

**IDEA AND
PERSPECTIVE**

Plant invaders and their novel natural enemies: who is naïve?

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Abstract

Introduced exotic species encounter a wide range of non-coevolved enemies and competitors in their new range. Evolutionary novelty is a key aspect of these interactions, but who benefits from novelty: the exotic species or their new antagonists? Paradoxically, the novelty argument has been used to explain both the release from and the suppression by natural enemies. We argue that this paradox can be solved by considering underlying interaction mechanisms. Using plant defenses as a model, we argue that mismatches between plant and enemy interaction traits can enhance plant invasiveness in the case of toxin-based defenses, whereas invasiveness is counteracted by mismatches in recognition-based defenses and selective foraging of generalist herbivores on plants with rare toxins. We propose that a mechanistic understanding of ecological mismatches can help to explain and predict when evolutionary novelty will enhance or suppress exotic plant invasiveness. This knowledge may also enhance our understanding of plant abundance following range expansion, or during species replacements along successional stages.

Keywords

Biological invasions, biotic resistance, co-evolution, enemy release, herbivorous insects, novel interactions, plant-herbivore interactions, plant-pathogen interactions, vertebrate grazers.

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THE PARADOX OF NOVEL SPECIES INTERACTIONS

An important role in understanding the invasiveness of introduced exotic species is often attributed to their release from natural enemies (Keane & Crawley 2002). However, enemy release is only one of several possible explanations for invasiveness (Mitchell *et al.* 2006) and the mechanisms that determine the outcome of interactions with native enemies in their new range are still poorly understood. Here, we explore underlying mechanisms of plant-enemy interactions and we ask how these mechanisms affect the outcome of novel, non-coevolved interactions. This analysis provides a framework for understanding host-enemy interactions in newly assembled communities. Our aim is to contribute to predictive theory that may help to further explain why some exotic species may and others may not become invasive in their new range.

The Enemy Release hypothesis (ER) proposes that introduced plants become invasive pests because they benefit from escaping their coevolved enemies (Keane & Crawley 2002). Whilst the benefits of leaving coevolved

enemies behind are evident and have received ample attention, it is less clear how an exotic plant is affected by novel, non-coevolved herbivores and pathogens that it encounters in its new environment. This, however, is an important component of ER (Keane & Crawley 2002; Colautti *et al.* 2004; Agrawal *et al.* 2005). Enemy release can be considered as the net effect of losing old enemies and acquiring new enemies. If an introduced plant suffers more from its novel enemies in its new range than that it did in its old range, its potential to become a successful invader is limited. The latter is consistent with the Biotic Resistance hypothesis (BR), that proposes that natural enemies (as well as competing plant species, Naeem *et al.* 2000) prevent successful establishment and spread of an invader in novel communities (Elton 1958; Maron & Vila 2001). Despite their contrasting consequences for introduced species, ER and BR are not mutually exclusive hypotheses (Mitchell *et al.* 2006). Rather, they highlight the fact that natural enemies can be invoked to explain both the success of some invaders and the failure of others. For instance, some studies have shown that introduced plant species overall harbour fewer

enemies in the novel range (the loss of old enemies exceeds the gain of new enemies, consistent with ER). At the same time, the introduced species that have acquired the most new enemies are the least invasive ones (consistent with BR) (Mitchell & Power 2003; Carpenter & Cappuccino 2005).

Empirical studies comparing populations of exotic species from their native and introduced ranges (biogeographic comparisons, *sensu* Colautti *et al.* 2004) have generally supported ER in terms of demonstrating reduced enemy abundance or diversity in introduced ranges (e.g. Wolfe 2002; Mitchell & Power 2003; Colautti *et al.* 2004; van der Putten *et al.* 2005; Liu & Stiling 2006). Few studies have provided additional support for reduced demographic impact (release from enemy effects, DeWalt *et al.* 2004). Studies comparing populations of exotic species in their new range with populations of (usually congeneric) indigenous species that are native to the invaded communities (community comparisons, *sensu* Colautti *et al.* 2004) have been more equivocal in their support for ER, with some studies actually showing higher, rather than lower incidence or damage by enemies on exotic species than on co-occurring indigenous congeners (Agrawal & Kotanen 2003; Parker & Hay 2005). Moreover, only few studies have explicitly investigated whether successful invasive exotics suffer less from enemies than non-invasive exotics (Mitchell & Power 2003; Cappuccino & Carpenter 2005; Carpenter & Cappuccino 2005; Liu & Stiling 2006). This would be a necessary condition for enemy release to drive the disproportionate abundance of invasive species in their new range.

While empirical tests of ER reveal mixed patterns, we know even less about the underlying factors that cause some introduced plants to suffer from their novel enemies whereas other introduced plants are able to escape from them. Introduced plants have become disconnected from their coevolved biotic relationships and engage in novel, non-coevolved relationships with herbivores and pathogens in their new range (Agosta 2006; Hallett 2006). Current thinking mainly stresses the potential benefits of evolutionary novelty for introduced plants. For instance, introduced plants may possess toxic compounds that evolved in their native range against their own enemies but which are novel to indigenous, non-coevolved, herbivores and pathogens that have not evolved adaptations to deal with the toxins. This can confer direct or indirect advantages to introduced plants in their interactions with indigenous enemies or competitors (Callaway & Aschehoug 2000; Vivanco *et al.* 2004). Indeed, Cappuccino & Arnason (2006) reported that introduced plants possessing defense chemicals that are different from indigenous plant species tend to be more invasive than introduced plants that share defense chemicals with indigenous plant species. Similarly, Louda & Rand

(2003) reported a close phylogenetic relationship between introduced and indigenous thistle species that enabled indigenous herbivores to recognize and exploit the introduced species, thus effectively suppressing its invasive potential.

The above-mentioned studies stress the advantage of evolutionary novelty for the invading plant, arguing that enemies or competitors have not been selected to resist or tolerate the 'novel' plant's defenses. In contrast, Parker *et al.* (2006) stressed the advantage of evolutionary novelty for the indigenous enemies. Faced with experimental evidence that vertebrate herbivores tend to suppress exotic plants more than indigenous plants, they argued that plants are especially susceptible to novel, generalist herbivores that they have not been selected to resist. In that case, evolutionary novelty could mean that the introduced plant fails to establish or spread successfully in its new range.

Thus, the evolutionary novelty argument has been used to explain both successful and unsuccessful invasions and both seem to be supported by empirical data. Resolving this paradox of novel species interactions and understanding why evolutionary novelty in some cases leaves plants defenseless against new enemies whilst in other cases it leaves enemies incapable of exploiting new hosts, requires consideration of the underlying mechanisms. Interactions between plants and their enemies are controlled by mechanisms of recognition, host selection and preference, as well as by offensive and defensive strategies. These mechanisms have been well studied in coevolved systems, but the consequences of these mechanisms for novel interactions during plant invasions have received much less attention (Parker & Gilbert 2004; Cappuccino & Arnason 2006; Hallett 2006; Mitchell *et al.* 2006). Depending on the time elapsed since introduction, the outcome of novel interactions will reflect instantaneous (ecological) matches and mismatches, or a combination of initial matching and rapid (co-)evolution following novel encounters. After introduction, rapid evolution in novel interactions is well-documented (Blossey & Notzold 1995; Müller-Schärer *et al.* 2004; Parker & Gilbert 2004; Carroll *et al.* 2005). Here, we focus on the consequences of initial mechanistic (mis-) matches in novel interactions, and we will briefly consider how the interactions are affected by subsequent evolutionary processes. We argue that evolutionary novelty leads to mismatching interaction systems and we show that mismatches in some defense mechanisms are intrinsically beneficial to introduced plants, while mismatches in other defense mechanisms are beneficial to their enemies. We will focus our discussion on biological plant invasions, but our results may also apply to range expanding plant species, e.g. due to climate warming, or to expansion along successional gradients.

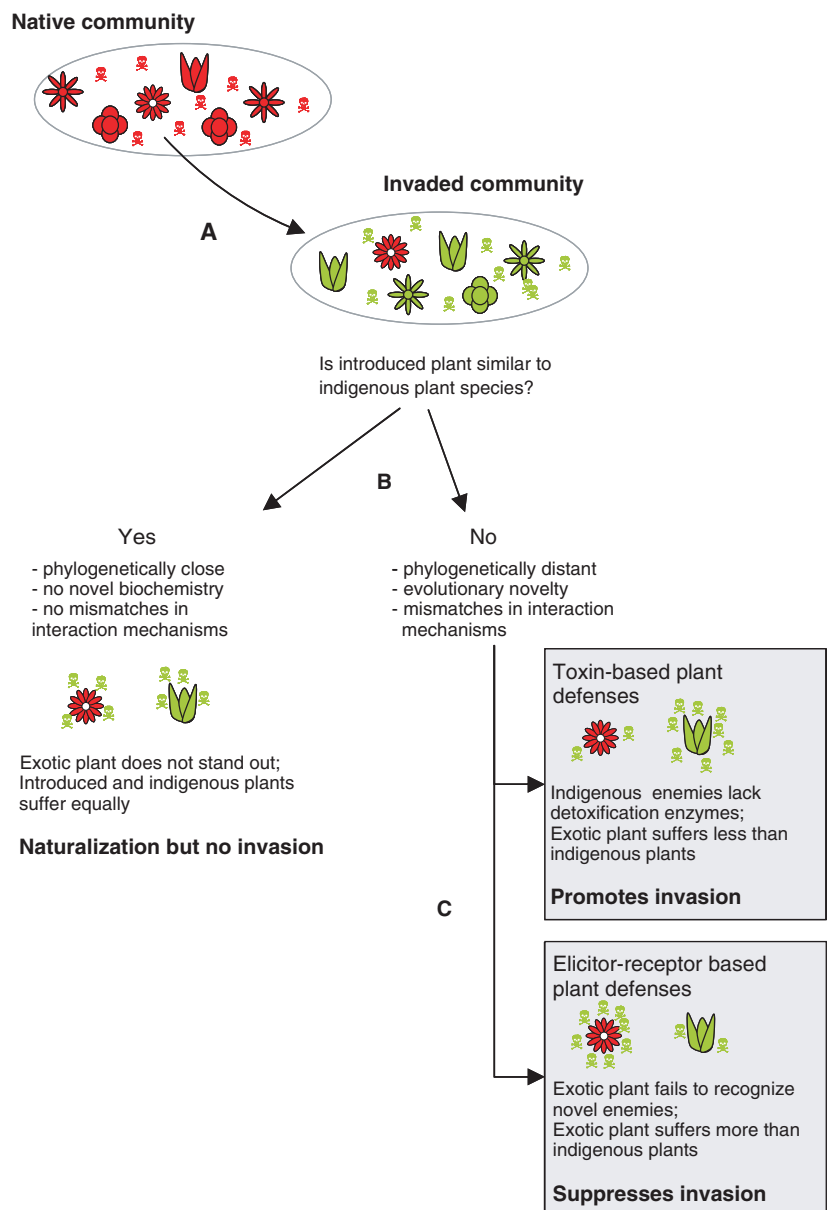
WHO IS NAÏVE IN NOVEL INTERACTIONS?

The paradox of novel species interactions can be illustrated by comparing two different and important interaction principles that frequently occur between host plants and their enemies: toxin-detoxifier and elicitor-receptor mechanisms (Kniskern & Rausher 2001) (Fig. 1). In toxin-detoxifier systems plants evolve secondary metabolites that are toxic to their enemies. Enemies evolve matching detoxification pathways, prompting hosts to evolve modified toxins, and this co-evolutionary process continues in time. Toxin-detoxifier systems are widespread and play an important role in many plant-insect herbivore interactions

(Gatehouse 2002). The molecular basis of such interactions, mediated by three major groups of genes, is well understood (Li *et al.* 2007). Recent studies, e.g. of Papilionids on Apiaceae (Li *et al.* 2003) and Pierids on Brassicaceae (Wheat *et al.* 2007) confirm the traditional view that plant chemical evolution has been followed closely by biochemical adaptation in insect herbivores, and that detoxification activity closely matches the distribution of host toxins both at the species and population level.

In elicitor-receptor systems plants evolve receptors that recognize enemy elicitor molecules, and this recognition is required in order for the plant to mount a defense response. Enemies evolve to evade recognition through modification or

Figure 1 Effects of evolutionary novelty and host-enemy interaction mechanisms in invasions. (a) Exotic plants leave native enemies behind (red skulls) and encounter new indigenous enemies in their new range (green skulls). (b) From the perspective of indigenous enemies, phylogenetic relationship between the exotic and indigenous plants determines if the exotic stands out or not. If the defense traits of the exotic plant are not novel to the indigenous enemies there is no reason to assume that the exotic and indigenous plants will suffer differently from indigenous enemies. (c) If the exotic's traits are novel there will be mismatches with the indigenous enemies, and it depends on the underlying interaction mechanisms whether these mismatches promote or suppress invasion. In *toxin-based defenses* plants evolve secondary metabolites that are toxic to their enemies. Through co-evolution enemies develop matching detoxification pathways, prompting hosts to evolve modified toxins, etc. Mismatches result in indigenous enemies lacking detoxification enzymes, contributing to enemy release and plant invasion. In *elicitor-receptor based defenses* plant receptors recognize enemy elicitor molecules, and this recognition triggers a defense response. Enemies evolve to evade recognition through modification or loss of the elicitor molecules. Hosts then evolve to target novel enemy-derived molecules, etc. Mismatches result in non-indigenous plants failing to recognize indigenous enemies, contributing to biotic resistance and suppressing invasion.



loss of the molecules that function as elicitors. Hosts then evolve to target novel enemy-derived molecules, and so on. Elicitor-receptor systems are the classic mechanisms underlying interactions between plants and microbial pathogens (Jones & Dangl 2006). The molecular basis (Dangl & Jones 2001) and evolutionary dynamics (Mcdowell & Simon 2006; Jiang *et al.* 2007) of these processes are well studied. One of the recent insights is that the involvement of such recognition systems is not restricted to specialized gene-for-gene interactions between highly diverged effector molecules encoded by avirulence genes (*Avr*) genes of biotrophic pathogens and the resistance gene (*R*) products of their hosts. Recognition systems are also involved in non-host and basal resistance, where transmembrane pattern recognition receptors (PRRs) recognize slowly evolving pathogen-associated molecular patterns (PAMPS) such as flagellins or chitins (Nurnberger & Lipka 2005).

In both systems local co-evolution involves reciprocal adaptation between the plant and its enemy, and either player can temporarily take the lead in the co-evolutionary process. The difference between the two systems is revealed in novel interactions, where mismatches between plant and enemy traits result from the fact that both players had been engaged in different co-evolutionary races. Mismatches in toxin-detoxifier systems confer an inherent advantage to plants, because naïve enemies lack proper detoxification mechanisms to unknown toxins. Such mismatches will contribute to enemy release and invasive spread. Mismatches in elicitor-receptor systems provide an inherent advantage to enemies as they will go undetected by naïve plants, and will therefore contribute to biotic resistance and the suppression of invasion.

Many of the best-studied examples of plant-pathogen and plant-herbivore interactions are characterized by combinations, or variations, of these two basic mechanisms. What types of mechanisms dominate interactions between plants and their most important enemies? Below, we explore the consequences of mismatches in a number of common or well-studied mechanisms of plant-pathogen, plant-insect herbivore and plant-mammalian herbivore interactions.

Host choice and foraging preferences

Many insect herbivores are relatively specialized (Bernays 1998) and rely on biochemical and visual cues from their host plants for recognition, feeding and oviposition (Renwick 2001; Chapman 2003; Rojas *et al.* 2003). All plants possess chemical fingerprints (reflecting phylogenetic history) and mismatches in the perception of such cues at any stage in the herbivore's life cycle can result in escape from herbivory (Feeny 1991). Perception mismatches by indigenous herbivores of cues from introduced exotic plants will therefore

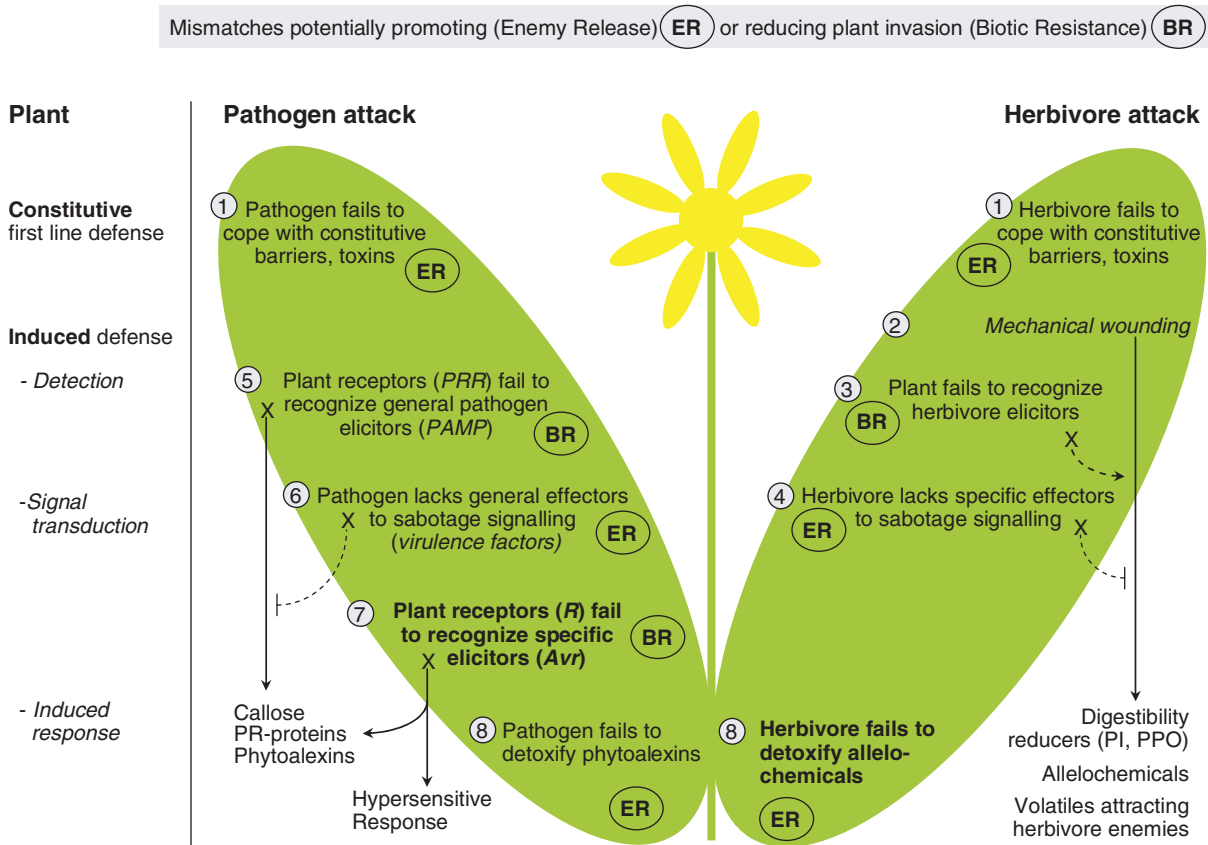
contribute to ER. For example, if an exotic plant possesses novel chemistry, then it may not be recognized by potential indigenous insect herbivores which fail to alight or oviposit on it even if it is a suitable host plant for development. Compared to insects, many mammalian herbivores are more generalist herbivores and can effectively deal with a broad range of different plant toxins (Freeland & Janzen 1974; Foley & Moore 2005). One consequence is that there is less scope for toxin-detoxifier mismatches and introduced plants are, therefore, much more likely to escape novel insect herbivores than novel mammalian herbivores. Moreover, mammalian generalist herbivores have been shown to forage selectively in order to minimize the toxic effects of plants (Iason & Villalba 2006; Sorensen & Dearing 2006). One strategy is to spread the toxin load effectively over different detoxification pathways. By switching between plants with different toxins, herbivores can ensure that no single toxin exceeds a critical metabolic threshold (Marsh *et al.* 2006). If an exotic plant produces toxins that are novel or rare in the indigenous plant community, generalist mammalian herbivores may thus prefer the exotic over indigenous plants when trying to avoid locally common toxin types. This would contribute to biotic resistance at the initial stages of invasion, when the introduced exotic plants occur at local low frequency. Similarly, some intestinal transporters of mammalian herbivores that regulate absorption of toxins appear to be activated by particular plant secondary metabolites (Sorensen & Dearing 2006). Generalist herbivores could take advantage of such compounds by including host plants producing these compounds in their diet to reduce absorption of toxic secondary metabolites from other plants.

Plant defenses

After having chosen a particular plant, enemies need to circumvent the plant's defenses for successful exploitation. Plant defenses are either preformed (constitutive defenses) or induced upon detection of enemy attack (Karban & Baldwin 1997; Mysore & Ryu 2004) (Box 1). Constitutive defenses such as structural barriers and toxins are potent defenses against a wide range of herbivores and pathogens except those that have suitable counter-adaptations like detoxification or excretion pathways (Gatehouse 2002; Pedras & Ahiahonu 2005). Some constitutive defenses are more widespread or more broad-spectrum in their functioning than others, and mechanistic mismatches will occur more readily with respect to plant toxins than with respect to some general structural defenses such as cell wall lignin and silica depositions. But when mismatches occur between constitutive chemical or structural plant defenses and novel enemies, this will contribute to ER and plant invasiveness. However, mismatches in the case of inducible defenses can either enhance or reduce invasiveness. In the chain of events

BOX 1. PLANT DEFENSE MISMATCHES IN NOVEL PLANT-ENEMY INTERACTIONS

Mismatches in plant-pathogen (left) and plant-herbivore interactions (right) may contribute to enemy release (ER; increasing plant invasion potential) or biotic resistance (BR; reducing plant invasion potential), depending on underlying interaction mechanisms. Solid arrows indicate induced responses, dotted lines indicate enhancement (arrows) or inhibition (vertical bars) of the induced response. X's at the beginning of a line indicates that the indicated mismatch results in failure of the response.



Constitutive defenses. As a first line of defense, plant enemies encounter physical or structural barriers (e.g. lignified cell walls) that provide little opportunity for mismatches, as well as constitutive chemical defenses (Gatehouse 2002; Mysore & Ryu 2004) (1). Toxin-detoxification mismatches at this stage (constitutive chemical defenses) will promote plant invasion due to ER, because enemies lack appropriate detoxification.

Initiation of induced defenses. Wounding by chewing insect herbivores (2) triggers the release of endogenous elicitors (e.g. systemin) that initiate a signalling cascade, activating induced defense responses including increased production of allelochemicals, digestibility reducers (e.g. proteinase inhibitors, PI, and polyphenol oxidases, PPO), and herbivore-induced plant volatiles (HIPV) (Gatehouse 2002). Wound-induced signalling responses can be enhanced or inhibited by compounds from insect herbivore saliva [e.g. volicitin and glucose oxidase, respectively (Musser *et al.* 2002)]. Failure of plants to recognize such elicitors (3) will reduce invasion potential due to BR, while lack of appropriate inhibitors in herbivores (4) may promote invasion potential due to ER. However, initiation of the wound response is rather general, and mismatches in downstream mechanisms that enhance or inhibit the defense response may have relatively minor effects.

By contrast, initiation of induced defenses against pathogens, including the production of phytoalexins and defense-related proteins, usually requires specific recognition of pathogens. In non-host and basal resistance, detection is primarily based on recognition of general elicitors (5), so-called PAMPs (pathogen-associated molecular patterns, e.g. flagellins, chitins) (Mysore &

Ryu 2004; Nurnberger & Lipka 2005). Since PAMPs are highly conserved, recognition mismatches may be rare, but if invading plants lack the transmembrane pattern recognition receptors (PRR) for local PAMP recognition it will reduce invasion potential due to BR. Pathogens require general effectors (6) (virulence factors) that inhibit signalling and downstream responses to successfully exploit their hosts (Alfano & Collmer 2004). Lack of appropriate virulence factors may promote plant invasion due to ER. The strongest and best-studied defense response of plants to pathogens, the hypersensitive response (HR, localized programmed cell death), is primarily mounted upon recognition of specific effector molecules (Avirulence factors, Avr) (7) by products of plant resistance (R) genes (Jones & Dangl 2006). Mismatches at this stage, i.e. failure to recognize pathogen Avr may reduce invasion potential due to BR.

Expression of induced defenses. Further mismatches may occur if indigenous pathogens or insect herbivores fail to effectively deal with induced toxic compounds (excretion, detoxification, absorption regulation, etc.) (Glendinning 2002; Pedras & Ahiahonu 2005) (8), promoting plant invasion via ER.

that lead from detection of attack via signal transduction to the expression of induced defenses, different types of molecular interactions take place between plant and enemy (see Box 1). Failure of an introduced plant to detect attack by novel enemies will contribute to BR. A detection mismatch may be difficult to envision when the cue for detection is very non-specific, such as herbivory detection via a generalized mechanical wounding response. Non-specific mechanisms do not discriminate between coevolved and novel enemies and do not actively contribute to either ER or BR. However, opportunities for detection mismatches increase when the cues used are more specific. For instance, the initiation and also the signal transduction pathway of induced defenses against coevolved pathogens depends critically on the recognition of specific pathogen molecules (Jones & Dangl 2006), which broadens the potential for mismatches that contribute to BR. In coevolved plant-enemy systems, a common strategy of herbivores and pathogens is to sabotage the plant's signaling pathway that leads to the induced defense response. They can produce compounds that interfere with the signaling pathway, and in return plants have evolved ways to neutralize these sabotaging efforts (see Box 1). Mechanistic mismatches in these systems between introduced plants and novel enemies could contribute to ER if attempts of enemies to block the plant's induced defense response are unsuccessful.

DIFFERENT EFFECTS OF DIFFERENT NOVEL ENEMIES?

Complex plant defenses against specific enemies typically contain both 'mismatch-leads-to-enemy release' elements and 'mismatch-leads-to-biotic resistance' elements (see Box 1). This means that exposure to almost any novel enemy could potentially contribute to either biotic resistance or enemy release. However, the relative importance of toxin-detoxifier and elicitor-receptor mechanisms may differ between different types of enemies, and this could lead to some general trends in how novel enemies affect exotic plants. For instance, the toxin-spreading selective foraging

strategy observed in mammalian generalist herbivores (Marsh *et al.* 2006), which could contribute to biotic resistance, may be less relevant to insect herbivores. Exotic plants may therefore be more vulnerable to biotic resistance from mammalian than from insect herbivores. Second, research in plant-pathogen interactions has traditionally emphasized elicitor recognition-based plant defenses (Parker & Gilbert 2004; Jones & Dangl 2006) while much of the plant-insect literature is focused on toxin-detoxification mechanisms (Gatehouse 2002). If these are the predominant mechanisms in plant-pathogen and plant-herbivore interactions, respectively, it suggests that mismatches between exotic plants and local pathogens contribute to biotic resistance while mismatches between exotic plants and insect herbivores may result in enemy release. It is clear that the situation is not this simple. For instance, non-host resistance against many potential pathogens may be based, at least in part, on constitutive, broad-spectrum antimicrobials and other non-specific preformed barriers (Nurnberger & Lipka 2005) that leave little room for mismatches. Nevertheless, induced defenses against herbivores may indeed be more easily triggered by non-specific cues (following wounding) than induced defenses against pathogens, which more strongly rely on specific recognition mechanisms (Box 1). While the complexity of underlying mechanisms may make it difficult in an individual case to accurately predict the outcome of novel plant-enemy interactions, certain mechanisms play an important role in determining the outcomes of ER or BR outcomes and insight into these mechanisms is needed to elucidate the different patterns that are observed for different enemy types (Cappuccino & Arnason 2006; Parker *et al.* 2006).

Based on mechanistic considerations described above, and ignoring complexities, is there a general trend showing that mammalian herbivores play an important role in biotic resistance? Or that novel exotics more easily acquire indigenous fungal pathogens while they tend to escape from novel insect herbivores? Testing such mechanistic predictions requires new data. Most previous studies on interactions between indigenous and exotic species and local

enemies have not accounted for differences in their introduction histories and time since introduction, making it difficult to single out effects of initial (mis-)matches. Most studies also focus on successful invaders, while evaluation of initial (mis-)matches requires knowledge of both successful and unsuccessful invasion attempts. Given these limitations, some observed patterns nevertheless appear to be consistent with mechanistic predictions. For example, exotic plants in Canada were found to suffer less from insect herbivory than indigenous plants (Cappuccino & Carpenter 2005; Carpenter & Cappuccino 2005) and plant biochemical novelty was negatively associated with herbivore damage and positively associated with invasion success (Cappuccino & Arnason 2006). This is consistent with a toxin-detoxification-mismatch-advantage for exotic plants when exposed to insect herbivores. In contrast, a similar analysis of the impact of native (mainly vertebrate) herbivores revealed a stronger suppression of exotic plants than of indigenous plants (Parker *et al.* 2006). This is consistent with the limited scope for toxin-detoxification mismatches between plants and broad generalist herbivores that in addition may forage selectively to avoid the over-consumption of locally common toxin types. Further, direct comparisons have shown that introduced plants can deter novel insects more easily than novel pathogens, even though this does not necessarily translate into invasion success (Parker & Gilbert 2007).

Other observations, however, are more difficult to interpret. If elicitor-receptor mechanisms play an important role in plant-pathogen interactions, then mismatches between invaders and novel pathogens should tend to suppress invasiveness because novel pathogens are not recognized by the plant. While pathogens have indeed been implicated in biotic resistance in some systems (Knevel *et al.* 2004), a considerable number of introduced exotic plants seem to be able to resist or escape novel pathogens and become invasive. For instance, black cherry (*Prunus serotina*) is controlled by soil pathogens in its native range but is apparently released from soil-borne pathogen control in its invaded range, despite the presence of various indigenous *Prunus* species in the invaded range (Packer & Clay 2000; Reinhart *et al.* 2003). An interesting twist to this story is that some invaders do accumulate pathogens or viruses in their new range, consistent with simple mechanistic predictions, but suffer relatively little fitness costs from these pathogens. On the contrary, the accumulated pathogens provide a reservoir that suppresses surrounding indigenous plants (Malmstrom *et al.* 2005; Mangla *et al.* 2008) and this can lead to an increase in the abundance of the introduced species (Eppinga *et al.* 2006). Thus, elicitor-receptor mismatches may result in failure of introduced plants to recognize novel pathogens, but this does not necessarily result in biotic resistance: novel host-pathogen interactions may promote

invasiveness via indirect effects on indigenous plants, thereby changing competitive relationships in the new range.

TEMPORAL CHANGES IN ENEMY IMPACT

During the course of an invasion exotic plants may encounter many novel enemies and evolutionary changes then allow the invader and its new suite of potential enemies to gradually adapt to each other. Previous work has emphasized the post-introduction evolution of exotic plants (Müller-Schärer *et al.* 2004). While an exotic plant's evolutionary potential could be constrained by limited genetic variation in small initial population sizes, some work suggests that considerable and rapid evolutionary changes are possible despite recent population bottlenecks (Sax *et al.* 2007). For instance, exotic populations of Canary Island St. John's Wort showed significant reductions in genetic variation in their new range but these populations evolved adaptive local differences in flowering phenology within a period of < 50 years (Dlugosch & Parker 2008). The evolutionary potential of exotics can be enhanced by repeated introductions from different source populations, that can lead to admixed exotic populations with high genetic variation (Lavergne & Molofsky 2007). The initial rarity of exotic species also creates asymmetries in selection that can be beneficial to them, as local enemies will experience little selection to adapt to exotics that they rarely encounter (Parker & Gilbert 2004), whereas exotics are under strong selection to adapt to their new enemies. However, as the population size increases, selection on enemies to exploit the exotic species also increases, and the enemies' evolutionary potential might exceed that of exotics. For instance, many microorganisms have large population sizes, rapid generation cycles, and may be capable of horizontal gene transfer (Ochman *et al.* 2000), factors which may accelerate the process of adaptation. Over time this can help pathogens, for instance, to overcome invaders' constitutive defenses and to efficiently exploit a host's resources after its defenses have been successfully circumvented.

In insect herbivores there is ample opportunity for fast genetic adaptation (Carroll *et al.* 2005; Strauss *et al.* 2006) and also for extremely rapid non-genetic change as feeding and oviposition choices are partly based on learned preferences (Renwick 2001). Specialized herbivores may initially avoid an invader because they do not recognize its chemical fingerprint while in fact they possess the necessary physiological tools to disarm its toxins. Through learning, which can overrule previous deterrent responses (Glendinning 2002), rapid host shifts are possible that could quite rapidly erode an invader's initial release from herbivory in the new range. Thus, invasion success based on enemy release is unlikely to last for long, and can be expected to

decrease with time (Hawkes 2007) and with the geographical area (Andow & Imura 1994) of the invasion. A number of invasive exotic plants have indeed shown a rapid decline, or even extinction, once adapted or novel pre-adapted enemies found and exploited them (Creed 2000; Simberloff & Gibbons 2004; Siemann *et al.* 2006).

It is, therefore, important to consider temporal processes in empirical tests of enemy release and biotic resistance. For instance, in studies that compare enemy impacts on exotic and co-occurring indigenous species (Agrawal *et al.* 2005; Parker *et al.* 2006; Parker & Gilbert 2007) it is crucial to distinguish between newly arrived exotic plant species, successfully spreading invaders and long-naturalized exotics that are no longer dominant. The first group includes successful species that may experience enemy release but also many unsuccessful ones that will be controlled by biotic resistance. The latter two groups are non-random subsets of introduced species, including only those species that at least have not perished due to biotic resistance. The potential for rapid enemy adaptation suggests that changes in enemy effects, at a local scale, might occur in a comparatively short period of time.

CONCLUSIONS

Research on plant invasions has focused largely on documenting patterns, but the underlying mechanisms that are responsible for the observed patterns have thus far received little attention (Levine *et al.* 2003). Studies on invasive species need to be linked more broadly with ecological and evolutionary theory (Callaway & Maron 2007; Sax *et al.* 2007) instead of developing as a distinct sub-discipline on their own. Enemy release and biotic resistance provide excellent opportunities for empirical studies on interaction mechanisms. Exploring the mechanisms underpinning these hypotheses can greatly contribute to understanding how the abundance of different species in natural communities are controlled in their non-native, as well as in their native ranges. A major feature of exotic species is that they have an evolutionary mismatch with natural enemies in the introduced range. Such mismatches have been argued to enhance (Cappuccino & Arnason 2006) or suppress (Parker *et al.* 2006) invasions. We conclude that these contrasting results do not represent opposing views, but that they reveal that plants can either benefit or suffer from mismatches in different underlying interaction mechanisms.

A mechanistic perspective of ecological mismatches exposes the underlying proximate causes of enemy release and biotic resistance, and can help to develop a better understanding as to why some introduced exotic plants become invasive while many others are suppressed. However, many important gaps still exist in our knowledge and some basic questions remain to be addressed in future

studies. Importantly, our knowledge of plant-enemy interactions is largely based on rather specialized systems where the largest scope for mismatches exists in mechanisms that are specific for coevolved interactions (such as specific effector recognition in pathogen defense; Box 1). On the other hand, many novel interactions will concern generalists (Keane & Crawley 2002). In these interactions, mechanisms of constitutive defense and non-host resistance (constitutive barriers, general pathogen elicitor recognition; see Box 1) can be more important. In order to further our understanding, the following questions need to be addressed:

- (1) Are there generalities in the strength of top-down control that are exerted by different types of natural enemies? And do these differ for novel and co-evolved interactions? Based on underlying mechanisms plants may more readily avoid some novel enemies than others, but their chances to become invasive will be higher if they avoid local enemies that have the capacity to exert severe top-down control.
- (2) In complex interaction mechanisms, what is the relative importance of 'toxin-detoxifier' and 'elicitor-receptor' elements? And does this differ for co-evolved and novel interactions? If mechanistic mismatches occur, the nature of the mechanism determines whether a plant benefits or suffers from the mismatch.
- (3) How specific are toxins and detoxifiers, and elicitors and receptors? What degree of specificity exists even in generalist enemies? And how much overlap exists in these mechanisms between species and communities? These factors determine the probability that mechanistic mismatches may occur between a plant and its novel enemies.

In addition, an unbiased assessment of the impact of novel enemies on exotic plants requires that we do not focus only on exotic species that became successful invaders. Some recent studies have included non-invasive exotics (e.g. Cappuccino & Arnason 2006), but overall we know little about the much larger group of introduced plants that have either survived in their new ranges but that have not become invasive pests, or that have been entirely unsuccessful. This likely underestimates the chances of biotic resistance, and makes it difficult to evaluate general patterns in how novel enemies affect introduced plants.

We have focused our discussion on the effect of mechanistic mismatches in novel interactions on plant invasiveness, but it is important to point out that the same mechanistic considerations apply when it is the enemy that is invasive. For instance, an exotic herbivore that relies on specific host chemical cues or that possesses specific detoxification enzymes is not expected to rapidly invade a novel plant community, unless this community has native species that are closely related to the herbivore's co-evolved

host (in which case host switching might not involve mismatches in underlying mechanisms). Examples of herbivores that readily switch from native to closely related non-native hosts are described in biological control literature (Rand & Louda 2004).

A mechanistic perspective also shows that, in principle, there is the potential for biotic resistance with respect to many different enemies, and acquisition of novel enemies can halt the spread of previously successful invaders (Creed 2000; Siemann *et al.* 2006). Considering this potential we may need to invest more effort in recruiting natural enemies from the invaded range, as opposed to seeking biological control agents from the original range, which requires extensive testing of agents for side effects on non-target species. Introduced enemies can switch hosts, and in field situations they may have a stronger impact on indigenous plants than on their original hosts (Callaway *et al.* 1999). In cases where the eradication of invasive exotic plants is impossible, for instance because the invader has spread too much already, an effective strategy could be to let populations of the invader develop in areas where the potential of biotic resistance (evolution) is highest. Those areas could then be considered as evolution grounds for indigenous enemies to become specialized on the invader. Designing various strategies of invader control, as well as developing an improved predictive power on the invasive potential of introduced exotic plants will benefit from a more intense mechanistic understanding of the key components of invaders' defense systems that affect novel interactions.

Novel plant-enemy interactions also affect processes other than biological invasions. During succession, for instance, late-successional plant species colonize communities that are dominated by pathogens and herbivores from early-successional plant species, and the order of species replacement may be driven in part by a plant's capacity to escape top-down control by enemies from earlier stages (van der Putten *et al.* 1993; De Deyn *et al.* 2003). Gradual range expansions, for instance due to climate warming (Parmesan & Yohe 2003), may proceed at different speeds for plants and their enemies, causing plants to be disconnected from their old enemies (van Grunsven *et al.* 2007) while becoming exposed to novel ones. As rapid climate warming and increased global trade and tourism are connecting and re-shuffling ecological communities, it will become increasingly important to understand and predict the consequences of novel biotic interactions.

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