LETTER

Do native predators benefit from non-native prey?

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Abstract
Despite knowledge on invasive species' predatory effects, we know little of their influence as prey. Non-native prey should have a neutral to positive effect on native predators by supplementing the prey base. However, if non-native prey displace native prey, then an invader's net influence should depend on both its abundance and value relative to native prey. We conducted a meta-analysis to quantify the effect of non-native prey on native predator populations. Relative to native prey, non-native prey similarly or negatively affect native predators, but only when studies employed a substitutive design that examined the effects of each prey species in isolation from other prey. When native predators had access to non-native and native prey simultaneously, predator abundance increased significantly relative to pre-invasion abundance. Although non-native prey may have a lower per capita value than native prey, they seem to benefit native predators by serving as a supplemental prey resource.

Keywords
Additive designs, biotic resistance, enemy release hypothesis, invasive species, non-native species, novel prey, optimal foraging theory, predator–prey interactions, substitutive designs.

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INTRODUCTION

Predator–prey interactions are a key process regulating population abundances and community dynamics. As such, predator–prey interactions have been a useful framework for studying and predicting the success of non-native species (Colautti *et al.* 2004; Sih *et al.* 2010). However, our knowledge of the role of predation in invasions is largely one-sided, with most studies of non-native species introductions focused on the predatory roles of invaders, as opposed to their role as prey (Parker *et al.* 2006; Salo *et al.* 2007; Carlsson *et al.* 2009). Those invasion studies that do examine non-native species as prey often do so with the short term and one-sided perspective of evaluating whether attack by native predators limits non-native prey populations and hence, invasion success. Specifically, through high consumption, native predators can provide biotic resistance to invasion by excluding or limiting the non-native prey population (deRivera *et al.* 2005; Cheng & Hovel 2010; Tetzlaff *et al.* 2010). Conversely, no or low consumption of non-native prey by native predators often leads to enemy release that may result in invasive establishment and rapid proliferation (Mitchell & Power 2003; Torchin *et al.* 2003; Shwartz *et al.* 2009). In both cases, the dependent variable of interest has been some measure of the non-native prey population, not that of the native predator. The effects of non-native prey on native predator populations themselves are seldom reported, despite the fact that several studies have shown that feedbacks on native predators from non-native prey can themselves lead to strong influences on invasion success and impact (Courchamp *et al.* 2000; Noonburg & Byers 2005). Thus, the one-sided perspective of predator–prey invasions highlights a gap in our understanding of the population-level and long-term fitness consequences of non-native prey on native predators, which limits a comprehensive understanding of the community-level impacts of invasions.

At least within the context of an isolated, two-species interaction, predators by definition are expected to have negative effects on prey, and prey a positive effect on predators. Would the non-native status of either the predator or prey make us expect anything different? Because predators and non-native prey often share no evolutionary history, non-native prey could be extremely vulnerable, in terms of lacking appropriate behavioural, morphological and chemical defences (Cox & Lima 2006; Sih *et al.* 2010). As a result, the positive effect of non-native prey on native predator populations could be extremely pronounced. Conversely, the lack of evolutionary history could also mean that a predator is much less efficient at capturing and consuming non-native prey or that the prey is of lower value to the predator. Even in this scenario, a lower relative value of the non-native prey may not adversely affect the predator if the new prey is simply an additional food option among many preferred native species. More specifically, if the predator–prey interaction is placed in the context of a multi-species community, then theoretically a non-native prey of lower value only would negatively affect a native predator population if the non-native prey is displacing higher value native prey and thus decreasing the availability of more profitable prey species.

Although a recent qualitative review about the effects of non-native prey on native predators drew attention to this gap in our understanding (Carlsson *et al.* 2009), to date there has not been a review quantifying to what extent non-native prey influence native predator populations. Since we know that in an absolute sense (i.e. in isolation) a prey must have a positive effect on a predator, the real question of interest is whether a non-native prey has a net positive or negative effect on native predators relative to the predator's fitness and abundance before the invasion. That is, does the presence of a non-native prey cause a native predator population to increase or decline from pre-invasion abundance? The net effect of the

prey invasion seems to depend on two key factors: the value (i.e. quality) of the non-native prey relative to native prey species and changes in prey species relative abundance that may come about through competitive interactions among prey species. In the simplest case, the addition of a non-native prey that does not influence the abundance of existing prey is purely additive and can have nothing but a positive effect on the native predator; it has simply added a further food item to the predator's choices. However, if a non-native prey is displacing native prey species, then its net influence depends very much on its relative value and densities of available prey. Therefore, quantifying whether non-native prey have a net positive effect on predators is crucial not just for understanding the success of the invasion and the interactions of those two species, but also because of its implications for the community-level impacts of invasion. To address this, we reviewed the literature for studies that quantified population abundance and individual-level fitness measures (growth rate, fecundity and survival) of native predators in both the presence and absence of non-native prey and conducted a meta-analysis to quantify the effect of non-native prey on native predator populations.

MATERIAL AND METHODS

Data selection

We searched the biological literature for studies that reported the effects of non-native prey on native predators. Specifically, we searched the literature using the ISI Web of Science database for combinations of the following keywords: 'exotic OR invasive OR non-native OR introd* OR non-indigeneous' AND 'predator OR prey' AND 'species'. Studies published before May 29, 2013 were collected for the analysis.

To look at the effects of non-native prey on native predators, we set four criteria for including a study in the meta-analysis. First, we only used studies that reported data on the following individual or population metrics as dependent variables: 1) predator population abundance, 2) individual growth rate (e.g. change in mass, length) or 3) individual fitness (i.e. survival and fecundity). Specifically, we included papers that reported estimates of these predator responses with and without a non-native prey (i.e. pre- and post-invasion, locations with and without the focal non-native prey, or experiments manipulating the presence of a focal non-native prey). We included studies that directly reported a mean along with an estimate of error and the sample size or a correlation coefficient along with the sample size. Second, we only used studies where the focal predator was native. Third, we only used papers where the focal prey was non-native. Finally, we limited and defined predator–prey interactions to those where both predator and prey were animals (i.e. excluded studies of native herbivores grazing on exotic plants).

Many studies included more than one experiment or native predator species within a single publication. All separate experiments or different native predator species evaluated in a single study were included, as long as they met the criteria for inclusion listed above. Although including all experiments and species from a single study could decrease the independence

of some data points, it allows us to explore responses of native predators across a broader range of species. However, to evaluate the effect of any bias that multiple data points from a single paper would impose, we calculated a single effect size for any paper that contained three or more data points. Results of the summary analyses indicated that although the overall effect size might have been different, the qualitative significance patterns remained the same (Appendix S1). Finally, if a study reported a response over time, then all time points were used to estimate a single mean effect size for the study (calculation described below in Data analysis). When not reported explicitly, data were mined from graphs using Engauge Digitizer Version 4.1 (Mitchell 2000).

Finally, our search produced six publications containing 13 data points looking at the effect of the non-native cane toad (*Bufo marinus* Linnaeus, 1758) on native predators. Because the cane toad is a highly toxic organism and has been frequently referenced as an evolutionary trap, i.e. a mistaken food item (Phillips & Shine 2004; Schlaepfer *et al.* 2005), we did not define its relationship with native carnivores as a classic predator–prey ($\pm$) interaction and excluded these studies from the data set. However, there were two published studies on cane toads that we included where three native predators species were documented to be resistant to cane toad toxins and thus, met the definition of a classic predator–prey interaction. To evaluate the effect of removing studies where cane toads were toxic to native predators, we conducted a supplemental analysis in which we included studies where cane toads were toxic to native predators, and their inclusion did not change the overall results of the meta-analysis (Appendix S2).

Data analysis

The effect of non-native prey on native predator populations was measured for each study as the natural log of the response ratio, where $lnR = \ln(R) = \ln(X_E/X_C) = \ln(X_E) - \ln(X_C)$, where X_E and X_C are the mean responses for the experimental and control groups (or post- and pre-invasion for observational studies). Response ratios quantify the proportional change in the native predator's response (e.g. population abundance, growth rate, etc.) resulting from the presence of the non-native prey. The variance of lnR is approximately $V_{lnR} = S_{pooled}^2(1/n_E(X_E)^2 + 1/n_C(X_C)^2$, where S_{pooled} is the pooled standard deviation. The approximate standard error is $SE_{lnR} = \text{sqrt}(V_{lnR})$ (Borenstein *et al.* 2009). The response ratios are often used because they relate responses as proportions, allowing studies with different response variables to be readily compared. Also, they have robust statistical properties and ease of biological interpretation (Hedges *et al.* 1999). For example a positive ratio indicates a positive effect of exotic prey on predators, whereas a negative ratio indicates a negative effect and a ratio of zero is interpreted as there being no effect of exotic prey on native predator populations.

We calculated the log response ratio from each study categorising each dependent variable as a measure of population abundance, individual growth rate, individual survival or individual fecundity. We used four separate random effects models to calculate the overall mean effect for each category of response variable. We chose a random effects model (as

opposed to a fixed-effects) because we were collecting data from a series of studies conducted by different researchers and across a broad range of taxonomic groups.

All meta-analyses were conducted in MetaWin Version 2. Ninety-five per cent bootstrap confidence intervals were estimated for the mean effect sizes and used to determine whether a mean effect size was significantly different from zero. To evaluate whether the observed overall effect was an artefact of publication bias (e.g. negative results less likely to be published), we calculated Rosenthal's fail-safe number. Rosenthal's fail-safe number is a sensitivity metric that relates the number of studies with no significant effect (i.e. effect size not significantly different from zero) that would be needed to change the significance of the meta-analysis (Borenstein *et al.* 2009). For example a fail-safe number of 398 suggests that there would need to be 398 additional studies with a response ratio of zero (i.e. no effect of non-native prey on native predators) before the cumulative effect would become no longer statistically significant. If the failsafe number is $> 5n + 10$ (where n is the original number of studies), then it suggests that there is a minimal chance of publication bias (Rosenthal 1979; Fragkos *et al.* 2014).

We used categorical meta-analyses to examine whether there was an effect of the study design on the mean effect size (Rosenberg *et al.* 1999). Aspects of the study design that we examined were (1) whether the study was a laboratory or field study (which was nearly synonymous with whether the data were experimental or observational respectively), and (2) whether the non-native prey was studied in isolation from alternative native prey or within the context of the entire prey community. This latter category is a key distinction. A study was categorised as being conducted in an 'isolated' context if the effect of each prey species on the predator population was evaluated in a substitutive or no-choice design, i.e. in isolation from alternative prey. In contrast, a study was categorised as being conducted in a 'community' context if the effect of the non-native prey was evaluated in an additive framework, i.e. in the presence of multiple alternative prey. Results from isolation studies reflect solely the relative value or quality of a non-native prey to a predator. Studies conducted in the 'community' context should reflect the integration of both the net value of the non-native prey relative to alternative prey and the relative abundance of all available prey. Of the four responses metrics we examined, only individual growth rates had sufficient studies of both the isolation and community type that could be directly compared to examine the influences of this study design aspect on effect size. Survival and fecundity studies had one study each done within the community context, each of which was removed before formal analysis. Abundance studies were all of the community context.

Finally, because the strength of novel predator–prey interactions could change over time as the species settle into a new equilibrium, we performed a continuous model meta-analysis of the time since invasion on each of the four response variables to determine if time since invasion influenced the effect of non-native prey on native predators. We report Q_M, the variation in effect sizes that is explained by the regression model.

RESULTS

Our search yielded 3905 publications. Fifty-two of those publications met our four selection criteria outlined above (Appendix S3). Within those 52 publications, there were 109 unique studies that were used in the meta-analysis. The studies covered 47 different non-native prey species and 93 native predator species (Appendix S4). Despite diverse representation at the species level, the studies were taxonomically skewed at higher levels of organisation. Non-native insects and crustaceans accounted for 49% and 20% of focal prey species respectively. Native birds and insects accounted for 35% and 27% of focal predator species respectively. A large majority of studies was conducted in the field (73%) as opposed to the laboratory (27%). Similarly, studies conducted in the community context represented 73% of the studies, as opposed to 27% conducted in isolation. All studies conducted in the community context were field studies and all studies conducted in isolation from alternative prey were laboratory studies.

Effect of non-native prey on native predator population abundance

Non-native prey have a significant positive effect on native predator abundance relative to native prey (Summary Effect size, lnR = 0.57, bootstrap 95% CI = 0.40–0.77, *n* = 68, Rosenthal's number = 1233*; Fig. 1). An asterisk indicates that the Rosenthal's number was $> 5n + 10$. All studies were field studies and all were conducted in the community context. The effect of non-native prey on native predator population abundance did not significantly change as a function of time since invasion ($Q_M = 0.09$, d.f. = 1, $P = 0.77$; Fig. 2).

Effect of non-native prey on individual-level responses of native predators

Non-native prey have a significant negative effect on native predator fecundity relative to native prey (Summary Effect
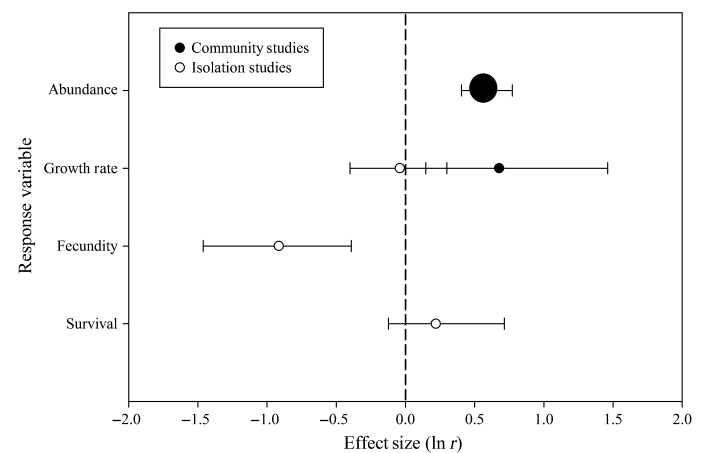

Figure 1 Mean effect of non-native prey on native predator population abundance, individual growth rate, fecundity and survival in the isolation and community contexts. Mean effect size and 95% confidence intervals are shown for all studies. Confidence intervals not overlapping zero indicate a significant effect of non-native prey on native predators. Size of the symbols is scaled to reflect differences in sample size among the response variables.
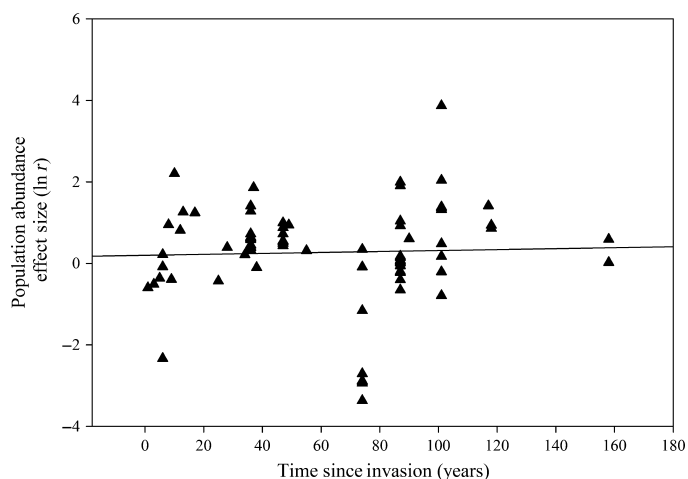
Figure 2 Relationship between time since invasion and the effect of non-native prey on native predator population abundance.

size, lnR = −0.92, bootstrap 95% CI = −1.46 to −0.39, n = 8, Rosenthal's number = 18; Fig. 1). The effect of non-native prey on native predator population fecundity did not significantly change as a function of time since invasions (Q_M = 0.49, d.f. = 1, P = 0.48).

Non-native prey did not have a significant effect on native predator survival relative to native prey (Summary Effect size, lnR = 0.22, bootstrap 95% CI = −0.12 to 0.71; Fig. 1). The effect of non-native prey on native predator population survival did not significantly change as a function of time since invasions (Q_M = 2.82, d.f. = 1, P = 0.09).

Non-native prey did not have a significant effect on native predator growth rate relative to native prey (Summary Effect size, lnR = 0.33, bootstrap 95% CI = −0.03 to 0.54). Ten of the 21 studies were conducted in the community and field context and 11 conducted in the isolation and lab context. There was a significant difference between studies conducted in the community verses isolation context (Q_M = 12.37, d.f. = 1, P < 0.001; Fig. 1). In the community context, non-native prey had a significant positive effect on native predator growth rate (Effect size, lnR = 0.67, bootstrap 95% CI = 0.15–1.15; n = 10, Rosenthal's number = 95*; Fig. 1). In the isolation context, non-native prey affected native predator growth rate no differently than native prey (Effect size, lnR = −0.04, bootstrap 95% CI = −0.40 to 0.30, n = 11; Fig. 1). The positive effect of non-native prey on native predator growth rate within the community context significantly increased with increasing time since invasion (Q_M = 4.54, d.f. = 1, P = 0.03; n = 10, Rosenthal's number = 72*). However, this result was driven by an outlier in this subset of 10 studies; when it was removed there was no effect of time since invasion. In contrast, the effect of non-native prey on native predator growth rate in the isolation context did not significantly change over time (Q_M = 0.05, d.f. = 1, P = 0.82; n = 11).

DISCUSSION

Native predator population abundance significantly increased following the arrival of non-native prey species. When prey

were studied embedded as part of the native prey community, individual predator growth rates also significantly increased following invasion of non-native prey species. In contrast, when prey were studied in isolation from alternative native prey, individual-level predator metrics were either not significantly different from pre-invasion levels (predator growth rates, survival) or significantly lower (fecundity).

Optimal foraging theory provides a useful framework to understand the increase in native predator abundance and growth rate following invasion of a non-native prey, as well as the discrepancy between the effects of non-native prey observed when prey are studied in isolation from, vs. embedded within, the native prey community. If a native predator is foraging optimally, then when given a choice, predators should choose the more profitable prey species (Krebs & Davies 1993). The neutral or negative effects on predator growth rate and survival when forced to consume only non-native prey suggest that on average, non-native prey are either of equal or lower value in contrast to native prey (Fig. 1). Therefore, when given a choice and allowed to forage optimally (as would be the case in most community studies), predators should typically either not favour or ignore non-native prey relative to native prey. The equal or lower relative value of non-native prey may, in fact, then be a mechanism contributing to the release of non-native prey from natural enemies.

Yet how predators perceive the value of non-native prey relative to native prey also should depend on the relative abundance of each prey species. The increase in abundance and growth rate of native predators in the community context following invasion suggests that native predators might not be experiencing or perceiving dramatic declines in the abundance of native prey as a consequence of a new invader. Otherwise, we would expect to see no change or a decline in native predator abundance and growth rate in community studies as we did in isolation studies. Optimal foraging predicts that non-native species (as the prey of equal or lower value) could serve a valuable role by supplementing the energetic demands of native predators when favoured, native prey are less abundant. Isolation studies are substitutive by design and do not allow predators to forage optimally on multiple prey species, so the additive effects of non-native prey in a supplementary role cannot manifest themselves as they can in community- or field-based studies. This is best seen in the effect of non-native prey on native predator growth rates, whereby growth rates were significantly greater in community studies in contrast to isolation studies. An extreme example of the contrast is also illustrated within a single paper and across two response variables. Dijkstra *et al.* (2013) evaluated the effects of non-native colonial ascidians serving as prey and found them to boost a native predator's abundance (the seastar, *Henricia sanguinolenta*) when studied in the community context, but to negatively affect predator growth rate relative to native prey when studied in isolation. Collectively, our findings suggest that the overall increase in native predator abundance and growth rate when studied in the community context following invasions of non-native prey is not the result of non-native prey having a higher per capita value as food, but rather because of their role as an additional, supplemental food

source. Such an additive role may also suggest an overall increase in biomass of the trophic level the non-native species is invading leading to larger scale community and food web ramifications.

On average, the equal or lower relative value of non-native prey when studied in isolation was somewhat surprising given that it is often thought that non-native prey may be easy targets of predation if they lack effective, co-evolved anti-predator defences (Sih *et al.* 2010), and as such, may be more profitable if search and handling times are lower relative to native prey. Parker & Hay (2005), e.g. found that native herbivores preferred non-native plants over phylogentically paired native species nearly 3–1. Furthermore, naïveté of *native* prey has been found to be a key factor driving the larger impacts of exotic over native predators on native prey (Wiles *et al.* 2003; Cox & Lima 2006). However, the continued invasion success and frequently observed large abundances of non-native prey suggests that native predators are not completely switching from consuming co-evolved native prey to non-native prey. Existing predator behaviours, skills or physiology may make native prey more profitable than non-native prey, despite any effect of non-native prey naiveté. A preference for native prey could impede the consumption and control of non-native prey until the relative profitability equalises or shifts in favour of the non-native prey. Although we know that the isolated effect of the non-native prey is neutral to negative relative to native prey, identifying the mechanisms generating differences in relative profitability of native and non-native prey (e.g. search, capture, handling, digestion) seems key to understanding if, when, and how non-native prey may experience an initial escape from natural enemies in their new environment.

We whole-heartedly caution against interpreting the increase in native predator population abundance or growth rate in the community context following invasion of non-native prey as evidence that non-native species are not harmful to native biodiversity and ecosystems. Indeed, the introduction of non-native species can clearly cause dramatic, negative changes to ecosystems and individual species (Vitousek *et al.* 1996; Wilcove *et al.* 1998; Parker *et al.* 1999; Mooney & Cleland 2001). Our data simply suggest that non-native prey may not be overly impacting the native prey base for native predators. In addition, our results still allow for the possibility that impacts on native prey species could arise from elevated abundances of native predators that result from non-native prey supplementing the prey base of predators, pushing native predators to higher equilibrium population sizes (Courchamp *et al.* 2000; Byers 2005; Noonburg & Byers 2005). For example over time the positive effect of non-native prey on native predator abundances could have indirect, negative consequences for native prey abundance (relative to pre-invasion abundance), especially if they remain the preferred prey.

Although our literature search produced 53 unique publications, containing 109 data points, most of these were not designed to explicitly examine the effects of non-native prey on native predator populations. Rather, the data on these interactions were collected in support of, but tangential to, the primary questions of interest in their studies. In addition, the magnitude of the observed responses could be partially related to characteristics of the dominant Classes represented in the data set (e.g. high intrinsic growth rates for insects) and therefore, warrant some caution with interpretation. Furthermore, even though our literature search was exhaustive, the large majority of the studies in this meta-analysis were observational studies and mensurative experiments conducted in the field as opposed to controlled, experimental settings. While observational studies are important to show the net bottom-line effect of non-native prey in the full community context, they do not isolate causal mechanisms of an interaction. Observational studies that have proper paired, contemporaneous controls where the non-native prey is not present (e.g. Before-After-Control-Impact-design) can implicate the non-native species as the causal influence of observed changes because such designs control for changes in climate or other exogenous factors that might coincide with the introduction of non-native prey. However, even when observational studies are properly controlled in such a way, it is conceivable that the positive effect of non-native prey on native predators can accrue through indirect pathways, e.g. by the non-native prey negatively affecting a focal predator's competitors or predators (i.e. meso-predator release). In at least one of our studies (Brown *et al.* 2011), this appears to have been a contributing factor. Specifically, the positive effects of invasive cane toads on five native snake predators (that were susceptible to the cane toads' toxins) possibly stemmed from cane toads poisoning one of these snakes' own predators (*Varanus panoptes* Storr 1980, a large varanid lizard) (Brown *et al.* 2011). Clearly in some systems these indirect effects can be contributing factors. More studies experimentally evaluating the effects of non-native prey on native prey and on other species (e.g. competitors and predators of the focal species) would help elucidate the relative role of direct verses indirect effects of non-native prey on native predators. However, because of the direct, immediate link from prey to predator it seems parsimonious and logical that at least a sizable portion of the witnessed positive effect of non-native prey on native predator is direct. Regardless, in either case, non-native prey benefit predators – whether by adding themselves as an extra prey or (perhaps less commonly) causing positive community indirect effects, e.g. cane toads killing top predators and driving meso-predator release.

The increase in predator abundance or fitness seems to arise very quickly after introduction of non-native prey. Specifically, our results suggest that the effect of non-native prey on native predator population abundance did not change over time, with an equal number of positive effects sizes found in recent invasions as in older invasions (Fig. 2). Recent evidence suggests that rapid plastic and evolutionary change can occur in recipient, native communities following invasion (Cox 2004; Freeman & Byers 2006; Strauss *et al.* 2006; Whitney & Gabler 2008). However, it is also possible that more time is needed to witness larger changes in effect size and our sample does not incorporate enough old invasions to witness such change. This possibility seems unlikely since even some of our older studies that extended to 150+ years showed no indication of a change in effect size. It is important to note, however, that although most studies showed a positive effect

size, there was a lot of variation among the studies included in our analysis (range of effect sizes: −0.79 to 3.87). Predator characteristics, phylogenetic or functional similarity between the native and non-native prey species, and other factors might contribute to this variation and the general lack of relationship between effect size and time since invasion. For example the degree to which a predator is a generalist or specialist presumably should influence whether a predator can switch prey and how quickly this may occur. The positive effect of non-native prey on native predator abundance underscores that most predators in our database were able to switch prey, and thus, were generalists. However, the degree of generality in the data set varied and was difficult to quantify (e.g. an 'insectivore generalist' vs. 'omnivore') and formally explore in analyses. Still, the degree of diet generality presumably could affect the speed at which a predator begins to consume a non-native prey. When more data are available, standardising across such factors might cause patterns to emerge.

Our study has shown that non-native prey when considered as part of the overall prey community have a net positive effect on native predators relative to the effects of native prey alone – an effect that is surprisingly seldom examined given the vast literature on invasive species. Perhaps, it is ignored because it seems obvious that addition of a prey would aid a predator population. However, studies conducted in isolation from alternative native prey reflect that non-native prey, on an individual level, are often equal or less beneficial compared to native analogues. A strong, suggested implication is that the positive effect of non-native prey stems not from their superior per capita benefit, but rather from invasions of non-native prey not displacing so many native prey that they drive down benefits to native predators. Rather, non-natives appear to be supplementing native food choices and augmenting native predators.

AUTHORSHIP

LMP and JEB developed the core idea, designed the study and reviewed the papers generated by the literature search. LMP extracted secondary data from the published literature, performed all data analyses and wrote the initial draft of the manuscript. LMP and JEB contributed substantially to revisions.

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