

## REVIEW

# Is invasion success explained by the enemy release hypothesis?

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## Abstract

A recent trend in invasion ecology relates the success of non-indigenous species (NIS) to reduced control by enemies such as pathogens, parasites and predators (i.e. the enemy release hypothesis, ERH). Despite the demonstrated importance of enemies to host population dynamics, studies of the ERH are split – biogeographical analyses primarily show a reduction in the diversity of enemies in the introduced range compared with the native range, while community studies imply that NIS are no less affected by enemies than native species in the invaded community. A broad review of the invasion literature implies at least eight non-exclusive explanations for this enigma. In addition, we argue that the ERH has often been accepted uncritically wherever (i) NIS often appear larger, more fecund, or somehow ‘better’ than either congeners in the introduced region, or conspecifics in the native range; and (ii) known enemies are conspicuously absent from the introduced range. However, all NIS, regardless of their abundance or impact, will lose natural enemies at a biogeographical scale. Given the complexity of processes that underlie biological invasions, we argue against a simple relationship between enemy ‘release’ and the vigour, abundance or impact of NIS.

## Keywords

Enemy inversion hypothesis, enemy of my enemy hypothesis, enemy release hypothesis, exotic species, increased susceptibility hypothesis, invasion success, non-indigenous species.

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Research on biological invasions has grown remarkably over the past few decades, yet ecologists still pursue fundamental questions such as why some communities are more invaded than others, or why particular species become widespread and abundant (Kolar & Lodge 2001; MacIsaac *et al.* 2001; Keane & Crawley 2002). The most straightforward and intuitively appealing explanation for the rapid establishment and proliferation of non-indigenous species (NIS) is that they are released from the effects of their natural enemies. The enemy release hypothesis (ERH) posits that the abundance or impact of some NIS – often measured as individual size, population abundance, or propensity to displace native species – is related to the scarcity of natural enemies in the introduced range compared with the native range (Keane & Crawley 2002; Torchin *et al.* 2002, 2003; Mitchell & Power 2003). Given its rising popularity, we sought to evaluate the ERH by comparing its predictions with a review of existing data, and to better explore the circumstances that give rise to a release from enemies.

Biological invasions may be thought of as a successful transition between a series of consecutive, obligatory stages including uptake, transport, release, introduction and establishment. Of those invaders that establish, only a small subset will proliferate and/or spread in the introduced range (Williamson 1996; Richardson *et al.* 2000a; Kolar & Lodge 2001). Our assessment of the ERH focuses on this subset (i.e. stage IV/V invaders *sensu* Colautti & MacIsaac 2004) – we ask whether the proliferation of NIS that become abundant or dominant in their introduced range is generally because of a release from the effects of enemies.

For the purposes of this review, we define ‘host’ to include plant and animal prey, and ‘enemy’ to describe parasites (and parasitoids), pathogens and predators. We refer to ‘natural’ enemies as those that are found in the native region of their introduced host, and ‘native’ enemies as those that are native to the invaded community.

## IMPORTANCE OF ENEMIES

Not surprisingly, strong evidence for the impact of enemies on host fitness can be found in numerous case studies, independent of host origin. These effects are particularly conspicuous in parasitological and plant–herbivore studies (Hoffman & Schubert 1984; Bigger & Marvier 1998; Torchin *et al.* 2001; Hudson *et al.* 2002). Likewise, the overwhelming success of several classical biological control (biocontrol) agents highlights the potential importance of natural enemies in controlling the population dynamics of their host (e.g. see McFadyen 1998); this has been cited as evidence for the ERH (DeLoach 1995). However, a large proportion (c. 40–80%) of biocontrol agents fail to effectively control their hosts despite careful screening procedures (Williamson 1996; Denoth *et al.* 2002). Even where successful, control of hosts by biocontrol agents may be attributable to processes that are unrelated to enemy release. For example, classical biocontrol agents (i.e. natural enemies) are themselves NIS and therefore may benefit from whatever processes are responsible for the profound success of other NIS. Release of the biocontrol agent itself from enemies and competitors is one such process (Keane & Crawley 2002), but others include environmental variables, human activity, selection for invasive genotypes, and facilitative interactions with other species in the community (Williamson 1996; Simberloff & Von Holle 1999; Richardson *et al.* 2000b; Kolar & Lodge 2001; Maron & Vilà 2001; Bruno *et al.* 2003; Daehler 2003; Duncan *et al.* 2003).

## TESTS OF THE ERH

We searched the ecological literature published over the past 10 years and found 25 studies that tested various aspects of the ERH, over half of which (60%) generally supported ERH predictions (Table 1). These studies could be divided into two categories based on the scale of analysis; ‘biogeographical’ studies examined native and introduced populations of a given host, while ‘community’ studies compared native species and NIS co-occurring within the same community. Each category could be further divided into studies that used a correlative approach and those that used experiments, field surveys, or other comparative methods (Table 1). Eight studies examined the presence or effects of parasites, pathogens or predators on native and introduced populations of a single host species (Table 1: ‘biogeographical/comparative’ studies). Of these, Fenner & Lee (2001) surveyed only the incidence of a seed predator, while Memmott *et al.* (2000) examined diversity and biomass of enemies without measuring their impact. Torchin *et al.* (2001) and Wolfe (2002) examined both incidence of enemies and their effect. Each study found support for the

ERH, but none used experimentation to confirm that enemies were responsible for the observed patterns. However, DeWalt *et al.* (2004) found a significant effect of fungicide and pesticide treatments in understory but not open habitats. Beckstead & Parker (2003) found evidence for a reduction in pathogenic nematodes in an introduced population of European beachgrass (*Ammophila arenaria*), but soil sterilization experiments revealed that this pattern did not translate into any increase in seed germination, seedling survival or growth rate. Conversely, Reinhart *et al.* (2003) and Callaway *et al.* (2004) found that soil pathogen exclusion improved performance of NIS grown on native soil more than those grown on soil from the introduced range. In the latter two cases, the authors suggested that a build up of soil pathogens resulted in a negative feedback that limited abundance of the host in the native range but less so in the introduced range.

In general, observational evidence at a biogeographical scale does suggest an important role for enemy release in invasive species, but only four studies used enemy exclusion to confirm significant, demographic impacts, and only two of these, both dealing with soil pathogens, found unconditional evidence to support the ERH. However, none of the soil microbe experiments in our review differentiated between the effects of pathogenic and facilitative interactions. Thus a reduction in the negative effects of soil microbes could be the result of a reduction in negative interactions or a corresponding increase in the effects of facilitators. We therefore stress caution when citing the results of soil microbe experiments as evidence for the ERH. Four additional studies each compared the diversity or richness of pathogen or parasite species, in native and introduced ranges, for a number of host NIS (Table 1: ‘biogeographical/correlative’ studies). All support the view that there are generally more species of enemy associated with NIS in their native than introduced range. Therefore, both comparative and correlative studies at biogeographical scales suggest that species experience a release from natural enemies.

If biogeographical studies examine a host’s release from its natural enemies, then community studies should give some indication of the relative impact of enemies on coexisting native species and NIS. Interestingly, support for the ERH at the community level is much more equivocal than support from biogeographical studies. For example, Clay (1995) found that grasses native to the United States have, on average, fewer pathogen species than co-occurring NIS (Table 1: ‘community/correlative’ studies). Twelve additional studies compared the effect of enemies on native and NIS (usually congeners) within the same community. Results from community level studies do not generally support the ERH as NIS were affected by enemies less than native species in only four of the 13 studies, with four

**Table 1** A review of recent studies (published since 1994) that test assumptions of the enemy release hypothesis (ERH). *Biogeographical* studies are those that compare native and introduced populations of the same species, while *community* studies examine native and non-indigenous species (often congeners) co-occurring within the same community. Each group is further divided into studies that used *correlative* statistical techniques of natural populations, and those that used common garden experiments, field manipulations, or other *comparative* methods. Studies that support the ERH are indicated by '+', those finding no support are indicated by 'n.s.' and those finding results opposite to ERH predictions are indicated by '-'. For the *comparative, community* group of studies, where NIS and native species were not paired for analysis, the numbers of species in brackets represent the subset of total species examined that were non-indigenous

Studies	Support for ERH	Number of host species
<b>Biogeographical</b>		
Comparative		
Beckstead & Parker (2003)	n.s.	One plant
Callaway <i>et al.</i> (2004)	+	One plant
DeWalt <i>et al.</i> (2004)	+	One plant
Fenner & Lee (2001)	+	One plant
Memmott <i>et al.</i> (2000)	+	One plant
Reinhart <i>et al.</i> (2003)	+	One plant
Torchin <i>et al.</i> (2001)	+	One aquatic invertebrate
Wolfe (2002)	+	One plant
Correlative		
Mitchell & Power (2003)	+	473 plants
*Poulin & Mouillot (2003)	+	Two fishes
†Torchin <i>et al.</i> (2002)	+/-	10 aquatic invertebrates
Torchin <i>et al.</i> (2003)	+	26 animals
<b>Community</b>		
Comparative		
Agrawal & Kotanen (2003)	-	15 congeneric pairs of plants
Bellingham (1998)	-	One pair of plants
Blaney & Kotanen (2001a)	n.s.	15 congeneric pairs of plants
Blaney & Kotanen (2001b)	n.s.	43 (21 NIS) plants
Blaney & Kotanen (2002)	n.s.	39 (20 NIS) plants
Goergen & Daehler (2001)	+	One pair of plants
Gross <i>et al.</i> (2001)	-	One pair of plants
Lesica & Miles (1999)	+	One pair of plants
Novotny <i>et al.</i> (2003)	n.s.	71 (two NIS) plants
Radho-Toly <i>et al.</i> (2001)	n.s.	Two congeneric pairs of plants
Schierenbeck <i>et al.</i> (1994)	+	One congeneric pair of plants
Siemann & Rogers (2003b)	+	One pair of plants
Correlative		
Clay (1995)	-	767 plants

\*Poulin & Mouillot (2003) found that introduced populations had higher taxonomic diversity, but that native populations had a higher total diversity; thus the results are not contradictory to the other papers in this category.

†Torchin *et al.* (2002) found fewer parasite species (+ support), but a higher overall prevalence (- support) in native populations.

studies showing the opposite trend (Table 1: 'Community' studies). Several studies that supported predictions of the ERH at a community level examined only a single pair of species, and as noted by Daehler (2003), several involved enemies that occurred at unusually high densities. In a common garden experiment on multiple host species, Agrawal & Kotanen (2003) noted that while some NIS were less affected by herbivory than native congeners, many were not, and the overall trend was actually in the reverse direction. Moreover, patterns of enemy release were not easily explained by the abundance or 'invasiveness' of the host NIS.

Overall there is evidence for enemy release of a few species at a community scale, but there is no apparent generality to this phenomenon. Studies of enemy release therefore represent somewhat of an enigma in that there

appears to be a general trend for a reduction in enemy diversity at a biogeographical scale, but with little evidence for 'release' from the effects of enemies in invaded communities. Below we explore some possible explanations for this apparent discrepancy, as outlined in Table 2.

## TWO TYPES OF ENEMY RELEASE

Studies of the ERH may have overlooked the differences between enemies with strong effects and those for which hosts have developed defences. Given that host species have evolved defences to some but presumably not all of their natural enemies, there are two pathways through which a host may be 'released' from the effects of enemies. The first occurs when a host species has low resistance to, and is therefore strongly regulated by, one or more enemy species.

**Table 2** Some explanations for the observed differences between biogeographical and community studies of enemy 'release'. Acronyms are used for non-indigenous species (NIS) and the enemy release hypothesis (ERH)

Section	Hypothesis	Examples
Two types of enemy release	<i>Compensatory vs. regulatory release</i> Failure to acknowledge two types of enemy release may have led to erroneous conclusions about the net effect of enemy loss at biogeographical scales	Fritz & Simms (1992); Blossey & Nötzold (1995); Strauss & Agrawal (1999)
Propagule bias and patterns of enemy diversity	<i>Propagule biases</i> Biogeographical patterns of enemy release are artefacts of sampling design	Southwood (1982); Clay (1995); Duncan <i>et al.</i> (2003); Colautti & MacIsaac (2004)
Invasion bottlenecks	<i>All NIS lose enemies</i> All NIS, regardless of their impact, are expected to lose enemies due to invasion bottlenecks, yet few studies have considered whether patterns of enemy release can account for innocuous, or non-invasive NIS	Torchin <i>et al.</i> (2002, 2003); Mitchell & Power (2003)
Endpoints of enemy release	<i>Other biotic and abiotic factors</i> Enemy release identified in <i>in vitro</i> experiments do not translate into increased vigour or fitness <i>in situ</i>	No studies reviewed here have tested this directly
The effect of native enemies	<i>Native enemies</i> NIS are naïve hosts for enemies native to the invaded community, offsetting a biogeographical release <i>Increased susceptibility hypothesis (ISH)</i> Genetic bottlenecks increase susceptibility of NIS to enemies in the introduced range <i>Loss of polymorphic defences</i> Bottlenecks and founder effects reduce the variability of polymorphic defences, resulting in stronger effects of native and natural enemies, despite a biogeographical release	Maron & Vilà (2001); Keane & Crawley (2002) See Barrett & Shore (1989) Indirect evidence only: Barrett & Shore (1989); Lively (1999); Holland (2001); Carr & Eubanks (2002)
The effect of natural enemies	<i>Enemy inversion hypothesis (EIH)</i> Novel biotic and/or abiotic factors reduce, or even reverse the net effect of enemies <i>Enemy of my enemy hypothesis (EEH)</i> Natural enemies have a stronger effect on native competitors; the NIS benefits through apparent competition, or hyperpredation, rather than enemy release	See Pearson <i>et al.</i> (2000); Pearson & Ortega (2001); Pearson & Callaway (2003) Reynolds (1988); Fritts & Rodda (1998); Courchamp <i>et al.</i> (1999); Tompkins <i>et al.</i> (2003)
Key areas of future research	<i>Sampling bias</i> Studies examining only a few host species are biased towards those finding positive results	We found no studies testing enemy release of innocuous invaders

In such cases, the loss of enemies during the invasion process could result in direct changes to survivorship, fecundity, biomass or other demographic parameters (i.e. a *regulatory release*). Alternatively, the loss of enemies against which a host is well defended would be of little consequence for the host populations. If, however, there were costs to defence, then the loss of enemies could result in an indirect release, as the limited resources utilized for defence were reallocated elsewhere (i.e. a *compensatory release*). Evidence for a trade-off between defence and other fitness parameters is accumulating (Fritz & Simms 1992; Bergelson & Purrington 1996; Strauss & Agrawal 1999), while regulatory effects are well documented (see 'Importance of Enemies' above). It

should be noted that regulatory and compensatory release are not mutually exclusive. For example, both forms of release could be active in an introduced population released from a predator that both caused significant damage to, and elicited a defensive reaction from, its host.

The distinction between regulatory and compensatory release is subtle but important for a number of reasons, a few of which we outline here. First, regulatory release is an immediate effect, whereas compensatory release may occur over ecological time, as limiting resources are re-allocated away from defence, or over evolutionary time, as genotypes with costly defences are selected out of introduced populations. However, the generality of the latter 'evolution

of increased competitive ability' (EICA; *sensu* Blossey & Nötzold 1995) has received conflicting support (Willis *et al.* 2000; van Kleunen & Schmid 2003 but see Leger & Rice 2003; Siemann & Rogers 2003a). Second, as noted above, available evidence seems to be skewed towards regulatory rather than compensatory release. For example, Agrawal *et al.* (1999) noted that trade-offs might only be apparent where multiple fitness characteristics are examined together, as slight improvements to each characteristic may be masked by statistical variance. It therefore seems necessary to question whether this low level of release can be responsible for the significant levels of abundance in, or dominance of, natural habitats that are characteristic of many stage IVb/V invaders. Finally, a distinction is important because release of specialized defences from co-evolved enemies is more likely to be skewed towards a compensatory release pathway. This owes to stronger host defences, and consequently reduced enemy effects, that are characteristic of co-evolutionary interactions. A host will not experience a *release* from enemies, but rather an *exchange*, if enemies in the invaded range elicit the same response as the enemies that are lost. NIS with native congeners in the invaded range may therefore benefit less from compensatory enemy release because host-switching will be more common than for distantly related NIS. However, it is uncertain how much variation in the success of NIS can be explained by the existence of congeners in the invaded community (Agrawal & Kotanen 2003).

Some confusion surrounding specific predictions of the ERH may arise through a failure to acknowledge the difference between regulatory release, which requires that enemies have an appreciable effect, and compensatory release, which assumes that enemies have a minimal effect because of costly defences. Despite these differences for the role of enemies, both predict an advantage for a 'released' host, albeit at different time scales. The disagreement between biogeographical and community studies in Table 1 may be explained if defences are not particularly costly. In such cases, the loss of many enemies with little regulatory effect would have little consequence for introduced populations of the host species.

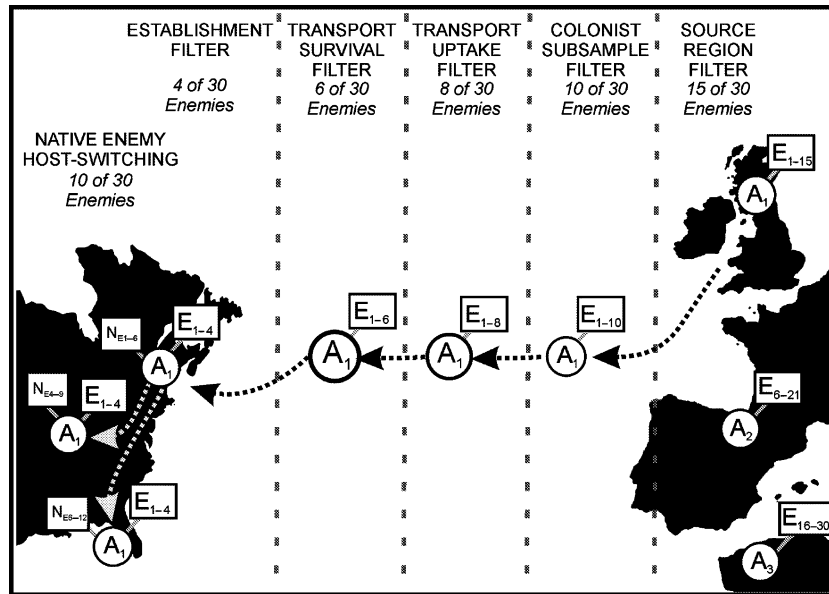
#### PROPAGULE BIAS AND PATTERNS OF ENEMY DIVERSITY

Patterns of enemy release that are based on the richness or diversity of enemy species may be confounded by biases in research effort or by the contrast group selected from the source region. Potential NIS and their enemies may be better studied in their native rather than their introduced ranges, and as such, more enemies would be expected in native populations simply because of sampling effort (Mitchell & Power 2003; Torchin *et al.* 2003). For example, of 26

randomly selected studies that addressed parasites of three globally invasive vertebrate species (i.e. rat, mosquitofish and rabbit), only five dealt with parasites found in the introduced ranges (Torchin *et al.* 2003). This problem should be particularly acute for recent invasions, wherein enemies of native populations are more likely to be studied because of a relatively larger range and longer residence time. In fact, the magnitude of this bias may be proportional to some function of the time since invasion over the native range area.

More importantly, richness-based measurements of 'enemy release' require knowledge of the number of enemies in the source *population*, rather than the native range *per se*. The native range of a given species may consist of many smaller populations, or may at least contain a heterogeneous assemblage of enemies. Studies that have explicitly compared range sizes with the number of co-occurring enemies for both introduced and native ranges of plant species have concluded that the best predictor of enemy diversity is the size of the host range, rather than status as native or introduced (Southwood *et al.* 1982; Clay 1995). Thus, spatial variation in enemy occurrence within the source range may be pronounced. For example, each population in the native range may have its own subset of enemies. As invading propagules are probably not drawn randomly from across their entire native range, the number of enemies available to be introduced to a new area with their hosts will be much lower than that represented by the total number available from across the realm (i.e. source region filter in Fig. 1). The use of cumulative numbers drawn from across an entire source biogeographical realm are therefore inappropriate because they could substantially overestimate the number of enemies available for transport to a new region, even if both native and introduced ranges are of similar size. We use the term 'propagule bias' to describe cases like this, where the confounding effects of non-random selection at early stages of the invasion process may bias patterns apparent at later stages (Colautti & MacIsaac 2004).

A more appropriate contrast would consider only those enemies found in the region(s) from which the colonist population was likely drawn. Where historical data is inadequate, identification of invasion pathways should help clarify the region(s) to be considered in developing candidate lists of enemies available for transport to new areas (MacIsaac *et al.* 2001; Hänfling *et al.* 2002). Where both genetic data and historical information are inconclusive, an alternative method may be to average the enemy diversity across a number of populations. However, it is unclear how representative this would be because introductions may often be non-random samples of native populations. In the Laurentian Great Lakes, for example, most aquatic NIS are believed to be derived from populations invading north-western Europe because of patterns of shipping traffic, which is the dominant vector of introduc-



**Figure 1** Mechanisms of apparent and realised enemy reduction for a host species (A). The size of A is related to the expected impact of enemy loss from each filter on host fitness. From right to left, subsampling of the biogeographical region (source region filter) results in an ‘apparent’ reduction in enemy species ( $E_{1-40}$ ) with no impact on introduced host populations. Subsampling of the actual source population (colonist subsample filter) is likely to cause the loss of only rare enemies, such that net effects on host population are uncertain. Transport of a subsample of enemies (transport uptake filter) that may experience mortality during transport (transport survival filter) or establishment (establishment filter) results in a ‘realized’ reduction in enemies that likely does lead to increased fitness. Finally, host switching by native enemies ( $N_{E1-12}$ ) in the introduced range may counteract the effects of ‘realized’ enemy reduction, while still maintaining a pattern of ‘apparent’ reduction at a biogeographical scale.

tion (MacIsaac *et al.* 2001; Ricciardi 2001; Grigorovich *et al.* 2003).

This potential for propagule bias at numerous invasion stages suggests to us that an analysis of regional enemy assemblages – such as the comparison of the number of enemy species on two different continents – may be a non-informative test of the ERH. A population-level analysis seems far more appropriate given that host species abundance is regulated at the level of population, not range. Propagule biases may help to explain the discrepancy between correlative biogeographical studies and the community-level studies in Table 1.

### INVASION BOTTLENECKS

Despite the problems inherent in biogeographical studies of enemy diversity, a number of mechanisms exist by which introduced populations may lose associated enemies that were present in native populations (see Paterson *et al.* 1999; Torchin *et al.* 2002). Because of the limited number of propagules typically associated with introduction events, their transportation to novel environments effectively results in a subsampling of source populations, reducing the likelihood of introducing rare enemies (i.e. a founder effect, see colonist subsample filter; Fig. 1). However, it is

unclear to what extent the loss of rare enemies will result in an effective ‘release’ for their host, as it is the most common enemies that typically have the greatest effects (Hudson *et al.* 2002). The number of transported individuals that become introduced may be further constrained by differential mortality of infected or parasitized propagules (Mitchell & Power 2003; Torchin *et al.* 2003) and by harsh conditions during transport (see transport survival filter; Fig. 1). Furthermore, transport vectors may predispose an invader to arrive without its enemies; for example, planktonic larval stages of aquatic invertebrates may lack parasites associated with adults (e.g. zebra mussels; Molloy *et al.* 1997; see transport uptake filter; Fig. 1). To complete their life cycle, many parasites (e.g. trematodes; Hudson *et al.* 2002) require multiple host species, and therefore would not establish in novel habitats without alternative hosts (see establishment filter; Fig. 1). Finally, human selection could influence the number of parasites available for transfer to the new habitat. For example, it is well established that female birds may preferentially select healthy-appearing mates with low parasite burdens (Andersson 1994; Saks *et al.* 2003; see transport uptake filter, Fig. 1); if human importers of plants or animals select colonists that are relatively free of parasites, then the number of enemies available for transfer to the new ecosystem will be correspondingly lower (see

transport uptake filter; Fig. 1). If transition through the stages of transport, introduction and establishment is dependent upon the health of the host NIS, then it may be expected that enemies with strong effects will be more readily excluded from introduced populations. We may therefore conclude that regulatory release will be more common than compensatory release in these circumstances.

Unlike 'propagule biases', the invasion bottlenecks outlined above are expected to impact host populations. However, given all the possible mechanisms of enemy release, most or all NIS will likely experience some degree of release from natural enemies at a biogeographical scale. Caution is therefore warranted when drawing inferences that are based merely on observed reductions of natural enemies, as this reduction is expected for all established NIS, independent of their invasion 'stage' or impact. This may help to further explain the discrepancy between studies at biogeographical and community levels because all NIS lose enemies at a biogeographical scale, regardless of their release from enemies at the community level.

#### END-POINTS OF ENEMY RELEASE

It has been noted that individuals in introduced populations are often larger than conspecifics in the native range (Crawley 1987; Grosholz & Ruiz 2003). It is unclear, although often speculated, that enemy release is responsible for this pattern. It is also unclear whether characteristics like increased size are even generally true for NIS (Thébaud & Simberloff 2001). Studies that examine the impact, rather than diversity, of enemies, typically examine reproduction, mortality and/or biomass of the host plant, although any number of demographic or life-history characteristics conceivably may be 'enhanced' through the loss of natural enemies. These parameters are likely chosen because they are generally accepted as correlates of fitness. However, even where results are significant *in vitro*, they may not be responsible for the increased abundance or dominance of NIS *in situ*. For example, Reinhart *et al.* (2003) found that *Prunus serotina* seedlings were harmed by soil pathogens in the native range but not the introduced range. However, Reinhart *et al.* (2003) also found that *Prunus* seedlings grew more than twice as well on non-native than on native soil, regardless of sterilization. In other words, soil pathogens increased the mortality of seedlings grown at high density in the native range, but something else, probably abiotic conditions of the soil, caused a doubling of biomass in soil from the introduced range. This raises an important question about the relative importance of enemy release compared with other factors in affecting patterns of NIS abundance or dominance *in situ*.

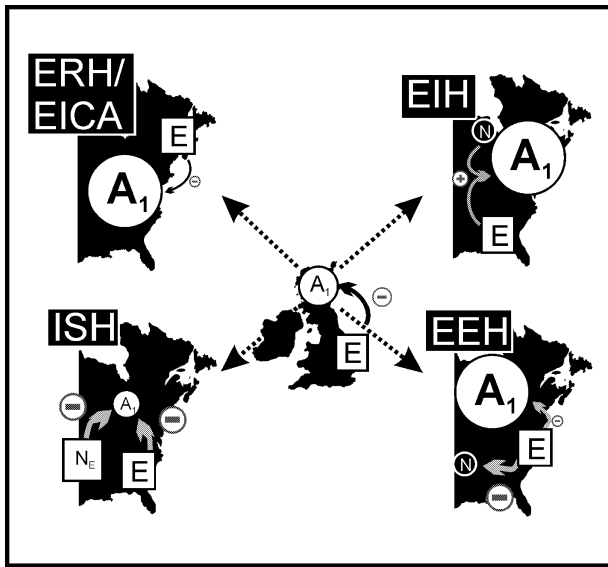
It is also important to consider that some characteristics may grant little advantage over competitors, even if there is a

fitness advantage over conspecifics. In some plant invasions, for example, increased fecundity or survivorship may provide little advantage where abundance is limited by competitive interactions with native species for limiting resources. Alternatively, increased competitive ability may not be useful where abundance is propagule limited, such as in highly disturbed sites. Here again, enemy release would not be an important driver of host abundance or dominance *in situ*, despite an apparent pattern of increased fitness *in vitro*. In other words, characteristics that increase fitness compared with conspecifics do not necessarily translate into an advantage over congeners or competitors. We therefore caution against acceptance of enhanced fitness characteristics as evidence for the ERH without demonstration of their cause (beyond a simple correlation with enemy impact), their relative importance compared with other factors, and their ultimate effect on the host population *in situ*. This could help to clarify results from biogeographical experiments, which show intraspecific fitness increases, and community experiments, which show little interspecific increase.

#### THE EFFECT OF NATIVE ENEMIES

Another key consideration for the ERH is whether NIS are less vulnerable to enemies in the invaded region than are native species. In other words, is host switching rare by native enemies in the introduced range, and where it occurs do they inflict less damage on NIS than on native species? Some evidence exists in support of this assumption, but it is by no means universal (Table 1; see also Maron & Vilà 2001; Keane & Crawley 2002; Agrawal & Kotanen 2003).

In fact, two lines of reasoning suggest that NIS should be more susceptible than native hosts to the effects of native enemies. First, invasion bottlenecks may reduce the genetic diversity of polymorphic defences (e.g. cyanogenic glycosides, recognition sites of the major histocompatibility complex) that are important in avoiding disease outbreaks (e.g. Lively 1999; Carr & Eubanks 2002). If this is true, then enemies will have disproportionate effects on populations of NIS compared with more genetically diverse native species. Thus, factors reducing the number of co-evolved enemy species could also result in higher levels of attack by not only native enemies, but by natural enemies that are successfully introduced. Although it is not known how strong a bottleneck must be to reduce polymorphic defences, genetic bottlenecks caused by founder effects have been identified in many NIS (Tsutsui *et al.* 2000; Cristescu *et al.* 2001) but not others (Holland 2001), and may be confounded by high rates of inbreeding among newly founded populations (see Barrett & Shore 1989). Second and more importantly, NIS represent naïve hosts to native enemies, which can result in novel, and sometimes profound instances of attack (i.e. 'new associ-



**Figure 2** Expected effects of enemies on the abundance or dominance of non-indigenous species (NIS). A host species ( $A$ ) in its native range (centre of diagram) is affected by natural enemies ( $E$ ) that may have varying effects in the introduced range: ERH/EICA, a reduction in the number of natural enemies leads to increased fitness or vigour of host NIS; EIH, disruption of complex species interactions reduces or reverses the effects of enemies, possibly through interactions with native species ( $N$ ); EEH, host switching by introduced enemies results in decreased fitness or vigour of native competitors ( $N$ ) and proliferation of  $A$ ; ISH, genetic bottlenecks lead to strong effects by a few introduced enemies ( $E$ ) and by some of those already present ( $N_E$ ), decreasing the vigour of  $A$ . Relative population responses by invading species ( $A$ ) and native species ( $N$ ) are denoted by size of the corresponding circles. Strength of negative ( $-$ ) and positive ( $+$ ) species interactions are indicated by size of the interaction circles. See text for definitions and examples of interaction acronyms.

ations principle'; Hokkanen & Pimentel 1989). Moreover, these two possibilities may interact synergistically such that naïveté is compounded by the loss of defences because of invasion bottlenecks. We call this the 'increased susceptibility hypothesis' (ISH; Fig. 2). Introduced populations could therefore be subjected to greater enemy effects than the source population, or native congeners in the same community, although it may involve a smaller complement of enemy species.

Contrary to current biocontrol practices, the ISH suggests that the best strategy for control of NIS may be the introduction of native enemies to newly founded populations of invaders. Unlike classical biocontrol, this method would not involve introducing NIS to control NIS, and therefore may not suffer many of the drawbacks of classical biocontrol methods (e.g. see Louda *et al.* 2003; Pearson & Callaway 2003). To the best of our knowledge, no studies

have tested the ISH directly. However, Torchin *et al.* (2002) noted that the average parasite prevalence for marine NIS was more than twice that of native populations, although the overall number of enemy species was reduced in introduced populations. This suggests that the ISH could be an important and under-appreciated consideration in studies of enemy release. This phenomenon may also help to explain the disjunction between biogeographical correlations of enemy release and experimental studies at the community level (Table 1), as NIS hosts lose several enemies from their native range, but gain a few with large impacts in communities where they are introduced. Reduced diversity of defences may be yet another alternative to the ERH to explain the success of certain biocontrol agents.

### THE EFFECT OF NATURAL ENEMIES

Studies of the ERH generally assume that NIS benefit from a loss of natural enemies during the invasion process. As noted above, however, the net effect of natural enemies may not be equal in the invaded and source regions. Alternative to the ISH, enemies may have a reduced, or even opposite effect on their host as a result of biotic or abiotic differences between communities in the native and introduced ranges. Two examples are outlined below.

#### Enemy inversion hypothesis

Natural enemies could have a reduced, or even opposite, net effect on their host between native and introduced ranges because of abiotic factors or through a restructuring of multispecies interactions (Pearson & Callaway 2003; Fig. 2). Inversions are likely to arise through direct changes, such as environmental conditions, or through subtle, indirect pathways because of complex species interactions in the new community. In one spectacular case, Pearson *et al.* (2000) found that larvae of two gall flies (*Urophora affinis* and *U. quadrifasciata*), introduced to control *Centaurea maculosa* (spotted knapweed), became a favoured meal of native *Peromyscus maniculatus* (deer mice), accounting for up to 86% of their diet. The mice readily consumed *Urophora*, reducing their impact to a level insufficient to control *Centaurea*. Furthermore, because *Urophora* larvae inhabit *Centaurea* flowerheads, the mice inadvertently consumed *Centaurea* seeds, providing a novel mechanism of local dispersal by the invasive plant (Pearson *et al.* 2000). Surprisingly, Pearson & Ortega (2001) later found viable *Centaurea* seeds in faecal pellets of Great Horned Owls (*Bubo virginianus*) that had apparently preyed upon the mice, thereby providing a novel mechanism for long-distance dispersal by *Centaurea*. Although deer mice in this example act as facilitators, it can be argued that the *Urophora* species have an indirect, but net positive impact on *Centaurea* in the



introduced range, despite being a 'well-behaved' biocontrol agent (Pearson *et al.* 2000). The importance of changes to complex interactions within communities in native and introduced ranges remains largely unexplored, likely because of the great challenge inherent in studying multiple interactions.

### 'Enemy of my enemy' hypothesis

The enemy of my enemy hypothesis (EEH) takes its name from the proverb 'the enemy of my enemy is a friend of mine', which is often used to describe tri-trophic interactions and other types of mutualisms mediated through a negative effect on an enemy or competitor (e.g. Sabelis *et al.* 2001). Thus, the EEH predicts a net positive effect of 'enemies' on co-occurring NIS (Fig. 2). As such, it could be considered as a special case of the enemy inversion hypothesis (EIH). The introduction of particular natural enemies sometimes increases the success of the original hosts by differentially impacting native species through apparent competition (Hoffman & Schubert 1984; Juliano 1998; Lafferty & Gerber 2002; Louda & O'Brien 2002). For example, introduced American crayfish (*Pacifastacus leniusculus*) carried a fungal parasite (*Aphanomyces astaci*) that wiped out most native crayfish populations in Europe (Reynolds 1988). Similarly, the on-going replacement of native red squirrels (*Sciurus vulgaris*) in the UK by introduced grey squirrels (*Sciurus carolinensis*) appears to be the result of enhanced vulnerability of the former to a parapoxvirus introduced with the latter (Tompkins *et al.* 2003).

Through a special form of apparent competition, termed 'hyperpredation' (Courchamp *et al.* 1999), a well-adapted prey might sustain an introduced predator population as the latter exerts pressure on the naïve native species, potentially driving them to extinction. Such was the case when successive invasions of Guam brought the brown tree snake (*Boiga irregularis*) into contact with its co-evolved lizard prey, which facilitated the elimination of over a dozen endemic species of birds, reptiles and bats through intense predation (Fritts & Rodda 1998). Despite several case studies, empirical evidence for the relative importance of the EEH is lacking. However, results of some studies of the ERH may be better explained by the EEH. The comparative community studies in Table 1 that examined the effects of multiple enemies usually did not distinguish between the level of attack from native and introduced enemies.

### KEY AREAS OF FUTURE RESEARCH

Our discovery of contradictory evidence for the ERH in community and biogeographical studies (Table 1) remains enigmatic. In addition to the possibilities outlined above,

studies finding positive support for the ERH may be over-represented if they are more likely to be undertaken where preliminary observations implicate the potential importance of enemies, or if studies rejecting the hypothesis (i.e. finding no difference in enemy effects) are less likely to be published. Nevertheless, we cannot rule out that NIS may be somehow more 'tolerant' than native species subjected to similar levels of attack within the invaded community. However, such a conclusion is premature given the dearth of studies of the same NIS at both biogeographical and community scales (Table 1). Given the myriad possible explanations for the success of NIS, this scenario cannot be an acceptable assumption without thorough research. Instead, the null hypothesis should be that NIS are no more 'released' from enemies than are native species. Clearly more research is needed. In particular, it is immediately apparent from Table 1 that comparative studies of the ERH are largely plant-biased, yet many of the cases we explicitly reviewed come from other taxonomic groups. Thus, experimental studies of the role of enemies for other taxa are needed to better understand the generalities and limitations of the ERH. Here we briefly outline some other areas of further research that will help to identify the limitations of the ERH and to differentiate among many of the alternative explanations outlined above.

### Enemy release or reduction?

Studies of the ERH have often used the number of enemy species as a measure of enemy release (e.g. Torchin *et al.* 2002, 2003; Mitchell & Power 2003). However, without knowledge of the net effects of these enemies on host population dynamics, we argue that such measurements represent an enemy *reduction*, rather than release *per se*. Patterns of enemy reduction may be prone to propagule biases, while patterns of enemy release may be erroneously inferred when significant experimental effects are insignificant *in situ*. We may therefore conclude that patterns of both enemy release and enemy reduction can be subdivided as *apparent* or *realized*, with the former resulting in false inferences. In other words, there could be a significant separation between apparent enemy reduction (i.e. an apparent loss of enemies) and realized enemy release (i.e. no net effect on host fitness). Differentiating between apparent and realized patterns therefore require careful consideration of the biases that might lead to apparent patterns that are not realized by the host at a population level. Understanding how reduction may translate into release requires a better understanding of the effects of specific enemies. Few of the studies reviewed in Table 1 that quantify the effects of enemies have examined multiple species of enemy, yet it seems important to understand the

interactions among different types of enemies. For example, a fruitful area of research may be quantifying the relative impacts of different types or 'functional groups' of enemies, like soil pathogens, root predators, herbivores and seed predators on plant hosts. Is the diversity of enemies *per se* a good predictor of host abundance or impact, or is it dependent upon the functional diversity of enemies, or upon a small number of enemies with particularly large effects (i.e. a 'lottery' effect)? In the case of the zebra mussel invasion of North America, Molloy *et al.* (1997) suggested that although no one enemy appears capable of significantly reducing zebra mussel populations, a diverse suite of enemies might have a limiting effect.

### Innocuous NIS

Notably absent from the ERH literature are studies of the impact of enemies on 'innocuous' NIS. A more informative test of the ERH than those reviewed in Table 1 would relate some measure of 'release' from enemies to the variation in impact or fitness among different NIS. Mitchell & Power (2003) found a relationship between the number of pathogens on NIS of plant and indices of 'invasiveness' or 'noxiousness' based on government reports. However, in addition to the problems with diversity comparisons outlined earlier, erroneous inferences could also result because qualification of NIS as 'invasive' or 'noxious' are often poorly and inconsistently defined (Richardson *et al.* 2000a; Chew & Laubichler 2003; Colautti & MacIsaac 2004). Nevertheless, a comparison of enemy release with the abundance or dominance of NIS should prove fruitful if empirical data are rigorous.

Perhaps an even better approach would be to examine multiple introduced populations of the same NIS that vary in their levels of abundance, dominance or impact (i.e. 'effect'). Callaway *et al.* (2004) noted high variability in the effects of soil pathogens on *Centaurea maculosa* among both native and introduced populations; results of soil sterilization ranged from a 24% decrease to a 900% increase in biomass. Although plants in the native range had, on average, a lower increase than those in the introduced range, no attempts were made to correlate pathogen release with the density of *Centaurea* at a population level. A correlation between the level of attack by enemies and the effect of the host at a population level would be an important first step in a comprehensive test of the ERH. The next logical step would be to attempt to equalize this variance through enemy exclusion and introduction experiments both *in situ* and in common garden experiments in both the native and introduced ranges. This would also allow for a distinction between the ERH and EIH as they predict opposite effects for the addition of particular enemies. The relative importance of ERH and EIH remains almost completely unex-

plored. Parallel common garden experiments in both ranges is particularly important for EICA experiments because phenotypic or life-history differences between populations may represent local adaptation to growing conditions in the common garden (e.g. solar incidence, day length).

Understanding how enemy attack varies over the time course of an invasion may prove to be another valuable area of research. How quickly do NIS accumulate native enemies over time, and how does this relate to the dynamics of invasion by the host? Is the accumulation of native and natural enemies responsible for the 'boom-and-bust' phenomenon that occurs in many introduced populations (Simberloff & Gibbons 2004)? What is the role of invasion 'vectors' in introducing more enemies from the native range of the host, both during and after invasion? The knowledge gained from comprehensive studies of NIS populations that pass through the invasion 'stages' could provide insights beyond those available from simple enemy exclusion experiments.

### The role of invasion vectors and bottlenecks

We are unaware of any studies that examine the effect of invasion vectors on co-introduced enemies, despite the potential importance of bottlenecks to the regulatory and compensatory release of NIS. For example, bottlenecks almost certainly act differently for ballast-mediated invertebrate introductions (Grigorovich *et al.* 2003) than for deliberately introduced plants for horticulture (Mack 2003) or for birds released by acclimatization societies in New Zealand (Duncan *et al.* 2003). In the first case, survival of parasites may depend on factors such as host residency time in a ballast tank, while in the latter two, humans may choose healthier individuals, or even treat them for disease, thereby excluding many pathogens and parasites. Invasion bottlenecks may differentially filter out enemies with the greatest impact, which could lead to a high regulatory release, because heavily infected hosts are less likely to survive introduction and become established. This suggests that regulatory release may be more important than compensatory release, but this remains to be tested.

### CONCLUSION

Studies of NIS that are abundant or dominant (i.e. stage IVb/V invaders *sensu* Colautti & MacIsaac 2004) often reveal that (i) the invader seems to 'perform' better in some way than conspecifics in the native range or congeners in the invaded community, and (ii) one or more natural enemies with known impacts are conspicuously absent from the introduced population. In countless systems, the ERH is inferred from these two points alone without critical

hypothesis testing to confirm that enemy release is responsible. We caution against such uncritical acceptance of the ERH and its use as justification for biocontrol given that (i) all NIS, regardless of impact, are expected to lose some natural enemies during their uptake, transport and introduction, and (ii) the ERH is only one of many hypotheses that can explain the abundance and/or impact of a given invader (EIH, climatic variables, selection for 'invasive' genotypes, human disturbance, etc.)

Rather than discount the effects of some enemies on particular hosts, we assert that the ERH is often accepted without critical examination. Observing that stage IVb/V invaders are less affected by enemies at a biogeographical or community scale is only a first step in confirming the ERH, while enemy exclusion provides more crucial, but still circumstantial evidence. Next, a comparison of the effects of natural vs. native enemies on NIS and native species in the same community would help to differentiate between the ERH and the EIH. Finally, tests of the ERH, as with any competing hypothesis, should not seek to confirm the importance of enemies, but to reject the importance of other factors. Where multiple factors may be responsible, experiments should seek to identify their relative importance. Although this may seem to be a daunting task, we cannot overstate the importance of a more critical approach to the ERH. Such an approach will serve to expand our understanding of the complex processes that likely underlie biological invasions, and improve our ability to manage natural ecosystems.

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