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LETTER

Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems

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Abstract

There exist few empirical rules for the effects of introduced species, reflecting the context-dependent nature of biological invasions. A promising approach toward developing generalizations is to explore hypotheses that incorporate characteristics of both the invader and the recipient system. We present the first general test of the hypothesis that an invader's impact is determined by the system's evolutionary experience with similar species. Through a meta-analysis, we compared the taxonomic distinctiveness of high- and low-impact invaders in several aquatic systems. We find that high-impact invaders (i.e. those that displace native species) are more likely to belong to genera not already present in the system.

Keywords
Biological invasion, community ecology, exotic species, impact, introduced species, nonindigenous.

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INTRODUCTION

Biological invasions are increasing in frequency worldwide and can produce substantial ecological damage, including the loss of native species (Mack *et al.* 2000; Kats & Ferrer 2003). However, most invasions cause no detectable impact (Williamson 1996). The ability to distinguish invaders likely to have a major impact from those having only minor effects is essential for prioritizing management efforts. Unfortunately, there exist few predictable patterns of impact, because of the context-dependent nature of invasions (Williamson 1996).

A popular, but largely untested, hypothesis is that a community's lack of evolutionary experience with invaders determines its vulnerability (Diamond & Case 1986; Cox 1999); therefore, the impact of an invader should be most severe in communities lacking similar species. This hypothesis is based on observations of higher virulence and mortality associated with the introduction of novel pathogens (Reynolds 1988; Anagnostakis & Hillman 1992) and the acute sensitivity of island communities to novel predators and herbivores (Ebenhard 1988). Remote oceanic islands, with their characteristically depauperate communities, are naïve to the effects of a broad spectrum of life forms (Diamond & Case 1986), which might account for the disproportionate number of extinctions linked to species introduced to islands (Atkinson 1989). Communities in lakes and river basins are similarly sensitive to species invasions, perhaps because of their evolutionary isolation (Ricciardi *et al.* 1998; Kats & Ferrer 2003). In virtually every well-documented inland fishery collapse attributable to invasions, the invader belongs to a novel genus (Spencer *et al.* 1990; Lester 1992; Kideys 1994; Hall & Mills 2000). However, given the relatively small size of a recipient community compared with the donor pool of potential invaders, many introduced species are likely to have novel attributes and unique taxonomic affiliations. Alternatively, the strong impacts of introduced predators and herbivores in insular ecosystems may simply be due to lack of refugia for native species (Simberloff 1995), although invaders can reduce native biodiversity even in large heterogeneous ecosystems (Ricciardi *et al.* 1998; Hall & Mills 2000). To our knowledge, there has been no general analysis of the relationship between the impact of an invader and the presence of closely-related species in the community. Here, we compare the taxonomic distinctiveness of high- and low-impact invaders across a set of aquatic systems.

METHODS

Classification

We examined the invasion histories of several aquatic systems that differ broadly in area, latitude, nutrient status, salinity, numbers of native species historically present, and numbers of invaders. These systems were located by searching the scientific literature (using internet databases; e.g. Aquatic Sciences and Fisheries Abstracts) for lakes, river basins and marine coastal regions with documented invasion histories and for which experimental or correlational impact studies were available for various invaders. For each system, we categorized all introduced fishes, invertebrates, algae and vascular plants according to their ecological impact. We included only introduced species that formed reproducing populations and that were present in the system for > 5 years. Invaders were classified as 'high-impact' if there was experimental or correlational evidence that they promoted the extirpation ($>$ 80% decline) of one or more native species in the system. This definition purposely excludes invaders whose impacts are due solely to hybridization (which is inversely correlated to taxonomic distinctiveness; Rhymer & Simberloff 1996), as these are obvious exceptions to the distinctiveness hypothesis. The remaining introduced species had untested, undetected or inconspicuous impacts, and were arbitrarily classified as 'low-impact' invaders.

After classifying the impact level of each invader, we determined if a native species in the same genus was present in the system. The taxonomic distinctiveness of high- and low-impact invaders was thus quantified by the number of genera they shared with native species. For many systems we examined (e.g. North Sea, Baltic Sea, Mediterranean Sea), there were extremely low proportions of documented high-impact species or shared genera. Because such cases can severely bias our results, we excluded systems for which (i) high-impact species represented $<$ 5% of the total number of species, or (ii) the number of shared genera comprised $<$ 10% of the total number of genera in the system.

Statistical treatment

To determine if high-impact invaders were more likely than low-impact invaders to belong to unshared genera, a one-tailed Fisher Exact test (Sokal & Rohlf 1995) was used to test the independence of row and column data in a 2×2 contingency table for each system (Table 1). We then conducted a meta-analysis of all systems using Fisher's method of combining probabilities from independent tests of significance (Sokal & Rohlf 1995). This method adds the logarithms of P-values from each Fisher Exact test to produce a single chi-square statistic (χ^2) as follows:

$$\chi^2 = -2\sum_i \ln P_i$$

The P-value for this chi-square statistic was computed with $2n$ degrees of freedom, where n is the total number of independent tests.

RESULTS

Our final data set consisted of seven independent aquatic systems. For four of these systems (the Laurentian Great Lakes, Hudson River, Potomac River, and New Zealand Coast), the Fisher Exact test rejected the null hypothesis that high- and low-impact invaders are equally likely to belong to unshared genera (Table 1). One additional system had a P-value that was suggestively low (San Francisco Bay, $P = 0.08$). Each system tended in the same direction: high-impact invaders shared fewer genera with native species. The significance of this overall tendency was confirmed by our meta-analysis ($\chi^2 = 62.0$, d.f. $= 14$, $P < 0.0001$), whose robustness is demonstrated by the absence of a disproportionate influence of any individual system on the combined test result; the two systems with the smallest P-values can both be eliminated without causing the chi-square statistic to become nonsignificant ($\chi^2 = 26.6$, d.f. $= 10$, $0.001 < P < 0.005$).

DISCUSSION

We consider our results to be conservative, because our study likely underestimated numbers of high-impact species for three reasons. First, experimental and correlational studies of impact are lacking for most introduced species; consequently, a substantial number of species may have been incorrectly classified as 'low-impact' invaders. Furthermore, our narrow definition of a 'high-impact' invader excludes many species that have caused detectable changes to ecosystem function and indirect effects on native species. Finally, because lag times of years to decades may occur between the introduction of a species and its maximum impact (Williamson 1996), studies of relatively recent invasions (or studies done early in the invasion process) may fail to identify 'high-impact' species.

Nevertheless, our meta-analysis revealed that the magnitude of an aquatic invader's impact is related to the invader's taxonomic distinctiveness within the recipient community. Diamond & Case (1986) hypothesized that much of the variation in an invader's impact across different communities can be explained by the community's 'prior experience with functionally similar species'. If species of the same genus tend to be functionally similar, i.e. if ecological distinctiveness correlates with taxonomic distinctiveness (as expected, given that genetic divergence decreases as taxonomic relatedness increases; Thorpe 1982), then our results support this hypothesis. Introduced species that share genera with native species in the invaded range are more likely to encounter enemies that can regulate their abundance and, thus, limit their impact (Agrawal & Kotanen 2003). Conversely, taxonomically distinct invaders are less

Table 1 Numbers of invaders belonging to genera shared and unshared by native species in aquatic systems

System	High-impact invaders		Low-impact invaders		
	Shared genera	Unshared genera	Shared genera	Unshared genera	*P*-value
Laurentian Great Lakes*	4	16	80	35	0.00004
Hudson River†	5	13	66	25	0.0005
Chesapeake Bay‡	2	5	19	45	0.66
Potomac River‡	2	7	34	23	0.04
San Francisco Bay§	1	11	44	96	0.08
Port Phillip Bay¶	2	5	31	59	0.55
New Zealand Coast**	0	8	59	42	0.001

P-values are from one-tailed Fisher Exact tests of the null hypothesis that the proportion of unshared genera (genera not represented among native species in the system) among high-impact invaders is no greater than that of low-impact invaders. The null hypothesis was rejected by a meta-analysis of the entire data set (Fisher's Combined Probability test, $P < 0.0001$).

Primary sources of data: *Mills *et al.* 1993, †Mills *et al.* 1996, ‡Ruiz *et al.* 1999, §Cohen & Carlton 1995, ¶Hewitt *et al.* 1999, **Cranfield *et al.* 1998.

likely to encounter potential victims or enemies that are adapted to them; this is the premise for neoclassical biological control, which purposely selects novel enemies against naïve target organisms lacking co-evolved defenses (Hokkanen & Pimentel 1989).

An alternative explanation to be considered is that our results reflect not a general pattern but merely the repeated impacts of the same small group of invaders in different systems. But this is not the case. In total, 66 species are classified as 'high-impact' invaders within the study systems, but only 14 are high-impact invaders of more than one system; 12 of these species occur in no more than two systems, and two species occur in three systems.

Although each system tended in the direction consistent with the hypothesis, two marine systems (Chesapeake Bay, USA and Port Phillip Bay, Australia) had highly nonsignificant *P*-values. Marine systems, in general, had higher *P*-values and lower proportions of high-impact invaders than freshwater systems. This may reflect a higher vulnerability of freshwater systems because of their greater insularity, but a larger dataset is needed to confirm this generalization.

Could our results be affected by variation in native species richness across systems? If species-poor systems are more invasible, as predicted by theoretical studies (although there is little empirical evidence for a species richness–invasibility relationship in aquatic systems; Ricciardi 2001), then by chance alone they may receive a higher number of taxonomically distinct invaders; but there is no theoretical reason that they should experience impacts greater than those experienced by species-rich systems. While species-rich systems are more likely to contain a shared genus, it is not apparent from our dataset that they are less vulnerable to high-impact invaders. For example, the New Zealand Coast possesses more than four times the number of native species found in Port Phillip Bay (8000 spp. vs. 650 spp., respectively; Hewitt *et al.* 1999; New Zealand Ministry of Environment 2000), yet has a similar number of high-impact invaders and a significantly larger proportion of unshared high-impact invaders (Table 1). We find no correlation between native species richness and the outcome of the individual Fisher Exact tests in our dataset. Although systems with historically low species richness are more naïve to the effects of a broader spectrum of invaders, strong impacts are observed even in species-rich systems invaded by organisms with novel traits, as demonstrated by the following examples. North American inland waters contain the planet's richest assemblage of freshwater mussels, which have no evolutionary experience with dominant fouling organisms; numerous native mussel populations have been extirpated by an invasive biofouling mollusc, the Eurasian zebra mussel *Dreissena polymorpha*. Such extirpations have rarely been reported from invaded European lakes and rivers, whose native fauna were previously exposed to *Dreissena* during the Pleistocene era (Ricciardi *et al.* 1998). Similarly, the cichlids of Lake Victoria were naïve to the effects of the Nile perch, a large predator whose introduction is implicated in the disappearance of nearly 200 endemic species (Hall & Mills 2000). As argued elsewhere (Simberloff 1995), the absence of entire groups of species (such as large piscivores or fouling bivalves), rather than low-species richness *per se*, predispose communities to be altered by certain invasions. Unfortunately, this caveat has little predictive value because the importance of any particular functional trait absent from a community is not apparent until a high-impact invader possessing that trait becomes established. A more practical approach for risk assessment, as suggested by our findings, is to consider a potential invader's taxonomic relationships to members of the recipient community.

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