REVIEW AND SYNTHESIS

Interactions between resource availability and enemy release in plant invasion

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Abstract

Understanding why some exotic species become invasive is essential to controlling their populations. This review discusses the possibility that two mechanisms of invasion, release from natural enemies and increased resource availability, may interact. When plants invade new continents, they leave many herbivores and pathogens behind. Species most regulated by enemies in their native range have the most potential for enemy release, and enemy regulation may be strongest for high-resource species. High resource availability is associated with low defence investment, high nutritional value, high enemy damage and consequently strong enemy regulation. Therefore, invasive plant species adapted to high resource availability may also gain most from enemy release. Strong release of high-resource species would predict that: (i) both enemy release and resources may underlie plant invasion, leading to potential interactions among control measures; (ii) increases in resource availability due to disturbance or eutrophication may increase the advantage of exotic over native species; (iii) exotic species will tend to have high-resource traits relative to coexisting native species; and (iv) although high-resource plants may experience strong enemy release in ecological time, well-defended low-resource plants may have stronger evolutionary responses to the absence of enemies.

INTRODUCTION

Understanding causes of exotic plant invasions is essential to identifying appropriate management strategies. As ecologists develop theories to explain invasion, however, they are faced with an enormous variety of both invaders and invaded systems. The difficulty of generalizing across disparate invasions has led to an array of hypotheses regarding mechanisms of invasion (Crawley 1987; Williamson 1999; Maron & Vila 2001; Shea & Chesson 2002). Of these hypotheses, two of the most well known and best studied are the enemy release hypothesis (ERH) (Elton 1958; Keane & Crawley 2002) and the resource hypothesis (Davis *et al.* 2000). The ERH attributes the success of exotic species to the possibility that they leave behind many diseases and herbivores upon invading a new range (Keane & Crawley

2002). While the ERH is generally supported by observations of decreased enemy richness, abundance and impact in species' exotic ranges (Wolfe 2002; Mitchell & Power 2003; DeWalt *et al.* 2004), comparisons of enemy damage among co-occurring native and exotic species have led to more mixed results (Colautti *et al.* 2004; Agrawal *et al.* 2005). Unlike the ERH, the resource hypothesis applies equally to native and exotic species (Davis *et al.* 2000). It proposes that colonization is facilitated by high resource availability, in turn due to either high resource supply or low resource uptake by competing species (Davis *et al.* 2000). The importance of resources in driving invasion is suggested by correlations between invasion and disturbance, which can increase resource availability by decreasing resource uptake or stimulating mineralization (Hobbs & Huenneke 1992; Davis *et al.* 2000), and between invasion and eutrophication (Bobbink *et al.* 1998). Increases

in invasion following experimental increases in resource availability provide direct support for the resource hypothesis (Huenneke *et al.* 1990; Milchunas & Lauenroth 1995; Davis & Pelsor 2001; Daehler 2003).

This review discusses the possibility that the concurrent importance of the enemy release and resource hypotheses may be causal rather than coincidental: fast-growing species adapted to high resource availability (henceforth 'high-resource species') may experience stronger enemy release than slow-growing species adapted to low resource availability ('low-resource species'; Blumenthal 2005). This hypothesis is a modification of the ERH, and will therefore be referred to here as the Resource-Enemy Release Hypothesis (R-ERH). For the R-ERH to hold, two conditions must be met: (i) stronger enemy regulation of high- than low-resource species; and (ii) enemy release of exotic species (Fig. 1). The objectives of this review are to evaluate evidence for each of these conditions
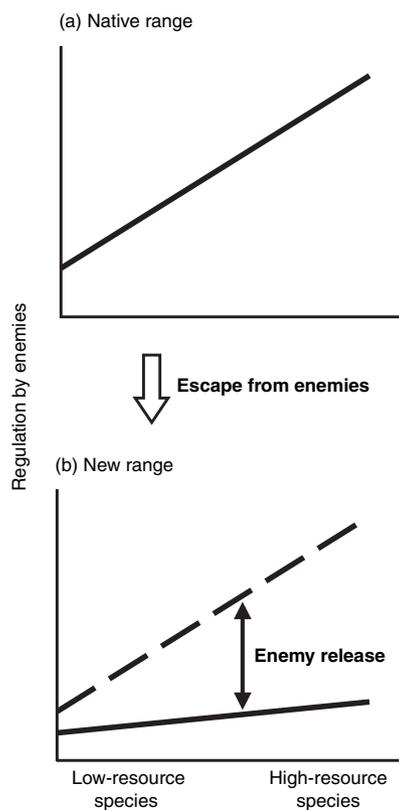

Figure 1 The resource–enemy release hypothesis. (a) Relative to low-resource plant species, high-resource plant species may be more strongly inhibited by enemies in their native range. (b) Consequently, high-resource species may have greater potential to escape those enemies upon moving to a new range (solid line) and be more strongly released, relative to native competitors from their new range (dashed line), than are low-resource species.

and to describe the predictions that follow from the R-ERH.

CONDITION 1: REGULATION BY ENEMIES INCREASES WITH THE RESOURCE AVAILABILITY TO WHICH A SPECIES IS ADAPTED

Two plant traits associated with high resource availability may increase susceptibility to enemies: low investment in defence and high tissue nutrient concentrations. The growth rate hypothesis of plant defence states that slow-growing plants from low-resource environments are likely to evolve greater investment in herbivore defence than will fast-growing plants from high-resource environments (Coley *et al.* 1985; Stamp 2003). In environments with low resource availability, plant tissue is expensive and difficult to replace, selecting for high investment in defence. As resource availability increases, the cost of replacing tissue goes down, and the cost in terms of growth rate of defending tissue goes up, selecting for lower investment in defence. In addition, high-resource species have high tissue nutrient concentrations, which not only allow for rapid photosynthesis and growth, but also lead to high nutritional value and therefore susceptibility to enemies (Mattson 1980; Reich *et al.* 1997). Evidence for these trends, described below, comes from multispecies relationships between growth rate or habitat resource availability with defence, nutritional value, enemy preference, enemy damage and enemy regulation.

Many studies of plant traits suggest that high-resource species are particularly susceptible to natural enemies. Chemical defences including phenolics and tannins have been found to decrease with increasing growth rate and resource availability among tropical forest trees (McKey *et al.* 1978; Coley 1983, 1987; Folgarait & Davidson 1995), although not among temperate herbaceous species (Poorter & Bergkotte 1992; Almeida-Cortez *et al.* 1999). Physical defences, including concentrations of lignin and cellulose, toughness and pubescence, decrease more consistently with increasing growth rate (Coley 1987; Loehle 1988; Poorter & Bergkotte 1992; Folgarait & Davidson 1995; Grime *et al.* 1997; Cunningham *et al.* 1999). The positive correlation between growth rate and tissue nutrient concentrations is well established (Chapin 1980; Mattson 1980; Poorter & Bergkotte 1992; Cornelissen *et al.* 1997; Grime *et al.* 1997; Reich *et al.* 1997). High tissue nutrient content, in turn, leads to high nutritional value for herbivores (Mattson 1980).

Studies of herbivore preference, which may reflect defence investment and nutritional value, provide direct tests of the susceptibility of high-resource species to herbivores. Many studies have found correlations between herbivore preference and traits associated with high-resource

environments. Fast-growing species are preferred by a wide variety of both terrestrial and aquatic herbivores (Sheldon 1987; Bryant *et al.* 1989; Price 1991; Wardle *et al.* 1998; Fraser & Grime 1999). Species with high nutritional quality, short-lived leaves and quickly decomposing litter are also preferred by herbivores (Rathcke 1985; Grime *et al.* 1996; Wardle *et al.* 1998; Cornelissen *et al.* 1999; Perez-Harguin-deguy *et al.* 2003). In addition, successional stage is related to herbivore preference, with palatability declining over the course of succession (Cates & Orians 1975; Lubchenco 1986; Sheldon 1987). To my knowledge, only one study has examined such relationships for pathogens, finding higher susceptibility to *Fusarium oxysporum* among fast- than slow-growing populations of *Raphanus sativus* L. (Hoffland *et al.* 1996).

Susceptibility to enemies translates into population regulation only if enemies are present. High-resource species might escape regulation by herbivores if their populations are sufficiently unpredictable in space or time (Rhoades & Cates 1976), or if their enemies are top-down regulated (Hairston *et al.* 1960; Crawley 1989). Nevertheless, patterns of enemy damage demonstrate that susceptible, high-resource species are often heavily damaged. Many field studies have shown high herbivore damage in high-resource environments or among fast-growing species (Coley 1980, 1983, 1988; Sheldon 1987; McNaughton *et al.* 1989; Fine *et al.* 2004). Further evidence that susceptible high-resource species are heavily damaged comes from a meta-analysis of herbivore damage studies (Cebrian & Duarte 1994). Across a range of species varying by several orders of magnitude in growth rate and herbivore damage, growth rate explained 83% of the variation in the percent of total biomass consumed.

Finally, a number of studies have directly examined regulation by herbivores and found stronger regulation of high- than low-resource plant species. Herbivores have been found to alter community composition by inhibiting species with high growth rates (Sheldon 1987; Fraser & Grime 1999; Olofsson 2001; Fine *et al.* 2004) or low concentrations of defensive compounds (Wardle *et al.* 2002). For example, Fine *et al.* (2004) found that herbivores inhibited fast-growing tropical trees typical of fertile clay soils more than slow-growing trees typical of infertile white sand soils. As a result, fast-growing species dominated plant communities on clay soils, where rapid growth compensated for high levels of herbivory, and on sand soils if herbivores were excluded. With herbivores present on sand soils, however, slow-growing species were able to out-compete heavily damaged fast-growing species. Such patterns demonstrate strong herbivore regulation of high-resource species, and together with broader patterns of herbivore damage (e.g. Cebrian & Duarte 1994), suggest a potential for strong enemy release among high-resource species.

CONDITION 2: PLANTS ARE RELEASED FROM ENEMIES IN THEIR EXOTIC RANGES, LEADING TO LOW ENEMY REGULATION OF EXOTIC RELATIVE TO NATIVE SPECIES

Regulation by enemies in the native range translates into enemy release in the exotic range if some of the regulating enemies are absent, and no near equivalents to the missing enemies are present, giving exotic species a competitive advantage over native species still burdened by their enemies (Maron & Vila 2001; Keane & Crawley 2002; Colautti *et al.* 2004) (Fig. 1). Reviews of the ERH suggest that species strongly regulated by enemies in their native range may experience strong enemy release, particularly short-lived species that rely heavily on current seed production (Maron & Vila 2001), and species that are poorly defended (Keane & Crawley 2002).

Biogeographical studies have consistently found decreased richness of, damage from or effects of enemies in plant species' exotic relative to native ranges (Colautti *et al.* 2004 and references therein; Vila *et al.* 2005). For example, DeWalt *et al.* (2004) found that common enemies of the neotropical shrub *Clidemia hirta* in its native Costa Rica were absent from its exotic range in Hawaii. Furthermore, insect and pathogen exclusion facilitated *C. hirta* establishment in its native but not its exotic range, suggesting that the absence of these enemies contributed to its invasiveness in the exotic range. More broadly, a comparison of pathogen richness among 473 plant species showed that not only do plants harbour fewer pathogen species in their exotic range, but also plants that lose more pathogens are more invasive (Mitchell & Power 2003).

Tests of the ERH comparing enemy damage among co-occurring native and exotic species have had less consistent results (Agrawal & Kotanen 2003; Colautti *et al.* 2004; Torchin & Mitchell 2004; Agrawal *et al.* 2005; Carpenter & Cappuccino 2005; Parker & Hay 2005). In a study of 30 taxonomically related native–exotic pairs, native plants were more damaged by both herbivores and pathogens than were exotic plants, despite having traits, such as tougher leaves and higher leaf C : N, which suggested that they should be relatively resistant to enemies (Agrawal *et al.* 2005). However, the opposite result has also been observed (Colautti *et al.* 2004). For example, Parker & Hay (2005) found an array of terrestrial and aquatic generalist herbivores to consistently prefer exotic over native plants.

Enemy release is most clearly expected from specialist enemies (Keane & Crawley 2002; Muller-Scharer *et al.* 2004; Torchin & Mitchell 2004; Joshi & Vrieling 2005). Because high-resource species may be particularly suscep-tible to specialist enemies (Coley *et al.* 1985), release

primarily from specialists could accentuate the pattern predicted by the R-ERH. The growth rate hypothesis of plant defence predicts that fast-growing, high-resource species have evolved not only low levels of defences, but also very low levels of quantitative defences, which are effective against specialists (Feeny 1976; Coley *et al.* 1985; Stamp 2003). Quantitative defences such as lignins and tannins are costly, both because they are required in high concentrations and because they are relatively immobile, and therefore lost with senescing tissue (Coley *et al.* 1985). This latter characteristic makes them particularly costly for plants with short-lived tissue, such as high-resource species (Coley *et al.* 1985). Consequently, high-resource species tend to invest little in quantitative defences (Coley 1987; Grime *et al.* 1997), and may be both highly susceptible to specialists in their native range and strongly released from specialists (the same enemies from which release is most likely) in their exotic range. In contrast, the potential role of generalists in the R-ERH is less clear, both because high-resource species often produce qualitative defences which are effective against generalists (Feeny 1976; Coley *et al.* 1985) and because exotic species may be inhibited by, rather than released from, generalist enemies in their new range (Levine *et al.* 2004; Parker & Hay 2005; Parker *et al.* 2006).

PREDICTION 1: ENEMY RELEASE AND RESOURCE AVAILABILITY MAY OFTEN ACT IN CONCERT TO FACILITATE INVASION

Given the small proportion of introduced species that become invasive (Williamson 1999), there is already reason to suspect that multiple factors may underlie successful invasions. The R-ERH provides the first indication that there may be a causal relationship between resource availability and enemy release. It suggests that the two mechanisms may co-occur because they facilitate invasion by the same type of species. Increases in resource availability help all high-resource species. Enemy release helps exotic high-resource species. Consequently, exotic high-resource species are likely to benefit from both high resource availability and enemy release (Fig. 2).

Where both resource availability and enemy release contribute to plant invasion, there may be a number of ramifications for management. Specifically, each mechanism may influence the success of control measures aimed at the other. For example, to the degree that high-resource species are most strongly released from enemies, particularly specialist enemies, they may also be most susceptible to biological control, the introduction of specialist enemies from their native range (Fig. 2). Biological control may also be particularly effective in
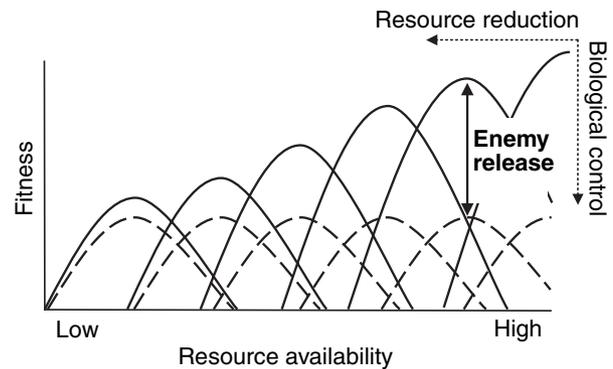

Figure 2 The influence of resource availability on the fitness of native (dashed lines) and exotic (solid lines) plant species. High resource availability selects for high-resource native and exotic species. If high-resource exotic species are more strongly released from enemies than are low-resource exotic species, high resource availability will indirectly increase enemy release, and therefore favour exotic over native species (prediction 2). Conversely, both biological control (vertical dotted line), which reduces enemy release directly, and control methods that reduce resource availability (horizontal dotted line), which favour low-resource species with less potential for enemy release, may reduce the advantage of exotic over native species (prediction 1).

environments with high resource availability, both because such environments select for potentially susceptible high-resource exotic species, and because high resource availability may increase the nutritional value of these species (Mattson 1980). Similarly, control measures aimed at limiting or reducing resource availability may favour native over exotic species. For example, immobilizing available N by amending soils with carbon can inhibit high-resource species (Blumenthal *et al.* 2003). If high-resource species have the most potential for enemy release (Fig. 2), N immobilization may inhibit strongly released species, thereby reducing enemy release and the advantage of exotic over native species.

The possibility that multiple causes of invasion interact could either strengthen or weaken the case for multiple solutions to invasion, or integrated pest management (Thill *et al.* 1991). Because biological control and resource reduction could each reduce the need for the other (Fig. 2), the most efficient approach may often be to use only one control method. However, there appear to be many situations where neither biological control nor resource reduction alone eliminates the advantage of exotic over native species (Blumenthal *et al.* 2003; Moran *et al.* 2005). In such situations, the possibility that both enemy release and available resources underlie invasion suggests that the most effective management may be a combination of biological control and resource reduction.

PREDICTION 2: EXOTIC SPECIES WILL HAVE A GREATER ADVANTAGE OVER NATIVE SPECIES IN HIGH- THAN LOW-RESOURCE ENVIRONMENTS

Hypotheses that explain why increases in available resources facilitate colonization do not explain why they favour exotic species in particular (Hobbs & Huenneke 1992; Davis *et al.* 2000). In contrast, the R-ERH predicts that increases in available resources will indirectly increase enemy release and therefore help exotic colonizers more than native colonizers (Fig. 2).

This prediction is consistent with observations of exotic species success in high-resource environments. The proportion of species richness or plant cover that is exotic tends to increase with moisture, soil fertility and disturbance (Crawley 1987; Rejmanek 1989; Kotanen *et al.* 1998; Hood & Naiman 2000; Cadotte & Lovett-Doust 2002; Kolb *et al.* 2002). Experimental studies also suggest that increased resource availability favours exotic over native species. In a meta-analysis of 79 studies that measured performance of both native and exotic species, Daehler (2003) found that exotic species tend to outperform native species in high- but not low-resource environments. These patterns might be explained by a larger proportion of high-resource species in exotic than native species pools (Kotanen *et al.* 1998). The R-ERH provides an additional explanation. It suggests that exotic species succeed in high-resource environments not only because low-resource native species are poorly adapted to such environments (Daehler 2003), but also because, among well-adapted high-resource species, enemy release favours exotics over natives (Fig. 2).

The potential for strong enemy release, and therefore strong advantages for exotic species, in high-resource environments provides another reason for concern about anthropogenic increases in resource availability. Humans increase plant-available resources by disturbing existing plant communities and by directly adding resources (Davis *et al.* 2000), and do so at a great variety of scales, from small-scale soil disturbances to regional increases in N deposition and global increases in CO_2. Such increases in resource availability can dramatically alter species composition and often decrease biological diversity (Vitousek *et al.* 1997). These changes are also known to facilitate colonization by both native and exotic high-resource species (Bobbink *et al.* 1998; Dukes & Mooney 1999; Davis *et al.* 2000). The R-ERH provides the first explanation for why such increases may help exotic high-resource species more than native high-resource species (Fig. 2) and predicts that increases in resource availability may lead to invasion even where native species are well adapted to high-resource environments.

PREDICTION 3: SUCCESSFUL EXOTIC SPECIES WILL HAVE HIGH-RESOURCE TRAITS RELATIVE TO COEXISTING NATIVE SPECIES

Within a given plant community, there are multiple reasons to expect that a larger proportion of exotic species than native species will be adapted to high-resource availability. For example, human tendencies to transport and create habitat for high-resource species may elevate propagule pressure for high- but not low-resource exotic species (Kotanen *et al.* 1998). The R-ERH predicts that relatively large proportions of exotic species will be adapted to high-resource availability even if native species and potential exotic species have similar ranges of resource adaptations. If, within the pool of exotic species that arrive in a plant community, high-resource exotic species are most strongly released, they may also be most likely to invade (Fig. 2). Consequently, the pool of *successful* exotic species in that community may have stronger adaptations to high-resource environments than do coexisting native species.

The degree of support for this prediction appears to depend on the scale of the study. Results of studies comparing traits of hundreds or thousands of native and exotic species have been inconsistent (Pysek *et al.* 1995; Thompson *et al.* 1995; Williamson & Fitter 1996; Crawley *et al.* 1997; Reichard & Hamilton 1997; Daehler 1998; Goodwin *et al.* 1999; Cadotte & Lovett-Doust 2002; Sutherland 2004; Hamilton *et al.* 2005). Some patterns do emerge, however; exotic species have been found to be tall and leafy, with high specific leaf area and long flowering periods, relative to native species. The lack of clear patterns with regard to other traits may not be surprising given that large databases are often limited to relatively coarse morphological and life history measurements, and comprise multiple ecosystems, and therefore different high-resource traits.

Identifying differences between native and exotic species appears to require detailed physiological measurements of particular life forms within particular communities: two types of community-specific studies have found higher values for high-resource traits among exotic than native species. Comparisons of many unrelated species within a single community have found exotic species to have higher specific leaf area and tissue nutrient concentration, more rapid photosynthesis and decomposition, and lower water use efficiency, tissue density and tissue construction cost than native species (Baruch & Goldstein 1999; Craine & Lee 2003; Allison & Vitousek 2004). Congeneric comparisons, each involving fewer species and measuring different variables, have together found exotic species to have faster growth, greater specific leaf area, higher tissue N, greater seed set and shorter tissue life-span than native species (Schierenbeck *et al.* 1994; Rejmanek & Richardson 1996; Radford & Cousens

2000; Durand & Goldstein 2001; Smith & Knapp 2001; Grotkopp *et al.* 2002; but see Schierenbeck & Marshall 1993).

To the degree that low defence investment is a trait of high-resource species (see condition 1), the R-ERH also predicts that exotic species will be less well defended than are coexisting native species. Although some of the high-resource traits described in the preceding paragraphs may be important to defence, explicit tests of differences in defensive traits among native and exotic species are rare. One study of 14 pairs of congeners in southern Ontario found that relative to native species, exotic species have high leaf water content, low leaf C : N and low leaf toughness (Agrawal *et al.* 2005).

PREDICTION 4: EVOLUTION OF INCREASED COMPETITIVE ABILITY WILL BE MOST IMPORTANT FOR WELL-DEFENDED SPECIES ADAPTED TO LOW-RESOURCE HABITATS

The evolution of increased competitive ability (EICA) hypothesis suggests that when exotic plants escape their enemies, they will evolve to allocate fewer resources to defence, particularly defence against specialists, and more resources to growth and reproduction (Blossey & Notzold 1995; Muller-Scharer *et al.* 2004; Joshi & Vrieling 2005). Thus, while well-defended, low-resource species may initially benefit little from enemy release, over time selection for lower investment in defence could increase their fitness. In contrast, high-resource species that replace rather than defend tissue (Coley *et al.* 1985) may immediately benefit from enemy release, but have little opportunity to evolve increases in those benefits. Therefore, EICA may be most important for low-resource species and environments, and low-resource species may be useful candidate species for such studies. However, it is important to note that other characteristics of low-resource species may limit their ability to evolve lower allocation to defence, including relatively long generation times (Rejmanek & Richardson 1996), and defences that also provide other benefits, such as tissue longevity, important in stressful low-resource environments (Coley 1980). There are currently too few studies available to evaluate prediction 4. Although common garden studies have found evidence both for and against EICA, results for many of the 23 species studied to date have been inconclusive (Bossdorf *et al.* 2005). Furthermore, few types of species have been tested for EICA. Most studies have examined either woody or herbaceous perennial dicots, and there are positive and negative results within both categories (Bossdorf *et al.* 2005).

TESTING THE R-ERH

Testing the R-ERH requires comparisons of enemy release among species varying in their adaptations to resource availability. A variety of measures are available for both resource adaptations and enemy release. Species adapted to high-resource habitats tend to grow quickly, and relative growth rate is closely related to a species' affinity for available resources (Chapin 1980; Coley *et al.* 1985). In addition, there are a variety of traits that are strongly correlated with relative growth rate and may be easier to measure, such as specific leaf area, tissue density or leaf longevity (Poorter & Bergkotte 1992; Grime *et al.* 1997; Reich *et al.* 1997).

Enemy release is best measured by using enemy exclusion experiments to determine how the effects of enemies differ between a species' native and exotic ranges (DeWalt *et al.* 2004). Differences in enemy richness or enemy damage among ranges are easier to measure but require assumptions about how each relates to enemy regulation. Enemy release can also be measured within an invaded community, by comparing effects of enemies among functionally similar native and exotic species. However, this approach should be used with caution in testing the R-ERH. If phylogenetic or functional group similarity does not reflect functional similarity (e.g. if exotic species have high-resource traits relative to native species; Agrawal *et al.* 2005), differences in origin could be confounded with differences in resource strategy.

The prediction that biological control will be most successful against high-resource species (prediction 1) could also be tested, by regressing the level of biological control success on resource strategy for a group of target species. Similarly, conducting common garden experiments with plants from both the native and exotic ranges of exotic species that vary in their resource strategy may shed light on the potential interaction between EICA and resources (prediction 4). The challenge in testing both the R-ERH and its predictions will be to determine resource strategy and either enemy release, biological control success or EICA for sufficiently large numbers of species.

ACKNOWLEDGEMENTS

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