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PERPECTIVES AND PARADIGMS

Insights from community ecology into the role of enemy release in causing invasion success: the importance of native enemy effects

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Abstract The enemy release hypothesis (ERH) predicts that the success of invasive species is caused by reduced enemy pressure in species' introduced ranges. The ERH is a highly-cited explanation for invasion success, yet rigorous evidence is lacking for most species and ecosystems. Most evidence comes from observations of enemies in native and introduced ranges. These studies assess one aspect of the ERH—"enemy loss." They do not provide a direct test of the ERH and overlook the assumption of "native enemy effects." This is a critical limitation as enemy release will not occur if enemies do not affect species in their native ranges, even if enemy loss occurs. Biogeographical experiments, providing a direct test of the ERH, are largely restricted to terrestrial plants. We present a synthesis of community ecology and invasion biology studies, including a novel meta-analysis of native enemy effects, to assess the potential for release for species in different taxonomic groups and ecosystems. We suggest that species that are subject to strong enemy effects in their native range will have a high potential for enemy release. We found that native enemy effects were stronger in aquatic systems than in terrestrial systems. They were particularly weak for terrestrial plants; and strong for marine organisms, and freshwater plants. Studies are needed for species that have strong potential for release, such as for aquatic invasive species. Alternative explanations should be explored for invasive species that are not affected by enemies in their native range, and future studies should emphasize native enemy effects rather than only enemy loss.

Keywords Community interactions · Enemy release hypothesis · Invasion success · Invasive species · Top-down effects · Native and introduced range

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Introduction

A key challenge in invasion biology is to determine what enables species to be particularly successful in their introduced ranges. Many introduced species attain higher abundances or greater biomass compared to conspecific populations in their native range (Elton 1958; Keane and Crawley 2002; Parker et al. 2013; e.g., Torchin et al. 2001; Ebeling et al. 2008; Prior and Hellmann 2013). This increased success enables some species to become invasive, if they negatively affect species, ecosystems, or society (e.g., D'Antonio and Vitousek 1992; Lodge et al. 1994; Prior and Hellmann 2010). The phenomenon of increased success leading to species becoming invasive is referred to as "invasion success" (Colautti et al. 2004; Torchin and Mitchell 2004). Shea and Chesson (2002) explain invasion success in a community context where net changes in abiotic and biotic conditions between native and introduced ranges of species governs success, post-establishment (also see Mitchell et al. 2006). This explanation of invasion success assumes that invasive species are successful in their introduced range because controlling factors in their native range are no longer present (Maron and Vila 2001; Shea and Chesson 2002; Mitchell et al. 2006).

Escape from enemies (e.g., herbivores, predators, pathogens, parasites) is one interaction that has gained considerable attention as an explanation of invasion success. The enemy release hypothesis (ERH) is one of the most often-cited explanations of invasion success with important implications for biological control (Keane and Crawley 2002; Colautti et al. 2004; Prior and Hellmann 2015). The ERH states that introduced species will lose enemies with a reduction in enemy pressure leading to increased performance (e.g., biomass or abundance) (Maron and Vila 2001; Keane and Crawley 2002; Torchin and Mitchell 2004). If the enemy community is more effective at controlling species in their native range than their introduced range, then species will experience release from enemy control. A key condition of the ERH is that "enemy loss" occurs, and an important assumption is that enemies have significant negative effects on species performance in their native range, i.e., "native enemy effects" (Maron and Vila 2001; Keane and Crawley 2002; Colautti et al. 2004; Torchin and Mitchell 2004; Prior and Hellmann 2015).

Most evidence for the ERH comes from observational studies that compare enemy abundance, richness, or attack rates between species' native and introduced ranges (Colautti et al. 2004; Heger and Jeschke 2014; Prior and Hellmann 2015; e.g., Mitchell and Power 2003; Torchin et al. 2003). Lower observations of enemies have been found in most studies, suggesting that enemy loss is a common phenomenon for introduced species (Fig. 1; Colautti et al. 2004; Heger and Jeschke 2014, Prior and Hellmann 2015). However, such observational studies fail to directly test the ERH (if enemy loss *causes* invasion success) as they do not measure the effect of enemies on prey performance in the context of other ecological interactions. They also overlook the assumption of native enemy effects (Maron and Vila 2001; Colautti et al. 2004; Williams et al. 2010; Prior and Hellmann 2013; Prior and Hellmann 2015). This oversight is critical because enemy release will not occur if enemies have little effect on species performance in their native range. For example, if species are largely controlled by ecological factors other than enemies they will not be released from enemies if introduced elsewhere (Maron and Vila 2001; Hierro et al. 2005; Keane and Crawley 2002; Colautti et al. 2004; e.g., Vermeij et al. 2009; Williams et al. 2010; Prior and Hellmann 2013).

A more direct test of the ERH is to compare the effect of the enemy community on prey performance in species' native and introduced ranges (Fig. 2; Colautti et al. 2004; Hierro et al. 2005; e.g., Callaway et al. 2004; DeWalt et al. 2004; Williams et al. 2010; Hellmann et al. 2012; Prior and Hellmann 2013). These experimental, "biogeographical comparisons" (sensu Colautti et al. 2004; Hierro et al. 2005) examine the effect of the enemy community on prey performance and assess the assumption of native enemy effects. Biogeographical experimental tests of the ERH are largely restricted to studies in a single taxonomic group, terrestrial plants [Fig. 1; Colautti et al. 2004; Pyšek et al. 2008; Roy et al. 2011; Prior and Hellmann 2015; except see Vermeij et al. 2009 (marine plants); Prior and Hellmann 2013 (terrestrial insect)]. Given the lack of rigorous tests of the ERH for species in other trophic levels and ecosystems, we argue that there is currently insufficient evidence for the ERH for invasive species in most taxonomic groups. This is a critical limitation given that the ERH is a widely invoked explanation for invasion success and used as a justification for biological control

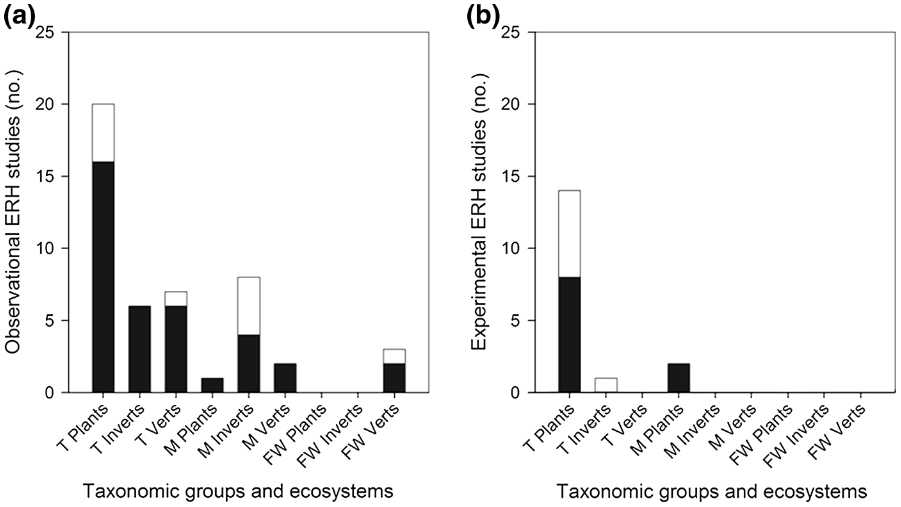

Fig. 1 Number of (**a**) observational and (**b**) experimental studies that have examined the enemy release hypothesis (ERH) using a "biogeographical comparison" approach for species in different taxonomic groups and ecosystems. *Black bars* represent the number of studies that found positive support for the ERH out of the studies that examined the ERH (*white bars*, 55 studies in total). Studies were found by searching the term "enemy release hypothesis" in ISI Web of Science and by searching through studies that were cited in and cited ERH reviews (e.g., Colautti et al. 2004; Torchin and Mitchell 2004). Searches ended in September 2011. See Prior and Hellmann (2015) for more details (Figure is adapted from this study). *FW* freshwater, *M* marine, *T* terrestrial

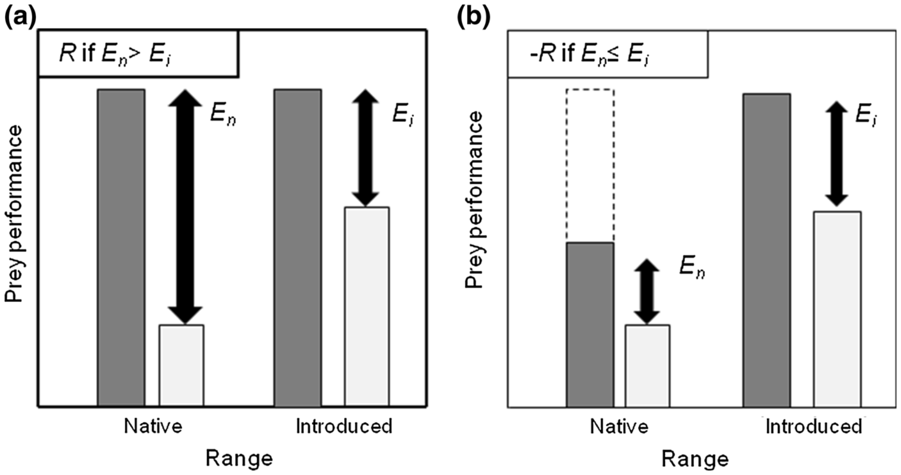

Fig. 2 Predictions of the enemy release hypothesis (ERH) using a "biogeographical comparison" experimental approach. Enemy effects (E) (*black arrows*) are defined as the effect of the enemy community on prey performance (abundance or biomass). Enemy effects can be estimated by measuring the result of experimentally reducing or excluding enemies on prey performance. *Dark grey bars* represent prey performance when enemies are excluded and *light grey bars* when enemies are allowed access to prey (controls). (**a**) Enemy release (R) will occur when prey experience stronger enemy effects in the native range (E_n) than in the introduced range (E_i). Enemy release (R) will not occur if enemies are not lost or if enemies are gained (e.g., if the *light grey bars* are equal in (**a**)). (**b**) Enemy release will also not occur if enemies do not negatively affect prey performance in the native range (i.e., *dark gray bar* is lower in the native than in the introduced range). This scenario could occur even if enemies are lost (e.g., *light grey bar* higher in introduced range), if some other factor(s) (*white hatched bar*) strongly reduces prey performance in the native range, but not in the introduced range (e.g., see Prior and Hellmann 2013 for an example of this scenario)

for many species and ecosystems (DeBach and Rosen 1991; Keane and Crawley 2002; Torchin et al. 2003).

There is reason to think that the generality of the ERH as an explanation of invasion success across different species and ecosystems is limited (Pyšek et al. 2008; Jeschke et al. 2012). One reason, that we highlight here, is that native enemy effects are not likely to be equal for species in different trophic levels or ecosystems (Hairston et al. 1960; Sih 1985; Shurin et al. 2002, 2006). Community ecology theory and empirical studies suggest that top-down processes are more prevalent in some trophic levels in certain ecosystems, are often stronger in aquatic systems, and are less prevalent in stressful or disturbed environments (e.g., Hairston et al. 1960; Fretwell 1977; Menge and Sutherland 1987; Polis 1991; Hunter and Price 1992; Strong 1992; Halaj and Wise 2001; Shurin et al. 2002). If systematic differences in the prevalence of top-down processes occur, then enemy release is likely not an equally plausible explanation of invasion success for all invasive species and ecosystems. Species that experience strong top-down pressure in their native range have a higher potential to undergo release, if they are introduced without their enemies, than species that are largely controlled by other ecological factors (also see Maron and Vila 2001; Blumenthal 2006; Blumenthal et al. 2009; Williams et al. 2010; Prior and Hellmann 2013).

Examining ecologically important factors that influence species in their native ranges is necessary to elucidate mechanisms that drive success (Hierro et al. 2005). Here, we conduct a novel meta-analysis of a central assumption of the ERH—"native enemy effects." We search for systematic patterns in native enemy effects among prey in different taxonomic groups in various ecosystems. Our meta-analysis is specifically designed to examine the importance of native enemy effects in the context of other ecological interactions. This is different from all previous reviews of top-down control, to which we compare our results (see below for further discussion of how our review differs from others) (e.g., Sih 1985; Shurin et al. 2002). We synthesize our results with theory and empirical studies from community ecology and invasion biology to inform general predictions about the potential for enemy release for prey in different taxonomic groups and ecosystems. These predictions follow from the claim that species that are subject to strong enemy effects in the native range will have a high potential for enemy release if introduced without their enemies.

Our intentions with this review are not to predict which types of species will *become* invasive because of enemy release as a multitude of factors other than enemies can predict the likelihood that a species becomes invasive (Kolar and Lodge 2001).The objectives of this review rather are to: (1) make suggestions for which types of invasive species is enemy release a likely explanation of invasion success; (2) highlight the lack of evidence for the ERH for certain types of invasive species and caution against making generalizations about the role of enemy release based on studies drawn largely from one taxonomic group; and (3) make suggestions for future efforts to improve our understanding of this central hypothesis of invasion success.

Definition of "native enemy effects" and "release"

The ERH is a broad hypothesis with various interpretations and sub-hypotheses (Jeschke et al. 2012; Heger and Jeschke 2014). Here, we present an interpretation of the ERH that we adopt using an equation from Torchin and Mitchell (2004). Demographic release (R) is an increase in a species performance (e.g., population size or biomass) resulting from a loss or reduction of some controlling factor, such as enemies. Enemy release is a function of the number of enemy species, their abundance, and their effect on prey performance. Torchin and Mitchell's (2004) equation describes release from parasite or pathogen enemies, but it can be expanded to include all types of enemies.

$$R = \sum_{n=1}^{N}(M_n * V_n) - \sum_{i=1}^{I}(M_i * V_i)$$

N is the total number of enemy species in the prey's native range, M is the enemy mean abundance (per enemy species), V is virulence or the effect on performance (per enemy species), n is the native range, i is the introduced range, and I is the total number of enemy species in the prey's introduced range (Torchin and Mitchell 2004). We define the summation terms as "enemy effects" (E), which is the effect of the enemy community on prey performance. Demographic release (R) will occur when enemy effects in the native range (E_n) are greater than enemy effects in the introduced range (E_i). Enemy effects can be estimated by removing or reducing the enemy community in situ and measuring the resulting effect on prey performance compared to controls that allow enemies to access prey (Fig. 2). It reflects the effect of the enemy community on prey performance in the context of other ecological interactions. The potential for a prey to undergo enemy release is high when E_n is high. Since few studies have examined the effects of enemies on prey performance in both ranges (Fig. 1; Prior and Hellmann 2015), most studies overlook the importance of E_n. We conduct a meta-analysis of native enemy effects (E_n) to inform the potential for release for invasive species in different taxonomic groups and ecosystems.

Meta-analysis of native enemy effects

To examine variation in native enemy effects (E_n) among taxonomic groups and ecosystems, we conducted a novel meta-analysis because previous reviews of top-down processes did not apply selection criteria appropriate for our definition of enemy effects as it relates to the ERH (see below for a detailed discussion), and did not include studies that spanned the breadth of prey types of interest to our question. Sih (1985) conducted a review most similar to ours in breadth, comparing predation effects among trophic levels and ecosystems. Our meta-analysis differs from this seminal review in a number of ways: (1) we used a formal meta-analysis, (2) we focused on studies published since this last major review, and (3) our selection criteria were tailored to the specific question at hand, regarding the relative effect of enemies in intact native communities. Other reviews of top-down processes across ecosystems have been conducted, but these reviews were restricted to a sub-set of studies that we included as they focused on certain elements of top-down processes (e.g., trophic cascades; Shurin et al. 2002); or certain enemy types (e.g., herbivores; Bigger and Marvier 1999), or ecosystems (e.g., terrestrial; Halaj and Wise 2001). We compare our results to these other reviews.

We conducted a systematic literature search of studies that examined the effects of removing natural enemies on native prey performance in their native range (E_n; see Fig. 2) (see Online Resources 1). We used the explanation of invasion success in a community context to design our selection criteria (Shea and Chesson 2002; Mitchell et al. 2006). Strong native enemy effects mean that enemies are important relative to other ecological interactions such that altering the enemy community has the potential to be an important driver of invasion success. Weak native enemy effects mean that other ecological factors (e.g., resources) are relatively more important than enemies in influencing performance. Thus, we targeted experimental studies that removed the natural enemy community and measured effects on prey performance in a prey's native, natural environments where ecological interactions were largely intact. Studies where enemies were added were excluded, as enemy addition experiments can inflate the magnitude of enemy effects relative to other interactions. When a study manipulated multiple factors, we used the treatment where the other ecological interaction(s) was kept intact. Studies were excluded if they measured enemy effects on introduced prey as these species may be experiencing low enemy effects. Additionally, studies where enemies were introduced (e.g., biocontrol studies) were excluded as these enemies may exert particularly strong effects on prey given that these enemies may be experiencing release from their natural enemies. Finally, agricultural studies were not included given their simplified communities and large resource base. If a study did not contain information about the origin of the prey or enemy, then external sources were used to determine if they were native (e.g., USDA Plants Database; Fish Base).

According to these constraints, studies included in our meta-analysis are field or common garden experiments and not experiments conducted in artificial environments. One exception was that some plant pathogen studies were conducted in greenhouses where plants were grown in soil collected from the field that had its natural soil community intact. Our 170 studies included 78 terrestrial, 51 marine, and 41 freshwater studies (see Online Resources 2 for list of studies). Some studies contained multiple "observations" (see Online Resources 1) that were used as independent data points in the meta-analysis, resulting in 615 observations, including: 283 terrestrial, 172 marine, and 160 freshwater observations.

Prey were classified into different taxonomic groups in different ecosystems: primary producers (e.g., plants and algae), invertebrates, or vertebrates in terrestrial, marine, or freshwater ecosystems. The lowest taxonomic group was always used (e.g., species, genera, or group of species such as periphyton). Since few studies examine invasive species in their native range (Hierro et al. 2005), studies in our meta-analysis were not restricted to species that have been introduced elsewhere. All of these taxonomic groups, however, contain important invasive species. Most studies that met our selection criteria investigated the effect of invertebrate or vertebrate enemies on prey performance. Pathogens and parasites can also exert top-down pressure on prey and are important agents of enemy release (Torchin and Mitchell 2004); however, due to our selection criteria we were only able to include terrestrial plant pathogen studies. Also, for vertebrate prey we only found studies that met our criteria on rodents in terrestrial systems and fish in aquatic systems. Marine studies and freshwater lotic studies were largely conducted in benthic habitats.

We included results where performance was measured as either prey biomass or abundance (see Online Resources 1). We only included studies that measured biomass, or some surrogate of (see Online Resource 1), at the population level (i.e., sum of individuals biomass), not the individual level. Thus, biomass measures reflected the effect of enemies on the abundance and size of prey populations. Plant studies in all ecosystems measured the effect of enemies on prey biomass and abundance, whereas animal studies often measure the effect of enemies on prey abundance. Only including studies that measured biomass at the population level enabled us to compare enemy effects measured as these different types of responses. Further, we found no differences in the enemy effects among response types within prey types (see Online Resources 3; Table S3.3).

Effect sizes for each observation were calculated using MetaWin 2.1 (Rosenberg et al. 2000) (see Online Resources 1 for full description of statistical methods). The effect size was calculated using Hedges' *d*, as the difference in prey performance in the absence and presence of native enemies (effect sizes represent native enemy effects; Fig. 2). A positive effect size reflects native enemy effects, and the magnitude of the effect size reflects the strength of enemy effects. Cumulative effect sizes and 95 % bias-corrected confidence limits using re-sampling tests (4,999 iterations) were calculated for the full dataset, each ecosystem, and each taxonomic group within ecosystems (Gurevitch and Hedges 1999). We examined if each taxonomic group experienced significant enemy effects, if confidence intervals did not bracket zero, and used mixed effects models to test for differences in enemy effects among ecosystems and taxonomic groups within each ecosystem. We also broke down our main groups further to search for patterns in native enemy effects among sub-groups: sub-prey groups (e.g., feeding guilds, growth forms, taxonomic groups), enemy types, and habitat types within ecosystems (see Online Resources 1). Patterns in enemy effects were largely robust to various study design elements such as the duration of the study, the type of exclosure, level of taxonomic resolution, or the response type (Online Resources 3, Tables S3.1 – S3.4). Also, we did not detect publication bias in our dataset (i.e., the "file-drawer problem") (Rosenberg et al. 2000) (Online Resources 1).

Results and discussion

Patterns in native enemy effects

Our meta-analysis revealed that native enemy effects were present in all taxonomic groups. The overall mean effect size for all observations ($n = 615$) was 0.73 and did not overlap zero (CI 0.65–0.83). An effect size of 0.2 is considered small, 0.5 moderate and 0.8 large (Cohen 1988), and, therefore, the overall effect of removing enemies on prey performance is moderate to large. This suggests that native enemy effects are important and that species from all taxonomic groups have potential of benefitting from losing enemies. However, we did find high heterogeneity among effect sizes ($QT = 937.34$; $P < 0.0001$; see Online Resources 4; Table S4.1) suggesting that underlying structure, such as differences in ecosystem type and taxonomic group exists. This suggests that species from certain taxonomic groups and ecosystems have a higher or lower potential of benefitting from losing enemies.

Mean enemy effects were lower in terrestrial systems (0.61) than in marine (0.86) and freshwater (0.86) systems and effect sizes were significantly different among these groups (Fig. 3). This suggests that enemy effects are stronger in aquatic systems than in terrestrial systems. However, given that none of the confidence limits crossed zero, enemy effects occurred at some level in all ecosystems. These findings support theories and results from other reviews of top-down processes (e.g., Sih 1985; Strong 1992; Polis 1991;

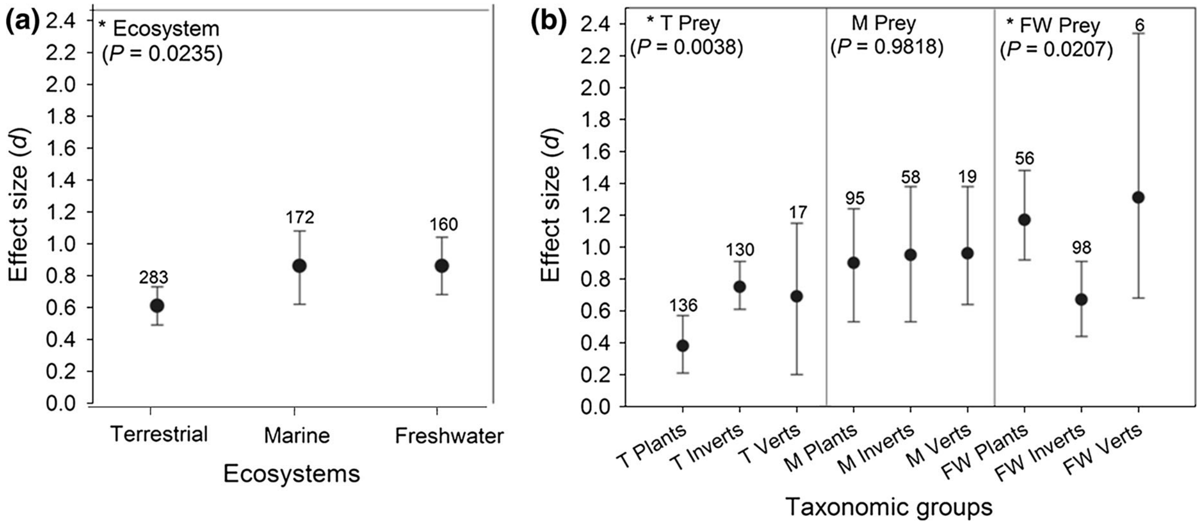

Fig. 3 Mean effect sizes (Hedges' *d*) of native enemy effects (E_n) on prey in different (**a**) ecosystems, and (**b**) taxonomic groups. The *bars* around the means denote bias-corrected 95 % bootstrap confidence intervals, and an effect size is different from zero if these confidence intervals do not overlap zero. The sample sizes (i.e., number of observations) are presented above the *bars*. The larger the effect size, the greater the effect of enemies on prey performance (measured as biomass and abundance). Statistical comparisons were performed among ecosystems and among taxonomic groups within each ecosystem. See statistical details in Online Resources 4. *FW* freshwater, *M* marine, *T* terrestrial

Hunter and Price 1992; Shurin et al. 2002; Shurin et al. 2006; except see Schmitz et al. 2000). Sih (1985), for example, found that predation effects were stronger in aquatic systems, especially rocky intertidal and lentic systems, compared to terrestrial systems. Shurin et al. (2002) similarly found that trophic cascades were strongest in lentic and marine benthos and weakest in marine plankton and terrestrial ecosystems. Our marine studies were largely conducted in benthic intertidal and reef systems, but we found no differences in enemy effects between lentic and lotic freshwater systems (plants; $P = 0.7535$, $n_{\mathrm{lentic}} = 22$, $n_{\mathrm{lotic}} = 33$) (invertebrates; $P = 0.9028$, $n_{\mathrm{lentic}} = 37$, $n_{\mathrm{lotic}} = 61$; see Online Resources 5 Tables S5.7, S5.8). Our results, in agreement with these two previous reviews, suggest that enemy effects tend to be stronger in aquatic than in terrestrial systems. Thus, many aquatic species have a high potential for enemy release if introduced without their enemies. This is an important result given that enemy release has been largely overlooked from a biogeographical perspective in aquatic systems, despite the fact that many species in these systems have high potential for release.

Enemy removal had significantly different effects among taxonomic groups in terrestrial ecosystems, with small to moderate effects on terrestrial plants (0.38) and moderate to large effects on terrestrial invertebrates (0.75) and vertebrates (0.69) (Fig. 3). Conversely, enemy effects were high for all marine prey types, including plants (0.90), invertebrates (0.95), and vertebrates (0.96) with no differences in mean effect sizes (Fig. 3). Finally, enemy removal had large effects on freshwater plants (1.17) and vertebrates (1.31) compared to freshwater invertebrates (0.67) (Fig. 3). Our results differed from Sih (1985) who found that predator effects were strongest at the lowest trophic levels in all ecosystems. We found that enemy effects were low for plants compared to higher trophic levels in terrestrial systems, and high for plants compared to higher trophic levels, or at least invertebrates, in freshwater systems. Sih (1985) results supported Menge and Sutherland's (1987) trophic theory that predicts high predation effects at low trophic levels. Our results provide some support for Hairston et al.'s (1960) and Fretwell's (1977) trophic theories that suggest top-down processes are less important for primary producers compared to herbivores on land, but more important for primary producers compared to herbivores in aquatic systems. Our results suggest that species in certain taxonomic groups, such as freshwater plants, marine organisms, and higher trophic levels in terrestrial systems, have high potential to benefit from enemy release.

Many factors likely contribute to variation in enemy effects among taxonomic groups and ecosystems in our meta-analysis. In some cases native enemy effects were weak because the direct affect of other ecological interactions on prey performance were stronger than enemies. In many instances, competitors, resources, or mutualists, had stronger effects on prey performance than did enemies (e.g., Huitu et al. 2003; Haag et al. 2004; Cornelissen and Stiling 2006; Miller 2008; MacDonald and Kotanen 2010). MacDonald and Kotanen (2010), for example, found that removing natural enemies of the invasive Common ragweed, *Ambrosia artemisiifolia*, in its native range had little effect on plant performance compared to soil disturbance and conspecific density. *Ambrosia artemisiifolia* has lost many of its enemies when introduced to Europe (Genton et al. 2005), but enemy release in this case may have played a small role in its invasion success because this species is not controlled by enemies in its native range.

Variation in native enemy effects also resulted from indirect effects of enemies on prey via interactions with other community members. For example, removing enemies decreased the performance of some terrestrial plants, marine plants and invertebrates, because these species were more limited by competition from other dominant species in the community that were preferred prey of enemies (i.e., apparent competition) (e.g., Lewis 1986; Bach 1994). Omnivory, intraguild predation, and compensatory predation can also dampen enemy effects in communities, and there were examples of these indirect interactions in many studies (e.g. Flecker 1992; Floyd 1996; Navarrete et al. 2000; Ho and Pennings 2008). Trophic theories suggest that terrestrial systems may have a higher degree of complexity compared to aquatic systems such that strong linear top-down effects are buffered by interactions with other species (e.g., Hairston et al. 1960; Polis 1991; Strong 1992; Shurin et al. 2002, 2006). One interpretation of enemy release invokes indirect effects. Apparent competition has been a suggested mechanism for plant invasions, in which the preference for native plant species over invasive plant species by native enemies in the introduced range may facilitate plant invasions via "enemy-mediated competitive release" (discussed in more detail below) (Keane and Crawley 2002).

Variation in native enemy effects also occurred as a result of variation in species traits (e.g., Barton 1986; Atlegrim 1998; Wootton 1992; Posey et al. 1995). Structural and chemical defenses are important traits in plants for defense against herbivores and pathogens. We found large differences in enemy effects between terrestrial and aquatic plants (Fig. 3). This could be because herbivory may be higher in aquatic systems than in terrestrial systems because aquatic plants are generally less defended and more nutritious than terrestrial plants (Shurin et al. 2006; Cebrian et al. 2009; except see Ostrofsky and Zettler 1986). How plant defenses and other life history strategies in plants relate to the potential for enemy release has been discussed in detail in other reviews (also see below) (Keane and Crawley 2002; Maron and Vila 2001; Blumenthal 2006; Blumenthal et al. 2009).

We also observed high heterogeneity in enemy effects within taxonomic groups and ecosystems, suggesting that many factors may cause variation in enemy effects (Fig. 3). Different types of prey within taxonomic groups, for example, may experience different levels of enemy effects (e.g., high versus low-resource plants) (Blumenthal 2006; Blumenthal et al. 2009). In our sub-group analysis we only found that enemy effects differed among marine plant types (Online Resources 5 Table S5.3). Certain enemy types, such as specialists, may exert especially strong pressure on prey (Keane and Crawley 2002); in fact we found that terrestrial plants and invertebrates were under stronger enemy effects by specialist invertebrates compared to generalist invertebrates (Online Resources 5; Tables S5.1, S5.2). As already discussed, enemy effects may be stronger in some habitat types (Sih 1985; Shurin et al. 2002), although we detected few patterns in enemy effects among habitat types (Online Resources 5). In addition, the presence and magnitude of enemy effects is likely context dependent. Variation in primary production, disturbance levels, and structural heterogeneity throughout species' ranges, for example, can vary the impact of enemies (Sih 1985). A full discussion of all factors that can influence predator effects is beyond the scope of this review. Importantly, despite this variation in enemy effects within groups, there were significant systematic differences in enemy effects among taxonomic groups and ecosystems.

Patterns in enemy loss

The strength of native enemy effects does not solely determine if species experience enemy release. Enemy release also depends on the change in enemy effects between species' native and introduced ranges (E_n–E_i) (Figs. 2, 4). Observational evidence of enemy loss between species' native and introduced ranges, suggests that it may be a common phenomenon for many invasive species (Mitchell and Power 2003; Torchin et al. 2003; Colautti et al. 2004; Heger and Jeschke 2014); for example, a recent review of biogeographical comparison studies found that enemy loss occurred in 79 % of observational studies (Fig. 1; Prior and Hellmann 2015). We did not conduct a novel analysis on this aspect of the ERH, nor do we provide a detailed review, as it has been reviewed and discussed elsewhere (Colautti et al. 2004; Liu et al. 2006; Jeschke et al. 2012; Heger and Jeschke 2014; Prior and Hellmann 2015). Here, we discuss how the potential for enemy loss may vary to help inform our predictions about the potential for release based on variation in native enemy effects.

Enemy loss occurs when enemies from the native range do not follow prey, and/or when enemies from the introduced range fail to effectively switch from alternative prey (Keane and Crawley 2002). The ERH provides clear predictions that introduced species are likely to lose specialist, pathogen and parasite enemies (Elton 1958; Keane and Crawley 2002; Torchin and Mitchell 2004). Many biogeographical comparison studies have in fact found that terrestrial invasive plants lose specialist invertebrate herbivores and pathogens (e.g., Memmott et al. 2000; Mitchell and Power 2003; van der Putten et al. 2005; Cripps et al. 2006); with DeWalt et al. (2004) finding experimental evidence for release of a terrestrial plant from specialist enemies. There is also good evidence for enemy loss of terrestrial invertebrates from pathogens and parasitoids (Cornell and Hawkins 1993; Menéndez et al. 2008; Prior and Hellmann 2013), and terrestrial and marine animals from parasites (Torchin et al. 2003). Given that these types of enemies can exert strong effects on prey performance (Hudson et al. 1998; Online Resources 5; Tables S5.1, S5.2) their loss may promote the success of introduced species.

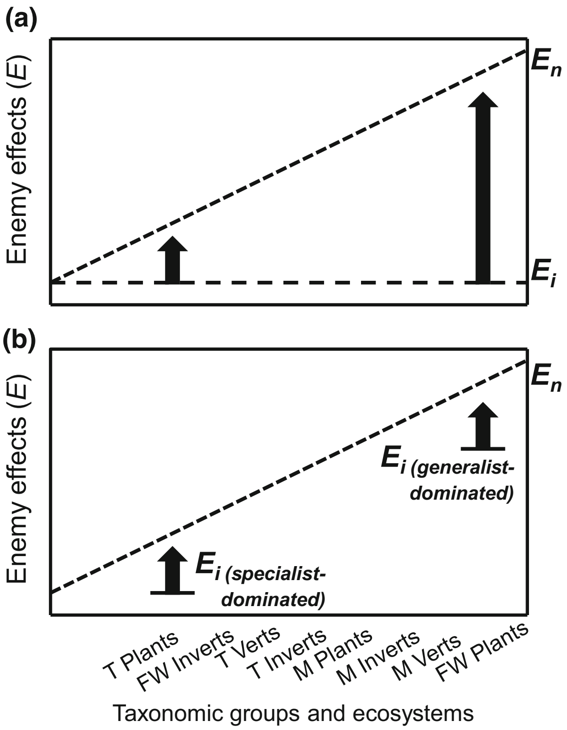

Fig. 4 Taxonomic groups are ranked in order from low to high mean native enemy effects (E_n) along the x axis (see Fig. 3). Freshwater vertebrates were not included due to the low sample size and high variation in this group. If (**a**) the change in enemy effects between the native (E_n) and introduced (E_i) range is high than some taxonomic groups (e.g., aquatic plants) have a higher potential for demographic release (R) than other taxonomic groups (e.g., terrestrial plants). *Top dashed line* represents native enemy effects (E_n), *bottom dashed line* represents enemy effects in the introduced range (E_i) (See Fig. 2 for definition of enemy effects). *Black arrows* represent examples for the potential for demographic release for species within taxonomic groups. Demographic release also depends on the magnitude of enemy loss (**b**) (or the change in enemy effects between the two ranges), such that prey experiencing high native enemy effects may have a similar potential for release than prey experiencing low enemy effects depending on enemy effects in the introduced range (E_i). For example, release may be dampened for prey occurring in some generalist-dominated communities if enemy effects are not low in the introduced range (e.g., aquatic communities) (the line corresponding to E_i generalist-dominated). Alternatively, in specialist-dominated communities enemy effects in the introduced range may be particularly low (E_i specialist-dominated) increasing the potential for enemy release for species that have low native enemy effects (E_n). Release does occur where the lines cross ($E_n = E_i$) and biotic resistance occurs when ($E_n < E_i$). Release will also not occur if E_n is ≤ 0 (also see Blumenthal 2006)

Predictions for how generalist enemies contribute to the success of invasive species is less clear, as generalists in the introduced range have the potential to switch to introduced prey (Keane and Crawley 2002; Parker 2006). Specialist enemies in the form of invertebrate herbivores or predators are more common in terrestrial than in aquatic ecosystems (Hay 1991; Shurin et al. 2006), and it has been suggested that enemy loss and subsequently enemy release may not be a common occurrence in generalist-dominated systems (Keane and Crawley 2002). However, few studies have conducted biogeographical comparisons in generalist-dominated systems, such as for invasive aquatic plants (Fig. 1; Prior and Hellmann 2015; except see Vermeij et al. 2009; Forslund et al. 2010). We argue that it is premature to discount the importance of enemy release in generalist-dominated systems especially given that prey in some of these systems can experience strong native enemy effects by generalist enemies (Fig. 3).

Although introduced species are less likely to lose generalist enemies than specialist enemies; there are many mechanisms by which prey can escape from generalist enemies (Verhoeven et al. 2009). For example, the generalist enemy community in the introduced range may simply lack traits that allow them to be effective enemies to novel prey. Shwartz et al. (2009) found that the rose-ringed parakeet, *Psittacula krameri*, undergoes reduced pressure from generalist enemies in its introduced range because predators there are too large to prey on eggs in nest cavities. Additionally local adaptation to alternative prey in the introduced range may preclude enemies from effectively attacking new prey (Vos and Vet 2004; Thompson 2005). Generally, if the advantage lies with the naïve prey, the outcome is enemy release. If the advantage lies with the naïve predators, the outcome is biotic resistance. There is evidence for both of these scenarios in nature, with the outcome depending on the inherent traits of the introduced species and of the native enemies (Cappuccino and Carpenter 2005; Colautti et al. 2004; Levine et al. 2004; Liu et al. 2006; Parker 2006; Parker and Gilbert 2007; Shwartz et al. 2009; Verhoeven et al. 2009).

Loss of generalist enemies can also occur if species are introduced into habitats that differ in the overall abundance of enemies (Pimm 1991; Shea and Chesson 2002). Oceanic islands, and estuaries and brackish seas, for example, have depauperate enemy communities and are often heavily invaded ecosystems (Cohen and Carlton 1998). Generalist enemy loss may also be important for the introduction of freshwater plants from tropical systems, which tend to have much higher levels of vertebrate herbivory than their temperate counterparts (Lodge 1991). Additionally, species in top trophic levels (especially vertebrates) are vulnerable to human stressors (Dobson et al. 2006; Carlsson et al. 2009); thus, many species could benefit from enemy loss if they are introduced into altered habitats that lack top predators (Carlsson et al. 2009). Finally, enemy richness decreases towards the poles (Janzen 1970; Rosenzweig 1995), and species introduced or moving polewards due to climate change could experience enemy loss due to this decreased richness (Menéndez et al. 2008; Prior and Hellmann 2013). Depauperate enemy communities could similarly benefit native and introduced species. A species may still experience release however relative to their native populations without having an advantage over other species in the introduced range (Mitchell et al. 2006; e.g., Vermeij et al. 2009).

Patterns in native enemy effects and enemy release

Using results from our meta-analysis and the theories and results from previous studies discussed above, it is possible to make general predictions about which types of invasive species have the highest potential of benefitting from enemy release, or where enemy release is the most likely explanation of invasion success (Fig. 4). In our meta-analysis, we found systematic variation in native enemy effects among prey and ecosystem types (Fig. 3). Prey that are under particularly strong enemy effects in their native range (E_n) should have the highest potential for release (R) (if introduced without their enemies [or if enemy effects are low in the introduced range (E_i)] (Fig. 4a; also see Blumenthal 2006). Given that there are systematic differences in native enemy effects among prey types, invasive species from different taxonomic groups have a higher or lower potential of benefitting from enemy loss.

We ranked taxonomic groups along the x-axis in the order of native enemy effects (Fig. 4). We did not include freshwater vertebrates given their small sample size and large variance. Based on patterns in native enemy effects, aquatic plants and marine organisms have a higher potential of enemy release than terrestrial organisms and freshwater invertebrates if enemy loss is high (Fig. 4a). This does not mean that all species in particular groups will or will not benefit from enemy release. Rather, we suggest that species from groups where native enemy effects are strong have a higher chance of being under strong top-down control and benefitting from enemy release if introduced without their enemies.

The likelihood of release not only depends on the strength of native enemy effects, but also on the change in enemy effects between the native and introduced ranges (E_n–E_i). Prey with specialist enemies are expected to more completely lose their enemies than prey with generalist enemies (Keane and Crawley 2002). Thus, the potential for enemy release could be dampened for species with strong native enemy effects if the change in enemy effects is low, such as for aquatic plants that are preyed on by generalist herbivores (Fig. 4b; E_i generalist-dominated). The potential for enemy effects could be enhanced for species with low native enemy effects that experience high enemy loss, such as for terrestrial plants that are preyed on by specialist herbivores (Fig. 4b; E_i specialist-dominated). As we argue in the previous section, however, enemy release should not be discounted in generalist-dominated systems given that there are many mechanisms by which generalist enemies can be lost. For example, invasive aquatic plants may have a high potential of benefitting from enemy release if they are introduced into enemy depauperate communities such as estuaries or from tropical freshwater systems to temperate freshwater systems.

Examples of experimental tests of the ERH and suggestions for future studies

Biogeographical comparisons that examine the effects of natural enemy communities on the performance of species in their native and introduced ranges are essential to uncover factors that cause invasion success. Here, we discuss two studies that highlight the importance of this experimental, performance-based approach. Prior and Hellmann (2013) examined the ERH for an invasive insect, *Neuroterus saltatorius*, using both an observational approach, and an experimental approach that reduced parasitoid attack on native and introduced populations of the invasive insect. Observational results supported the ERH, with parasitoid attack rates being lower and *N. saltatorius* density being higher in the introduced range compared to the native range. Despite lower attack rates, experimental results revealed that factors other than enemies were likely driving this species' success. This was because background mortality (in the parasitoid reduction treatment) was higher in the native range than in the introduced range (e.g., see Fig. 2b). This change in background survivorship contributed more to the increased survivorship of *N. saltatorius* in its introduced range than did lower parasitoid attack. Thus, while enemy pressure was lower in the introduced range, enemy loss was not driving this species' success. Factors, such as host plant suitability, likely played a larger role in causing invasion success. This study clearly demonstrates how observational studies of enemy loss could lead to erroneous support of the ERH.

Even more powerful are studies that manipulate additional factors in both regions to examine the relative effects of multiple ecological factors on invasion success (Mitchell et al. 2006). Williams et al. (2010) manipulated specialist enemies and disturbance in the native and introduced ranges of the invasive plant houndstongue, *Cynoglossum officinale*, to examine causes of invasion success. They integrated the effect of these factors on different life stages into population demographic models to examine what drives differences in demographic growth in the species native and introduced range. They found that escape from specialist enemies contributed little to increased demographic growth; rather response to disturbance had a much larger effect on growth rates the introduced range. This was not because there were more disturbed sites; rather other plants were slower to colonize disturbed sites in the introduced range. This study highlights another limitation of most ERH studies (that is not unique to invasion studies). While invasion success is a demographic process, most studies only examine the effects of enemies on prey performance (or one demographic parameter), which will not necessarily scale up to population growth.

Based on our review of native enemy effects, we suggest that future studies examining invasive terrestrial plants should also test the role of other potentially important interacting factors (e.g., resources and competitors) (also see Blumenthal 2006; Mitchell et al. 2006). Additionally, we need more rigorous studies that employ experimental approaches and demographic modeling in species' native and introduced ranges to examine the role of enemies in causing invasion success. This is especially important for species in groups where interactions with enemies are strong and the potential for enemy release is high, such as for aquatic organisms or terrestrial species in higher trophic levels.

Researchers should tailor their studies and hypotheses of invasion success based on fundamental ecological and evolutionary knowledge about the species or taxa in question (Gurevitch et al. 2011). This approach would result in more relevant hypotheses and experiments rather than relying on broad hypotheses that may not apply to species in all taxonomic groups and ecosystems. For example, the ERH has largely be formulated to explain the success of invasive plants (e.g., Blossey and Nötzold 1995; Keane and Crawley 2002; Blumenthal 2006; Mitchell et al. 2006; except see Shea and Chesson 2002; Torchin and Mitchell 2004). Components from plant-derived explanations of the ERH may not be relevant to describe enemy release for other species. For example, Keane and Crawley (2002) invoke the importance of competitive interactions, suggesting that apparent competition or enemy-mediated competitive release is important in causing plant invasions. This form of enemy release may not be important for species in communities that are not strongly structured by interactions with competitors that share enemies (e.g., Prior and Hellmann 2013).

Enemy release and invasive terrestrial plants?

Although we found that native enemy effects are relatively low for terrestrial plants, we are not suggesting that enemies play no role in their invasion success. Evidence for the ERH in plants has been found in 57 % of experimental studies (Fig. 1; Prior and Hellmann 2015). These results provide evidence in support of ours and others' predictions: that while enemy release is important in some cases, it is not a ubiquitous explanation for plant invasion success (Fig. 4; Maron and Vila 2001; Keane and Crawley 2002; Blumenthal 2006; Williams et al. 2010). Furthermore, while enemy effects were the lowest for terrestrial plants confidence limits did not cross zero suggesting that enemies on average have negative effects on plants, effects are just not as strong or do not occur as frequently as for species in other groups. Plants with certain traits such as poor defense, short life cycles that rely on current seed production, and adaptations to high resource conditions are all thought to be particularly sensitive to enemy control and are predicted to have a high potential for release (Maron and Vila 2001; Keane and Crawley 2002; Blumenthal 2006).

Also, as mentioned above, one way that enemy release is predicted to occur for terrestrial plants is via enemy-mediated competitive release. This form of release may occur if introduced plants benefit from competitive release from native plants that are preferred by native enemies. This may be especially important for driving invasions of well-defended plants with generalist herbivore enemies (Keane and Crawley 2002; Kalisz et al. 2014; except see Parker 2006). Studies examining this type of release are in the form of "community comparison" studies, comparing enemy prevalence or effects on native and invasive species in introduced ranges (Colautti et al. 2004). Preferences or larger effects on native plants are cited as evidence for the ERH, and support has been found to be equivocal (Colautti et al. 2004; Agrawal et al. 2005; Parker 2006). We did not review these types of studies as they have been reviewed elsewhere (Colautti et al. 2004; Liu et al. 2006; Parker 2006).

Conclusions

Enemy release is a highly-cited explanation for the success of invasive species. We highlight that this hypothesis still needs critical evaluation to confirm its importance. Overlooking the assumption of native enemy effects can lead to erroneous conclusions about the role of enemies in facilitating invasions. We found systematic heterogeneity in native enemy effects among taxonomic groups and ecosystems. Thus, enemy release should not be expected to be an equally plausible explanation of success for all types of invasive species. Studies that examine enemy effects in both regions are needed for terrestrial animals and species in aquatic systems that have the potential to undergo strong release and where studies are lacking (e.g., Vermeij et al. 2009; Prior and Hellmann 2013). Additionally, future studies on invasive terrestrial plants should assess the effects of multiple interacting factors, such as enemies and resources (Blumenthal 2006; Mitchell et al. 2006; Williams et al. 2010). These types of studies will greatly advance our ability to uncover processes that cause invasion success. This is a critical step towards improving the management of invasive species.

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References

Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989

Atlegrim O (1998) Exclusion of birds from bilberry stands: impact on insect larval density and damage to the bilberry. Oecologia 7:136–139

Bach CE (1994) Effects of a specialist herbivore (*Altica suplicata*) on *Salix cordata* and sand dune succession. Ecol Monogr 64:423–445

Barton AM (1986) Spatial variation in the effect of ants on an extrafloral nectary plant. Ecology 67:495–504

Bigger DS, Marvier MA (1999) How different would a world without herbivory be? A search for generality in ecology. Integr Biol 1:60–67

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. J Ecol 83:887–889

Blumenthal D (2006) Interactions between resource availability and enemy release in Plant invasion. Ecol Lett 9:887–895

Blumenthal D, Mitchell CE, Pysek P, Jarosik V (2009) Synergy between pathogen release and resource availability in plant invasion. Proc Natl Acad Sci USA 106:7899–7904

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427:731–733

Cappuccino N, Carpenter D (2005) Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biol Lett 1:435–438

Carlsson NO, Sarnelle O, Strayer DL (2009) Native predators and exotic prey –an acquired taste? Front Ecol Environ 7:525–532

Cebrian J, Shurin JB, Borer ET, Cardinale BJ, Ngai JT, Smith MD, Fagan WF (2009) Producer nutritional quality controls ecosystem trophic structure. PLoS ONE 4:e4929

Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Earlbaum Associates, New Jersey

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Cornelissen T, Stiling P (2006) Responses of different herbivore guilds to nutrient addition and natural enemy exclusion. Ecoscience 13:66–74

Cornell HV, Hawkins BA (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. Am Nat 141: 847–865

Cripps MG, Schwarzländer M, McKenney JL, Hinz HL, Price WJ (2006) Biogeographical comparison of arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges. J Biogeogr 33: 2107–2119

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

DeBach P, Rosen D (1991) Biological control by natural enemies. University Press, Cambridge

DeWalt SJ, Denslow JS, Ickes K (2004) Natural enemy release facilitates habitat expansion of the invasive tropical shrub, *Clidemia hirta*. Ecology 85:471–483

Dobson A, Lodge D, Alder J, Cumming GS, Keymer J, McGlade J et al (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87:1915–1924

Ebeling SK, Hensen I, Auge H (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. Divers Distrib 14:225–233

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Flecker AS (1992) Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. Ecology 73:927

Floyd T (1996) Top-down impacts on Creosotebush herbivores in a spatially and temporally complex environment. Ecology 77:1544–1555

Forslund H, Wikström SA, Pavia H (2010) Higher resistance to herbivory in introduced compared to native populations of a seaweed. Oecologia 164:833–840

Fretwell SD (1977) Regulation of plant communities by foodchain exploiting them. Perspect Biol Med 20:169–185

Genton BJ, Kotanen PM, Cheptou P-O, Adolphe C, Shykoff JA (2005) Enemy release but no evolutionary loss of defence during ragweed invasion of France: an inter-continental reciprocal transplant experiment. Oecologia 146:404–414

Gurevitch J, Hedges LV (1999) Statistical issues in ecological meta-analyses. Ecology 80:1142–1149

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from synthesis of conceptual frameworks for biological invasions. Eco Lett 14:407–418

Haag JJ, Coupe MD, Cahill JF (2004) Antagonistic interactions between competition and insect herbivory on plant growth. J Ecol 92:156–167

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421

Halaj J, Wise DH (2001) Terrestrial trophic cascades: how much do they trickle? Am Nat 157:262–281

Hay ME (1991) Marine-terrestrial contrasts in the ecology of plant chemical defenses against herbivores. Trends Ecol Evol 6:362–365

Heger T, Jeschke JM (2014) The enemy release hypothesis as a hierarchy of hypotheses. Oikos 123:741–750

Hellmann JJ, Prior KM, Pelini SL (2012) The influence of species interactions on geographic range change under climate change. Ann NY Acad Sci 1249:18–28

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15

Ho CK, Pennings SC (2008) Consequences of omnivory for trophic interactions on a marsh shrub. Ecol 89:1714–1722

Hudson PJ, Dobson AP, Newborn D (1998) Prevention of population cycles by parasite removal. Science 282: 2256–2258

Huitu O, Koivula M, Korpimäki E, Klemola T, Norrdahl K (2003) Winter food supply limits growth of northern vole populations in the absence of predation. Ecology 84:2108–2118

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Jeschke JM, Aparicio LG, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14:1–20

Kalisz S, Spigler RB, Horvitz (2014) In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proc Natl Acad Sci USA 111:4501–4506

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 1:199–204

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Liu H, Stiling P, Pemberton RW, Peña J (2006) Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: implications for the enemy release hypothesis. Fla Entomol 89:475–484

Lodge DM (1991) Herbivory on freshwater macrophytes. Aquat Bot 41:195–224

Lodge DM, Kershner MW, Aloi JE, Covich AP (1994) Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75:1265–1281

MacDonald AAM, Kotanen PM (2010) The effects of disturbance and enemy exclusion on performance of an invasive species, common ragweed, in its native range. Oecologia 162:977–986

Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373

Memmott J, Fowler SV, Paynter Q, Sheppard AW, Syrett R (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. Acta Oecol 21:213–222

Menéndez R, Gonzáez-Megías A, Lewis OT, Shaw MR, Thomas CD (2008) Escape from natural enemies during climate-driven range expansion: a case study. Ecol Entomol 33:413–421

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757

Miller TEX (2008) Bottom-up, top-down, and within-trophic level pressures on a cactus-feeding insect. Ecol Entomol 33:261–268

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN et al (2006) Biotic interactions and plant invasions. Ecol Lett 9:726–740

Navarrete SA, Menge BA, Daley BA (2000) Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? Ecology 81:2264–2277

Ostrofsky ML, Zettler ER (1986) Chemical defenses in aquatic plants. J Ecol 74:279–287

Parker JD (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461

Parker IM, Gilbert GS (2007) When there is no escape: the effects of natural enemies on native, invasive, and noninvasive plants. Ecology 88:1210–1224

Parker JD, Torchin ME, Hufbauer RA, Lemoine NP, Alba C, Blumenthal DM et al (2013) Do invasive species perform better in their new ranges? Ecology 94:985–994

Pimm SL (1991) The balance of nature?. University of Chicago Press, Chicago

Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. Am Nat 138:123–155

Posey M, Powell C, Cahoon L, Lindquist D (1995) Top down vs. bottom up control of benthic community composition on an intertidal tideflat. J Exp Mar Biol Ecol 185:19–31

Prior KM, Hellmann JJ (2010) Impact of an invasive oak gall wasp on a native butterfly: a test of plant-mediated competition. Ecology 91:3284–3293

Prior KM, Hellmann JJ (2013) Does enemy loss cause release? A biogeographical comparison of parasitoid effects on an introduced insect. Ecology 94:1015–1024

Prior KM, Hellmann JJ (2015) Does enemy release contribute to the success of invasive species? A review of the enemy release hypothesis. In: Keller R, Cadotte M, Sandiford G (eds) Invasive species in a globalized world. University of Chicago Press, Chicago

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

Rosenberg MS, Adams DC, Gurevitch, J (2000) MetaWin: statistical software for meta-analysis, Version 2.0. Sinauer Associates, Massachusetts

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Roy HE, Lawson Handley LJ, Schönrogge K, Poland RL, Purse BV (2011) Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? Biocontrol 56:451–468

Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am Nat 155:141–153

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B et al (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785–791

Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. Proc R Soc B 273:1–9

Shwartz A, Strubbe D, Butler CJ, Matthysen E, Kark S (2009) The effect of enemy-release and climate conditions on invasive birds: a regional test using the rose-ringed parakeet (*Psittacula krameri*) as a case study. Divers Distrib 15:310–318

Sih A (1985) Predation, competition, and prey communities: a review of field experiments. Ann Rev Ecol Syst 16:269–311

Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754

Thompson JN (2005) The geographic mosaic of coevolution. University of Chicago Press, Chicago

Torchin ME, Mitchell CE (2004) Parasites, pathogens, and invasions by plants and animals. Front Ecol Environ 2:183–190

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol Invasions 3:333–345

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Van der Putten WH, Yeates GW, Duyts H, Schreck Reis C, Karssen G (2005) Invasive plants and their escape from root herbivory: a worldwide comparison of the root-feeding nematode communities of the dune grass *Ammophila arenaria* in natural and introduced ranges. Biol Invasions 7:733–746

Verhoeven KJF, Biere A, Harvey JA, Van der Putten WH (2009) Plant invaders and their novel natural enemies: Who is naïve? Ecol Lett 12:107–117

Vermeij MJA, Smith TB, Dailer ML, Smith CM (2009) Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. Biol Invasions 11:1463–1474

Vos M, Vet LEM (2004) Geographic variation in host acceptance by an insect parasitoid: genotype versus experience. Evol Ecol Res 6:1021–1035

Williams JL, Auge H, Maron JL (2010) Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. Ecology 91:1355–1366

Wootton JT (1992) Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology 73:981–991