



Origin matters: alien consumers inflict greater damage on prey populations than do native consumers

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ABSTRACT

Aim Introduced alien species are frequently implicated in ecosystem disruption and biodiversity loss, but some ecologists have recently argued that efforts to manage ecosystems should be refocused on known problematic species without regard to whether such species are native or alien. This argument rests on the premise that native and alien species in general do not differ in their impacts. Although there are numerous cases that suggest alien predators and herbivores can sometimes cause severe declines or even local extinctions of native species, very few studies have compared the impacts of native and alien consumers on native populations.

Location World-wide.

Methods We have conducted a meta-analysis on a global dataset to compare the effects of native and alien predators and herbivores on native populations occupying a broad range of terrestrial and aquatic environments.

Results The distribution of positive, negative and neutral effects on native prey abundance differed significantly by consumer origin, with alien consumers associated with more negative and fewer positive effects than expected, opposite the finding for native consumers. The effect size of alien consumers was 2.4 times greater than that of native consumers and did not differ between predators and herbivores. The impact of alien consumers did not differ significantly in aquatic (lakes, rivers, oceans) versus terrestrial (continental, island) habitats. Similarly, there was no significant interaction between consumer origin and location, as consumers had similar effects in insular (freshwater, island) and open (continental, marine) systems – contrary to the notion that alien species impacts are mainly problematic for island biota.

Main conclusions We hypothesize that the ecological naïveté of native biota facilitates their enhanced suppression by alien predators and herbivores relative to native enemies. Our results counter the assertion that the biogeographical origin of species has no bearing on their ecological impact.

Keywords

Biodiversity, biological invasions, invasive species, non-indigenous, non-native, prey naïveté, trophic interaction.

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INTRODUCTION

Invasions by alien (i.e. non-native) species are increasing globally (Ricciardi, 2007), and many are known to have significantly altered biological communities, physical habitats and ecosystem processes (Parker *et al.*, 1999; Mack *et al.*, 2000; Simberloff *et al.*, 2013). It may often be difficult to

determine the extent to which alien species are drivers, rather than passengers, of observed ecological change (Didham *et al.*, 2005), because impacts and their causes have not been investigated for the vast majority of invasions (Parker *et al.*, 1999; Hulme *et al.*, 2013). Nevertheless, a growing number of case studies implicate alien species as a major cause of native population loss and extinction (e.g. Witte *et al.*, 1992;

Kats & Ferrer, 2003; Clavero & Garcia-Berthou, 2005; Parker *et al.*, 2006; Clavero *et al.*, 2009; Medina *et al.*, 2011). Mechanisms by which alien species contribute to native species decline include predation (Witte *et al.*, 1992; Fritts & Rodda, 1998; Kats & Ferrer, 2003; Blackburn *et al.*, 2004; Dorcas *et al.*, 2012), herbivory (Parker *et al.*, 2006; Spear & Chown, 2009), hybridization (Ayres *et al.*, 2004), competition (Spencer *et al.*, 1991; Ricciardi *et al.*, 1998; Ricciardi, 2004; Baider & Florens, 2011), disease transfer (Wyatt *et al.*, 2008) and physical habitat alteration (Mack *et al.*, 2000). The impacts of these mechanisms appear to be magnified by the lack of evolutionary adaptations in native species to the effects of aliens for which there are no naturally occurring analogues in the invaded system (Short *et al.*, 2002; Ricciardi & Atkinson, 2004; Cox & Lima, 2006). Insular systems, in particular, contain native species that are naïve to the behaviours of a broad range of consumers and thus appear to be disproportionately vulnerable to suppression by alien predators and herbivores (Witte *et al.*, 1992; Fritts & Rodda, 1998; Courchamp *et al.*, 2003; Blackburn *et al.*, 2004; Berglund *et al.*, 2009).

In spite of this evidence, several authors claim that concern over alien species has been exaggerated or misplaced (Gurevitch & Padilla, 2004; Goodenough, 2010; Davis *et al.*, 2011; Schlaepfer *et al.*, 2011a). Moreover, some ecologists have recently argued that efforts to manage ecosystems should be refocused on known problematic species without regard to whether such species are native or alien (Davis *et al.*, 2011). They base this argument on the premise that alien species have no particular propensity to cause ecological damage and are just as likely to confer benefits to ecosystems and the biodiversity they contain (Davis *et al.*, 2011; see also Schlaepfer *et al.*, 2011b). This untested premise may fuel growing calls to consider intentional introductions ('assisted colonization' or 'managed relocation') of species beyond their native range as a strategy for conservation and resource management (Hoegh-Guldberg *et al.*, 2008; Briggs, 2008; Schwartz *et al.*, 2012; but see Ricciardi & Simberloff, 2009).

Parker *et al.* (2006) determined that native herbivores suppressed non-native plant abundance but not their diversity, whereas non-native herbivores enhanced the abundance and diversity of non-native, but not native, plants. To date, no study has compared the effect sizes of native and alien consumers (encompassing both predators and herbivores, and vertebrate and invertebrate animals) on populations of plant and animal prey. Here, we conducted a global meta-analysis to examine the effects of alien and native predators and herbivores on the abundance of prey populations in terrestrial, freshwater and marine environments. Specifically, we tested the following null hypotheses: (1) alien and native consumers do not differ in their impact (i.e. they have similar effect sizes and are equally likely to exert positive and negative effects) on prey populations across all biomes; and (2) insular (freshwater systems and islands) and 'open' (continental and marine) prey populations are equally suppressed by alien consumers.

METHODS

We searched Thomson Reuter's Web of Science for peer-reviewed articles published in 2010 and 2011 using the following keywords: *introduced species*, *alien species*, *non-indigenous species*, *non-native species*, *colonizing species* or *exotic species*; we then combined that search with one using the keywords *predat**, *herbivore** or *prey*. To obtain more studies involving native consumers and native prey, we conducted another search following the same methodology but using the keywords *native predator*, *native herbivore* or *native prey*. The total search yielded 1417 published studies, of which 1355 were discarded as they did not provide quantitative descriptions of consumer impact on native prey populations. The resulting dataset allowed us to study the frequency and magnitude of effects ('effect size') of alien and native consumers on native prey populations. Effect size was measured as a log response ratio $R = \ln(X_{+pred}/X_{-pred})$, incorporating population abundance (biomass or numerical density) measured in the presence (X_{+pred}) and absence (X_{-pred}) of a predator or herbivore. Thus, a positive or negative ratio indicates that native prey populations increased or decreased in abundance, respectively, in the presence of the consumer. We recorded positive, negative and neutral effects of alien and native consumers, and used a Chi-square test (in SYSTAT version 12.00.08; Systat Software, Inc., Chicago, IL, USA) to compare the frequency distribution of these categories for all native prey species (184 populations) identified in the studies.

Where studies reported effects on multiple prey, we calculated the mean effect size across all prey species to avoid pseudoreplication. In cases involving multiple species of consumers feeding on the same assemblage (see Appendix S1 and S2 in Supporting Information) and where their individual effects could not be distinguished, a combined effect of these consumers was reported; however, such cases were included only when it was known (or when the study indicated) if all the consumers were either native or non-native. When the individual effects of multiple consumers were examined in the same study, the data were treated as individual records. In cases involving omnivorous consumers (e.g. black rats) feeding directly on plants (or on animals), the data were used in calculations of the overall effect of herbivores (or predators). When data from multiple sampling dates were available for a given experiment or field survey, we used only the final sampling date in the effect size calculation. We included experimental studies with both replicated and unreplicated data, field surveys that were either temporally or spatially replicated, and mesocosm experiments that were conducted in the laboratory or in the field.

We tested for differences in effect size by consumer origin (1) across biomes (freshwater, terrestrial, marine); (2) between insular habitats (lakes, rivers and islands) and 'open' (mainland/marine) habitats; (3) between predators and herbivores; and (4) between experimental studies and field surveys, using either *t*-tests (with separate variances) or 2-way

ANOVA, as appropriate, with SYSTAT version 12.00.08. We used an unweighted effect size metric in our meta-analysis because many studies did not report sampling variances and sample sizes for the response variables measured. Exclusion of these studies would greatly reduce the sample size of our dataset and possibly introduce biases into our analyses (Englund *et al.*, 1999). Therefore, we used standard parametric statistical tests and acknowledge that our estimated *P*-values may be less precise, and our tests less powerful, compared with weighted analyses (Gurevitch & Hedges, 1999). However, our approach allowed us to include a greater number of studies and thus likely reduced the probabilities of both type I and type II errors (Lajeunesse & Forbes, 2003).

RESULTS

Some studies reported a positive impact of consumers on prey populations; these effects were less likely to be associated with alien consumers as compared with native consumers, whereas negative effects were more commonly observed with alien consumers ($n = 184$; $\chi^2 = 7.76$, d.f. = 2, $P < 0.03$).

Altogether, 73 mean effect sizes were collated from 62 peer-reviewed studies. The overall mean effect of alien consumers was 2.4 times that of native consumers ($t = -3.15$, d.f. = 68.7, $P = 0.002$; Fig. 1). There was no significant difference in effect sizes yielded by experimental and field survey data ($F_{1,69} = 0.04$, $P = 0.835$), and so all other analyses were carried out using the combined dataset. Effect sizes did not differ between alien predators and alien herbivores ($F_{1,69} = 0.62$, $P = 0.436$). Contrary to predictions, effect size differences between alien and native consumers did not vary between insular and open systems ($F_{1,69} = 1.07$, $P = 0.305$),

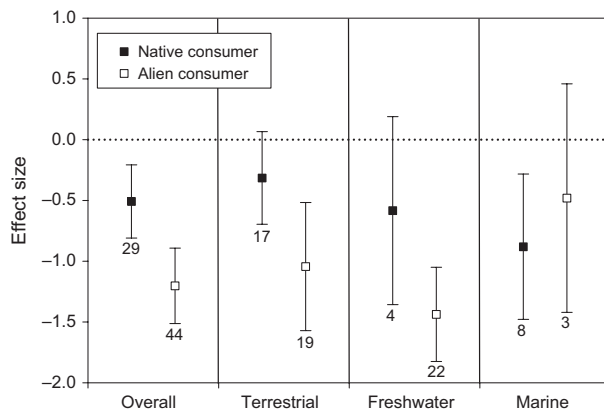


Figure 1 Mean effect sizes (ln-response ratios) of consumers on native prey populations in different biomes. Bars represent 95% confidence intervals; numbers under each bar are sample sizes. Large positive or negative effect sizes indicate increased or decreased prey abundance, respectively, in the presence of the consumer. Differences between native and alien consumers were significant overall (*t*-test, $P < 0.003$); effect sizes for native and alien consumers did not differ among biomes (ANOVA, $P > 0.05$).

and alien consumers had a slightly but insignificantly greater effect in aquatic than in terrestrial ecosystems ($F_{1,69} = 2.54$, $P = 0.115$); however, the mean effect of alien consumers in freshwater systems did not differ with those of terrestrial or marine systems ($F_{2,67} = 0.62$, $P = 0.542$; Fig. 1). Interaction terms in the aforementioned ANOVA models were non-significant in each case ($P > 0.05$).

DISCUSSION

Significance of predator origin

A fundamental weakness of recent criticisms of invasion ecology (e.g. Davis *et al.*, 2011) is that they ignore evolutionary context – the roles of co-evolution and prey naïveté, that is, lack of predator recognition (and effective antipredator defences and behaviours that would enhance survivorship) as a consequence of isolation from alien predator types. Prey naïveté could be a principal reason for the differential effects of alien and native consumers revealed in our meta-analysis. In contrast to co-evolved consumer–prey interactions, prey naïveté may produce a mismatch in the hunting tactics of a novel predator and in the anti-predatory defences of resident prey, which can result in surplus killing (Short *et al.*, 2002) and increased vulnerability to extinction (Gillespie, 1999; Berglund *et al.*, 2009). Unlike prehistoric species introductions, which were dominated by intraoceanic or intracontinental dispersal, modern invasions resulting from long-distance (e.g. intercontinental) transfers of species are common (Ricciardi & MacIsaac, 2000; Ricciardi, 2007) and have resulted in an increasing frequency of evolutionarily mismatched predator–prey or plant–herbivore combinations. The importance of prey naïveté in determining the outcome of predator–prey interactions is well documented (e.g. Cox & Lima, 2006; Polocavia *et al.*, 2010; Sih *et al.*, 2010), although most studies do not compare prey responses with alien and native predators alike (Kovalenko *et al.*, 2010; but see Parker *et al.*, 2006). Indeed, a shortcoming of our analysis is the relative dearth of studies ($n = 3$) available in which native and alien consumers impacts on native prey were assessed in the same system. Naïveté can also explain enhanced plant vulnerability to alien herbivores (e.g. Parker *et al.*, 2006; Verhoeven *et al.*, 2009; Desurmont *et al.*, 2011; Morrison & Hay, 2011), and there is abundant evidence demonstrating the influence of naïveté on the impacts of alien pathogens and parasites (Martin, 2001; Tompkins *et al.*, 2003; Wyatt *et al.*, 2008). The impacts of naïveté can be severe even for continental biota (Anagnostakis, 1987; Short *et al.*, 2002), as suggested by the greater negative mean effect size of alien ($R = -0.895$) consumers compared with natives ($R = -0.315$) in continental areas.

Gurevitch & Padilla (2004) questioned whether alien species are a major cause of extinction and suggested that they were more often passengers than drivers of biodiversity change (but see Clavero & Garcia-Berthou, 2005). However, even where environmental stressors have previously caused some native population declines, experiments and modelling

studies have shown that alien species can accelerate these declines (Ricciardi *et al.*, 1998; Ricciardi, 2004; Light & Marchetti, 2007; Clavero *et al.*, 2009; Hermoso *et al.*, 2011). When we exclude non-experimental data from our analysis, alien consumers ($R = -1.018$) had a slightly but non-significantly ($t = -1.67$, $P = 0.103$) greater negative effect size than native consumers ($R = -0.527$). In a previous meta-analysis that examined predator–prey interactions among terrestrial vertebrates, Salo *et al.* (2007) found that alien predators had twice the impact of native predators. They acknowledge that their results may have been influenced by strong impacts recorded in Australia – an isolated region with few large native carnivorous mammals (Short *et al.*, 2002) and which accounted for half of their data records. A pattern remarkably similar to our overall result (Fig. 1) was found by Parker *et al.* (2006), whereby native and alien herbivores both had negative mean effects on native plants, but those of alien herbivores were stronger. Our analysis considered vertebrate and invertebrate predators and herbivores in terrestrial and aquatic systems world-wide, and our results suggest that the dominant negative impact of alien consumers is more general in scope than previous evidence indicated. Strong impacts can also be extended to non-native plants; in a study of vascular plants in the United States, Simberloff *et al.* (2012) reported that naturalized non-native species were 40 times more likely to be perceived as invasive pests than were native plants. Collectively, these studies refute the assertion by Davis *et al.* (2011) that the biogeographical origin of species has no bearing on their impact.

A potential limitation of our analysis might be that the ecological literature is biased towards reporting impacts of alien species whose effects are conspicuous and extreme. However, a similar bias would occur for native predators and herbivores that are studied because they are suspected, or known, to be keystone consumers. We can find no reason why a ‘file drawer’ problem (*sensu* Koricheva, 2003; Cassey *et al.*, 2004) of underreporting of non-significant impacts would differ between studies of alien and native consumers. Moreover, we deliberately limited our literature search to 2010 and 2011, because in recent years, ecologists have become more aware of the potential positive effects of alien species and, as such, are perhaps more inclined to conduct studies that addressed these effects. Rather than focus our data collection to particular journals, our search was comprehensive and, therefore, was more likely to include studies in which non-significant results were reported. It is also possible that the differences between alien and native species would have been amplified had our analysis considered additional mechanisms of interaction (e.g. competition, disease transfer, habitat alteration).

A second potential limitation is that, although the diversity of consumers and systems allows us to test for generality, some confounding biases may be created by heterogeneity in the data. For example, vertebrates comprise a larger proportion of alien consumers than native consumers in our dataset (78% vs. 22%, respectively), which could bias our results if

vertebrate consumers have stronger impacts than invertebrate consumers (see Parker *et al.*, 2006). In fact, our limited data suggest the opposite, with the mean effect size slightly greater for alien invertebrates ($R = -1.321$) than for alien vertebrates ($R = -1.134$). We also note that some of the largest trophic effects observed in aquatic ecosystems are the result of invertebrate consumers (Ricciardi & MacIsaac, 2011). Clearly, there may exist numerous interactions involving combinations of factors (e.g. predator/herbivore, vertebrate/invertebrate, insular/open, terrestrial/aquatic), and resolving the relative importance of these interactions to changes in prey populations would require a much larger dataset.

Impacts of alien consumers in insular versus open systems

An unexpected result from our study was that the magnitude of the alien effect did not differ between insular and open (mainland, marine) systems. Insular systems have long been thought to be particularly sensitive to predator addition (Elton, 1958; Ebenhard, 1988), and indeed, there are some dramatic cases of extinctions following such introductions (e.g. Witte *et al.*, 1992; Fritts & Rodda, 1998; but see Simberloff, 1995). Fritts & Rodda (1998) noted that oceanic islands typically have a complex of vulnerabilities that predispose them to being severely disrupted by introduced consumers: (1) prey naïveté (lack of coevolution between predator and prey); (2) anthropogenic disturbance that simultaneously favours the predator and renders prey populations more susceptible to extinction; and (3) the presence of alternative, often co-evolved, prey sources to maintain the predator at high densities as it drives the prey to extinction (hyperpredation). These vulnerabilities are also found in freshwater habitats (Cox & Lima, 2006), which have higher extinction rates than terrestrial mainland habitats (Ricciardi & Rasmussen, 1999) and appear to contain a greater proportion of high-impact alien species than marine systems (Ricciardi & Kipp, 2008). We observed a higher mean effect size of alien consumers on native prey in all aquatic ($R = -1.322$) than in all terrestrial ecosystems ($R = -1.044$). Although not significantly different, the mean effect of alien consumers tended to be greater in freshwater ($R = -1.437$) than in terrestrial or marine ($R = -1.044$ and $R = -0.481$, respectively) ecosystems. We attribute this result largely to insufficient statistical power owing to small sample sizes. An alternative explanation is that the result reflects the broad novelty of consumers that are being increasingly transferred across large (e.g. intercontinental) spatial scales to both insular and ‘open’ systems, which, as a consequence, contain biota that are similarly naïve to a growing number of introductions.

Management implications

If, as our results suggest, alien consumers are more likely to damage native prey populations, then community

assemblages may suffer major changes when native predators are replaced by alien predators, contrary to the notion that alien species can beneficially fill vacancies created by native extinctions (Schlaepfer *et al.*, 2011b). Thus, our study warns against proposals for deliberately introducing threatened predators beyond their native range as a conservation method (e.g. Donlan *et al.*, 2005; Hoegh-Guldberg *et al.*, 2008). The addition of alien consumers may exacerbate local extinction rates of native populations by rendering them more vulnerable to other anthropogenic stressors and to stochastic extinction dynamics (Brook *et al.*, 2008).

The more novel the introduced consumer is to the resident species assemblage, the more severe its interaction with resident species is likely to be (Short *et al.*, 2002; Ricciardi & Atkinson, 2004; Cox & Lima, 2006; Parker *et al.*, 2006). Prey naïveté is arguably a continuous, rather than dichotomous, condition that is altered by degrees of experience, adaptation and natural selection (Cox & Lima, 2006; Mitchell *et al.*, 2010; Parker *et al.*, 2012). As such, alien predator–native prey interactions (and indeed any other type of antagonistic interaction) should evolve to become less severe for the prey. There exists very little data to estimate how long it may take for this integration to occur, but a recent study suggests that for some mammalian carnivores, it is on the order of thousands of years (Carthey & Banks, 2012). We hypothesize that this time period will be inversely proportional to the phylogenetic distance between the consumer and its closest native functional counterpart within the invaded region.

The premise that the biogeographical origin of species be ignored in management (Davis *et al.*, 2011) portends another problem. If strongly interacting alien species are introduced to novel ecosystems, it may well be impossible – and at a minimum, prohibitively expensive – to eradicate or control them by the time severe ecological or economic harm is determined to have occurred (Crooks, 2005; Simberloff *et al.*, 2013). Previous studies have demonstrated the economic value of pre-border screening programmes designed to prevent introduction of alien species (e.g. Leung *et al.*, 2002; Finnoff *et al.*, 2007). Such programmes include open-ocean ballast water exchange by ships (Bailey *et al.*, 2011) and use of only heat- or chemically treated wood packing materials, that is, dunnage (Haack *et al.*, 2010). These programmes may assist in preventing the introduction of not only alien invasive species known to be associated with a vector, but also any unknown harmful species hitchhiking with them.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data and impact ratios of prey population abundance (biomass or numerical density) in the presence (X_{+pred}) and absence (X_{-pred}) of a consumer for the 62 studies used in this meta-analysis.

Appendix S2 List of references.

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