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REVIEWS AND SYNTHESIS

Biotic interactions and plant invasions

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Abstract

Introduced plant populations lose interactions with enemies, mutualists and competitors from their native ranges, and gain interactions with new species, under new abiotic conditions. From a biogeographical perspective, differences in the assemblage of interacting species, as well as in abiotic conditions, may explain the demographic success of the introduced plant populations relative to conspecifics in their native range. Within invaded communities, the new interactions and conditions experienced by the invader may influence both its demographic success and its effects on native biodiversity. Here, we examine indirect effects involving enemies, mutualists and competitors of introduced plants, and effects of abiotic conditions on biotic interactions. We then synthesize ideas building on Darwin's idea that the kinds of new interactions gained by an introduced population will depend on its relatedness to native populations. This yields a heuristic framework to explain how biotic interactions and abiotic conditions influence invader success. We conclude that species introductions generally alter plants' interactions with enemies, mutualists and competitors, and that there is increasing evidence that these altered interactions jointly influence the success of introduced populations.

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INTRODUCTION

For a plant species to be demographically successful in a novel region, it must be transported from its native range to that area, colonize it, survive and reproduce, then spread more widely. Each of these stages presents an ecological filter through which introduced plants must pass. These same filters will also act on enemies, mutualists and competitors from the invader's native range. As a result, it is almost inevitable that introduced plant populations will interact with a subset of the species with which their conspecific native populations interact (Colautti *et al.* 2004). On the other hand, the introduced populations will encounter novel species of potential enemies, mutualists and competitors (Richardson *et al.* 2000; Levine *et al.* 2004; Parker & Gilbert 2004). Our central question is, what are the consequences of such losses and gains of biotic interactions for the demographic success of introduced plant populations?

We equate demographic success with long-term large-scale population abundance. Defined as such, demographic success

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is a chief driver of the ecological impact of introduced species (Parker *et al.* 1999). Empirical studies commonly focus on one of the many components of demographic success, including individual plant performance, local population density, local population growth rate, rate of spread at larger spatial scales and niche breadth or habitat use. Demographic success can be gauged against a variety of standards, including native competitor species or conspecific native populations (community and biogeographic comparisons, respectively, sensu Colautti *et al.* 2004). While testing fundamentally different questions, both comparisons shed light on important aspects of biological invasions. Comparison with conspecifics in their native range is useful because it is relative to these populations that invaders gain and lose interactions with enemies, mutualists and competitors. Also, the ecological and evolutionary dynamics of introduced populations will be constrained, in part, by the evolutionary history of the native populations from which they are introduced. On the other hand, introduced species are of interest in part because of their effects on native biodiversity, and they may acquire enemies and mutualists from resident competitors. For brevity, we hereafter refer to the demographic success (or any of its components) of an introduced population as 'invader success'.

Currently, we have little predictive understanding of what controls variation in invader success among introduced populations (Colautti *et al.* 2004; Hierro *et al.* 2005). Many of the hypotheses to explain variation in invader success invoke biotic interactions. Abiotic environmental conditions can directly influence both invader success and the outcome of biotic interactions. We suggest that, for any introduced species, invader success will be a function both of additive effects of enemies, mutualists, competitors, and abiotic conditions, and of interactions between these factors. As a step towards understanding their additive effects, we begin by reviewing evidence for the major current hypotheses on biotic interactions and invasions that focus on single factors. We then discuss the potential for these factors to jointly influence invader success. We argue that interactions with enemies, mutualists, and competitors are lost and gained through common causes, feed back to influence invader success through similar mechanisms, and can be understood through a unified conceptual framework.

SINGLE-FACTOR HYPOTHESES

Many of the current hypotheses on the role of biotic interactions in plant invasions focus exclusively on either enemies, mutualists or competitors (Table 1). We briefly review current conceptual progress on some of the chief single-factor hypotheses. We then seek to promote conceptual integration across these hypotheses by highlighting concepts that may be applicable across these groups.

Disease and herbivory

The enemy release hypothesis argues that the loss of interactions with natural enemies allows introduced populations to attain greater abundances. Supporting this idea, current studies indicate that introduced plant populations are exposed to fewer species of pathogens and insect herbivores (reviewed by Colautti *et al.* 2004; Hinz & Schwarzlaender 2004; Torchin & Mitchell 2004, but see Van der Putten *et al.* 2005), are less impacted by pathogens and herbivores (DeWalt *et al.* 2004, but see Beckstead & Parker 2003), and are less negatively impacted by soil organisms (Reinhart & Callaway 2004; Torchin & Mitchell 2004; Wolfe *et al.* 2005) than are native conspecific populations. On the other hand, within-community comparisons indicate that introduced species do not consistently receive less damage from natural enemies than do resident competitors (reviewed by Colautti *et al.* 2004 and Torchin & Mitchell 2004; see also Agrawal *et al.* 2005; Carpenter & Cappuccino 2005; Parker & Hay 2005). These within-community comparisons have been cited as contrary to the enemy release hypothesis (Colautti *et al.* 2004). However, many relied on assessments of visible damage. Because plant species vary in their ability to tolerate or compensate for a given amount of visible damage (Gilbert 2002; Muller-Scharer *et al.* 2004), comparisons of visible damage rates across species do not necessarily indicate effects on plant performance or demographics, and thus invader success. For example, the invasive Chinese tallow tree (*Sapium sebiferum*) experienced less herbivory, in terms of percentage leaf area damaged, than a native competitor, yet experimental exclusion of herbivores revealed greater impacts of herbivory on the invader because it was less tolerant of herbivory (Siemann & Rogers 2003). Additionally, many of the published within-community comparisons have relied largely on comparisons of invaders to congeneric native species. Controlling for phylogenetic relatedness is important, in part because invaders with native congeners may be more likely to acquire new enemies from them (Mack 1996; Parker & Gilbert 2004). The invaders selected for these studies may therefore be less released from enemies than invaders in general, making them a conservative test of enemy release (Agrawal *et al.* 2005). Together, these two points indicate that the available within-community comparisons are insufficient to discount the enemy release hypothesis. To more directly test this hypothesis, we advocate experiments that: (i) directly manipulate enemy attack rates; and (ii) more directly test the role of phylogenetic history, for example, by incorporating diverse invaders known to vary in their relatedness to the native flora.

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Table 1 Hypotheses that invoke enemies, mutualists, competitors or favourable abiotic conditions to explain invaders' demographic success

Hypothesis	Enemy	Mutualism	Competition	Abiotic	Select references
Enemy release	+				Darwin (1859), Colautti *et al.* (2004) and Torchin & Mitchell (2004)
Evolution of increased competitive ability	+				Blossey & Nötzgold (1995) and Bossdorf *et al.* (2005)
Biotic resistance from enemies	−				Elton (1958) and Maron & Vila (2001)
New associations	−				Hokkanen & Pimentel (1989) and Colautti *et al.* (2004)
Mutualist facilitation		+			Richardson *et al.* (2000)
Invasional meltdown		+		+	Simberloff & Von Holle (1999) and Bruno *et al.* (2005)
Biotic resistance from competitors			−		Elton (1958) and Levine *et al.* (2004)
Empty niche			+		Elton (1958) and Hierro *et al.* (2005)
Novel weapons			+		Callaway & Aschehoug (2000) and Callaway & Ridenhour (2004)
Habitat filtering				+	Darwin (1859) and Kriticos *et al.* (2005)
Mutualism–enemy release	+	+			Wolfe (2002)
Competition–enemy release	+		+		Tilman (1999) and Shea & Chesson (2002)
Mutualism–competition		+	+		Marler *et al.* (1999) and Callaway *et al.* (2004)
Enemy of my enemy	+		+		O'Connor (1991) and Colautti *et al.* (2004)
Mutualism disruption		+	+		Roberts & Anderson (2001) and Brown *et al.* (2002)
Subsidized mutualism		+			Bever (2002)
Resource–enemy release	+			+	Blumenthal (2005)
Fluctuating resources			+	+	Davis *et al.* (2000)
Opportunity windows	+	+	+	+	Johnstone (1986) and Agrawal *et al.* (2005)
Naturalization	+	+	+	+	Darwin (1859) and Daehler (2001)

Each hypothesis either predicts net increased (+) or decreased (−) invader success as a result of the specified combination of factors. Selected references are early formulations and recent reviews or examples.

The loss of natural enemies may have not just ecological consequences, but evolutionary consequences as well. The evolution of increased competitive ability (EICA) hypothesis suggests that decreased enemy attack on introduced populations may select for increased competitive ability because plants can allocate resources to competition instead of defence (Blossey & Nötzgold 1995; Maron *et al.* 2004; Bossdorf *et al.* 2005). Invaders are typically more completely released from specialist than generalist enemies (Andow & Imura 1994; Hinz & Schwarzlaender 2004; Knevel *et al.* 2004; Torchin & Mitchell 2004; Van der Putten *et al.* 2005). Recent studies suggest that, in response, introduced populations evolve lower allocation to defences against specialist, but not generalist enemies (Muller-Scharer *et al.* 2004; Joshi & Vrieling 2005; Stastny *et al.* 2005). Thus, differences in enemy species composition between plants' native and introduced ranges figure centrally in the current iteration of this theory. Additionally, intra- and interspecific hybridization, which is facilitated by species introductions (Ellstrand & Schierenbeck 2000), can influence interactions with enemies (Fritz *et al.* 1999). Finally, native enemies may evolve to attack introduced plants (Carroll *et al.* 2005). The ecological and evolutionary dynamics of introduced populations may often be intertwined, perhaps playing at the same time on the same stage.

The effect of enemies on introduced populations will be a function of both the loss of old enemies and the gain of new ones. The gain of new enemies from the resident community is a form of biotic resistance to invasion (Elton 1958; Mack 1996; Maron & Vila 2001; Levine *et al.* 2004). In North America, introduced plants that accumulated more new pathogens (Mitchell & Power 2003) or that experienced more herbivory (Carpenter & Cappuccino 2005) were less frequently reported as invasive, suggesting that biotic resistance decreases invasiveness. In a meta-analysis of experimental tests, excluding native herbivores increased both invader establishment and individual performance (Levine *et al.* 2004), and native crayfish preferred to feed on introduced aquatic plants (Parker & Hay 2005). Such observations of biotic resistance from enemies are not incompatible with simultaneous and strong enemy release (Mitchell & Power 2003). Many approaches to study competition incidentally integrate any effects of apparent competition (Connell 1990; Mitchell & Power 2006). One recent study suggested that the effects of plant species composition on biotic resistance to invasion resulted not from resource competition, but from apparent competition mediated by nematodes (van Ruijven *et al.* 2003). Apparent competition may be an underappreciated mechanism for biotic resistance.

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New enemies acquired by introduced plants may have stronger negative effects than enemies with which the plant has coevolved because there has been no selection in the new associations for greater resistance or reduced virulence (the new associations hypothesis; Hokkanen & Pimentel 1989). Thus, this hypothesis predicts that changes in enemy species composition from native to introduced ranges will decrease invader success. Colautti *et al.* (2004) suggested that this effect might be compounded by plants' loss of genetic variation for defence during population bottlenecks in the introduction process. Analyses of crops and a few wild species have been consistent with the new associations hypothesis (Hokkanen & Pimentel 1989). However, one of its key assumptions that coevolution generally reduces the effects of natural enemies, remains a topic of debate (Jarosz & Davelos 1995; Parker & Gilbert 2004; Carroll *et al.* 2005; Parker & Hay 2005). Additionally, the evolution of greater defence against generalist enemies (Joshi & Vrieling 2005) would reduce the impacts of new associations on introduced populations.

A crucial and unresolved aspect of enemy release is its durability. If enemy release occurs, subsequent temporal accumulation of enemies seems almost inevitable. At what rate do enemy species accumulate? Studies examining the correlation between time since introduction and enemy richness have not detected clear patterns of enemy accumulation across plant species (Andow & Imura 1994; Torchin & Mitchell 2004; Carpenter & Cappuccino 2005). Rates of accumulation may be difficult to estimate if they are very slow on the time scales for which we have data or if, as might be more likely, they are obscured by other sources of variation among species such as geographical range size or phylogeny. A better understanding of the temporal dynamics of enemy accumulation would inform our understanding of the fate of introduced populations.

Mutualism and facilitation

The mutualist facilitation hypothesis argues that the replacement of lost mutualists from plants' native ranges with new mutualists in their introduced ranges is key to invaders' establishment and spread (Richardson *et al.* 2000). Shifts in mutualist species composition from plants' native to introduced ranges are pervasive, and the acquisition of new mutualists is often essential for the establishment of introduced populations (Richardson *et al.* 2000). Might the identity of these new mutualists help explain variation in the success of established populations? Studies documenting variation among mutualist species in their per capita or per-interaction effects on plants (Schemske & Horvitz 1984; Bever 2002; Klironomos 2003) suggest the answer is yes. Changes in mutualist species composition may limit invader success or even prevent successful establishment and naturalization, if the pool of mutualists available to an introduced plant does not include species on which it has evolved to depend (Nadel *et al.* 1992). On the other hand, widespread host generalism among plant mutualists (Waser *et al.* 1996; Richardson *et al.* 2000) and the large geographical ranges of many mutualists (Richardson *et al.* 2000) suggest that there might be insufficient variation in mutualist species composition among comparable plant species for composition to influence invader success. Moreover, recent results indicate that population-level effects of plant mutualists are driven not by their effects on a per-interaction basis, but by the frequency of their interactions with the plant (Morris 2003; Vázquez *et al.* 2005), suggesting that any effects of mutualist species composition on invader success will be overridden by variation in interaction frequency.

As well as species composition, the richness of mutualists may differ between plants' native and introduced ranges. Some studies have detected effects of mutualist species richness on plant performance (van der Heijden *et al.* 1998; Jonsson *et al.* 2001), but others have not (Morris 2003). Simulating pollinator extinctions using empirical data predicts that lower pollinator richness ultimately decreases pollination service to plants, but most plants are highly buffered against all but the largest changes in richness (Morris 2003). On the other hand, controlled inoculation experiments with arbuscular mycorrhizal fungi have revealed that greater mycorrhizal species richness can increase plant growth across a suite of diverse species (van der Heijden *et al.* 1998; Jonsson *et al.* 2001). One recent study found that mycorrhizal infection enhanced pollination success (Wolfe *et al.* 2005), suggesting that adding or losing mutualists of different functional types can have synergistic impacts on plant performance.

Finally, introduced plant populations can enhance invader success for subsequently introduced plants through facilitative interactions (Bruno *et al.* 2005). This is a common example of the broader invasional meltdown hypothesis (Simberloff & Von Holle 1999). A variety of mechanisms for such facilitation have been reported, including increased nitrogen availability, soil salinity and fire frequency (Simberloff & Von Holle 1999).

Competition

Competition from resident species is a chief mechanism for biotic resistance to invasion. The negative effects of competition on invader performance increase with greater competitor species richness (Levine *et al.* 2004). While positive correlations between native and introduced species richness at large spatial scales have been used to argue that native richness does not inhibit invader success (Stohlgren *et al.* 2003), recent analyses indicate that these positive correlations arise because both native and invader richness are correlated with spatial heterogeneity in abiotic

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conditions (Davies *et al.* 2005). Greater resident plant species richness and composition can decrease resource availability for invaders through multiple mechanisms (e.g. Fargione & Tilman 2005).

The empty niche and novel weapons hypotheses argue that invaders succeed because they are able to acquire resources by avoiding competition. The empty niche hypothesis posits that invader success is greater when species are introduced into communities where they can take advantage of unutilized resources (Elton 1958). Put into a biogeographical context, this implies that, in their native ranges, plants are limited by competitors that do utilize these resources. Thus, introduced populations benefit from a difference in the species composition of competitors relative to that in their native range. In the terminology of the enemy release hypothesis, this idea essentially describes 'release from competition'. Consistent with this hypothesis, several case studies have found invaders can access resources that native species do not, but no studies have compared these interactions to resource competition in the plant's native range (reviewed by Hierro *et al.* 2005).

The novel weapons hypothesis for plant invasions argues that some invaders are more successful than in their native range because competitors in their native range have evolved to tolerate allelopathic compounds while competitors in the introduced range lack such tolerance (Callaway & Ridenhour 2004). Research on the invaders *Centaurea diffusa* and *Centaurea maculosa* suggests that invaders can benefit from a change in species composition from allelopathy-tolerant species with stronger per capita competitive effects to allelopathy-intolerant species with weaker per capita competitive effects (e.g. Callaway & Aschehoug 2000; Bais *et al.* 2003; Callaway & Ridenour 2004; Vivanco *et al.* 2004, but see Blair *et al.* 2005).

Abiotic environment

The abiotic environment, including both climatic and edaphic conditions, has long been regarded as a fundamental determinant of the potential distribution of introduced plant populations. These conditions are thought to fundamentally limit the habitat available to invaders through habitat filtering. Numerous studies have used climate matching algorithms to predict the potential geographical ranges of introduced species (Pearson & Dawson 2003), with the understanding that the predicted ranges may be conservative in extent because they do not allow for changes in biotic interactions (Kriticos *et al.* 2005).

The general importance of species composition

Current work on the enemy release, EICA, new associations, empty niche and novel weapons hypotheses (reviewed above) all point to major effects of shifts in the species composition of enemies and competitors on invader success. There are at least two ways in which species composition may influence invader success. First, there might be differences in species composition between plants' native and introduced ranges that are biased either towards or against greater invader success. The novel weapons (Callaway & Ridenhour 2004), new associations (Hokkanen & Pimentel 1989), and recent extensions of the biotic resistance (Parker & Hay 2005) hypotheses propose that such biases arise from plants sharing a longer coevolutionary history with species in their native range than in their introduced range. Second, even when there are no such biases, invaders may still by chance encounter biotic environments that enhance their success relative to that in their native ranges. Such communities with more benign species compositions may be the initial beachheads for invasion.

MULTIFACTOR HYPOTHESES

While many hypotheses to explain invader success consider only a single factor, we have seen that it will be rare for just one factor to differ between populations of an introduced species. Invader success may thus be better understood by considering the joint effects of enemies, mutualists and competitors, including interactions between them on introduced populations. These interactions can take the form of indirect effects that result from either interaction modifications or interaction chains (Wootton 1994). Additionally, biotic interactions are pervasively modified by abiotic environmental conditions (Smith & Read 1997; Mitchell *et al.* 2003; DeWalt *et al.* 2004). Spatial and temporal variation in these conditions may thus indirectly influence invader success by modulating the strength of biotic interactions. Finally, biotic interactions experienced by introduced populations may depend strongly on the phylogenetic relatedness of the invader to the resident species (Darwin 1859; Mack 1996; Parker & Gilbert 2004; Ricciardi & Atkinson 2004). We consider how the phylogenetic dependence of the effects of enemies, mutualists, and competitors, as well as abiotic conditions, may jointly explain variation in invader success. We begin by outlining a unified framework for evaluating the joint effects of biotic interactions and abiotic conditions on invader success.

A unified framework

We use R to represent any demographic response variable, such as population growth rate, density or rate of spread. To make explicit the dependence of R on its causal factors, we write it as a generic function $R(E_1,\ldots,E_e, M_1,\ldots,M_m, C_1,\ldots,C_c, A_1,\ldots,A_a$, where E_i, M_i, C_i, and A_i represent the abundance of enemy, mutualist or competitor species or

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the value of abiotic variable i, and there are e, m, c and a enemy, mutualist and competitor species and abiotic factors, respectively, which influence the response variable. We write the difference in abundance of enemy species j between the introduced and native ranges as $\Delta_j = E_j^{\mathrm{i}} = E_j^{\mathrm{n}}$ (where superscripts i and n denote introduced and native ranges respectively), and similarly for mutualist and competitor species and abiotic variables. We can write the difference in the response variable between the introduced and native ranges, ΔR, using the Taylor series expansion for a multivariate function:

$$\Delta R = \sum_{j=1}^{e} \Delta E_j R_{E_j} + \sum_{j=1}^{m} \Delta M_j R_{M_j} + \sum_{j=1}^{c} \Delta C_j R_{C_j} + \sum_{j=1}^{a} \Delta A_j R_{A_j} + O(\Delta^2). \quad (1)$$

Terms such as R_{E_j} are shorthand notation for the partial derivatives of the response variable with respect to the factors that affect it, evaluated at the values of these factors in the native range. For example, $R_{E_j} = \partial R/\partial E_j$ represents the sensitivity of the response variable to a change in the abundance of enemy species j, and can be assumed as the per capita interaction strength of this enemy species on the potential plant invader. We consolidate terms involving products of two or more differences into the single term $O(\Delta^2)$ which we assume to be small; as shown below, the first-order terms implicitly incorporate both direct and indirect effects. This framework expands the one developed for parasites alone by Torchin & Mitchell (2004). While eqn 1 explicitly compares biotic interactions in the plant's introduced range to its native range, we note that it could also be applied to differences between two populations in the introduced range.

Interaction modifications

Change in the abundance of one species may change the per capita effect of a second interacting species, even if the abundance of the second species does not differ between the two ranges (interaction modifications, sensu Wootton 1994). Such indirect effects enter eqn 1 through the partial derivatives (e.g. $R_{E_j} = \partial R/\partial E_j$). Here, we focus on interaction modifications involving two species of enemy, mutualist or competitor that each interact directly with an introduced plant. For example, consider a simple model for the per capita population growth rate of an introduced plant (P) interacting with a pollinating mutualist (M) and an enemy (E):

$$\frac{1}{P}\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{rM}{a + M + bE}\left(1 - \frac{P}{K}\right) - \frac{\mathrm{d}E}{1 + cP}. \quad (2)$$

The first term on the right-hand side of eqn 2 is the invader's per capita birth rate. When the invader's density is low ($P \ll K$), its birth rate increases to an asymptote r (with half-saturation constant a) as mutualist density increases in the absence of enemies. But if enemy damage makes flowers less attractive to pollinators (Strauss & Irwin 2004), the invader's birth rate will decline with enemy density (at a rate controlled by b). The invader birth rate also declines to zero when all K safe sites for invader recruitment are occupied. The second term on the right-hand side is the per capita invader death rate due to enemy attack. The per-enemy attack rate is assumed to reach an asymptote d/c (with half-saturation constant $1/c$) as invader density increases (i.e. enemy attack follows a Type II functional response). If R is the invader's per capita population growth rate at low density (i.e. when $P \ll K$ and $P \ll 1/c$), then

$$\frac{\partial R}{\partial E} = \frac{-brM}{(a + M + bE)^2} - d. \quad (3)$$

Equation 3 reveals that the effect of increasing enemy abundance on invader growth rate includes both a direct negative effect on mortality (the $-d$ term) and an indirect negative effect resulting from reduced pollination (the first term on the equality's right-hand side). This indirect effect would occur even if there were no change in pollinator abundance. Because both terms are negative and are multiplied by a negative ΔE in eqn 1 (if the enemy is less abundant in the introduced range), both the direct and the indirect effects of lower enemy density act to enhance the invader's growth rate (Fig. 1). Thus, when introduced plants are released from specialist herbivores, they may receive increased visitation by pollinators and decreased loss of flowers, fruits and seeds, enhancing the effects of enemy release.

Such synergistic effects may be common. Herbivores often, although not universally, decrease pollination and reproductive success (Strauss & Irwin 2004). For example, because introduced populations of *Silene latifolia* in North America experienced less floral herbivory (Wolfe 2002), they may receive additional benefit from pollinators relative to native populations. Other groups of enemies and mutualists may also interact to influence invader success. Herbivores generally reduce mycorrhizal colonization, and mycorrhizal fungi in turn commonly affect rates of herbivory, either positively or negatively (Gehring & Whitham 2002). A meta-analysis indicated that root nematodes decreased the effects of arbuscular mycorrhizal fungi on plant growth, and mycorrhizal fungus-inoculated plants were more impacted by nematodes (Borowicz 2001). The pattern of interaction was opposite for fungal pathogens and mycorrhizal fungi, with mycorrhizal fungi typically suppressing the pathogens (Borowicz 2001, but see

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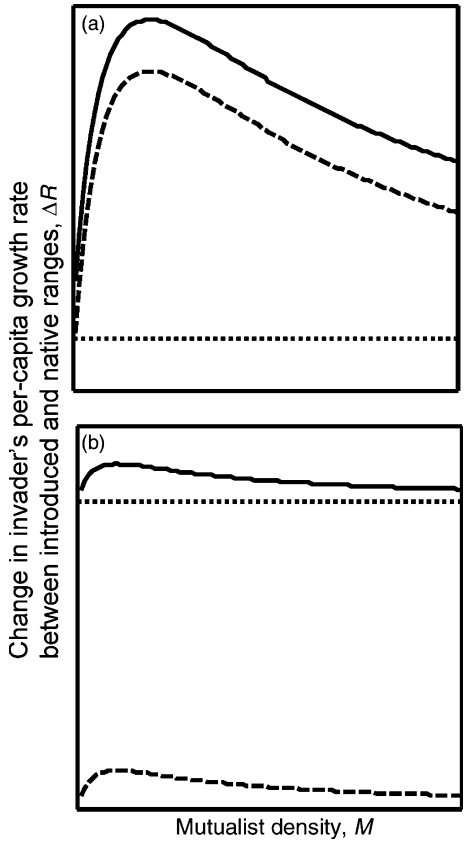

Figure 1 The total effect of enemy release (solid lines) predicted by eqn 2 is the sum of the direct effect (dotted lines) of lower herbivory-induced mortality and the indirect effect (dashed lines) of more effective pollination due to lower floral damage. The indirect effect is small at low mutualist density (because the invader's per capita birth rate is already low due to pollinator scarcity) and at high mutualist density (because pollinator abundance ensures adequate reproduction even in the face of floral damage). The indirect effect can be large (a) or small (b) relative to the direct effect, depending on whether pollinator deterrence or mortality is the predominant effect of herbivory.

Graham 2001). These studies suggest that the effects of enemy release may be compounded by allowing plants to receive greater net benefits from mutualists (the mutualism–enemy release hypothesis). Such an effect could result either from effects of enemies on plant allocation to mutualism (Gehring & Whitham 2002) or from direct effects of enemies on the mutualists (Borowicz 2001). Above-ground, a recent set of experiments documented that horizontally transmitted fungal endophytes of cacao greatly reduced the infection by pathogenic fungi (Arnold *et al.* 2003). Together, these studies suggest great potential for enemy–mutualist interactions to influence invader success.

Enemy attack and competition may also have interactive effects on invader success. Pathogens can decrease plant per capita competitive ability by acting as long-term sinks for nutrients and photosynthate, by altering plant allocation, and sometimes by releasing phytotoxic compounds (Paul 1989; Alexander & Holt 1998; Gilbert 2002). Herbivores can also decrease plant competitive ability (e.g. Carson & Root 2000). Increased ability to compete for resources as a result of enemy release is one possible mechanism for invader success (Tilman 1999). Thus, the benefits of enemy release may be greater under more intense competition (Keane & Crawley 2002; Shea & Chesson 2002), the competition–enemy release hypothesis.

Finally, there is growing evidence that invader success may depend on interactive effects of mutualists and competitors. Many plant mutualists such as pollinators and fruit dispersers directly increase plant density (e.g. by increasing seed set, seed dispersal or plant establishment) much more than they enhance plant per capita competitive ability, and therefore are more likely to be involved in interaction chains than interaction modifications. However, mycorrhizal fungi can directly increase plant per capita competitive ability by increasing resource uptake, and thereby indirectly alter the outcome of plant competition (e.g. Zabinski *et al.* 2002). In at least one case, this has been shown to favour an introduced plant over a native competitor, the mutualism–competition hypothesis. In two greenhouse experiments and one field experiment, the presence of arbuscular mycorrhizal fungi increased the per capita competitive effect of the introduced forb *C. maculosa* on the native grass *Festuca idahoensis* (Marler *et al.* 1999; Zabinski *et al.* 2002; Callaway *et al.* 2004), although not some other native species (Callaway *et al.* 2004).

Interaction chains: apparent competition and indirect facilitation

Invader success may be influenced by the abundance of enemies, mutualists or competitors that may or may not interact directly with the invader, but alter the abundances of other species that do (interaction chains, sensu Wootton 1994). Consider, for example, a generalist herbivore that consumes an introduced plant and its competitors in both the plant's native and introduced ranges, but is less abundant in the introduced range. Its lower abundance in the introduced range would have direct positive effects on the invader relative to the native range. But, it may also have indirect negative effects on invader success because the invader's competitors will also benefit from its lower abundance, potentially more so than the invader (Fig. 2a). Thus, an invader may experience release relative to native conspecific populations without simultaneously enjoying an advantage over competitors native to its introduced range (Keane & Crawley 2002; Shea & Chesson 2002; Torchin & Mitchell 2004).

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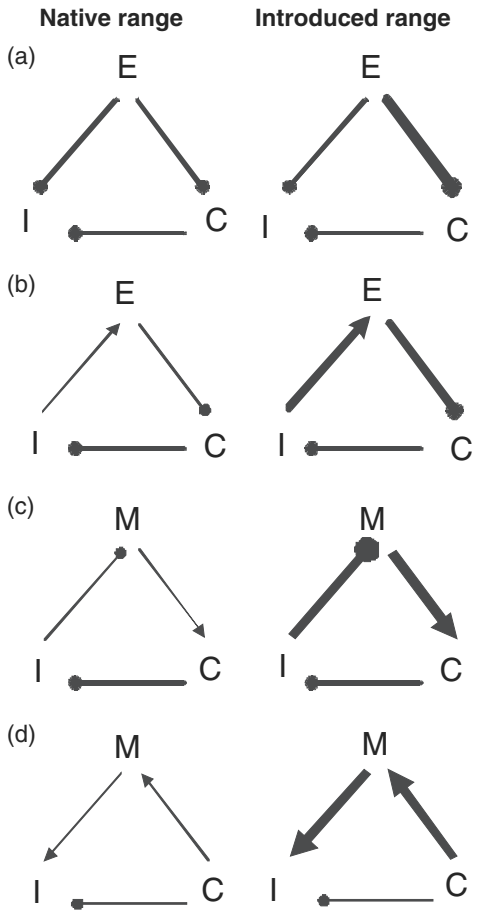

Figure 2 Four hypothesized interaction chains that may influence the success of introduced populations relative to native populations of the same species. Arrows represent positive effects on species densities and clubs represent negative effects. Relative thickness of lines indicates strength of interaction (measured per capita) relative to the same interaction in the other range (native or introduced). For each interaction, only one direction is shown to highlight the direction of the hypothesized interaction chain. *I* represents the introduced plant species, *E* represents an enemy species and *C* represents competing plant species. (a) If introduced plant species are less vulnerable to generalist enemy attack in the introduced range (perhaps because a coevolved enemy was introduced with the invader), competitors may benefit more from enemy release than the introduced species. (b) An introduced plant could facilitate its own success by increasing the density of enemies which have stronger negative effects on competitors in its introduced range than in its native range because of the difference in coevolutionary history. (c) An introduced plant could indirectly suppress competitors by decreasing the density of their mutualists. (d) Competitors in the introduced range may subsidize mutualists that benefit the introduced plant species.

Alternatively, invaders may benefit from enemy release relative to resident species but not relative to native conspecifics. For example, invader success may be enhanced by generalist enemies that accompany it from its native range, if the introduced species and its competitors in its native range have evolved mechanisms of resistance or tolerance to those enemies, but resident species in its introduced range have not (the enemy of my enemy hypothesis; Colautti *et al.* 2004). In this scenario, the introduced plant would inhibit competitors in its introduced range, but not those in its native range, via apparent competition by increasing the density of a shared enemy (Fig. 2b). This is an extension of the new associations hypothesis discussed above (Hokkanen & Pimentel 1989). For example, introduced grazers such as pigs, goats, deer, cows and bison can facilitate invasion of grazing-adapted plant species by decreasing the biomass of grazing-intolerant natives (O'Connor 1991; DiTomaso 2000; Hobbs 2001). Recently, Rand & Louda (2004) found that a native thistle was more heavily colonized by a weevil introduced as a biocontrol agent for an introduced thistle when it co-occurred with the invader. Thus, while invaders' specialist enemies are expected to consistently decrease invader success, generalist enemies (whether native or introduced) may decrease or enhance it depending on whether enemy impacts are greater on introduced or resident species (Noonburg & Byers 2005).

Mutualists can also mediate interactions between plant species, potentially enhancing invader success by either providing greater benefits to invaders or by being inhibited by invaders (the mutualism disruption hypothesis). For example, the invasive garlic mustard produces chemicals that inhibit mycorrhizal fungi (Roberts & Anderson 2001). Invaders can also attract pollinators away from natives, decreasing visitation rates and seed set (Chittka & Schurkens 2001; Brown *et al.* 2002). Such negative effects on competitors' interactions with mutualists may be greater in plants' introduced ranges (Fig. 2c), for example, if enemy release allows increased allocation to antifungal root exudates or floral displays.

Alternatively, native plants may increase the density of mutualists that benefit introduced plants, indirectly facilitating invader success (the subsidized mutualism hypothesis). Introduced plants, for example, may benefit from pollinators that are attracted by, or whose populations are supported, by native plants (Feldman *et al.* 2004; Moeller 2004). Bever (2002) found that a native grass increased the density of two species of mycorrhizal fungi which then strongly benefited the growth of an introduced plantain. Similarly, an introduced grass was found to benefit from the rhizosphere bacteria that accumulate with a native grass (Westover & Bever 2001). Invader success would be enhanced when such subsidies of mutualists by other plant species are greater in plants' introduced ranges than in their native ranges (Fig. 2d).

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Abiotic influence on biotic interactions

Introduced plants' interactions with enemies, mutualists and competitors will commonly take place under environmental conditions that differ from those in their native ranges. Additionally, biological invasions will always take place across environmental gradients and heterogeneity. The strength of herbivory, disease, mutualism and competition all commonly depend on the abiotic environment, particularly resource availability and climate. Increased resource availability can increase or decrease resistance and tolerance to pathogen infection (Givnish 1999; Mitchell *et al.* 2003; Gilbert 2005), and plant diseases have long been known to be highly sensitive to climatic variation (Coakley *et al.* 1999; Harvell *et al.* 2002; Scherm 2004). The outcome of plant–herbivore dynamics can also vary greatly across environmental gradients in sunlight, productivity or elevation (Louda & Rodman 1996; Olff *et al.* 1997). One recent study reported that release from environmentally dependent enemy attack allowed an introduced plant to expand both its geographical and environmental range (DeWalt *et al.* 2004). In a recent review, the outcome of competition between native and introduced plants depended on abiotic context in over half of the studies that tested for context dependence (Daehler 2003). Increased resource availability may interact with enemy release because introduced species with rapid growth rates may get the greatest advantage from both (the resource–enemy release hypothesis; Blumenthal 2005). The benefit derived from mutualistic interactions can be similarly environmentally contingent. For example, benefits of mycorrhizal fungi to host plants are greatly reduced in more nutrient-rich soils or by nutrient addition (Smith & Read 1997). Introduced species that do not require mycorrhizal associates may be able to flourish in eutrophic conditions. Finally, increased resource availability from natural or anthropogenic sources can decrease competition for those resources, facilitating the establishment and spread of introduced species (the fluctuating resources hypothesis; Davis *et al.* 2000).

Together, the well-documented dependence of biotic interactions on abiotic conditions leads to an important prediction: introduction to a new region may influence a plant's biotic interactions not only directly through the gain and loss of enemies, mutualists and competitors, but also indirectly by putting interactions with the same species in a different environmental context. Further, the ability of introduced populations to establish and spread will depend not only on the structure of the resident biotic community, but also on the local abiotic conditions, rather on their joint effects. In general, invader success should be enhanced in situations in which abiotic conditions reduce enemy impact or enhance mutualist impact on the invader relative to residents, or in which they increase invader competitive ability relative to residents. Introduced populations may be able to utilize places and times of jointly beneficial biotic and abiotic conditions to establish, then subsequently spread more broadly (the invasion opportunity windows hypothesis; Johnstone 1986; Agrawal *et al.* 2005).

Darwin's naturalization hypothesis

Darwin (1859) proposed that introduced species that are more closely related to the resident species are less likely to become naturalized (Darwin's naturalization hypothesis; Daehler 2001). Several studies have reported this general pattern (e.g. Mack 1996; Wu *et al.* 2004), but others that tested for it have not (Daehler 2001; Duncan & Williams 2002). The chief mechanism proposed for this pattern is that more closely related species compete more strongly because resource use requirements are more similar among closer relatives. However, this mechanism has not been directly tested. In our framework, this hypothesis and mechanism predict that plants introduced to communities with more closely related species will gain more new competitors with more negative competitive effects on the introduced species and have lower invader success. This hypothesis can be expanded to incorporate the joint effects of enemies, mutualists and abiotic conditions on invader success.

The opposite pattern, greater invader success for species more closely related to residents, would be expected if more closely related species require more similar abiotic environmental conditions (Daehler 2001). Spatial scale may be crucial in determining whether common abiotic requirements or resource competition dominate the success of particular species. Webb *et al.* (in press) found that at small spatial scales plant species were more likely to be successful if surrounded by plants species that were not closely related, whereas at larger spatial scales they found the opposite pattern. These results suggest that plant performance is reduced by competition from more closely related species at the neighbourhood scale, but at larger spatial scales more closely related species respond positively to the same abiotic factors. Thus, we predict that the balance between competition and environmental suitability will depend on spatial scale and degree of relatedness.

Introduced species more closely related to resident species may acquire more enemies from them (Mack 1996; Parker & Gilbert 2004). The host ranges of herbivores and pathogens exhibit a strong phylogenetic signal. Although there are exceptions, they are more likely to feed on or infect more closely related plant species (Coley & Barone 1996; Novotny *et al.* 2002; Parker & Gilbert 2004). As a result, invaders more related to the resident species should acquire additional enemies, particularly generalist enemies that previously attacked resident relatives. Available data support the hypothesis that greater phylogenetic relatedness

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increases accumulation of pathogens and insect herbivores by introduced plants (Connor *et al.* 1980; Blaney & Kotanen 2001; Parker & Gilbert 2004). Phylogenetic dependence of enemy accumulation has implications for the interpretation of experimental designs comparing introduced and native congeners (reviewed by Colautti *et al.* 2004 and Torchin & Mitchell 2004). Specifically, it implies that these studies may be conservative tests of the difference in enemy attack on native vs. introduced species in general because choosing introduced species with native congeners selects for species with greater potential to accumulate enemies.

The capacity for introduced species to form new associations with resident mutualists seems unlikely to depend strongly on phylogenetic relatedness (Richardson *et al.* 2000). However, even if multiple plant species all form associations with a given mutualist, they can vary widely in the degree to which they benefit from that association (van der Heijden *et al.* 1998; Bever 2002; Klironomos 2003). If the magnitude of benefits from a mutualist covaried with plant phylogeny, then this would facilitate the success of plants introduced into communities including close relatives.

Weaving these threads together, the reported variation among communities in the relationship between phylogenetic relatedness and naturalization (Mack 1996; Daehler 2001; Duncan & Williams 2002; Wu *et al.* 2004) may result from variation in the phylogenetic dependence of the effects of enemies, mutualists, competitors and suitable abiotic conditions. These mechanisms are potentially countervailing. The success of more closely related invaders is expected to be reduced by greater accumulation of enemies and competitors, but enhanced by greater accumulation of mutualists and more suitable abiotic conditions (Fig. 3). The direction of predicted outcomes for invader success will depend on the relative phylogenetic dependence of the four factors (the slopes of the lines in Fig. 3) and the strength and form of the interactions between the factors. Thus, Darwin's naturalization hypothesis is predicted to operate for combinations of introduced species and resident communities in which the phylogenetic dependence of the effects of enemies and competitors outweighs the phylogenetic dependence of the effects of mutualists and abiotic conditions.

Considering the potential for joint phylogenetic dependence of the effects of enemies, mutualists, competitors and abiotic conditions also allows specific predictions of which mechanisms are likely to explain invader success for different combinations of introduced and resident species (Table 2). For species introduced to communities including close relatives, rates of accumulation of enemies, mutualists and competitors should all be relatively high, and abiotic conditions should be relatively favourable. This suggests that invaders with low success in communities including close relatives are limited by the accumulation of enemies or competitors (biotic resistance; Table 2a). Invaders with high success in communities including close relatives are predicted to be facilitated by more favourable abiotic conditions (habitat filtering) or perhaps the accumulation of mutualists (Table 2b). For species introduced to communities without close relatives, rates of accumulation of enemies, mutualists and competitors should all be relatively low, and abiotic conditions may be unfavourable. In this case, invaders with low success are likely limited by unfavourable abiotic conditions (habitat filtering) or perhaps by the loss of mutualists for which there are no suitable resident replacements (Table 2c). Invaders with high success in communities without close relatives are likely facilitated by release from enemies or competitors (enemy release or empty niche; Table 2d). Finally, we emphasize that there is

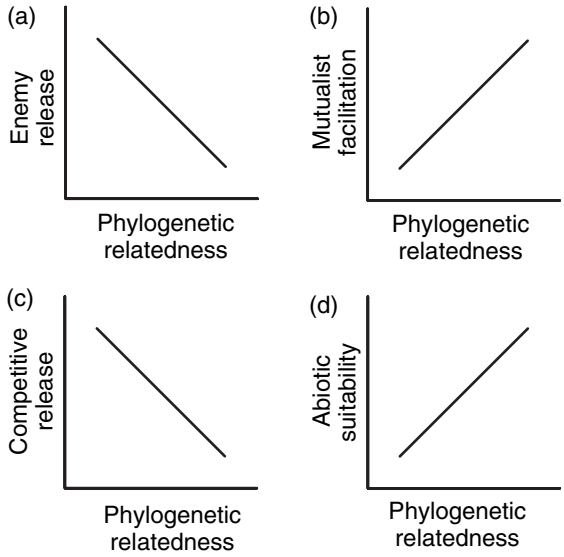

Figure 3 Hypothesized dependence of four proposed mechanisms for biological invasions on the phylogenetic relatedness of an introduced species to resident species, integrated across all those species. (a) The contribution of release from natural enemies to invader demographic success is predicted to be greater in communities of resident species less related to the introduced species, assuming that enemies are phylogenetically specialized. (b) The contribution of resident mutualists to invader success is predicted to be greater when the introduced species is more closely related to resident species, assuming that mutualists or their benefits are phylogenetically specialized. (c) The contribution of competitive release to invader success is predicted to be lower in communities of resident species more related to the introduced species, assuming that more related species have greater niche overlap. (d) The contribution of a suitable abiotic environment to invader success is predicted to be greater in communities of resident species more related to the introduced species, assuming that more related species are adapted to similar abiotic conditions. (a–d) To the degree that each of these assumptions is violated, the slopes of the hypothesized relationship would approach zero.

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Table 2 Predicted mechanisms for the success (lower vs. higher) of invaders that either have or do not have close relatives present in the resident community

	Invader success	
	Lower	Higher
Close relatives present	(a) Enemy or competitor accumulation (biotic resistance)	(b) Mutualist accumulation Favourable abiotic conditions (habitat filtering)
Close relatives not present	(c) Mutualist loss Unfavourable abiotic conditions (habitat filtering)	(d) Enemy release Competitor release (empty niche)

potential for interaction between the individual mechanisms outlined in each of the four combinations of invader success and relatedness. This cross-classification provides a general heuristic framework to guide hypothesis testing, and perhaps management strategies, for specific combinations of invaders and resident communities.

APPROACHES

Answering the numerous outstanding questions on biotic interactions and invasions will require biogeographical, taxonomical, and analytical integration. Here we highlight four approaches that may be particularly valuable in understanding how plant introductions alter biotic interactions, and how these interactions feed back to influence invader success. In general, we expect that the level of integration required to answer questions of how biotic interactions influence plant invasions will require increased scientific collaboration, including international collaboration bridging the native and introduced ranges of key study species.

Demography

There is a fundamental need for more studies of the demography of plants in both their native and introduced range, and particularly for studies that link demography to species interactions. Comparative demographic studies can shed light on the particular vital rates that change between ranges, and by how much. Demographic studies can also assess the efficiency of particular management strategies (Rees & Paynter 1997; Shea & Kelly 1998; McEvoy & Coombs 1999; Parker 2000). Because enemies, mutualists and competitors may often influence different life-history stages of a plant, demographic studies also provide an integrative framework for examining their joint effects at the population level. Population models parameterized with demographic data can be used to infer how population growth rates of an invader differ between the native and introduced range, an approach that has yet to be widely adopted (but see Grigulis *et al.* 2001).

Factorial manipulations

Descriptive demography studies should be complemented with experimental quantification of the effects of enemies, competitors, and/or mutualists on demography in both the plant's native and introduced range. Experiments are the strongest test of causal effects of biotic interactions on invader success, and the most reliable way to decouple the potentially complex feedbacks at play. An excellent first example of the power of this approach was recently provided by DeWalt *et al.* (2004), who used factorial exclusion of herbivores and pathogens in two habitat types in both the native and introduced range of the neotropical shrub *Clidemia hirta* to reveal the role of enemies in habitat expansion in the introduced range.

Phyloecology

The loss and gain of enemies, mutualists and competitors, as well as the suitability of abiotic conditions, all are expected to depend on phylogenetic relatedness of introduced and resident species. Testing these predictions requires measuring the phylogenetic similarity between introduced species and members of the recipient communities they enter. Qualitative assessments at the genus or family level have been a valuable starting point, but new methods to quantify the phylodiversity of plant neighbourhoods promise to provide a more powerful approach (Webb *et al.* in press).

Ontogeny of invasion

Enemies, mutualists and competitors may influence different stages in the invasion process, such as colonization, growth and spread, and long-term adaptation. For example, herbivores may exert strong control over invaders in small, incipient patches, but not once densities are high (e.g. Fagan & Bishop 2000). Therefore, studies should be designed to take advantage of chronosequence sites that vary in invasion stage (e.g. Siemann & Rogers 2001; Torchin *et al.* 2001). By turning introduction status from a categorical to a

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continuous variable, the chronosequence approach is a logical and potentially more powerful extension of biogeographical approaches testing for differences between plant's native and introduced ranges (Hierro *et al.* 2005).

CONCLUSIONS

We have outlined numerous ways in which biotic interactions can influence the dynamics of biological invasions by plants. Several general points emerge. Introduced populations interact with different species of enemies, mutualists and competitors, and do so under different abiotic conditions, than do the native populations from which they stem. Evidence is accumulating that the corresponding shifts in species composition of enemies and of competitors contribute to the demographic success of introduced populations. Similar studies of mutualists are more limited and more ambivalent. Enemies, mutualists and competitors of introduced plants can interact to influence invader success through both interaction modification indirect effects and interaction chain indirect effects. Because these indirect effects will commonly involve resident species, they are also potential mechanisms for impacts on native biodiversity. The effects of biotic interactions on invaders will also depend on abiotic environmental conditions. These conditions are not only naturally variable in space and time, but increasingly driven by anthropogenic processes and sometimes by biological invasions themselves. Ultimately, work to date shows clearly that biological invasions dramatically alter biotic interactions, and suggests that these interactions may commonly feed back to influence invasion dynamics.

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