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BIODIVERSITY RESEARCH

Predicting the number of ecologically harmful exotic species in an aquatic system

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ABSTRACT

Most introduced species apparently have little impact on native biodiversity, but the proliferation of human vectors that transport species worldwide increases the probability of a region being affected by high-impact invaders – i.e. those that cause severe declines in native species populations. Our study determined whether the number of high-impact invaders can be predicted from the total number of invaders in an area, after controlling for species–area effects. These two variables are positively correlated in a set of 16 invaded freshwater and marine systems from around the world. The relationship is a simple linear function; there is no evidence of synergistic or antagonistic effects of invaders across systems. A similar relationship is found for introduced freshwater fishes across 149 regions. In both data sets, high-impact invaders comprise approximately 10% of the total number of invaders. Although the mechanism driving this correlation is likely a sampling effect, it is not simply the proportional sampling of a constant number of repeat-offenders; in most cases, an invader is not reported to have strong impacts on native species in the majority of regions it invades. These findings link vector activity and the negative impacts of introduced species on biodiversity, and thus justify management efforts to reduce invasion rates even where numerous invasions have already occurred.

Keywords

Aquatic ecosystems, biological invasions, ecological impact, invasive species, propagule pressure, risk assessment, Tens Rule.

INTRODUCTION

Introduced species are implicated as a major cause of extinction (Clavero & García-Berthou, 2005; Light & Marchetti, 2007). Their impacts on native species can be particularly severe in insular systems (Witte *et al*., 1992; Ricciardi *et al*., 1998; Hall & Mills, 2000), but are highly variable geographically (Atkinson, 1985; D'Antonio *et al*., 2000; Ricciardi, 2003). This raises the fundamental question of why certain areas are more severely affected by invasions and whether they fit any general statistical pattern. Owing to their evolutionary history, some species assemblages are naïve to the effects of a broad range of invaders (Diamond & Case, 1986; Cox & Lima, 2006), whereas others contain native predators or competitors that can limit the impact of invaders (Robinson & Wellborn, 1988; Reusch, 1998; DeRivera *et al*., 2005). The invasion history of an area might also influence the impact of new invaders. An accumulation of invaders could conceivably lead to biotic resistance in the form of increased interference and other antagonistic interactions that progressively reduce the impacts of late arrivals (Case, 1990; Vance-Chalcraft & Soluk, 2005). Conversely, through positive interactions invaders may augment each other's impact and produce synergistic effects (Simberloff & Von Holle, 1999; Richardson *et al*., 2000; Ricciardi, 2001; Ross *et al*., 2004; Blackburn *et al*., 2005). Otherwise, differences in the number of high-impact (HI) invaders across sites may simply reflect variation in propagule pressure (the number of organisms or species released into an area per unit time), such that those sites that receive more invaders are more likely to acquire HI species by chance alone.

Thus, if there is a relationship between the number of HI invaders and the total number of invaders within a given region, it may be described by one of the following models (Fig. 1):

(1) A linear function, which can arise from a sampling effect in at least two ways. It may be generated by the proportional sampling of a constant number of HI species, in which case the expected proportion (the regression coefficient or slope of the line) could theoretically be known *a priori*. For example, Rejmanek & Randall (2004) found a linear relationship between 'noxious' vs. 'non-noxious' plant invaders across 50 states within the USA. Their study precategorized the impact status of each plant invader: if a species was reported to be noxious in any one state, it was counted as a noxious species in every state in which it was

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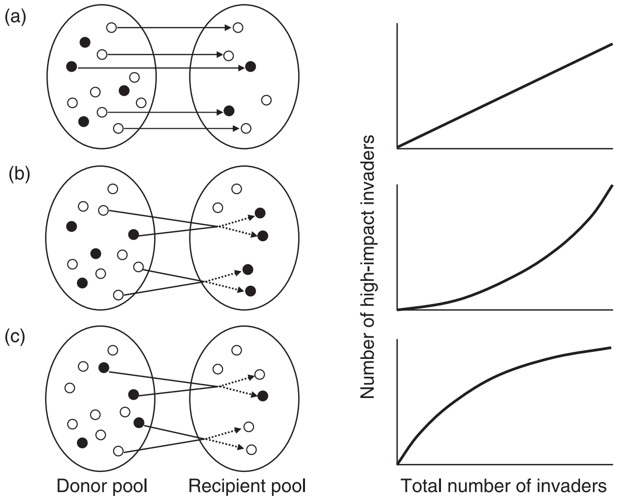

Figure 1 Hypothesized relationships between the number of high-impact (HI) invaders and the total number of invaders within an area: (a) a linear sampling effect – resulting either from simple proportional sampling of a fixed number of HI invaders, or from sampling species with varying potential to become HI invaders in the new environment; (b) a synergistic effect – where the impacts of an invader are enhanced in the presence of other invaders; and (c) an asymptotic effect resulting from antagonism (if interference or other negative interactions between invaders diminish their impacts) or pool depletion (if HI invaders colonize more rapidly than other species). HI invaders are indicated by solid circles; other invaders are indicated by open circles.

known to occur; thus, the resulting correlation reflects simple proportional sampling. However, case studies suggest that the same species may not have strong effects everywhere it invades (Atkinson, 1985; D'Antonio *et al.*, 2000; Ricciardi, 2003), and so there should be no predetermined number of HI species in any given donor pool.

Alternatively, the linear function could arise from sampling a pool of invaders whose potential to become HI species in the recipient region is regulated by extrinsic factors, e.g. resource availability, habitat structure, disturbance, or the diversity, composition and evolutionary naïveté of the recipient community (Byers, 2002a,b; Ricciardi, 2003; Huston, 2004; Ricciardi & Atkinson, 2004; Ruesink, 2007). Spatial variation in the regression coefficient may also be generated by biases in detection effort and scientific attention. In either case, the proportion of HI species cannot be known from merely sampling the donor pool, but it can be expected to be small because most invasions do not produce extinctions (Simberloff, 1981).

(2) A concave-upward (polynomial or exponential) curve, reflecting the situation where opportunities for synergistic interactions increase disproportionately with the total number of invaders.

(3) A convex curve, which can arise in at least two ways. An increasing number of invaders may create more interference with each other, thereby constraining each other's abundance and, thus, their impact. Or, if HI species are better colonizers and have the same opportunity to invade as low-impact species, then they will establish early and subsequent invasions by HI species will decline with time as the source pool becomes depleted; however, this latter scenario seems unlikely as there is no evidence of a correlation between the impact of an introduced species on native species populations and its ability to spread (Ricciardi & Cohen, 2007).

The objective of our study was to determine whether the total number of aquatic invaders in a given system or region is a reliable predictor of the number of HI species and, if so, which of the above scenarios best describes this relationship. We also tested the effects of area and native species richness as covariables.

METHODS

We compiled two separate data sets for analysis. We examined the invasion histories of aquatic systems that differ broadly in area, location, the number of native species historically present, and the number of invaders. These systems were located by a search of the scientific literature and internet databases for lakes, river basins, estuaries, and marine coastal regions with well-documented invasion histories. 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 more than 5 years. Invaders were classified as 'high-impact' (HI) if there was experimental or correlational evidence that they caused a substantial (> 50%) decline in a native species population – or, alternatively, if there was a published reference to them having been associated with the displacement, extirpation, or severe reduction of a native population – anywhere within the system. We excluded systems that had fewer than two HI species and a documented invasion history spanning less than 50 years, in order to reduce the influence of time lags in detection of impacts (Ruesink, 2003). The resulting data set consisted of 16 spatially independent aquatic systems, including seven marine and nine freshwater systems. We used the documented number of native fishes historically present as a proxy of native species richness in each system.

A second data set was compiled from lists of introduced fishes for regions worldwide provided by Lever (1996). Numbers of native species historically present in each region were obtained through FishBase (Froese & Pauly, 2007). We omitted regions that reported no established non-indigenous fishes (according to Lever, 1996), leaving a total sample of 149 regions. HI fish invaders were identified using the same criteria as above. Least-squares regression was used to test the relationships between the number of HI invaders and the total number of invaders in a given system or region. Multiple regression analysis [generalized linear model (GLM) and stepwise regression, SAS version 8; SAS Institute, Cary, NC, USA] was used to test the effects of area and the number of native species (both log-transformed) as covariates.

RESULTS

In aquatic systems, the number of HI invaders is positively correlated to the total number of invaders, which explains 59% of the

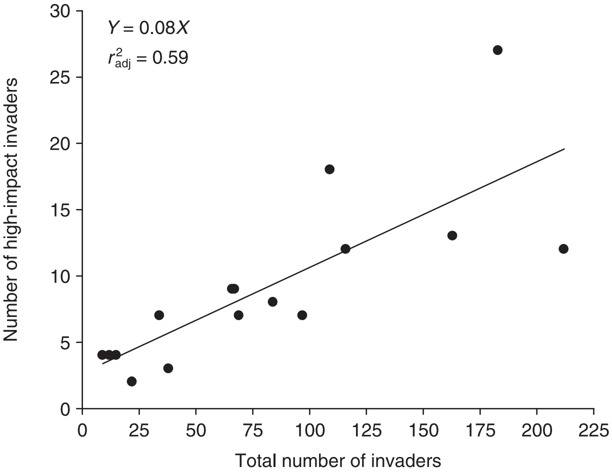

Figure 2 Relationship between the number of high-impact invaders and the total number of invaders in freshwater and marine systems.

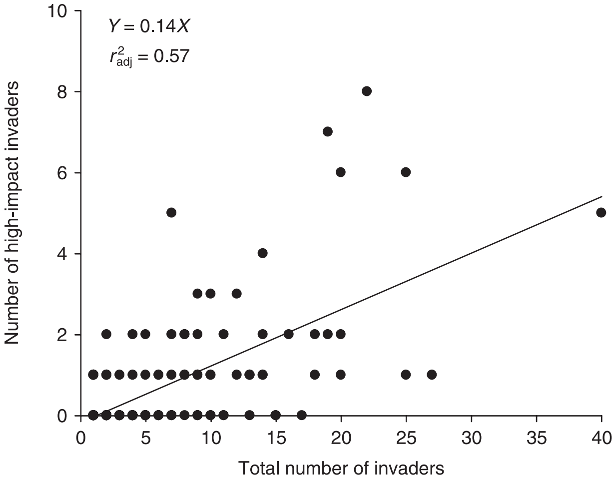

Figure 3 Relationship between the number of high-impact fish invaders and the total number of fish invaders for 149 regions. The data point corresponding to the USA is outside the range shown.

variance ($P < 0.0003$; Fig. 2). This relationship is not driven by a species–area effect; system area is not correlated with the number of HI invaders ($P = 0.09$), although it is weakly correlated with the total number of invaders ($r^2_{adj} = 0.237$, $P < 0.032$). A simple linear function provides a better fit to the untransformed data (more variance explained, lower residual mean square error) than a polynomial or exponential function, suggesting that the mechanism behind this relationship is a sampling effect. Logarithmic transformation did not improve the fit. As expected, the y-intercept was not significant. On average, 8% of invaders exert strong negative impacts on biodiversity in these systems (95% confidence limits = 4–12%). Freshwater systems tended to have higher proportions of HI invaders than marine systems (regression coefficients ± 95% CI: 0.11 ± 0.05 vs. 0.04 ± 0.04, respectively; ANCOVA, $P = 0.05$).

A nearly identical linear relationship exists between the number of HI invaders and the total number of fish invaders in a given region ($P < 0.0001$; Fig. 3). Both variables increase with area (for HI invaders: $r^2_{adj} = 0.12$, $P < 0.0001$; for all invaders: $r^2_{adj} = 0.13$, $P < 0.0001$), but they remain correlated with each other after controlling for species–area effects; log-transformed area is not a significant covariate in the relationship (Proc GLM, $P > 0.15$). Here again, a simple linear function provides the best fit to the data. The USA has the highest recorded number (~80 species) of established foreign fishes but is not an outlier nor has any significant leverage: the regression coefficients are 0.14 ± 0.02 with the USA ($r^2_{adj} = 0.57$, $P = 0.0001$) and 0.13 ± 0.03 without the USA ($r^2_{adj} = 0.39$, $P = 0.0001$). Moreover, the regression coefficient is not significantly different from that obtained for mixed assemblages of invaders in aquatic systems.

The log-transformed number of native species was not a significant covariate in the relationship between the number of HI invaders and the total number of invaders in either of the two data sets (Proc GLM, $P > 0.20$). The total number of invaders was the only variable to be retained as a predictor of HI invaders in stepwise regressions that included the log-transformed number of native species and area as candidate variables (Proc stepwise, $P = 0.15$ for variable entry and retention).

DISCUSSION

We recognize that invasions do not divide up simply into those that are harmful and those that are not (Carlton, 2002). We presume that every invasion will have an ecological impact on the environment, but that these impacts are distributed along a skewed continuum in which the most severe impacts are relatively rare, i.e. the upper tail of a log-normal distribution (Williamson & Fitter, 1996). Therefore, we have applied an arbitrary quantitative criterion to a specific type of impact: whether an invader contributed to a substantial (> 50%) decline of a native species population. This does not imply that invaders that fail to meet this criterion have no significant impacts on the resident community, but it provides a practical benchmark for categorizing invaders that have a particularly strong negative effect on one or more native species populations in the invaded area.

Although positive interactions among exotic species are common in some aquatic systems and can produce strong synergistic impacts (Ricciardi, 2001, 2005), we found no evidence that such interactions have augmented the frequency of native species declines in highly invaded areas. There is also no evidence of increased interference resulting in reduced impacts on native species, consistent with the view that antagonistic interactions among species generate observable patterns only at local scales (Levine & D'Antonio, 1999; Shea & Chesson, 2002). The distributions of many invaders may not overlap within a system or region, and while larger systems accommodate more species they are also more heterogeneous, thereby reducing the frequency of interactions between invaders.

Our study found that approximately 10% (8–14%) of aquatic invaders have strong negative impacts on native biodiversity.

This is in agreement with some regional studies: the proportion of marine invaders implicated in the displacement of native species from coastal waters is 9% (5/53) in Britain (Eno, 1996) and 7% (8/109) in New Zealand (Cranfield *et al.*, 1998). By contrast, hardly any HI invaders have been recorded from coastal areas of France (Goulletquer *et al.*, 2002) and India (Subba Rao, 2005), perhaps reflecting a paucity of impact studies in these regions. Similarly, the ecological impact of the vast majority of invaders in the Mediterranean Sea is poorly known, but at least 4% of the ~500 non-indigenous species recorded from the region appear to be linked to declines in native species populations (Galil, 2007), which is consistent with our estimate for marine systems. A high proportion (24%) of HI invaders is found among the introduced inland fishes of California, a relatively well-studied fauna (Moyle, 2002). Freshwater systems tended to have higher proportions of HI invaders than marine systems in our dataset (11% vs. 4%, respectively). Although this finding resonates with the conventional view that insular systems are more vulnerable to the impacts of invaders (Williamson, 1981; Cox & Lima, 2006), it must be interpreted with caution, given the small number of systems available for comparison.

At first glance, our findings appear to be in agreement with the Tens Rule, in which between 5% and 20% of established introduced species become ‘pests’ (Williamson & Fitter, 1996). However, invaders that do not contribute significantly to native species declines may nonetheless disrupt their new environment in myriad ways. For example, common carp (*Cyprinus carpio*) and grass carp (*Ctenopharyngodon idella*) frequently damage or destroy beds of aquatic plants, thereby altering physical habitat for other fishes and invertebrates; additional negative effects of aquatic invaders include hybridization, the transfer of new parasites and diseases, and trophic alterations leading to declines in productivity (Moyle *et al.*, 1987; Lever, 1996; Simon & Townsend, 2003). Thus, the proportion of invaders that exert significant ecological impacts is likely to be substantially larger than what we derived for those species that are specifically associated with native population declines – as indicated by a review of fish invasions in Europe, which found that 50–86% of the most frequently introduced species had conspicuous ecological effects, although these include positive as well as negative effects (García-Berthou *et al.*, 2005). For the vast majority of invasions, impacts are not quantified or may be strongly underestimated due to insufficient baseline data (Parker *et al.*, 1999); therefore, the expected value of 10% for HI invaders is probably highly conservative.

Nature of the relationship: sampling effect with local regulation

The mechanism driving these correlations is likely a sampling effect, but it is not merely the proportional sampling of a constant number of ‘repeat offenders’. In fact, repeat offenders appear to constitute a minority of invaders, although this may be biased by the variable quality and availability of impact data, which is sometimes lacking even for species with conspicuous effects (Parker *et al.*, 1999). Most invaders are not reported to have strong impacts on native species in the majority of regions which they invade (Fig. 4). Among the fishes that invaded multiple (≥ 3) regions, those that were a HI species in at least one region were HI species in only 19% (median = 14%) of the regions they invaded, on average. For example, Nile tilapia (*Oreochromis niloticus*) has invaded at least 19 countries in Africa and Eurasia, but has been reported as a HI species in only six of them (Lever, 1996). There are very few common characteristics of HI species (Ruesink, 2003; but see Keller *et al.*, 2007) and their impacts are context dependent (Ricciardi, 2003), suggesting the importance of local regulation by extrinsic environmental variables (e.g. Byers, 2002a,b; Ricciardi & Atkinson, 2004).

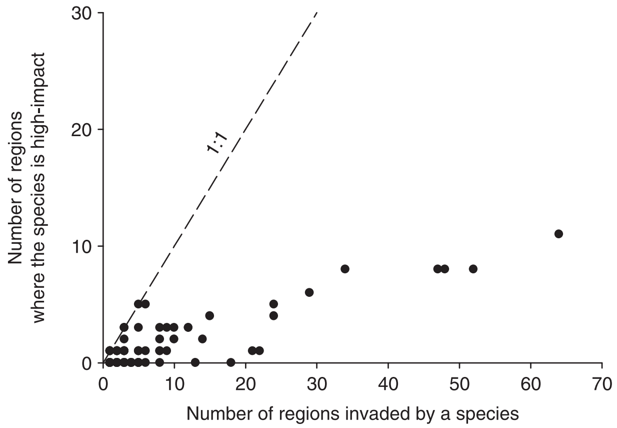

Figure 4 The impacts of a fish invader on biodiversity are highly variable across regions. The 1 : 1 line indicates where the number of regions in which a species is a high-impact invader equals the number of regions it has invaded.

We found no evidence that native species richness is a regulatory variable at the spatial scale of our analysis. The relationship between native diversity and the impacts of invaders is complex (Ortega & Pearson, 2005; Ruesink, 2007). The composition of the recipient community may be a more important regulator than species richness *per se*. For example, invaders introduced to areas where predators are absent have had highly disruptive effects on communities (Pimm, 1987). Generalist predators can constrain the abundance and impact of some invaders (Robinson & Wellborn, 1988; Reusch, 1998; DeRivera *et al.*, 2005), especially in areas that lack prey refugia (Eklöv & VanKooten, 2001; Harvey *et al.*, 2004) or where abiotic conditions are unfavourable to the invader (Baltz & Moyle, 1993; Byers, 2002a). However, the presence of even a diverse assemblage of consumers does not necessarily prevent invaders from becoming dominant; a diverse community of herbivores did not prevent an invasive green alga from proliferating on New Zealand’s rocky shores (Trowbridge, 1995), nor did a diverse and abundant native planktivore community prevent the predatory waterflea *Bythotrephes longimanus* from extirpating native species in the lower Great Lakes (Boudreau & Yan, 2003). In fact, interference competition among multiple predators could reduce mortality among introduced prey in some instances (Soluk, 1993), and the net effect of a predator could be to exacerbate the impact of an introduced prey on native species through apparent competition (Noonburg

& Byers, 2005). A diverse recipient community can simultaneously exert antagonistic and facilitative effects on invaders (Ruesink, 2007). The synergistic influence of recipient communities, habitat attributes, and other extrinsic factors poses a considerable challenge to the development of general predictive models of impact, and makes the discovery of any strong statistical pattern all the more remarkable.

Implications for risk assessment and management

As Lockwood *et al.* (2001) argued, simply knowing that some proportion of invaders will have a strong impact is not obviously useful for resource management. However, the statistical expectation that at least 10% of invaders within an area will pose a severe threat to native species populations should encourage managers to closely monitor the long-term effects of exotic species in highly invaded systems, or in systems that have experienced a recent increase in propagule pressure (e.g. through a change in shipping activity), which may elevate the rate of invasion (Lockwood *et al.*, 2005; Thuiller *et al.*, 2005; Ricciardi, 2006). Our findings suggest a link between propagule pressure and impact, and thus a justification for investing in methods to reduce the invasion rate of a region even where numerous invasions have already occurred. In San Francisco Bay, for example, if the current rate of invasion persists, four new HI invaders can be expected to arrive within the next decade.

It would be interesting to study highly invaded systems or regions in which the number of HI species deviates strongly from the expected value, as these areas may reveal environmental conditions that regulate the impact of invaders on biodiversity. Finally, the expected value could also be used as a baseline to identify taxonomic groups of species that have a greater than expected chance of being HI invaders in each system or region within their invaded range. Our findings support the contention that most species could become HI invaders in at least part of their invaded range if distributed sufficiently widely (Fig. 4; Ruesink, 2003).

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REFERENCES

Atkinson, I.A.E. (1985) The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *Conservation of Island birds* (ed. by P.J. Moors), pp. 35–81. International Council for Bird Preservation, Cambridge, UK.

Baltz, D.M. & Moyle, P.B. (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications*, **3**, 246–255.

Blackburn, T.M., Petchy, O.L., Cassey, P. & Gaston, K.J. (2005) Functional diversity of mammalian predators and extinction in island birds. *Ecology*, **86**, 2916–2923.

Boudreau, S.A. & Yan, N.D. (2003) The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1307–1313.

Byers, J.E. (2002a) Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia*, **130**, 146–156.

Byers, J.E. (2002b) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, **97**, 449–458.

Carlton, J.T. (2002) Bioinvasion ecology: assessing invasion impact and scale. *Invasive aquatic species of Europe: distribution, impacts and management* (ed. by E. Leppäkoski, S. Gollasch and S. Olenin), pp. 7–19. Kluwer, Dordrecht, The Netherlands.

Case, T.J. (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA*, **87**, 9610–9614.

Clavero, M. & García-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110.

Cox, J.G. & Lima, S.L. (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, **21**, 674–680.

Cranfield, H.J., Gordon, D.P., Willan, R.C., Marshall, B.A., Battershill, C.N., Francis, M.P., Nelson, W.A., Glasby, C.J. & Read, G.B. (1998) *Adventive marine species in New Zealand*. NIWA Technical Report 34, NIWA, Wellington, New Zealand.

D'Antonio, C.M., Tunison, J.T. & Loh, R.K. (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient. *Austral Ecology*, **25**, 507–522.

DeRivera, C.E., Ruiz, G.M., Hines, A.H. & Jivoff, P. (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology*, **86**, 3364–3376.

Diamond, J. & Case, T.J. (1986) Overview: introductions, extinctions, exterminations, and invasions. *Community ecology* (ed. by J. Diamond and T.J. Case), pp. 65–79. Harper & Row, New York.

Eklöv, P. & VanKooten, T. (2001) Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, **82**, 2486–2494.

Eno, C. (1996) Non-native marine species in British waters: effects and controls. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **6**, 215–228.

Froese, R. & Pauly, D. (2007) *FishBase*. Online publication. www.fishbase.org, version (5/2007).

Galil, B.S. (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine Pollution Bulletin*, **55**, 314–322.

García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G. & Feo, C. (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 453–463.

Goulletquer, P., Bachelet, G., Sauriau, P.G. & Noel, P. (2002) Open Atlantic coast of Europe – a century of introduced species in French waters. *Invasive aquatic species of europe: distribution, impacts, management* (ed. by E. Leppäkoski, S. Gollasch and S. Olenin), pp. 276–290. Kluwer, Dordrecht, The Netherlands.

Hall, S.R. & Mills, E.L. (2000) Exotic species in large lakes of the world. *Aquatic Ecosystem Health and Management*, **3**, 105–135.

Harvey, B.C., White, J.L. & Nakamoto, R.J. (2004) An emergent multiple predator effect may enhance biotic resistance in a stream fish assemblage. *Ecology*, **85**, 127–133.

Huston, M.A. (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions*, **10**, 167–168.

Keller, R.P., Drake, J.M. & Lodge, D.M. (2007) Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. *Conservation Biology*, **21**, 191–200.

Lever, C. (1996) *Naturalized fishes of the world*. Academic Press, London.

Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

Light, T. & Marchetti, M.P. (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, **21**, 434–446.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.

Lockwood, J.L., Simberloff, D., McKinney, M.L. & Von Holle, B. (2001) How many, and which, plants will invade natural areas? *Biological Invasions*, **3**, 1–8.

Moyle, P.B. (2002) *Inland fishes of California*. University of California Press, Berkeley, California.

Moyle, P.B., Li, H.W. & Barton, B. (1987) The Frankenstein effect: impact of introduced fishes on native fishes of North America. *Fish culture in fisheries management* (ed. by R.H. Stroud), pp. 415–426. American Fisheries Society, Bethesda, Maryland.

Noonburg, E.G. & Byers, J.E. (2005) More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology*, **86**, 2555–2560.

Ortega, Y.K. & Pearson, D.E. (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications*, **15**, 651–661.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Pimm, S.L. (1987) Determining the effects of introduced species. *Trends in Ecology & Evolution*, **2**, 106–108.

Rejmanek, M. & Randall, J.M. (2004) The total number of naturalized species can be a reliable predictor of the total number of alien pest species. *Diversity and Distributions*, **10**, 367–369.

Reusch, T.B.H. (1998) Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. *Marine Ecology Progress Series*, **170**, 159–168.

Ricciardi, A. (2001) Facilitative interactions among aquatic invaders: is an 'invasional meltdown' occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2513–2525.

Ricciardi, A. (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology*, **48**, 972–981.

Ricciardi, A. (2005) Facilitation and synergistic interactions among introduced aquatic species. *Invasive alien species: a new synthesis* (ed. by H.A. Mooney, R.N. Mack, J. McNeely, L.E. Neville, P.J. Schei and J.K. Waage), pp. 162–178. Island Press, Washington, D.C.

Ricciardi, A. (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, **12**, 425–433.

Ricciardi, A. & Atkinson, S.K. (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, **7**, 781–784.

Ricciardi, A. & Cohen, J. (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, **9**, 309–315.

Ricciardi, A., Neves, R.J. & Rasmussen, J.B. (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology*, **67**, 613–619.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions: the role of mutualisms. *Biological Reviews*, **75**, 65–93.

Robinson, J.V. & Wellborn, G.A. (1988) Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: fish predation effects. *Oecologia*, **77**, 445–452.

Ross, D.J., Johnson, C.R., Hewitt, C.L. & Ruiz, G.M. (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. *Marine Biology*, **144**, 747–756.

Ruesink, J.L. (2003) One fish, two fish, old fish, new fish: which invasions matter? *The importance of species – perspectives on expendibility and triage* (ed. by P. Kareiva and S.A. Levin), pp. 161–178. Princeton University Press, Princeton, New Jersey.

Ruesink, J.L. (2007) Biotic resistance and facilitation of a non-native oyster on rocky shores. *Marine Ecology Progress Series*, **331**, 1–9.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, **17**, 170–176.

Simberloff, D. (1981) Community effects of introduced species. *Biotic crises in ecological and evolutionary time* (ed. by M.H. Nitecki), pp. 53–81. Academic Press, New York.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Simon, K.S. & Townsend, C.P. (2003) Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, **48**, 982–994.

Soluk, D. (1993) Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, **74**, 219–225.

Subba Rao, D.V. (2005) Comprehensive review of the records of biota of the Indian Seas and introduction of non-indigenous species. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 117–146.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.

Trowbridge, C.D. (1995) Establishment of the green algae *Codium fragile* spp. *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. *Journal of Ecology*, **83**, 949–965.

Vance-Chalcraft, H.D. & Soluk, D.A. (2005) Multiple predator effects result in risk reduction for prey across multiple prey densities. *Oecologia*, **144**, 472–480.

Williamson, M. (1981) *Island populations*. Oxford University Press, Oxford.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.

Witte, F., Goldschmidt, T., Wanink, J., Oijen, M., Goudswaard, K., Witte-Maas, E. & Bouton, N. (1992) The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes*, **34**, 1–28.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Data and references for the 16 aquatic systems used in this study.

Appendix S2 Data for non-indigenous fishes in 149 regions.

This material is available as part of the online article from:
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