Why does predator abundance increase after invasion of a non-native prey?

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Abstract

Invasive species have been shown to have substantial effects on native food webs though their potential roles as novel predators or novel prey. As novel prey, invasive species have been recently shown to cause native predator populations to increase in abundance and growth rate following introduction. However, we know little about whether the magnitude of the effect of invasive species as novel prey depends on particular traits of native predator species. The goal of this study was to conduct a literature search to identify the characteristics of native predators that might influence the magnitude of effect that non-native prey might have on predator abundance. Specifically, we recorded whether a predator was a generalist or specialist and then quantified the number of different prey types consumed by that native predator. In general, the lowest level of taxonomic resolution that could be obtained for most prey consumed by predators in the dataset was Order. We conducted a simple linear regression to look at whether the number of orders consumed by a predator explained variation in the magnitude of effect size that a non-native, prey species had on the predator's abundance. Results suggest that there is no relationship between the number of taxonomic orders consumed by the predator and the estimated effect size of a non-native prey on the native predator. There is, however, a relationship between whether a predator is a carnivore or omnivore and their change in abundance. Carnivorous predators exhibited a larger change in effect size post invasion of a non-native prey. Future work may be aimed at understanding whether different classifications of generalist or specialist predators influence the effect of non-native prey on native predators. The long-term goal of this work is to determine why and how specific predators benefit from exotic species as prey.

Introduction

The invasion of alien species beyond their native range has been shown to have significant effects on the ecosystems in which they're invading (Parker et al. 1999; Mooney & Cleland 2001). In the United States, invasive species are estimated to have caused almost $120 billion in environmental damages per year (Pimentel et al. 2004). Additionally, invasive species are one of the leading causes of loss of biodiversity (Clergeau 2006). In particular, novel alien predators are significantly decreasing native prey species (Carthey & Banks 2014). A significant amount of work has been done determining the effect of this relationship, however, much less is known about the impact of alien prey species on native predators (Carlsson et al. 2009). Although less work has been done examining this relationship, studies have shown that the interaction of native predators and invasive prey play a significant role in invasion success (Noonburg & Byers 2005). Predator – prey interactions are important to examine when researching invasion ecology because predators play a role in the regulation of prey species – including possible invaders (Carlsson et al. 2009; Walsh 2014).

Novel prey can affect predators in different ways. For example, non-native prey might be expected to have a neutral to positive effect on native predators, depending on the degree of naiveté between the predator and prey species. For example, naïve predators might not have the predatory skills to consume prey, but conversely the prey might equally be naïve and not exhibit the appropriate anti-predator behavior. Additionally, non-native prey might affect native predators by becoming a highly abundant food source. Following optimal foraging theory, when given an option, predators are predicted to consume prey that are most profitable (Krebs & Davies 1993). Depending on the quality of the non-native prey, relative to native prey, this could greatly benefit the native predator if the non-native prey is energetically profitable. However, if its energetically less profitable than native prey, a highly abundant non-native prey might reduce the encounter rate with more profitable native prey and have a negative effect on the native predator. One-way non-native prey might become more profitable than native prey is by becoming highly abundant Based on these expectations, the availability and profitability of a prey species can influence how predator species and the ecosystem respond to prey.

Recent evidence suggests that non-native prey actually increase the abundance of native predator populations (Pintor & Byers 105). Specifically, Pintor & Byers (2015) quantified the effect of non-native prey on native predators through a quantitative meta-analysis and found that following invasion, predator abundance increased. Their meta-analysis was based on 52 publications and 109 unique studies examining exotic prey effects on native predators. These native predators included 69 different unique predator species from both aquatic and terrestrial systems. These species represented a wide range of predatory traits such as active vs. sit-and-wait foragers, diurnal/nocturnal foragers, etc. The objectives of this study were to examine how diet breadth and trophic status (e.g. carnivore vs. omnivore) influenced the effect of a non-native prey on a native predator. Specifically, I attempted to answer two questions 1) how does predator diet breadth influence the abundance of predators after the establishment of a non-native prey species and 2) do non-native prey have a different effect on carnivorous verses omnivorous predators? I hypothesized that predators with a wider diet would exhibit a larger change in abundance following the invasion of a non-native prey. Additionally, omnivorous predators will show a larger change in abundance following the invasion of a non-native prey. To test these hypotheses, I conducted a literature search to quantify the diet of native predators and examined whether predator diet influenced the effect of non-native prey on predator abundance.

Methods

To estimate the effect size of non-native prey on a native predator, I used the reported effect sizes of 68 different predator-prey interactions that were included in the Pintor & Byers (2015) meta-analysis dataset. This subset of interactions examined in this study were ones that quantified change in the abundance of native predators following the invasion of a non-native prey species. Effect size in this study was measured as the natural log of the response ratio. The response ratio quantifies the proportional change in the native predator's abundance (Pinter & Byers 2015) following the invasion of a non-native prey species. There were eight different predator classes and eight different prey classes included in this subset of data (Figure 1). In all of the studies examined, the invasive prey was not classified as a novel class or order when compared to the predator's original diet.

To quantify diet breadth for each predator species in the dataset, I conducted a literature search on each predator species and quantified the number of taxonomic orders eaten by each predator (Figure 1). For organism's diets where this level of taxonomic resolution was not able to be obtained, number of taxonomic classes was recorded. Additionally, we categorized all 68 predators as carnivores or omnivores. A predator was classified as a carnivore if it consumed only live prey. A predator was cataloged as an omnivore if it consumed both live prey and plant material (e.g. leaves, seeds, fruit, eggs) (Figure 3).

I performed a weighted linear regression (e.g. weighted to take into account the sample size and variance associated with the effect size estimated for each individual study) to test for an effect of the number of orders eaten by a predator on the effect size of each predator (MetaWin

Version 2) I performed a categorical meta-analysis to test for an influence of omnivory on the effect of non-native prey on native predator abundance (MetaWin Version 2).

Results

52 predator's diets were classified to this level. In this sample set, 33 predators were labeled as carnivores, and 35 were labeled as omnivores. Results of the weighted linear regression indicated that there is no significant relationship between the number of taxonomic orders consumed by the predator and the estimated effect size of a non-native prey on the native predator (Q_m = 0.03, df = 51, p = 0.173) (Figure 2). Although there appears to be a slightly negative relationship, it is not statistically significant. Additionally, through the categorical meta-analysis, I found that carnivorous predators exhibited a significantly larger increase in abundance following the invasion of a non-native prey than omnivorous predators (Q_m = 9.7051, df = 67, p = 0.016*) (Figure 3).

Future Directions

Future work may also include exploring other predator-related traits such as nocturnal vs. diurnal foraging behavior, and solidarity vs. group foraging. By examining these traits, we can determine the how a predator may respond to new prey items. We can also examine the predators willingness to add a new prey item into its diet. Additionally, traits of the invasive prey (e.g. anti-predator behaviors) might also provide insights into the effect of non-native prey on native predators. By examining the prey species ability to hide from or escape from a predator may assist in determining why not all predator incorporate the novel prey into their diet. Furthermore, this could give us insight into how energy beneficial the novel prey is to the predator. For example, if the invasive prey is efficient at escaping a predator, a predator may not integrate it into its diet due to lack of energy gained from the prey. Furthermore, a predator may be more likely to incorporate the novel prey into its diet based on the abundance of both native and invasive prey. The influence of geography as a factor could also be incorporated to determine if the effect of an invasive prey varies depending on region in which the interaction is occurring. Finally, the examination of phylogeny as a factor in the effect of novel prey on native predators would give us more insight to how novel the invasive prey is. This would allow for interactions to be weighted differently in analysis. Overall, further studies should be done to examine different ways to quantify predator diet breadth. This would allow for the relationship between the effect size examined in this study to be compared to predator diet in additional methods.

Discussion

I did not find support for my hypothesis that the effect of a non-native prey on a native predator would be a function of the number of orders consumed by the predator. Opposite my hypothesis, I found that predators with omnivorous diets exhibited a smaller change in abundance following invasion.

A possible explanation as to why I did not find a significant relationship between number of orders consumed and effect size due to the restriction of the analysis to order. This taxonomic resolution may be too course of a measurement to examine the influence of invasive species on native predators. By using a different comparison making the variable more specific, we may be able to see a relationship. Additionally, by examining all of the studies together, we may blend possible relationships together. For example, we could examine difference in diet breadth among species within a particular taxonomic group, e.g. when looking at just birds, we may see a stronger or different pattern. Increasing the sample size beyond the studies analyzed here would also allow us to gain a better idea of the relationship between taxonomic orders and effect size (Clergeau 2006).

The relationship between omnivorous/carnivorous diet and effect size may due to the fact that predators with a wider diet already have numerous prey to choose from. Therefore, one additional prey species might not have a particularly large impact on its abundance. For example, a predator that eats a broad range of prey, including seeds, nuts, and plants, has a lot of options when choosing a food source, therefore, they will eat the most energy beneficial prey item (Krebs & Davies 1993). Due to them eating the most energy beneficial prey, they may not incorporate the exotic species into their diet as much as a predator who only eats other animals. If they do not incorporate the exotic species into their diet as much, their abundance will not increase at the same rate that predators that are classified as carnivores.

The long-term goal of this work is to determine why and how specific predators benefit from non-native species as prey. This relationship can assist in predicting the effect that non-native species have the ecosystems in which they're invading. This can aid in the creation of models to help determine how ecosystems will change over time after the invasion of the alien species. Additionally, by examining this interaction, we can prevent the spread of invasive species in the future. Due to the many factors that determine the success of invasive species, the understanding of predator-prey interactions can provide more insight into the ecosystem impacts of exotic species (Walsh 2014).

Limitations

One challenge of this study was the difficulty of quantifying predator diet to lower order classifications, e.g. genus or species. A majority of studies did not report prey types below Order. In some studies, the lowest classification found was Class. Additionally, we were unable to include how variation within each taxonomic level varied between studies. For example, a predator may only feed on insects but due to insects being a large class, it may actually eat more variable prey than an organism that feeds on other classes.

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Appendix

Native Predator Taxonomic Classes	**Non- Native Prey Taxonomic Classes**
• Actinopterygii (bony fishes) • Arachnida (spiders and mites) • Asteroidea (sea stars) • Aves (birds) • Gastropoda (snails) • Insecta • Mammalia • Reptilia	• Actinopterygii (bony fishes) • Amphibia (frogs) • Arachnida (spiders and mites) • Ascidiacea (ascidians) • Gastropoda (snails) • Insecta • Malacostraca (crayfish) • Mammalia

Figure 1: Native predator and non-native prey taxonomic classes examined in this study

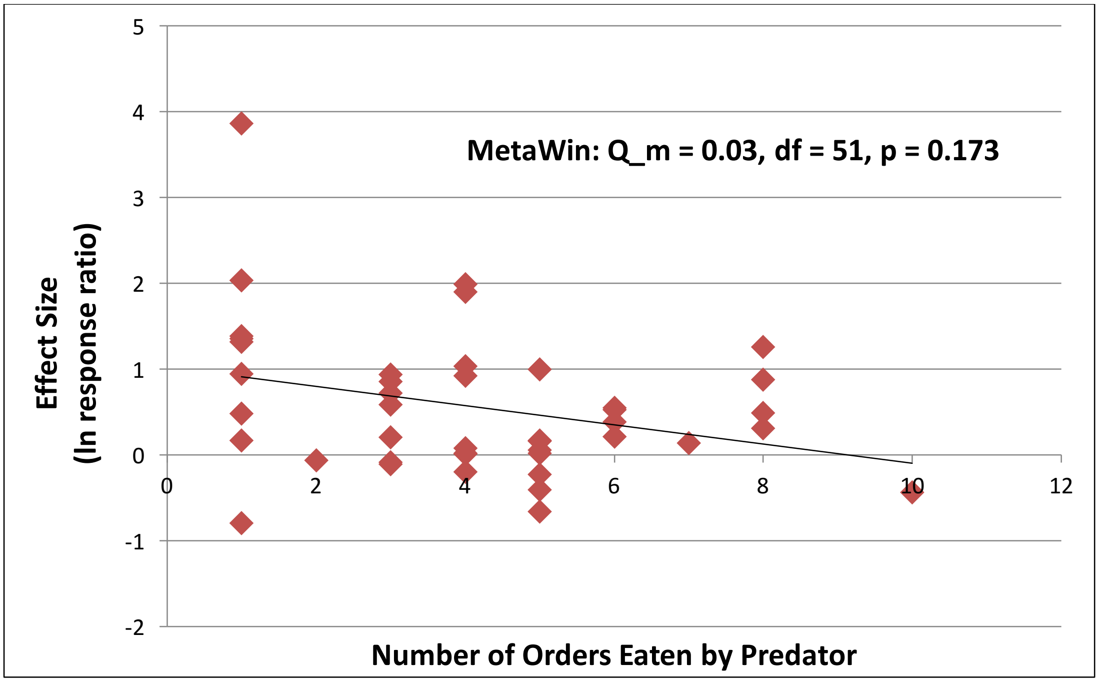

Figure 2: Results of a continuous model meta-analysis indicated that the effect of a non-native prey on native predator abundance did not change as a function of the number of orders eaten by a predator.

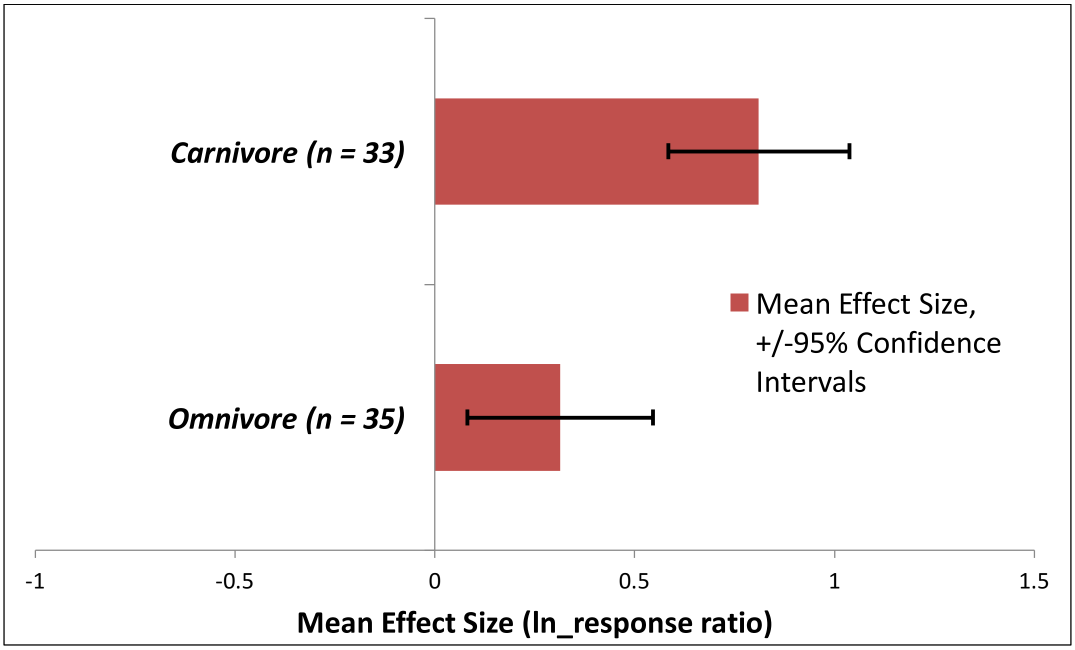

Figure 3: Results of categorical meta-analysis indicated that carnivores experienced a larger change in abundance following invasion of a non-native prey. Omnivores were defined as predators that also feed on fruit, nuts, seeds, or eggs.