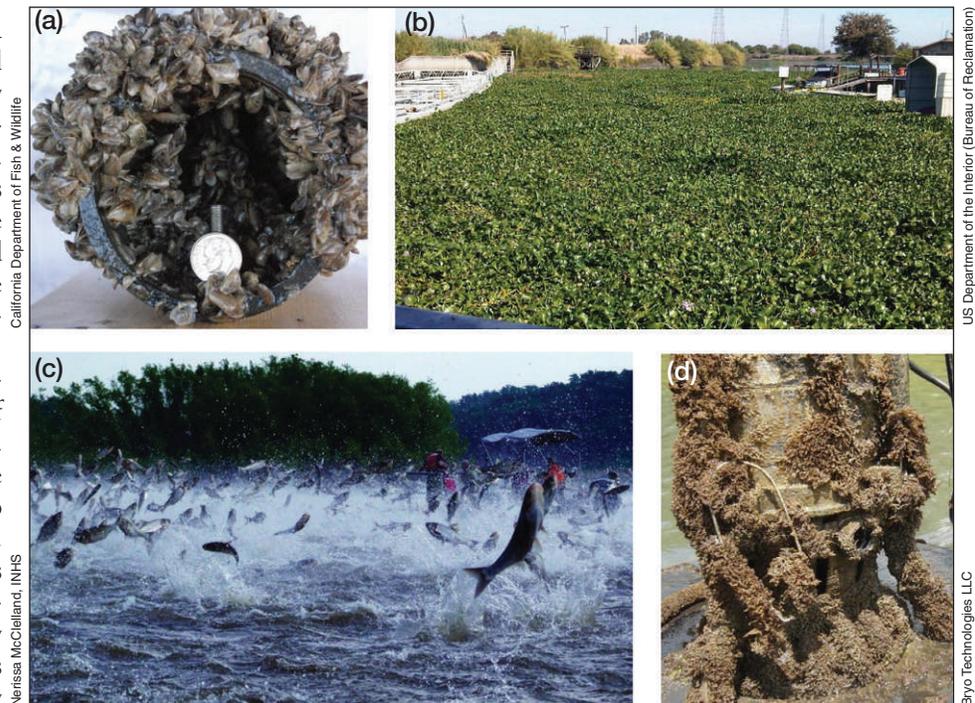


Figure 1. Examples of freshwater pest species: (a) The Eurasian quagga mussel (*Dreissena rostriformis bugensis*), a fouling pest in the Great Lakes and, more recently, in the western US. (b) Water hyacinth (*Eichhornia crassipes*), a globally invasive pest of waterways. (c) Silver carp (*Hypophthalmichthys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

Table 1. Pest and benign freshwater species in North America and Europe

| 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 <i>et al.</i> (2008); USDA ¹ |
| Fishes | 5 | 76 | 3 | 327 | 0 | 1061 | Fuller <i>et al.</i> (1999); Lévêque <i>et al.</i> (2005) |
| Mollusks | 6 | 35 | 0 | 23 | 0 | 813 | Lévêque <i>et al.</i> (2005); USGS ² |
| Crustaceans | 3 | 37 | 2 | 48 | 1 | 870 | Lévêque <i>et al.</i> (2005); USGS ² |
| Bryozoans | 2 | 1 | 0 | 2 | 5 | 22 | Lévêque <i>et al.</i> (2005); USGS ² |
| Cnidarians | 1 | 1 | 0 | 0 | 0 | 22 | Lévêque <i>et al.</i> (2005); USGS ² |
| Total | 34 | 340 | 8 | 481 | 23 | 3415 | |

Notes: ¹USDA (US Department of Agriculture) PLANTS database, accessed May 2013; <http://plants.usda.gov/java/>. ²USGS (US Geological Survey) Nonindigenous Aquatic Species Database, accessed May 2013; <http://nas.er.usgs.gov/>.

| 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 <i>et al.</i> (2008); Hussner (2012) |
| Fishes | 1 | 95 | 1 | 57 | 0 | 360 | Lévêque <i>et al.</i> (2005); Gherardi <i>et al.</i> (2009) |
| Mollusks | 2 | 31 | 1 | 13 | 1 | 176 | Lévêque <i>et al.</i> (2005); Gherardi <i>et al.</i> (2009) |
| Crustaceans | 4 | 101 | 1 | 44 | 0 | 445 | Lévêque <i>et al.</i> (2005); Gherardi <i>et al.</i> (2009) |
| Bryozoans | 0 | 1 | 0 | 2 | 3 | 19 | Massard and Geimer (2008); Gherardi <i>et al.</i> (2009) |
| Cnidarians | 0 | 14* | 1 | 1* | 0 | 15 | Lévêque <i>et al.</i> (2005); Gherardi <i>et al.</i> (2009) |
| Nematodes | 1 | 0 | 0 | 0 | 0 | 84 | Lévêque <i>et al.</i> (2005); Gherardi <i>et al.</i> (2009) |
| Total | 20 | 325 | 6 | 135 | 22 | 1578 | |

Notes: * refers to species counts of "other macroinvertebrates" in Gherardi *et al.* (2009).

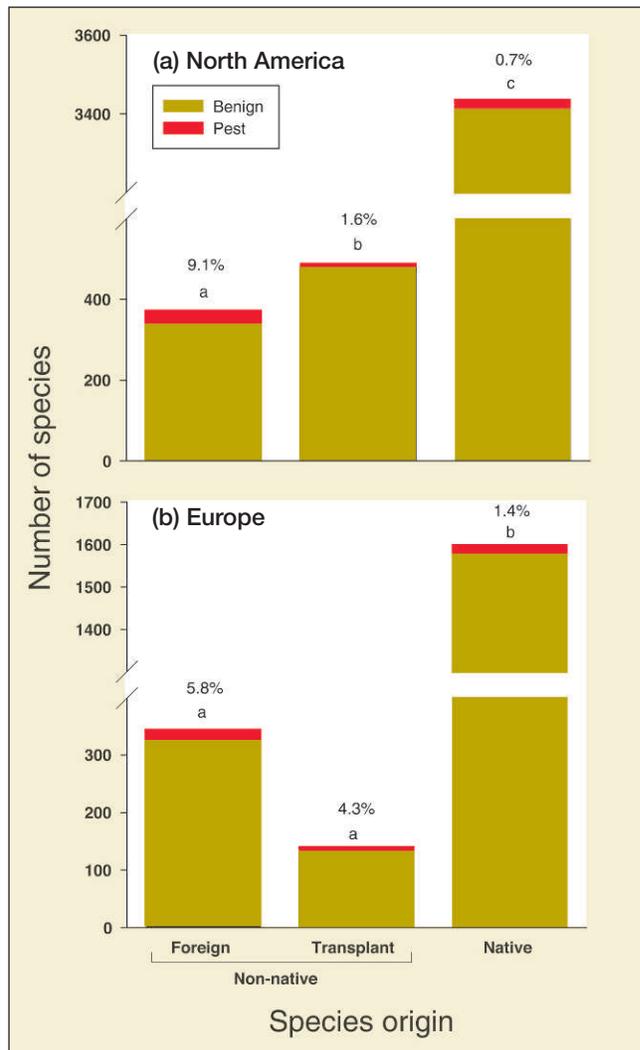


Figure 2. Number of freshwater pest and benign species in (a) North America and (b) Europe. Percentages above bars indicate proportion of pest species per origin category. Different letters above bars indicate significant differences in proportions ($P < 0.05$).

historically and are thought to have evolved there. We obtained total numbers of native, foreign, and transplanted species in North America and Europe using online databases and published volumes (Table 1). 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. Furthermore, the native/non-native origin of a species throughout the study region may be poorly known; for example, the native and introduced ranges of some bryozoan taxa are conflated owing to their 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 as

benign in another. Given that transplants are a subset of native species within a continent, transplant species are used twice in our analysis: their pest status is evaluated in both their native and non-native (transplanted) ranges. The final dataset included the total number of species in each continent organized by origin and pest status, arranged into 2×2 contingency tables, and analyzed by 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

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 (WebTables 1 and 2). The majority (60%) of pests were non-native in origin (ie transplant or foreign). After pooling data for North America and Europe, 5.3% of non-native species and 0.9% of native species were found to be socio-economic pests. The relationship between pest status and species origin was highly significant ($P < 0.0001$).

In both North America and Europe, foreign species contain the highest proportion of pests, followed by transplants, and then natives (Figure 2). 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 difference 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 foreign invaders, followed by transplants, and then natives (Figure 3). Proportions of foreign, transplant, and native animal pests differ significantly from one another ($P < 0.001$ for all comparisons). Among plants, foreign species are more likely than native species to be pests ($P < 0.0001$), although there are no significant differences either between foreign and transplant invaders or between transplant invaders and natives.

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, because 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 aquatic systems (Ricciardi 2006; Jackson and Grey 2012). The non-native species already established in North America and Europe will likely continue to expand their range at a greater rate than native species (cf Simberloff *et al.* 2012), thus 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 because Europe is not isolated from other continents to the same extent as North America, the distinction between foreign and transplant species in the former region is not as relevant evolutionarily. Alternatively, this discrepancy may be attributable to a majority of European pests being plants (67% in Europe as compared with 57% in North America). Among animals in our study, 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). The relationship is somewhat more tenuous for plants, with no difference between foreign and transplant invaders. This is perhaps explained by the contrasting nature of the economic impacts of aquatic plants and animals. The economic impacts of aquatic animals in North America and Europe appear to be derived primarily from consequences of ecological interactions (eg declines in sport fish populations, spread of pathogens) mediated by evolutionary novelty (Ricciardi and Atkinson 2004; Cox and Lima 2006), which conceivably increases with biogeographic distance. Economic impacts for aquatic plants are derived from their excessive growth (eg blocking waterways and impeding recreation; WebTables 1 and 2), which, for native plants, tends to be associated with changes in land use, nutrient pollution, or other disturbances (Cook 1990; Simberloff *et al.* 2012).

Caveats

We attempted to use a method of data collection that would generate an unbiased sample of socioeconomic pest species. In our literature review, we relied on search terms that explicitly excluded any reference to origin; we consulted

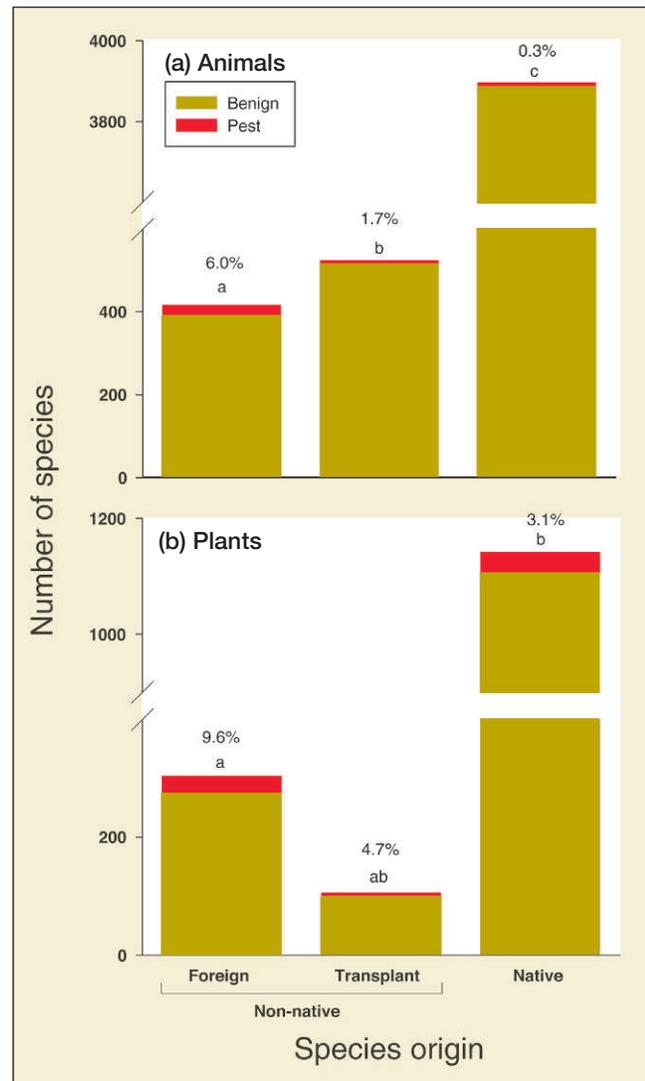


Figure 3. Number of freshwater pest and benign species in North America and Europe combined, classified as (a) animals and (b) plants. Percentages above bars indicate proportion of pest species per origin category. Different letters above bars indicate significant differences in proportions ($P < 0.001$).

alien species databases only to confirm details on species already identified as pests through our initial search. Given these methods, our dataset 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 is equally conservative; therefore the observed differences in pest proportions illuminate genuine 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, thereby exaggerating their pest proportion. In recognition of this possibility, we restricted our study to conspicuous species groups (fish, vascular plants, and macroinvertebrates) that are generally well recognized in North America and Europe. Even when taxonomically problematic species (eg bryozoans, cnidarians, nematodes) are removed from the analysis, foreign and

transplanted species still comprise the majority of socio-economic pests (63%) and remain significantly more likely than native species to be pests.

Another potential bias may be generated by increased attention to non-native species in recent decades. However, our study encompasses literature spanning the previous century, and we also included species that were historically pests but are not currently problematic (eg owing to effective management). Furthermore, 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 (eg Figure 1, a and d). However, fouling species are usually studied without explicit consideration of their biogeographic origin (eg 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 (eg Cook 1990).

Why non-native species are more likely to be pests

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 selection that determines the non-native species composition in a region. Because some key traits of successful invaders – eg high fecundity, asexual modes of reproduction, ability to colonize disturbed habitats (Rejmánek and Richardson 1996; Kolar and Lodge 2001) – are also common in aquatic pests (Cook 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 analog 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 US (Simberloff *et al.* 2012), and it counters claims that the native/non-native origins of potential pest species are irrelevant to management (Davis *et al.* 2011; 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). This being the case, researchers (eg 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 that such action is likely to be more feasible and beneficial if applied early in an invasion (Lodge *et al.* 2006).

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Erratum: An earlier version of this paper was posted on e-View on 1 Apr 2014; Table 1 and Figures 2 and 3 have been slightly revised in this version.

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