

# A mechanistic framework of enemy release

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## Abstract

The enemy release hypothesis (ERH) is the best-known hypothesis explaining high performance (e.g., rapid population growth) of exotic species. However, the current framing of the ERH does not explicitly link evidence of enemy release with exotic performance. This leads to uncertainty regarding the role of enemy release in biological invasions. Here we demonstrate that the effect of enemy release on exotic performance is the product of three factors: enemy impact, enemy diversity, and host adaptation. These factors are modulated by seven contexts: time since introduction, resource availability, phylogenetic relatedness of exotic and native species, host-enemy asynchronicity, number of introduction events, type of enemy, and strength of growth-defence trade-offs. ERH-focused studies frequently test different factors under different contexts, leading to inconsistent findings, which characterise current evidence for the ERH. For example, over 80% of meta-analyses fail to consider ecological contexts that can modulate study findings; we demonstrate this by re-analysing a recent ERH synthesis. Structuring the ERH around factors and contexts promotes generalisable predictions about when and where exotic species may benefit from enemy release, empowering effective management. Our mechanistic factor-context framework clearly lays out the evidence required to support the ERH, unifies many enemy-related invasion hypotheses and enhances predictive capacity.

## Introduction

The enemy release hypothesis (ERH) is the most well-known hypothesis in invasion biology (Enders *et al.* 2018) and is frequently invoked to explain the success of exotic species in their non-native range (Mitchell & Power 2003; Torchin *et al.* 2003; Connolly *et al.* 2014). According to the ERH, invaders can leave their natural enemies behind when introduced beyond their home range, releasing them from enemy regulation and consequently enabling increased growth, reproduction, or survival in their invaded range (Keane & Crawley 2002; Prior *et al.* 2015; Mlynarek *et al.* 2017). The ERH has an intuitive mechanistic basis, seemingly straightforward tests and direct link with biosecurity and invasive species management. For example, when the ERH holds true, introduced specialist biocontrol agents can be a way of controlling populations of invasive species (Clewley *et al.* 2012; Walsh *et al.* 2023). However, using the ERH to effectively prioritise or guide management requires identifying invasions (or potential future invaders) that have been (or may be) facilitated by enemy release.

Not all exotic species show evidence for the ERH or will benefit from enemy release, but it is currently unclear why some exotics benefit while others do not. For example, Reinhert *et al.* (2003) and te Beest *et al.* (2009) tested belowground enemy release with nearly identical experimental designs (though with different exotic species). The two studies reached opposite conclusions: Reinhert *et al.* (2003) showed that release from belowground pathogens promoted exotic success, while te Beest *et al.* (2009) found no release from soil-borne enemies. The context in which a test is carried out could explain why the occurrence or strength of enemy release can vary between studies (Catford *et al.* 2022; Chiuffo *et al.* 2022). However, relevant contexts are rarely reported in ERH studies, leaving no clear path for synthesising circumstances where enemy release promotes exotic success and potential invasive impacts. It is thus not possible to surmise why the exotic species in the Reinhert *et al.* (2003) study benefitted from enemy release while those examined by te Beest *et al.* (2009) did not. Individual contexts have previously been predicted to be important in determining the

likelihood and strength of enemy release, such as resource levels (Blumenthal 2006), time since introduction (Hawkes 2007) or phylogenetic relatedness of exotic and native species (Mitchell *et al.* 2006). However, an overarching framework for integrating these contexts is absent, hampering effective predictions of when and how enemy release may affect invasion success (see inconsistencies in Table S1).

We propose a new framework for the ERH (Fig. 1). Our framework emphasises exotic performance as the key outcome of the ERH, explicitly linking enemy release with the relative success of exotic populations. We introduce three component factors – enemy diversity, enemy impact, and host adaptation – that influence exotic performance. We then show how effects of these factors are modulated by seven key ecological contexts: (i) time since introduction; (ii) resource availability; (iii) phylogenetic relatedness of exotic and native species; (iv) host-enemy asynchronicity; (v) number of introduction events; (vi) type of enemy; and (vii) the strength of growth-defence trade-offs. In later sections we outline three ways in which current understandings of the ERH are improved by our framework and provide recommendations to guide data collection and documentation when testing the ERH. Other frameworks have been suggested that propose splitting the ERH into sub-hypotheses (e.g. Schulz *et al.* 2019) or splitting the ERH according to how it is tested (e.g. Heger & Jeschke 2014). These frameworks ably highlight the complexity of the ERH. However, they do not attempt to propose the circumstances where one sub-hypothesis should be more likely than another, or why different tests may come to different conclusions. In contrast, by considering how factors interact with specific contexts, we provide a more mechanistic understanding of observed patterns. Our framework aids the prediction of circumstances when enemy release may facilitate invasion and assists effective synthesis of studies testing the ERH.

## Understanding exotic performance requires a mechanistic framework of the ERH

### *Current conception of the ERH: a phenomenological framework*

The ERH was designed as a hypothesis to explain exotic species performance. Here, we take ‘performance’ to mean population growth (following Keane & Crawley 2002), which could be measured by demographic metrics such as population growth rate, or geographic metrics such as rate of spread (Table 1a). In Keane & Crawley’s (2002) seminal paper, the ERH was laid out as a three-step argument:

*Step 1:* Natural enemies are important regulators of species fitness;

*Step 2:* Exotic species experience reduced enemy pressure relative to native species;

*Step 3:* Exotics can capitalise on reduced enemy pressure, resulting in increased competitive ability and population growth.

Keane & Crawley (2002) highlight that the advantages in Steps 2 and 3 are inherently biogeographic (i.e. they relate to the exotic in its invaded vs home range), but they should also lead to advantages relative to the native community (see Box 1).

There are many reasons why performance of exotic species may increase in their invaded range (Díaz *et al.* 2023), not all of which are related to release from enemies (Buckley & Catford 2016). Therefore, support for the ERH requires evidence for both Step 2 (exotics experience reduced enemy pressure) and Step 3 (this reduced enemy pressure leads to increased performance). Whether this reduced enemy pressure is compared to the exotic species in its home range or to native species in the invaded range depends on the goals of the researcher (Box 1). If evidence for these two steps exists, then Step 1 is redundant, as the combination of Steps 2 and 3 implies that enemies were regulating species fitness.

The dominant interpretation of the ERH has focused on the release of enemy pressure itself (i.e. Step 2), with Steps 1 and 3 gaining less attention (Prior *et al.* 2015). Worryingly, evidence that enemies have been lost has been taken as evidence that the ERH is supported (Prior *et al.* 2015). Exotic performance is seldom assessed. For example, of the 85 biogeographic comparisons compiled by Jeschke & Heger (2018) in their review of evidence for the ERH (hi-knowledge.org), just 16 of 85 (19%) considered performance, with 7 of those 16

(44%) supporting the ERH. Further, performance is influenced not just by enemy richness or abundance, but by the effect of those enemies, and other biotic and abiotic factors (Chiufo et al. 2022). With a small number of studies testing Step 3, and no clear framework to integrate the range of potential influences on performance, it is extremely difficult to determine why the ERH has support in some cases but not others.

### *New conception for the ERH: a mechanistic framework*

Our framework emphasises exotic performance as the key outcome of the ERH (Fig. 1a; Table 1a). By making exotic performance the outcome, we re-emphasise the ERH as fundamentally a hypothesis to help predict and explain exotic naturalisation and invasiveness (Box 1). This approach reduces the likelihood that evidence for individual steps will be misconstrued as providing evidence for the whole 3-step hypothesis.

As noted above, we argue that ERH-induced increases in exotic performance are the product of three factors: enemy diversity, enemy impact, and host adaptation (Fig. 1b; Table 1b). Our three-factor framework does not directly map onto the three steps of Keane & Crawley. The steps of Keane & Crawley are phenomenological, while our framework is mechanistic. Broadly, we take their Step 3 (exotic performance) as the overall outcome of the ERH at the top of our framework (Fig. 1a). Keane & Crawley’s Steps 1 and 2 are observations of how enemies affect species, and how they may affect native and exotic species differently. The drivers underlying these observations are captured by our three factors (Fig. 1b). Our framework adds further nuance by highlighting seven contexts that influence the strength of these three factors (Fig. 1c; Table 1c); our contexts have no analogue in the steps of Keane & Crawley.

We believe our mechanistic framework complements and offers advantages over a phenomenological one. Conceptualising the ERH phenomenologically – as with the steps of Keane & Crawley – allows for a valuable documentation of trends and could help prioritise exotic species particularly worthy of further investigation. However, to effectively make predictions, generalise and deal with context, a mechanistic framework is required (Johnston et al. 2019).

In the sections below, we introduce the three factors in detail and describe the data required for robustly testing the ERH. We highlight how context modulates effects of the three factors and discuss the wider benefits of a mechanistic framework for the ERH. As the ERH has been especially studied in plants (Jeschke et al. 2012), examples are drawn from plant invasions, though we posit that our framework applies to any taxonomic group. Given our plant focus, ‘enemies’ refers to herbivores, parasites and pathogens of plants in this paper. We use the community comparison as our basis (Box 1), and so all discussion and figures focus on the differences between exotic and native species in the invaded range. Nevertheless, the framework could equally be applied to biogeographic comparisons (comparing exotic species in their home vs invaded ranges), and the principles that we discuss should hold for either comparison. By synthesising the factors and contexts of the ERH that influence exotic performance (Fig. 1b, c), we believe that our framework will provide insight into why some exotic species benefit from enemy release while others do not.

### **Three factors influence exotic performance**

Below we introduce the three component factors that collectively influence exotic performance in the context of the ERH. We first define each of the factors and outline their importance, before specifying ways in which they can be measured. Not every aspect of our framework will be applicable in every case. However, the framework provides a general outline for the way the ERH may apply to invasion, and what factors determine its role in exotic establishment, naturalisation, and invasiveness.

#### *Factor 1: Enemy Impact*

Enemy impact is the negative *per capita* effect that an enemy has on a plant or plant population (Fig. 1b, orange box; Table 1b). This factor explicitly considers how a given enemy affects performance of individual plants or plant populations, including their likelihood of survival, growth and reproduction. This factor acknowledges that the same enemy species can have different effects on plants depending on whether they are growing in the species’ native or invaded range.

Enemy damage is typically used to assess impact (e.g. % of leaves eaten). However, it would ideally be measured in terms of individual plant performance (Chun *et al.* 2010) and population vital rates (survival, growth or reproduction), which ultimately determine exotic success (Ramula *et al.* 2008) (Table 1b). Although extent of enemy damage likely correlates with vital rates (e.g. more damage leads to a greater reduction in growth rate), the shapes of these relationships are largely unknown and reductions in one vital rate can be compensated for by increases in another (Livingstone *et al.* 2020). We accordingly emphasise that damage provides only an indirect measure of enemy impact. Enemy impact is arguably the most difficult of the three factors to reliably measure, which likely explains why only half the studies of the ERH provide direct estimates of enemy impact (Table S2). Future studies on enemy impact are important to comprehensively quantify the occurrence and strength of enemy release.

### *Factor 2: Enemy Diversity*

Changes in enemy diversity accounts for the loss (or gain) of enemy species upon invasion, as well as changes in enemy abundances (Fig. 1b, green box; Table 1b). Higher reductions in enemy diversity have been shown to increase geographic extent of exotic plants in the invaded range (Mitchell & Power 2003; Hawkes 2007) (but see van Kleunen & Fischer 2009). Identifying which exotics have the potential to experience large reductions in enemy diversity could therefore inform predictions about invasion risk.

Enemy diversity can be measured with enemy abundance (the prevalence of a given enemy species, or the number of individuals of that enemy per host) and richness (the total number of enemy species per host) (Table 1b). Together, richness and abundance determine the total enemy load faced by an exotic plant. Both are important to measure where possible: different enemy species may target different tissues and cause different fitness costs, while enemy abundances will determine the extent of those fitness costs.

### *Factor 3: Host Adaptation*

Host adaptation is the directional investment in defence or growth (Fig. 1b, blue box; Table 1b). Enemy release can drive selection by reducing the need for costly defences (Cipollini *et al.* 2014). Selection can lead to an evolutionary advantage for exotics as they can invest in less expensive generalist defences or reduce the absolute quantity of defences, freeing up resources for growth instead (Blossey & Notzold 1995; Joshi & Vrieling 2005). Host adaptation can also reflect phenotypic changes over the lifetime of a plant, mediated by features such as the jasmonate pathway (Howe & Jander 2008). As the focus of our synthesis is the ERH, we only consider adaptation caused by changes in enemy impact and diversity (see arrows in Fig. 1b).

Host adaptation is typically tested in common gardens, comparing the growth, defence, or tolerance of home and invaded populations of exotic species (Rotter & Holeski 2018) (Table 1b). To support the ERH, these measurements also need to be accompanied by evidence of changes in enemy diversity or impact, as there are many reasons beyond enemy release why growth and defence may change in an invaded range (Felker-Quinn *et al.* 2013).

### *Testing the ERH with our mechanistic framework*

Using our framework, robust tests of the ERH require either: (a) data about population-level exotic performance and data for at least one of the factors that influence exotic performance; or (b) data for at least two of the factors that influence exotic performance. Approach (a) would provide the most rigorous test of the ERH, but approach (b) is more feasible.

The ERH was designed to explain population-level performance, so metrics of performance are the gold standard (approach a). Performance measures must be coupled with data on one or more of the three factors to ensure that performance is linked with enemy release; exotic performance could increase for reasons unrelated to enemies (Felker-Quinn *et al.* 2013), so it is important to discount that. Measuring population-level performance is difficult though, so most tests of the ERH will likely use approach (b). Of the two requisite factors that need to be measured in approach (b), enemy diversity and enemy impact seem the most beneficial and feasible combination. Host adaptation is difficult to measure, and the degree of host

adaptation from enemy release will be driven by changes in enemy diversity and impact (Fig. 1b), so it makes most sense to focus on those two factors.

Using approach (b), where both enemy diversity and impact are measured, is important because evidence for one factor alone does not robustly test the ERH. We demonstrate this in Figure 2. Two exotic populations (A & C) experience identical levels of enemy pressure, and both are under higher enemy pressure than natives (Fig. 2). However, this identical enemy pressure between populations A and C would not be detected by looking at enemy diversity alone (Figs. 2a *vs.* 2b), nor by looking at the impact of certain enemies alone (Figs. 2c *vs.* 2d). In contrast, exotic population B experiences lower enemy pressure than co-occurring native species, and lower enemy pressure than populations A and C. However, it would be assumed to be identical to population A if only diversity was studied, or identical to population C if only impact was studied. Studies that assess total enemy diversity *and* estimate their impact on host individuals are rare (Table S2). In particular, studies on exotic impact are underrepresented in the ERH literature (Prior *et al.* 2015). The combination of enemy diversity and the impact of those enemies (enemy pressure) determines relative release for exotics (Fig. 2) and the likelihood and strength of exotic host adaptation (Fig. 1b). Appropriately measuring total enemy pressure is therefore critical to testing the ERH.

We suggest that studies of performance under field conditions are particularly valuable. Field conditions allow an assessment of native and exotic vital rates in the context of their complete enemy suites. These enemy suites can be indirectly assessed through a metric such as total damage at a leaf- or plant-level (Table 1b), as directly determining total enemy diversity is likely difficult. Field studies therefore allow for the interaction of multiple ERH factors to be seen. Further, relevant trade-offs in invader performance (i.e., growth and defence) are often only expressed under interspecific competition (Cipollini *et al.* 2014; de Vries *et al.* 2019), and competition can change a plant’s response to enemies (Honor & Colautti 2020). More studies of enemy release should take place in intact communities, providing further insight into the ERH under more realistic field scenarios.

### Seven contexts can alter the influence of each ERH factor

Ecological context modulates the occurrence and strength of the component factors contributing to the ERH (Table 1c; Figs. 1c, 3). These seven contexts contribute to inconsistencies between studies when not accounted for (Box 2; Fig. 4). Once accounted for, apparent ‘inconsistencies’ can become explicable by ecological context (Catford *et al.* 2022), enabling predictions on how future invaders experiencing similar contexts may or may not benefit from enemy release. For brevity, we discuss only three of the seven contexts in detail: time since introduction; relative resource availability in species’ home and invaded ranges; phylogenetic relatedness of native and exotic plants. In each case, we describe how the context influences enemy impact, enemy diversity and host adaptation, before discussing appropriate ways to measure the context. We then briefly introduce the four other contexts (temporal and spatial asynchronicity; number of introduction events; type of enemy; strength of growth-defence trade-offs), highlighting the factors they especially influence. These seven contexts are key moderators of the ERH based on our review of the literature, but this list is not necessarily exhaustive.

#### *Time since introduction*

*Effect on enemy impact:* Immediately after arrival in a new range, exotic species may experience a lower enemy impact relative to natives (Fig. 3a). This lower impact is because generalist enemies in the invaded range can be less effective at exploiting exotic species (e.g. Beaulieu *et al.* 2019). Lower impact on exotics will enhance performance relative to co-occurring native species over short time scales, even if enemy richness is the same for native and exotic populations. Through time, this benefit to exotics can erode as generalists in the new range evolve to target the exotic more efficiently (Carroll *et al.* 2005) and thus increase their impact on the exotic (Fig. 3a). Alternatively, enemy impact on exotics could also further reduce with time, as exotics develop new defences against generalists (Müller-Schärer *et al.* 2004).

*Effect on enemy diversity:* Invaders lose and (re)gain enemies through time (Fig. 3b). There should be an immediate reduction in specialist enemies upon introduction, as specialists that only target the invasive plant

are absent from the invaded range (Keane & Crawley 2002). The diversity of local generalist enemies could also be initially low on the exotic, as they may be poorly adapted or unused to targeting it (Bezemer *et al.* 2014). Over time there is typically a steady accumulation of generalists as they, for example, become familiar with the chemical signature of the plant (Novotony *et al.* 2003; Iqbalet *al.* 2021).

*Effect on host adaptation:* Host adaption caused by enemy release is a phenotypic- or genetic-based response to reduced enemy impact or diversity (Inderjit *et al.* 2005; Medina-Villar *et al.*2022). How quickly host adaptation occurs will depend on the generation time of the host plant in question, the strength of selection (the degree to which enemy pressure is reduced, Fig. 2) and other contexts that affect investment into growth and defence, such as resource availability (see Context ii below; Fig. 3f).

*Measurement:* Time since introduction should be measured in the number of generations of the exotic species, rather than in an absolute measure such as years since introduction. 150 years means something very different to an annual daisy than it does to an oak tree. Further, ‘generations since introduction’ should be considered at a population level (Table 1c). An exotic species may have multiple distinct populations in the invaded range, that have been established for different lengths of time. These populations could show different support for the ERH, especially if they are isolated (Fig. 4).

#### *Relative resource availability in home and invaded range*

*Effect on enemy impact :* Relative resource availability refers to difference in resource levels between the home and invaded range of an exotic population. The impact of enemies is strongly correlated with the availability of resources. Plants in high-resource environments tend to be more resource-acquisitive, a characteristic of invasive species (van Kleunen *et al.* 2010a, b). High resource availability encourages investment in growth rather than defence, so herbivores perform better on resource-acquisitive plants (Morrow *et al.* 2022). Therefore, if exotics come from a high-resource environment relative to the invaded environment, enemy impact is likely to be higher on the exotic than co-occurring native species, as exotics are more palatable than natives (Fig. 3d, red line). Contrastingly, species from low-resource environments show higher investment in defence, as tissue is less easily replaced and more valuable (Endara & Coley 2011). Therefore, enemy impact relative to natives is likely to be lower on exotics from resource-poor home ranges (Fig. 3d, blue line). In the absence of host evolution or phenotypic adaptation where a plant upregulates growth and downregulates defence (but see Fig. 3f), these differences should persist through time.

*Effect on enemy diversity:* High resource availability encourages poorly defended, nutrient-rich plants, promoting a high diversity of natural enemies (Blumenthal 2006; Allen *et al.* 2017). Exotics coming from resource-rich environments have more enemies to lose (Fig. 3e, red line) and are particularly likely to benefit from enemy release (the resource-ERH: Blumenthal 2006; Blumenthal *et al.* . 2009). However, exotics from resource-rich environments also accumulate enemies at a faster rate than exotics from resource-poor environments because their poorly defended and nutrient-rich tissues are more attractive to generalist enemies (Ebeling *et al.* 2021; Morrow *et al.*2022) (Fig. 3e).

*Effect on host adaptation :* Resource availability can alter trade-offs between growth and reproduction (Agrawal 2020). Exotics coming from low-resource environments likely have a lower growth-defence ratio than co-occurring natives (Endara & Coley 2011) (Fig. 3f, blue line). If they are released from enemies and have more resources available, exotic plants will evolve to invest more in growth than defence (Coverdale & Agrawal 2022). This adaptation can happen in as little as 150 growing seasons (Wolfe *et al.* 2004) and underpins the well-known evolution of increased competitive ability (EICA) hypothesis (Blossey & Notzold 1995). Alternatively, if exotics experience reduced resource availability in their invaded range and can no longer use growth to compensate for high enemy damage, exotics from high-resource environments may evolve to invest more in defence and less in growth (Fig. 3f, red line).

*Measurement.* We define relative resource availability as the difference in resource availability between the home and invaded range of an exotic population (Table 1c). While absolute resource availability is important, there is evidence for fine-scale responses to resources even within low-resource populations (Hahn *et al.* 2021), suggesting the potential for exotic adaptation even if they are moving between two sites with low levels of

absolute resource availability. Therefore, we present the difference in resources between the home and invaded range as the key metric of this context.

### *Phylogenetic relatedness of exotic and native species*

*Effect on enemy impact:* Phylogenetic relatedness represents the evolutionary distance between exotic and co-occurring native plants. Exotics that are phylogenetically close to the native community usually show lower reductions in enemy impact (Fig. 3g, blue line). This is because specialist enemies in the invaded range can more effectively exploit closely related exotics (Castells *et al.* 2013; Harvey *et al.* 2013; Aldorfová *et al.* 2020). Distantly related exotics have novel defences to which enemies in the invaded range are naïve (Cappuccino & Carpenter 2005). Enemy impact will then increase through time, as generalists in the invaded range evolve to target exotics (Carroll *et al.* 2005), as noted above. However, enemy impact can saturate at a lower level for distantly related exotics even over prolonged time scales (Beaulieu *et al.* 2019; Liu *et al.* 2023) (Fig. 3g, blue and black lines). While Fig. 3g represents our general prediction, we note the opposite can also be true. Phylogenetically close exotics may possess defences that are well adapted to the herbivores in an invaded range (Ricciardi & Ward 2006; Morrison & Hay 2011).

*Effect on enemy diversity:* Distantly related exotics typically experience greater reductions in enemy diversity (Fig. 3h, blue line), as the ability for enemies to switch from co-occurring natives is lower (Ebeling *et al.* 2008). In contrast, exotics with congeners in the invaded range tend to accumulate enemies quickly (Mitchell *et al.* 2006; Fig. 3h, black line), or are targeted by enemies to such an extent they show no evidence for release at all (Iverson *et al.* 2023; Fig. 3h, red line). Enemy diversity will generally saturate until exotic and native plants have similar enemy numbers (Fig. 3h), though the rate at which this occurs is contested (Hawkes 2007; Mitchell *et al.* 2010).

*Effect on host adaptation:* Distantly related exotics experience greater reductions in enemy pressure (because of lower enemy impact and diversity) than exotics that are closely related to co-occurring natives. Distantly related exotics may therefore adapt to invest less in defence and more in growth, evolving more competitive phenotypes that increase invasiveness (Fig. 3i).

*Measurement:* Phylogenetic relatedness can be measured in various ways (Pinto-Ledezma *et al.* 2020), but we suggest that evolutionary distance to the most closely related co-occurring native species (“nearest neighbour”) is the most relevant metric (Table 1c). An exotic that is distantly related on average to the community but with one very close native relative is more likely to be immediately affected by that native’s specialists than an exotic with intermediate average relatedness and no close relative. However, mean relatedness might also be important when considering overall native-exotic competition and how this interacts with release, and it would also be important to consider weighting the abundance or frequency of potential “nearest neighbour/s” as has been done with functional traits (Gallien *et al.* 2014; Catford *et al.* 2019). We do not explore these nuances further here but suggest that aspect of the ERH warrants further development. We also note that phylogenetic relatedness may not always map on to phenotypic similarity or result in closely related specialist enemies. Considering shared traits (which are not necessarily phylogenetically conserved) may also be valuable (Cadotte *et al.* 2017).

### *Temporal and spatial asynchronicity between plant and enemy populations*

Temporal or spatial asynchronicity between exotic plants and their potential enemies affects the diversity of enemies that accumulate (Gsell *et al.* 2023). Temporally, exotic species can benefit from ‘invasion windows’ if generalist enemies are less abundant in a given season (Agrawal *et al.* 2005; Geppert *et al.* 2021). Within a single season, exotics can flower at different times to natives and so avoid periods of intensive native herbivore activity (Fan *et al.* 2016), leading to higher reproductive success than natives the following season (García & Ehrlén 2002). Spatially, there may be microhabitats or microclimates in the invaded range where disease or herbivore pressure is lower (Parker & Gilbert 2007; Halliday *et al.* 2021). This is because the niche breadth of exotic plants can exceed that of generalist enemies, facilitating increased exotic survival in enemy-free areas (Luet *et al.* 2013; Kambo & Kotanen 2014). We predict that enemy diversity will generally decline as exotic plants and generalist enemies become more asynchronous.

### *Number of introduction events*

The number of introduction events affects enemy diversity (over ecological time scales), and host adaptation (over evolutionary time scales). Ecologically, an increasing number of introduction events increases the likelihood of co-introducing specialist enemies from the home range, eroding the initial benefit of lowered enemy diversity (Mitchell & Power 2003; Mitchell *et al.* 2010; Schultheis *et al.* 2015; Warren & Bradford 2021). This effect is not captured by simply accounting for time since first introduction. Evolutionarily, the number of introduction events alters the genetic potential for host adaptation. Founder effects could limit adaptive potential (Felker-Quinn *et al.* 2013; Harvey *et al.* 2013; Smith *et al.* 2020) or promote rapid divergence from the home range (Bossdorf *et al.* 2005), both of which are ameliorated by greater numbers of introduction events. Therefore, considering the number of introduction events is crucial when testing the ERH, independently of the time since (first) introduction.

### *Type of enemy*

The likelihood and impact of losing or gaining an enemy will vary depending on enemy type. The distinction between specialists and generalists is fundamental when considering changes in enemy diversity. Specialists should be lost to a much greater degree than generalists on movement to a new range (Joshi & Vrieling 2005; Zhang *et al.* 2018) (Fig. 3b). The likelihood of losing specialists partly depends on functional attributes of the specialist; for example, plants are more likely to lose insect herbivores than fungal pathogens or viruses that can co-invade with exotic seeds (Hawkes 2007; Parker & Gilbert 2007). The type and generation times of enemies also affects their impacts. For example, generalist mammalian herbivores provide the strongest biotic resistance to exotic plant spread compared to other types of enemy through their consumption of whole plants (Levine *et al.* 2004). Enemies with fast generation times (e.g. viruses) can adapt faster to an exotic, and thus exert a larger impact more quickly. Because different types of enemy may be lost and gained at different rates, and have different impacts through time, reporting trends for a limited number of enemies may not fully capture the degree of enemy release (Fig. 2).

### *Presence and strength of trade-offs*

The presence and strength of growth-defence trade-offs affect the likelihood and strength of host adaptation mediated by enemy release. Although there is evidence for trade-offs *between* species (i.e. one species has high defence and low growth, while another species has the opposite; Lind *et al.* 2013; Rotter & Holeski 2018; Heckman *et al.* 2019) (but see Chauvin *et al.* 2018; Hinman *et al.* 2019), evidence for within-species trade-offs is weaker (Heckman *et al.* 2019; Hahn *et al.* 2021) yet this is more pertinent as host adaptation requires within-species variation. However, specific plant organs can show trade-offs related to defence and growth (Agrawal *et al.* 2012; Medina-Villar *et al.* 2022), and there is evidence that some species can adaptively lower defence and increase growth in response to lower enemy pressure (Wolfe *et al.* 2004; Coverdale & Agrawal 2022). Evolutionary changes in growth and defence because of enemy release should only benefit exotics that show strong growth-defence trade-offs. These clear trade-offs may be relatively uncommon, as plant resource management strategies are complex so a single trade-off axis is unlikely (Lau & Schultheis 2015; Agrawal 2020).

## **A mechanistic framework highlights research gaps and reasons for inconsistencies**

### *Assessment of factors and contexts in previous ERH syntheses*

Categorising meta-analyses by the contexts and factors they examine reveals reasons for previous inconsistencies (Table S1). We examined 16 ERH meta-analyses and meta-syntheses to ascertain whether existing syntheses capture the component factors of the ERH and the extent to which they consider context. Our results revealed that individual syntheses provide only partial tests of the ERH, and many cannot be directly compared (Fig. 5; Table S1). For example, Mitchell & Power (2003) tested how enemy diversity changes after invasion, using the metric of species richness, whereas González-Browne *et al.* (2016) tested whether enemy impact varies between exotic and native plants, using the metric of reproductive potential (Fig. 5).

Both meta-analyses provide valuable information but analyse quite different things. Several meta-analyses combine different metrics into a single effect size (and, in two cases, different factors into a single effect size: Lamarque *et al.* 2011; Felker-Quinn *et al.* 2013; Fig. 5), likely increasing uncertainty and variance around that effect size due to underlying methodological differences, which can result in apparent context dependence (Catford *et al.* 2022).

Ecological context seems to have been under-explored in the 16 meta-analyses (Fig. 5). Not all contexts are relevant for all factors, and some meta-analyses implicitly account for certain contexts in their design by, for example, accounting for resource availability by only including common garden comparisons. However, explicit tests were included in just 17 of 88 cases (19%) where context could affect meta-analysis results (Fig. 5). In 15 of those 17 cases (88%), they were found to be a significant moderator of effect sizes (Fig. 5). Ecological context therefore has huge potential to explain variation both within and between meta-analyses yet is rarely accounted for.

#### *Importance of accounting for context: a re-analysis as proof of concept*

To illustrate the importance of considering context when testing the ERH, we re-analysed a recent synthesis (Xu *et al.* 2021). Xu *et al.* used the dataset of Turcotte *et al.* (2014), which reports annual herbivory damage for a range of plant species. Xu *et al.* categorised each plant species in the dataset as ‘exotic’ or ‘native’ and compared their damage rates, accounting for plant growth form and latitude of each observation. We repeated their analysis, but also included information about enemy type, which was available in Turcotte *et al.* (2014) (context = type of enemy). See Supplementary Analysis for details.

We found that damage rates were generally higher on native than exotic species ( $F_{1,1660}=9.12$ ,  $p=0.003$ , Fig. 6a;  $N=137$  [exotics],  $N=1527$  [natives]), consistent with the conclusion of Xu *et al.* (2021). However, when we included the type of enemy as a random variable, we found no difference in damage between native and exotic species ( $\chi^2_1=0.13$ ,  $p=0.719$ , Fig. 6b). We suggest that these distinct findings can be largely attributed to vertebrate impacts. Effects of vertebrates were only recorded on natives (Fig. 6b;  $N=0$  [exotics],  $N=76$  [natives]), and as vertebrates cause higher mean damage than other types of enemy in the database, average damage on natives was disproportionately higher than damage on exotics. In this case study, unless type of enemy is explicitly accounted for, it can erroneously appear that overall damage is lower on exotics, as found in Xu *et al.* (2021)’s study. In fact, if only damage from insects is examined ( $N=84$  [exotics],  $N=1341$  [natives]), damage appears higher on exotics than natives (Fig. 6b), contradicting the ERH and the conclusion of Xu *et al.* (2021). This brief example demonstrates how evidence for the ERH is contingent on context, and failure to account for context affects conclusions. It also highlights that examining context can reveal data gaps (here, vertebrate herbivory on exotic plants) that should be prioritised in future work.

#### **Benefits of a mechanistic framework for the ERH**

We describe three ways that our proposed framework can increase understanding of the ERH, including predictive understanding.

##### *Explain inconsistencies within and between studies*

Context increases variation in evidence for the ERH, both within and between studies. If context is appropriately reported, then this variation has the potential to be informative, as the above reanalysis example shows (Fig. 6). As another example, by explicitly considering the local environment and resource availability of populations of *Clidemia hirta*, Dewalt *et al.* (2004) found evidence that populations in its invaded Hawaiian range had experienced enemy release, but only when compared with understory sites in its home range. This was likely because open sites in its home range provided enough resources (light) for *C. hirta* to compensate for enemy damage (DeWalt *et al.* 2004). Due to this variation, Jeschke & Heger (2018) list this study’s evidence for the ERH as “undecided”, as the current conception of the ERH is not nuanced enough to capture these sorts of dynamics. In contrast, our framework emphasises that reporting key ecological contexts is vital for contextualising the results of individual studies and provides a checklist of these contexts. The Dewalt *et al.* (2004) example highlights apparent inconsistencies within the *same* study system

but shows that these inconsistencies and ‘undecided’ nature of the results are explicable when ecological context (resource availability) is considered (Box 2; Fig. 4). Not all studies can be carried out on large scales encompassing multiple contexts (or broad ranges of a single context), nor is it easy to study all three factors that underpin the ERH (Fig. 1b). However, the factors and contexts pertinent to each study must be considered and reported as explicitly as possible (Catford *et al.* 2022). The near-absence of several contexts from ERH meta-analyses to date (i.e. time since introduction, asynchronicities, number of introductions; Fig. 6) would at least partly reflect lack of information in the primary literature.

### *Reduce redundancy in invasion hypotheses*

At least eight enemy-related hypotheses have been proposed in invasion ecology (Table 2; see also Catford *et al.* 2009). Our framework effectively integrates these hypotheses by showing that they share the same set of factors and contexts, and represent variations of the same underlying concepts (Jeschke 2014; Enders *et al.* 2018) (Table 2). For example, ‘enemy release’ and ‘enemy reduction’ functionally represent the same process, just to a different degree. If the set of factors or conditions underlying different hypotheses are not integrated, we are left with a “heady mix of acronyms” (Evans 2008) and a suite of loosely related hypotheses with little way of predicting when one is more likely than another. Highlighting possible conditions that lead to each hypothesis (Table 2) should facilitate better predictions of when, where and how exotics may benefit from the ERH.

### *Identify gaps in meta-analyses and meta-syntheses and reduce unexplained variation*

The power of meta-analyses and -syntheses can be improved by explicitly incorporating the factors and contexts of the ERH. A meta-analysis’ power is hampered when spurious variation is introduced, leading to inconsistencies between different meta-analyses (Table S1). A key goal of meta-analyses is to attribute this variation to meaningful predictors (Spake *et al.* 2022). To comprehensively test the ERH, we suggest that a meta-analysis of the ERH should consider evidence of one metric for at least two of the three factors (Table 1b) and report them as discrete effect sizes. Meta-analyses that comprehensively test one factor are still valuable, but they should be reported as *partial* examinations of the ERH, and should not combine results from studies that focus on different factors or metrics into a single effect size. When information is available, contexts should be included as moderator variables to better reveal generalities (i.e., parameterising Fig. 3) and reduce ‘unexplained’ variance (Fig. 6), both within and between meta-analyses. We refer readers to a rich literature that provides specific guidance on effective strategies and approaches to account for within- and between-study variance and for incorporating context into studies, including meta-analysis and meta-synthesis (e.g. Koricheva & Gurevitch 2014; Doncaster & Spake 2018; Catford *et al.* 2022; Spake *et al.* 2022, 2023).

## **Conclusion**

In this paper, we have demonstrated that contradictions in evidence for the ERH exist both within and between studies (Table S1), but that these apparent inconsistencies can be the result of explicable factors and contexts, rather than unpredictable variation (Fig. 4; Box 2). We posit that greater acknowledgement of the factors and contexts of the ERH will reduce apparent contradictions, reconcile apparently contrasting enemy-related invasion hypotheses and increase our ability to determine when and how enemy release contributes to plant invasions (Figs. 3, 4; Table 2).

It is unlikely that the ERH is universally true or false, but rather that enemy release is important in some circumstances and not others. Our framework provides a way to predict what those circumstances will be (Fig. 1, Table 1). As few studies have explicitly considered exotic performance, we cannot reliably say whether the ERH is a rare or prevalent mechanism for successful invasion. Outlining the core set of factors and contexts that can lead to a wide array of observed patterns in exotic performance enables greater theoretical clarity in invasion ecology. This should improve the quality of ERH studies and comparisons between them, guiding future research into the role of enemy release in invasions.

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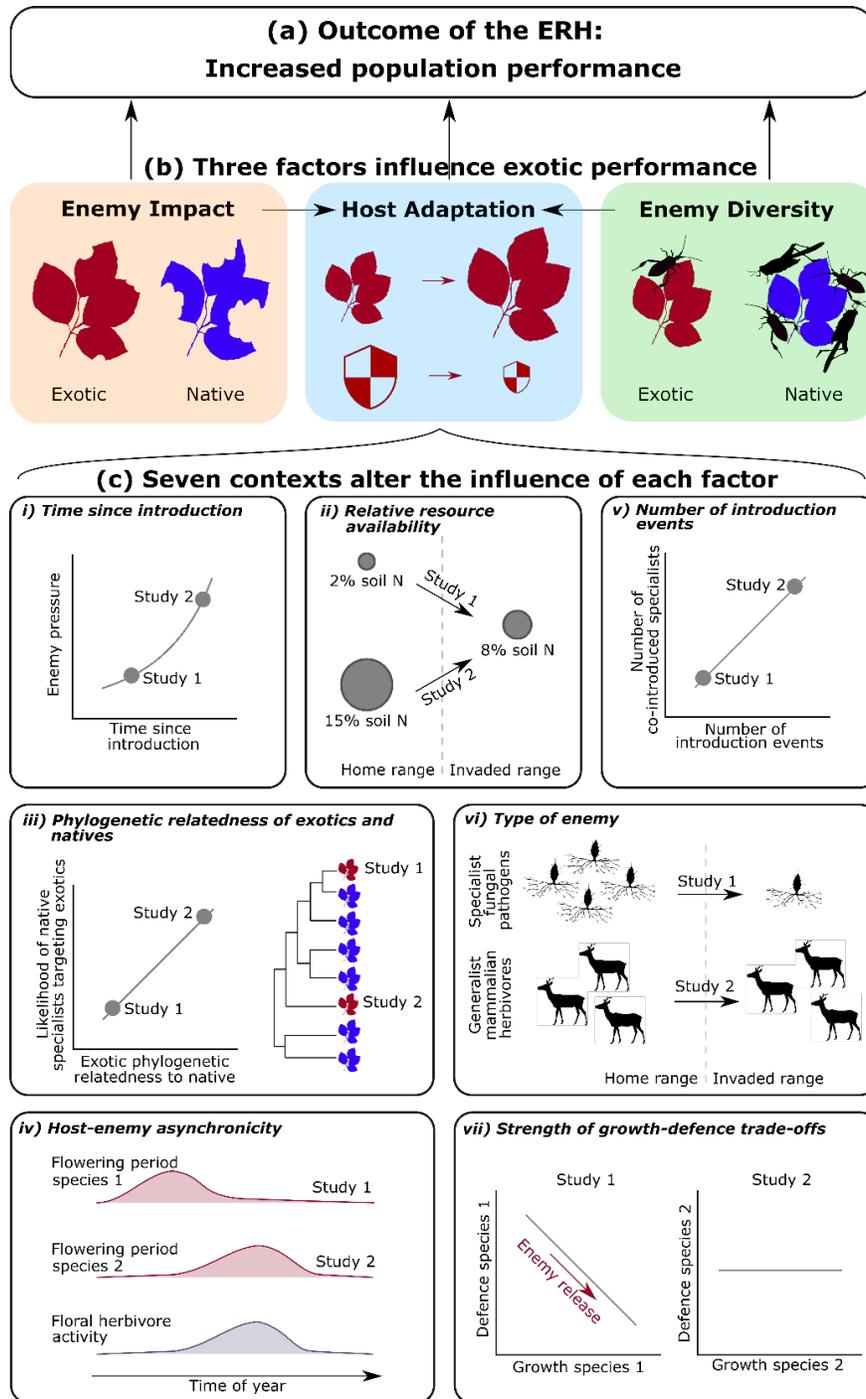
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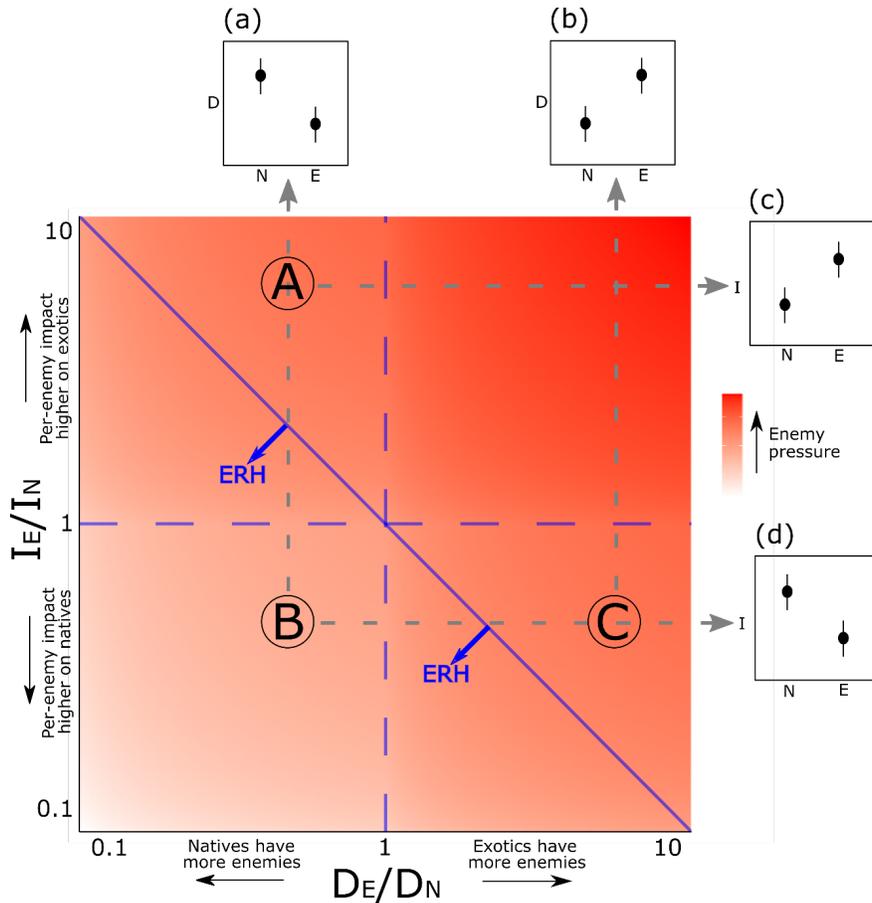
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## Figures and Figure legends

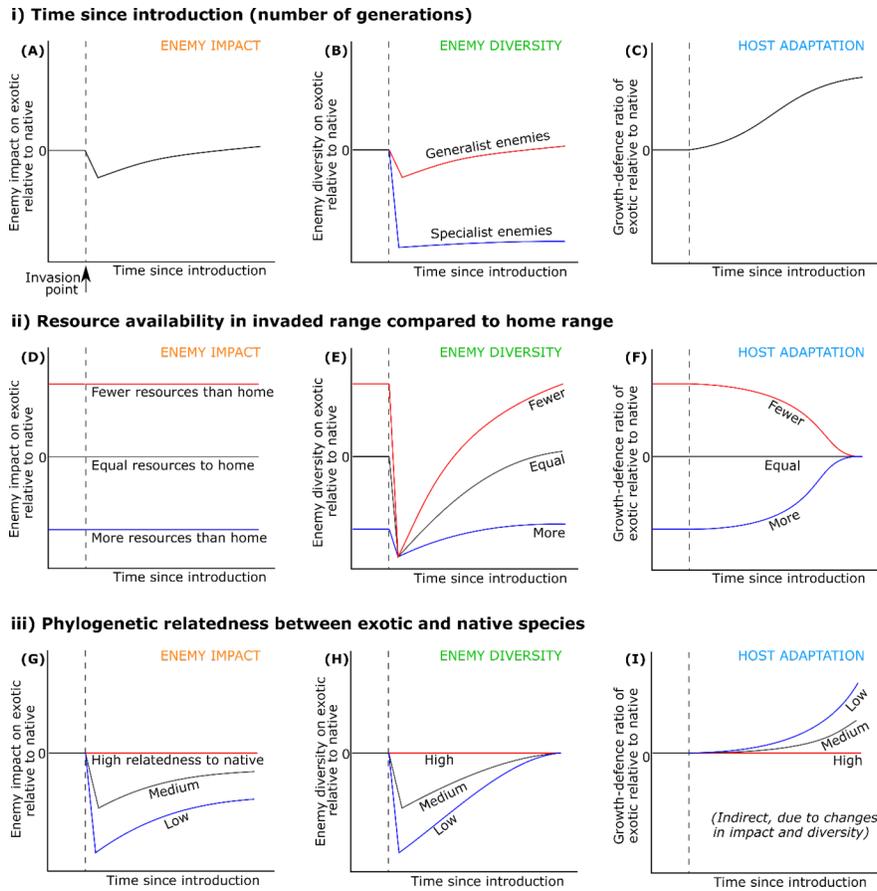


**Figure 1:** The enemy release hypothesis as an explanation for (a) increased exotic performance is the product of (b) three factors, which are modulated by (c) seven contexts. Three factors: 1) the difference in per-capita effect of enemies (compare damage on leaves); 2) the difference in enemy diversity, which incorporates enemy abundance (number of individuals) and richness (number of species); and 3) host adaptation, which involves changes in exotic growth (plant size) and defence (shield size). Changes in any one factor will benefit the exotic, assuming the other factors are held constant (e.g. reductions in enemy impact will lead to release,

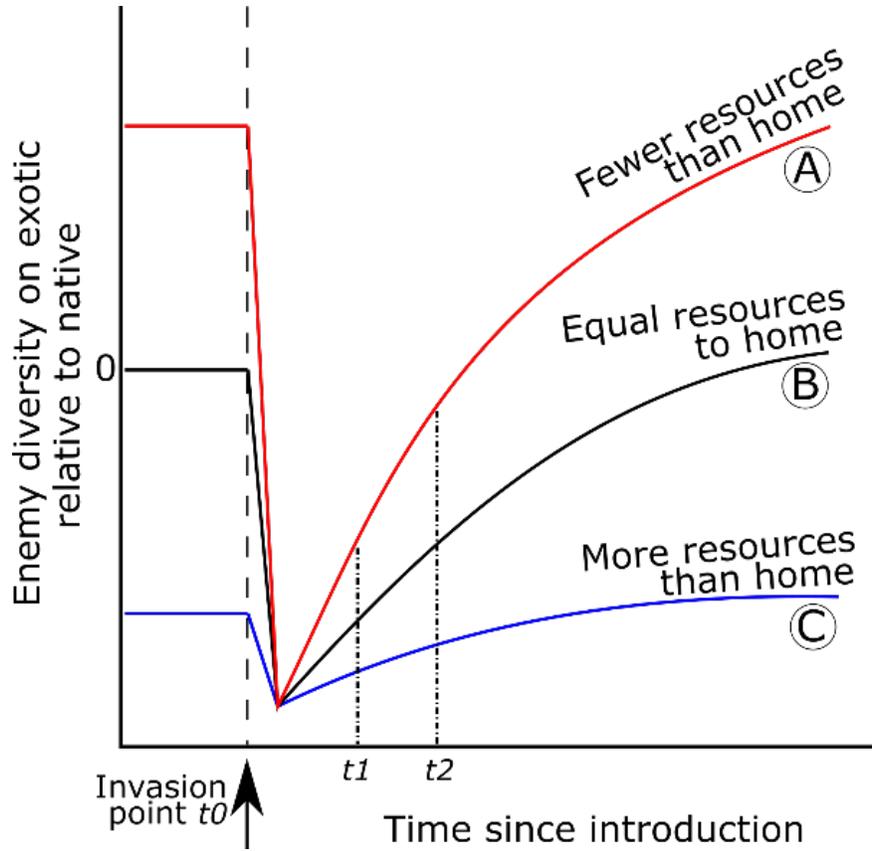
even if enemy diversity remains unchanged). The influence of these factors and our ability to detect them changes with seven contexts. Each panel in (c) shows two hypothetical studies that examine different levels of a given context, and so would give contrasting support for the ERH. While context dependence is visualised in terms of two different exotic species, the contexts are equally applicable to a single exotic species arriving to different native communities, or different source populations of a single exotic species invading the same native community. All images in public domain (phylopic.org) except shield (Akash Yadav, Noun Project).



**Figure 2 :** Three exotic E populations (A, B, C) experience different levels of enemy pressure relative to native species (N), depending on the product (enemy pressure  $P = D \cdot I$ ) of proportional differences in both enemy diversity ( $D = D_E/D_N$ , and  $I = I_E/I_N$ ).  $P > 1$  indicate enemies have a stronger negative effect on exotic species,  $P < 1$  indicate enemies have a stronger negative effect on natives. Dashed grey lines from each population link to exterior squares that show how those populations would look if only a single process was studied (diversity, a and b; or impact of a few select enemies, c and d). Dashed blue lines indicate equal enemy diversity (richness, abundance or their combination) between natives and exotics (vertical), and equal per-capita impact of those enemies (horizontal). The solid blue line indicates where enemies affect the performance of native and exotic species equally, with support for the ERH below this line. Axes are logged to facilitate symmetrical interpretation (i.e. on the x-axis, 0.1 corresponds to natives having ten times as many enemies as exotics; 10 corresponds to aliens having ten times as many enemies as natives).



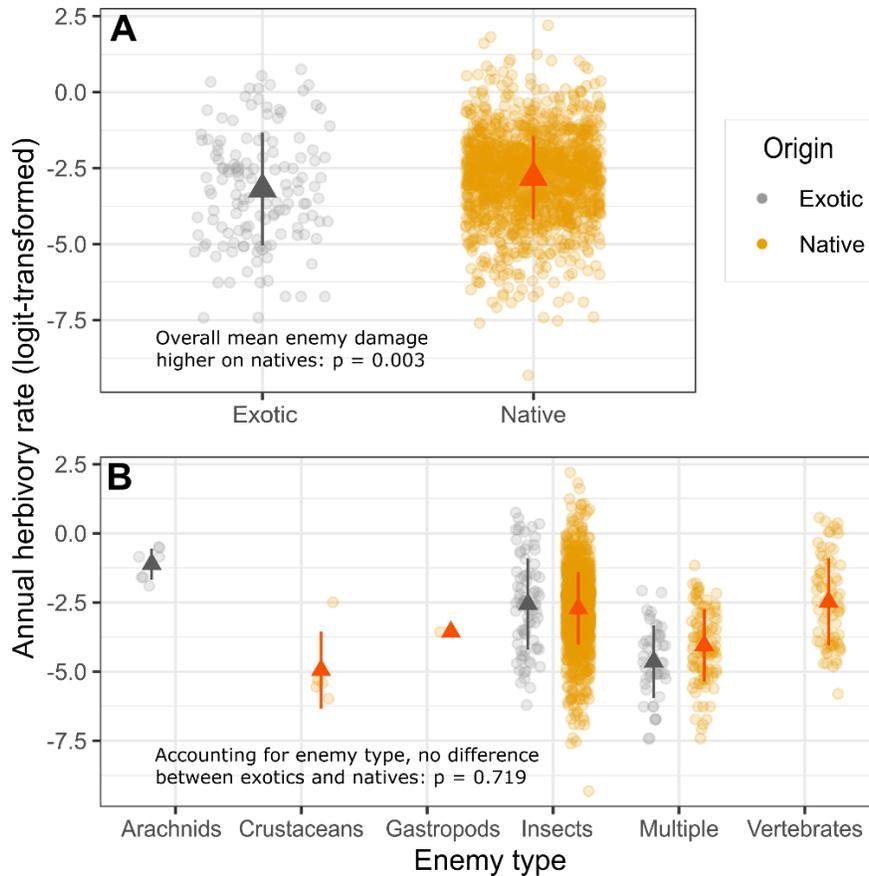
**Figure 3** : Ecological context affects the factors of the ERH. Three of the seven contexts (time, A-C; relative resource availability, D-F; phylogenetic relatedness, G-I) are shown for brevity, and how these contexts affect the processes of changing enemy impact (A, D, G), changing enemy diversity (B, E, H), and host adaptation (C, F, I). Trajectories are drawn assuming that the other two processes are held constant, though there may be complex feedbacks between them. For example, evolutionary changes to the growth-defence trade-off under different resource regimes will alter the relative impact of enemies through time. These are predictions but other trajectories are possible: we aim to demonstrate generally how context interacts with factors to drive the likelihood of the ERH occurring, and its strength.



**Figure 4** : Three hypothetical exotic species or populations (A, B, C) that occur in different contexts (Context ii: relative resource availability) and that are studied in terms of their enemy diversity at different times ( $t_1$  vs.  $t_2$ ) produce a wide range of possible interpretations (Box 2). Details as per Fig. 3e: exotics that come from high-resource ranges (population A, red line) likely lose a high number of enemies but also accumulate them quickly, while exotics from low-resource ranges (population C, blue line) both lose and accumulate a lower diversity of enemies. Population B is intermediate.



**Figure 5:** Summary of meta-analyses and meta-syntheses that test the ERH or related sub-hypotheses. ‘Scope of meta-analyses’: Each coloured box represents an effect size and is positioned to reflect what factor of the ERH the meta-analysis tested, and what metric of that factor it examined. Multiple boxes per row indicate that the meta-analysis calculated different effect sizes for different metrics and/or factors – long boxes spanning multiple metrics indicate a single effect size that combined all those metrics. ‘Contexts’: Each box indicates whether the meta-analyses accounted for the seven key contexts of the ERH. Codes in boxes are as follows: Grey shading, the effect of that context was tested for; red star, the context was found to be significant; solid diagonal line, the context was controlled for in meta-analysis design (e.g. accounting for resource availability by only including common garden studies); dashed diagonal line, the context was controlled for in design for the process of host adaptation only; NA, the context is not applicable for the process that the meta-analysis tested.



**Figure 6** : A re-analysis of Xu *et al.* (2021), incorporating additional information about type of enemy (Context vi). Dots are individual observations; triangles and error bars represent mean  $\pm$  1 standard deviation. (A) Analysis of annual herbivory rates of exotic and native species ignoring type of enemy (same findings as Xu *et al.* 2021). (B) Analysis of annual herbivory rates categorised by enemy type (different finding to Xu *et al.* 2021).

## Tables

**Table 1:** A reframing of the enemy release hypothesis, focused on the key outcome of exotic population-level performance. This outcome is driven by three factors, which are affected by seven contexts. Summaries of broad predictions are given; references highlight key papers for each prediction but are not comprehensive. See text for complete discussion and justification.

Component of ERH	Definition
Outcome of the ERH: increased exotic performance	Outcome of the ERH: increased exotic performance
Population-level performance	Enhanced performance of an exotic population after introduction
Three factors influence exotic performance	Three factors influence exotic performance
1: Enemy impact	Change in the per-capita effect of enemies on the exotic after introduction
2: Enemy diversity	Change in the diversity of enemies attacking exotic after introduction
3: Host adaptation	Adaptive changes to investment in growth and defence by exotics
Seven contexts alter the influence and strength of each factor	Seven contexts alter the influence and strength of each factor
i) Time since introduction	Time elapsed since a specific local exotic population established
ii) Resource availability	Difference in the level of resources between the home and introduced range

Component of ERH	Definition
iii) Phylogenetic relatedness of exotic and native species	Genetic relatedness of an exotic population to the native (in)
iv) Host-enemy asynchronicity in space or time	Difference between the observed spatial and temporal occur
v) Number of introduction events	Propagule pressure of an exotic species to a given location
vi) Type of enemy	Functional and taxonomic characteristics of the enemy spec
vii) The strength of growth-defence trade-offs	The degree to which individuals with high growth have lowe

**Table 2:** Summary of hypotheses that fall under an enemy framework and how they can be encompassed by process and ecological context. The proposed explanations are examples only; e.g. a high relatedness to native species could mean an exotic is more vulnerable to enemies (because it is a more familiar target for enemies in the invaded range), or less vulnerable to enemies (because it likely possesses defences that will be effective against enemies in the invaded range). Our goal is not to suggest which hypotheses are more or less likely overall, but to highlight the conditions that could lead to each one and demonstrate how considering a core set of factors and contexts can unify the hypotheses into a single tractable framework. List and summary of hypotheses is from Catford *et al.* 2009 and references therein.

Hypothesis	Summary of hypothesis
Enemy-mediated biotic resistance (BR)	Enemies in the invaded range limit invasive ability (Levine et al. 2000)
Enemy inversion (EI)	An exotic’s natural enemies have reduced effect in invaded range (C
Enemy of my enemy (EE)	Enemies affect native species more than exotics (Colautti et al. 2004)
Enemy reduction (ERD)	A partial (rather than a total) loss of enemies (Colautti et al. 2004)
Evolution of increased competitive ability (EICA)	Loss of enemies leads to loss of defences and upregulation of growth
Increased susceptibility (IS)/New associations (NAS)	Low genetic diversity increases susceptibility to enemies in invaded r
Resource-Enemy release (R-ER)	Resource-acquisitive species have more enemies to lose, and will ben
Shifting defence (SDH)	Loss of specialists stimulates investment in cheaper generalist defenc

## Boxes

### Box 1: Biogeographic and community approaches to the ERH: exotic naturalisation versus exotic impact?

The key outcome of the enemy release hypothesis (ERH) is increased exotic performance in the invaded range (Fig. 1). But increased relative to what? There are two possible comparators: 1) Exotic performance can be compared to conspecifics in the home range – a *biogeographic* comparison; or 2) Exotic performance can be compared to co-occurring natives in the invaded range – a *community* comparison. The original conception of the ERH (Keane & Crawley 2002) does not explicitly state which comparator is appropriate, or why they may differ. Later conceptions incorporate both. For example, Sarabeev et al. (2022) premise their discussion of the ERH around two predictions, one biogeographic and one community.

Potential differences between biogeographic and community comparisons depends on underlying assumptions. The ‘universal trade-off hypothesis’ (Tilman 2011) suggests that biogeographic and community comparisons should yield the same result. This hypothesis posits that there is a ubiquitous trade-off surface along which all species lie. Release from enemies in the invaded range could cause an exotic to move off this shared trade-off surface (Catford et al. 2018). The exotic should therefore gain a performance advantage relative to conspecifics in its home range (biogeographic), and also relative to natives in the invaded range (community). In contrast, the ‘evolutionary imbalance hypothesis’ (Fridley & Sax 2014) proposes that old, highly diverse regions with large population sizes produce species that should be superior competitors to species from younger, more depauperate regions. Under these circumstances, biogeographic and community comparisons may produce distinct findings. For example, an exotic from a species-poor region may experience enemy release and compare favourably with conspecifics in its home range, but perform poorly in a community

context if it has invaded a species-rich area with highly competitive natives.

Empirical evidence suggests that biogeographic and community comparisons often yield different results (Colautti et al. 2004). Biogeographic (home vs invaded range) comparisons tend to support the ERH more than community (native vs exotic species) comparisons. However, very few studies employ biogeographic and community comparisons together. It is therefore unclear whether this is the result of a meaningful ecological pattern (e.g., that evolutionary imbalance is more likely than universal trade-offs), or due to different types of study employing different methods to test biogeographic and community comparisons. When comparisons are made using the same metric (e.g. ‘insect diversity’), results between biogeographic and community tests are similar (Meijer et al. 2016). We suggest that one reason for the inconsistencies between biogeographic and community comparisons is that they emphasise different aspects of exotic performance and use different metrics. Biogeographic comparisons emphasise successful establishment and naturalisation, and tend to focus on enemy richness and abundance. In contrast, community comparisons emphasise the impacts of exotic species, and typically focus on the relative performance of exotic and native species (Jeschke & Heger 2018).

Whether a biogeographic or community comparison should be used thus depends on the goals of the researcher:

If a researcher is interested in the likelihood of successful colonisation and naturalisation, a biogeographic comparison is appropriate. A key barrier to successful colonisation is initial survival. If a universal trade-off holds (Tilman 2011), exotics are more likely to cross this barrier if they lose enemies, or if enemies have lower impact compared to in their home range. A biogeographic comparison tests whether these losses have occurred.

If a researcher is interested in exotic species’ impact and dominance in their invaded range, a community comparison is appropriate. Whether an exotic becomes invasive (becomes dominant and has a negative impact on the co-occurring native species or the recipient ecosystem) can only be fully understood relative to co-occurring native species (Zhang & Jiang 2006). A community comparison is required to compare performance against natives.

When choosing a comparator, a researcher should consider both the goals of the study, and the underlying assumptions about whether the two comparators should differ. This may vary depending on the stage of invasion (see ‘*Context i: Time since introduction*’ in main text).

### **Box 2: Context changes how we observe biotic interactions**

The component factors of enemy release interact with context. If this is not accounted for, this interaction produces inconsistencies in evidence for the ERH. To demonstrate this we discuss Fig. 4 in detail. Fig. 4 shows how different levels of resource availability affect enemy diversity through time. Three exotic populations (A, B, C) may be studied at the same time point ( $t_1$  or  $t_2$ ) in their invasion. If the populations come from different ecological contexts, their relative enemy diversities may differ. Alternatively, two populations could follow different trajectories because of their ecological contexts but appear to be on the *same* trajectory if they are studied at different points in time (enemy diversity on population A at  $t_1$  is identical to population B at  $t_2$ ). In this case, the equivalence is misleading; the ERH appears to be equally influential in both cases, but population B will saturate at a lower total enemy diversity. Finally, populations with the same trajectory can appear to be very different if they are studied at different points in their invasion history (e.g. population A at  $t_1$  vs.  $t_2$ ).

Depending on when populations A-C are studied, trends could range from ‘complete’ enemy release (all three populations shortly after  $t_0$ ), to enemy reduction (all three populations at  $t_1$ , populations B and C at  $t_2$ ) to biotic resistance (population A in later invasion). As individual case studies, they would all tell different stories but can all be explained by the interaction of factors with context.