Ballari SA, Kuebbing SE, Nuñez MA. 2016. Potential problems of removing one invasive species at a time: a meta-analysis of the interactions between invasive vertebrates and unexpected effects of removal programs. PeerJ 4:e2029 https://doi.org/10.7717/peerj.2029

Potential problems of removing one invasive species at a time: Interactions between invasive vertebrates and unexpected effects of removal programs

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Although the co-occurrence of nonnative vertebrates is a ubiquitous global phenomenon, the study of interactions between invaders is poorly represented in the literature. Limited understanding of the interactions between co-occurring vertebrates can be problematic for predicting how the removal of only one invasive—a common management scenario—will affect native communities. We suggest a trophic food web framework for predicting the effects of single-species management on native biodiversity. We used a literature search and meta-analysis to assess current understanding of how the removal of one invasive vertebrate affects native biodiversity relative to when two invasives are present. The majority of studies focused on the removal of carnivores, mainly within aquatic systems, which highlights a critical knowledge gap in our understanding of co-occurring invasive vertebrates. We found that removal of one invasive vertebrate caused a significant negative effect on native species compared to when two invasive vertebrates were present. These unexpected results could arise because of the positioning and hierarchy of the co-occurring invasives in food web (e.g. carnivore-carnivore or carnivore-herbivore). We consider that there are important knowledge gaps to determinate the effects of multiple co-existing invaders on native ecosystems, and this information could be precious for management.

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Potential problems of removing one invasive species at a time: Interactions between invasive vertebrates and unexpected effects of removal programs

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Abstract

Although the co-occurrence of nonnative vertebrates is a ubiquitous global phenomenon, the study of interactions between invaders is poorly represented in the literature. Limited understanding of the interactions between co-occurring vertebrates can be problematic for predicting how the removal of only one invasive—a common management scenario—will affect native communities. We suggest a trophic food web framework for predicting the effects of single-species management on native biodiversity. We used a literature search and meta-analysis to assess current understanding of how the removal of one invasive vertebrate affects native biodiversity relative to when two invasives are present. The majority of studies focused on the removal of carnivores, mainly within aquatic systems, which highlights a critical knowledge gap in our understanding of co-occurring invasive vertebrates. We found that removal of one invasive vertebrate caused a significant negative effect on native species compared to when two invasive vertebrates were present. These unexpected results could arise because of the positioning and hierarchy of the co-occurring invasives in food web (e.g. carnivore-carnivore or carnivore-herbivore). We consider that there are important knowledge gaps to determinate the effects of multiple co-existing invaders on native ecosystems, and this information could be precious for management.

Keywords

animals, carnivores, co-occurrence, invasional meltdown, meta-analysis, nonnative

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1. INTRODUCTION

Invasive vertebrates can alter native communities and ecosystems through many pathways including predation, competition, reducing food web complexity, hybridization, competitive exclusion, and increasing the risk of extinction of native species (White et al., 2008; Doherty et al., 2015). Many ecosystems now host numerous invasive species that directly or indirectly interact with one another and impact native species populations and ecosystem processes (Courchamp et al., 2011; Meza-Lopez & Siemann, 2015). Interactions between these co-occurring invaders are of superlative interest for wildlife management because frequently managers can only control or eradicate a single invasive species at a time (Glen et al., 2013). Without prior knowledge of invader interactions, removal of only a single invader can lead to an increase in the population size of other invasives or decrease in the population size of native species (Zavaleta et al., 2001; Campbell et al., 2011; Ruscoe et al., 2011).

Predicting the community-level consequences of management of a single invasive species requires an understanding of both the interactions between co-occurring invaders and their combined impacts. In an initial review of 45 invasive animal interaction studies, Jackson (2015) showed that the combined ecological impacts of multiple invaders were additive, but the mean effect size was non-additive and lower than predicted. This analysis included many animal taxonomic groups (with no mammalian cases) and ~96% the reported interactions were from aquatic environments. In our study, we focus on invasive vertebrates because it is a homogeneous group to compare and includes some of the most damaging and widespread invasive species that are frequent targets for management (White et al., 2008; Dawson et al., 2015).

Interactions between nonnative species can be positive, negative or neutral (Kuebbing & Nuñez, 2015; Jackson, 2015), but most research on invasive species interactions focused on facilitative interactions (i.e., invasional meltdown hypothesis, Simberloff & Von Holle, 1999; Simberloff, 2006). Other alternative scenarios to invasional meltdown include replacement of one invasive by another invasive (Lohrer & Whitlatch, 2002), or competition between two invaders, which can lead to the combined effects of both invaders to be less than the sum of their individual impacts (Kuebbing &, Nuñez 2015).

It may be possible to predict the type of interactions between vertebrate invaders and their potential impacts because the interactions between two invasive species should vary depending on the traits and trophic position of the co-occurring invasive and native species in the community. For example, two invasive carnivores in the same trophic position may predate on similar native species or utilize similar habitats, which could lead to both invaders investing energy to compete against one another (Fig. 1d). Thus, the removal of only one invasive predator could release the population of the second invasive predator, which could ultimately cause a greater impact on the native prey species (Murphy et al., 1992). We may also expect different outcomes of single-species management when multiple co-existing invasive species occupy different positions in food webs (Fig. 1). In a hypothetical coexistence scenario of an invasive carnivore predator and an invasive herbivore, we might expect that the removal of the invasive carnivore could reduce predation pressure on the invasive herbivore prey and allow its population to increase. The consequence of this herbivore release may indirectly affect native herbivores through competition, or directly threaten a native plant through herbivory (Fig 1b). On the other hand, if the removed species is the invasive herbivore, the invasive carnivore predator would be forced to change their diet and search for native prey (Fig 1c). These hypothetical examples illustrate how the coexistence of invasive vertebrates and subsequent removal of one of them can lead to unexpected impacts on native biodiversity, which could depend on the invaders position in the food chain.

We assessed whether the trophic positions of invasive vertebrates could predict the consequences of removal of only a single invasive species on native species. To do this, we conducted an extensive literature search of studies that evaluated the impact of removing a single invasive vertebrate while leaving a second invasive present on native biodiversity. We focused on invasive vertebrates owing to their biological and socioeconomic importance and because there are still many gaps of information on management of invasive vertebrates. We ask the following questions: (1) What is the combined effect of two invasive vertebrate species on native biodiversity relative to a single invasive vertebrate?; (2) Does the removal of a single invasive vertebrate reduce the impact on native species?; and (3) What traits of invasive vertebrate species, including trophic position, predict these interactions?

2. MATERIAL AND METHODS

We searched for peer-reviewed literature on invasive vertebrate interactions using the database Web of Science® and the methodology proposed by Kuebbing & Nuñez (2015). We used the keywords "species" AND "invas*" OR "alien" OR "nonnative" OR "non-indigenous", and also used as search terms the genres of mammals, birds, reptiles, amphibians and fish described in the list of 100 most damaging invasive species in Global Invasive Species Database (http://www.issg.org/database/species/) and categories filter (Supporting Information 1, Literature Search). From the final list of articles (n=403), we selected those that met the following criteria: (1) studied the impact of an invasive vertebrate on a native species; (2)

included a treatment where two invasive vertebrate species were present; and (3) included a treatment where one invasive vertebrate species was removed. This selection restricted our meta-analysis to eight published studies that comprised 128 individual observations (Supporting Information 2: Table 2). Finally, to investigate if there were any species or habitat characteristics that affected the type of interaction, we recorded the following information for each observation: (1) location of study; (2) habitat type (temperate forest, oceanic island, freshwater terrestrial wetland, freshwater aquatic systems); (3) invasive species studied; (4) native species studied; (5) trophic position (e.g., carnivore, herbivore, omnivore) of each native and invasive species; and (6) if the invasive species overlapped in their native ranges. We estimated mean effect sizes using Hedges' $d+$, which measures the difference between treatment groups (i.e., performance of a native species in the presence of one invasive species) and control groups (i.e., performance of a native species in the presence of two invasive species). This method corrects for small sample size bias and avoids overestimating effect sizes when study sample size is low (Gurevitch & Hedges, 2001; Lajeunesse & Forbes, 2003). When necessary, we extracted data with extraction software (ImageJ 1.449p© 2015 Wayne Rasband). We considered all response variables in each study (e.g., if a study measured fitness and growth of a native animal). We consider a mean effect size to be significant when its 95% confidence intervals do not overlap zero. Because of potential publication bias against studies with negative results or studies with higher sample sizes having a probability of finding effects, we assessed potential publication bias by plotting the sample size against the Hedges' d value (e.g., funnel plot analysis, Palmer, 1999). We found a funnel-shape distribution of data that is expected in the absence of publication bias (Supporting Information 3: Figure 3).

3. RESULTS

We found that the removal of a single invasive species always led to a negative or neutral mean effect on native species performance or survival (Fig. 2; Table 1). Surprisingly, we never found a positive effect size where the removal of one invasive led to an increase in native performance (Table 1). Related the trophic position, we found that the majority of the invasive vertebrates studied were strict carnivores (52.9%, n=9), while the minority were herbivores (23.5%, n=4) or omnivores (23.5%, n=4; Supporting Information 4: Table 3). Likewise, the vast majority of observations included interactions between two carnivorous species (82.8%, n=106), while only 11 observations included interactions between an invasive herbivore and omnivore (8.6%) and a single observation between two omnivores. Of the 17 species reviewed, there were 8 fish, 6 mammals, 2 amphibians and 1 marsupial (Table 1). Regarding the location, the majority of the observations were from North America (Canada and United States, 82.8%, n=106), while only 12.5% were in Oceania (New Zealand, n=16) and 4.7% in Europe (United Kingdom and Spain, n=6). Only 14.8% (n=19) of the observations were on islands. Finally we found significantly negative mean effect sizes regardless of the whether the nonnative species overlapped in their native range, and across habitat types (Table 1).

4. DISCUSSION

Our results show that the removal of a single invasive species led to a negative or neutral mean effect on native species performance or survival. This fact could suggest, in accordance with Jackson (2015), that the interactions between vertebrate invaders are antagonistic and reduce the population size and impact of other invaders. However, the studies we reviewed overwhelming considered the effects of two carnivorous species on native biodiversity (82.8%, n=106). We suggest that it is likely that in scenarios where the co-occurring invaders are not competing predators, that positive effects on native biodiversity are likely or occur at different trophic levels (Fig 1b-d), and that terrestrial ecosystems may have varied patterns.

While we never recorded a positive effect size where the removal of one invasive led to an increase in native performance, in nature, there are some examples where the removal of an invasive species might affect the presence of another invader, and consequently a positive effect on the native biodiversity (e.g., invasive host and pathogens, invasive specialize mutualisms). However, we have not found studies supporting this potential scenario.

We found many gaps in our review concerning the impacts of removing a single invasive vertebrate species on native biodiversity, which highlights research areas in need of further study. First, the majority of the invasive vertebrates studied were strict carnivores, while the minority were herbivores or omnivores. Likewise, most of the observations included interactions between two carnivorous species, while few recorded interactions between an invasive herbivore and omnivore or two omnivores. Globally, there are many examples of co-occurrence of invasive vertebrates that occupy these missing trophic positions (herbivorous (h) – omnivorous (o) or their combinations h-h or o-o). For example, in South American and New Zealand islands and mainland, large nonnative herbivores such as cattle, goat, and deer modify and alter plant communities, which affects other invasive herbivore species such as rabbits and hares, and/or omnivores like wild boar, rats, and opossums (Glen et al., 2013; Lantschner et al., 2013; Whitehead et al., 2014). However, we did not find studies that evaluated the consequences or the individual effects of single-invader eradication of these species. Finally, the studies we found lacked information of some vertebrate groups like reptiles and birds. However, in different regions of the world, several species of invasive reptiles (e.g. in USA, Engeman et al., 2011) or invasive birds (e. g. in Israel, Orchan et al., 2013) coexist and affect native biodiversity. These gaps could contribute more insight into the implications of single-species invasive removal and potentially expand the results found in this work.

Interactions among invasive vertebrates could also be affected by the habitat type (Norbury et al., 2013) or by the overlap in native range of the invaders (Kuebbing & Nuñez, 2015). In this study we found significantly negative mean effect sizes regardless of the whether the nonnative species overlapped in their native range, and across habitat types. However, we believe that we do not have enough evidence to determine if exist some relevant traits of invasive vertebrate species or environmental and manipulated features can influence the coexistence, interactions and combined impacts of invasive species.

It is important for wildlife management efforts to know and understand the outcomes of the removal of only a single invasive species in a scenario with multiple invasive species. But also, it is clear that we need more studies and experiments across different regions, invasive species combinations, and management strategies to test if we can predict or anticipated the results of this invasive interactions. When possible, management initiatives should consider integrated management of invasive species in whole food web context to be attempt to detect possible direct or indirect unexpected consequences for native species and ecosystems (commonly called "surprise effects", e.g. Zavaleta et al., 2001; Caut et al., 2009; Ruscoe et al., 2011; Glen et al., 2013).

We suggest that considering the trophic positions of the co-occurring invasive vertebrates might provide a predictive framework for understanding when single-species management will lead to “surprise effects”, but more data is necessary to test this hypothesis. We call for more studies of the effects of co-occurring invasive vertebrates, particularly of scenarios where invaders occupy the following trophic positions: predator-herbivore; predator-predator; predator-omnivore; omnivore-herbivore, herbivore-herbivore. These studies will clarify and bring to light possible outcomes of the removal of single-invaders on native biodiversity.

Authors' contributions

SAB designed the study, conducted the literature search and data collection, and wrote the first draft of the manuscript; SEK help in the design of the study, the statistical analyses, and provided comments on the manuscript; MAN participated in the design of the study, coordinated the study, and provided comments on the manuscript**.** All authors gave final approval for publication.

Acknowledgments

The authors thank Mariano Rodriguez Cabal for thoughtful comments on previous versions of this manuscript. S.A. Ballari and M.A Nuñez acknowledge support from CONICET.

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Figure 1(on next page)

PRISMA flow diagram

Figure 1. A flow diagram of the screening protocol for paper selection in this study (from Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6(6): e1000097. doi:10.1371/journal.pmed1000097)

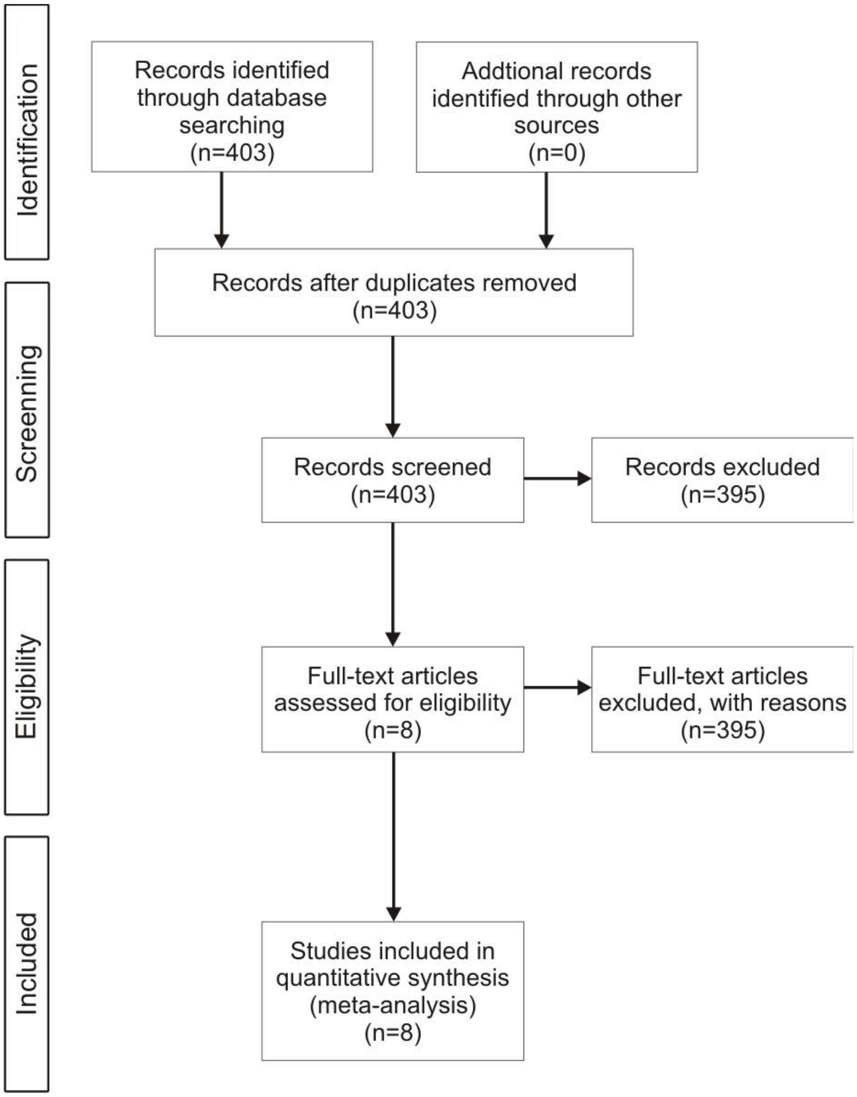

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Figure 2(on next page)

Hypothetical food interaction webs with co-occurring native and invasive species.

Figure 2. Hypothetical food interaction webs with co-occurring native and invasive species (a). The trophic level of co-occurring invaders could influence outcomes when a single invasive species is removed (red cross; b, c, d). In "b" the removal of a carnivore releases nonnative herbivores, and native omnivores and predators. In "c" the removal of a nonnative herbivore reduces population size of the competing native herbivore. In "d" the removal of only one invasive carnivore releases the other invasive carnivore predating on native herbivores and native omnivores reducing their populations.

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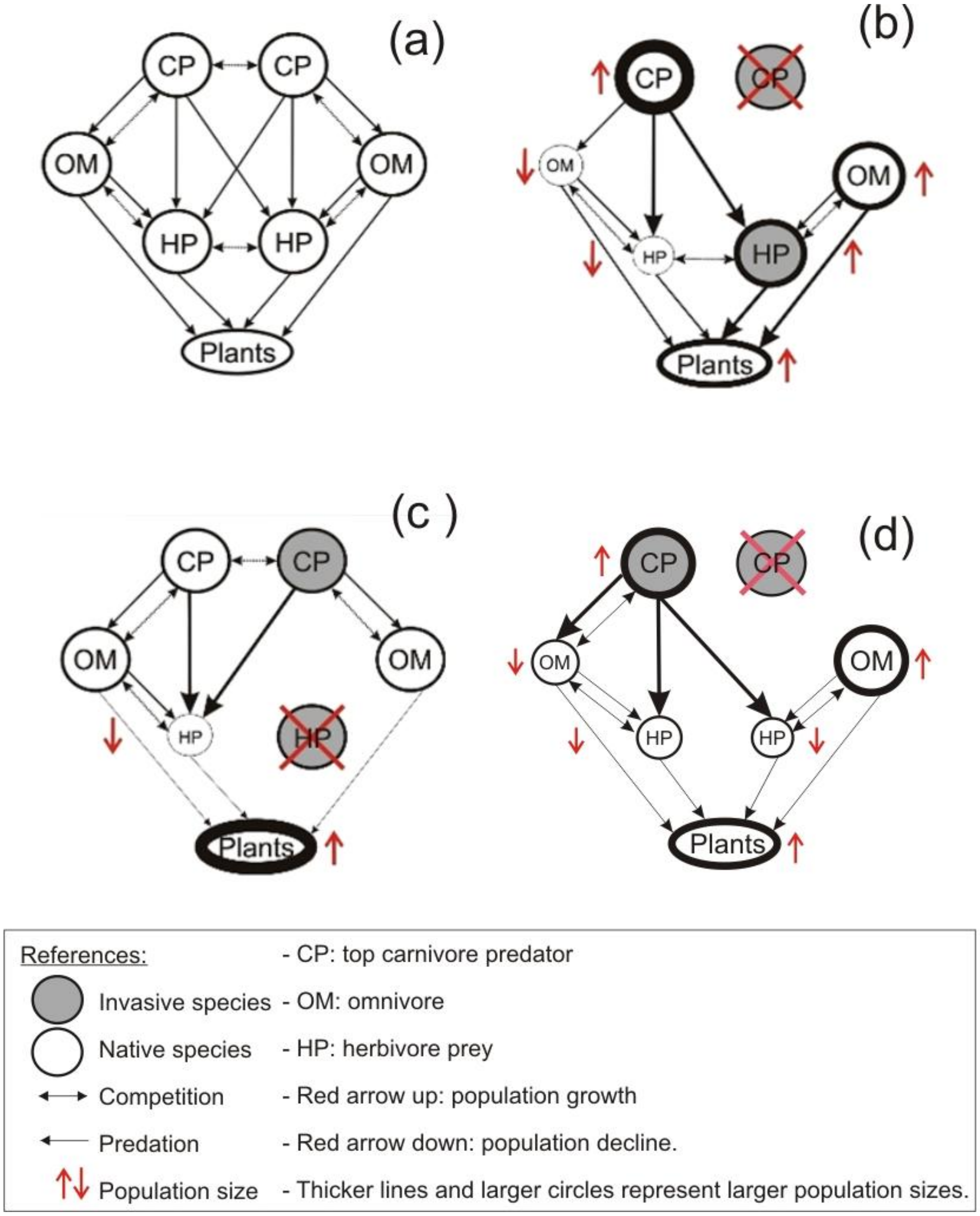

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Figure 3(on next page)

Mean effect on native diversity performance or survival across all trophic levels of nonnative vertebrates.

Figure 3. In ecosystems invaded by two nonnative vertebrates, the removal of only a single invader had a negative mean effect on native diversity performance or survival (Hedges' d+) across all trophic levels. Error bars represent 95% confidence intervals of the mean.

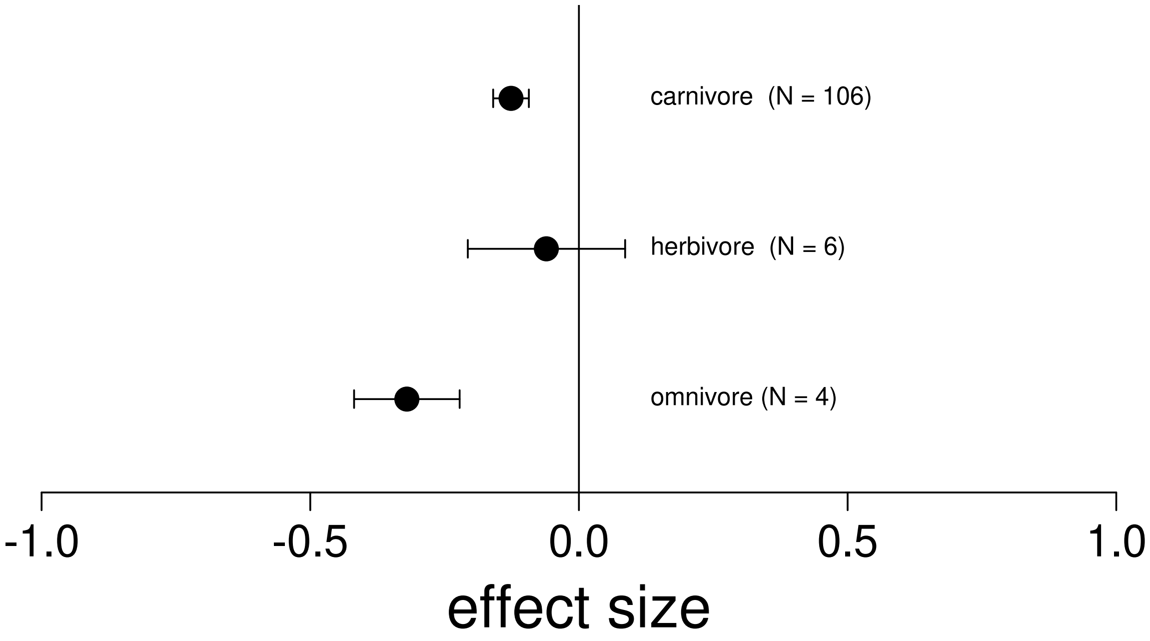

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Table 1(on next page)

Meta-analysis

Table 1. Results from a meta-analysis of 8 published manuscripts entailing 128 observations of invasive vertebrate interactions. We report the mean effect size and 95% confidence intervals (Hedge's d+) and bold values when the 95% CI does not overlap zero. Mean effect sizes were calculated for the entire data set and subsets of the data that compared the effect of mixed and single groups of invasive vertebrates on native biodiversity.

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	N	**direction**	**Hedge's *d+***
HABITAT TYPE			
forest	**16**	**-**	**- 0.29 ± 0.10**
wetland	**36**	**-**	**- 0.13 ± 0.05**
freshwater	**73**	**-**	**- 0.11 ± 0.05**
garrigue	**3**	**-**	**- 0.16 ± 0.15**
NATIVE RANGE OVERLAP			
overlapping ranges	**46**	**-**	**- 0.21 ± 0.07**
non-overlapping ranges	**72**	**-**	**- 0.13 ± 0.03**
INVASIVE FUNCTIONAL GROUP			
amphibian	16	0	- 0.13 ± 0.13
mammal	**19**	**-**	**- 0.25 ± 0.08**
fish	**93**	**-**	**- 0.13 ± 0.03**
TROPHIC POSITION OF REMOVED INVADER			
carnivore	**106**	**-**	**- 0.13 ± 0.03**
herbivore	6	0	- 0.06 ± 0.15
omnivore	**4**	**-**	**- 0.32 ± 0.10**

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