

# A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range

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## Summary

**1** Most theory and empirical research on exotic invasions is based on the assumption that problematic exotics are much more abundant in the regions where they invade than in the regions where they are native. However, the overwhelming majority of studies on exotic plants have been conducted solely within the introduced range. With few exceptions, ecologists know surprisingly little about the abundance, interaction strengths and ecosystems impacts of even the best-studied exotics in their native range.

**2** We argue that taking a biogeographical approach is key to understanding exotic plant invasions. On a descriptive level, unambiguous quantification of distributions and abundances of exotics in native and introduced ranges are crucial. Experiments conducted at a biogeographical scale are also necessary to elucidate the mechanisms that enable highly successful exotics to occur at substantially higher abundance in their introduced vs. native communities.

**3** We summarize the leading hypotheses for exotic plant success. We assert that tests of these major hypotheses for invasions (the natural enemies, evolution of invasiveness, empty niche and novel weapons hypotheses) require comparative biogeographical approaches.

**4** In addition to focusing on comparative work in the native and introduced range, we also suggest other approaches that could yield important insight into processes that influence exotic success.

**5** Increased understanding of invasions has the potential to provide unique insight into fundamental ecological theory, including that on individualistic-holistic structure, the role of trophic interactions in population regulation, and the importance of co-evolution in communities.

*Key-words:* biological invasions, comparative biogeography, disturbance, EICA, empty niche hypothesis, evolution of invasiveness, exotic plants, natural enemies hypothesis, novel weapons hypothesis, plant demography

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## Introduction

Contemporary biological invasions result from man expanding the distributional range of organisms. Species are taken from a native range where their populations are controlled by one set of factors and moved beyond natural dispersal barriers to regions where their abundance may be influenced by a different set of parameters. Although the ecological responses to this breaching of natural barriers to dispersal are funda-

mentally biogeographical phenomena, until recently the lion's share of studies of species in the new regions (hereafter exotics) have focused exclusively on their ecology in the communities to which they have been introduced, and ignored the ecology of these species where they are native. While research in recipient communities has certainly enhanced understanding of the detrimental economic (Pimentel *et al.* 2000) and ecological (D'Antonio & Vitousek 1992; Mack *et al.* 2000; Sala *et al.* 2000) effects of exotics and has identified factors that may influence susceptibility of communities to invasion (Crawley 1987; Lonsdale 1999; Davis *et al.* 2000; Mack *et al.* 2000; Sakai *et al.* 2001), progress in

understanding the processes that enable exotics to dominate recipient communities could be greatly accelerated by an increased emphasis on the comparative ecology of plants where they are native and introduced.

Why might such a biogeographical approach to invasion biology be useful? At the descriptive level, comparative studies are needed simply to establish the degree to which conspecifics occur at different densities or distributions in their native and introduced range. Currently, the assumption of greater abundances and overall impacts of species in recipient than in native communities is based almost exclusively on non-quantitative observations. While this assumption appears to be true for a number of species – *Centaurea maculosa* Lam. (spotted knapweed), *Alliaria petiolata* (Bieb.) Cavara & Grande (garlic mustard), *Lonicera japonica* Thunb. (Japanese honeysuckle), and *Bromus tectorum* L. (cheatgrass) come immediately to mind – many exotics occur at only moderate densities in recipient communities and may actually occur at similar densities in communities where they are native. The fraction of exotics that actually occur at significantly higher densities when introduced is not known, mostly because there are few direct comparisons of the density or overall abundance of particular plants in their native and introduced range (but see Woodburn & Sheppard 1996; Edwards *et al.* 1998; Grigulis *et al.* 2001; Paynter *et al.* 2003; Jakobs *et al.* 2004). While there are reports documenting the fact that some species are rare at home and abundant or even superabundant in introduced communities (Lonsdale & Segura 1987; Braithwaite *et al.* 1989; Malecki *et al.* 1993; Eckert *et al.* 1996; Meyer & Florence 1996; Bruce *et al.* 1997; Paynter *et al.* 1998; Memmot *et al.* 2000), these observations remain largely anecdotal.

Beyond documenting differences in abundance of exotics at home and away, a biogeographical perspective is needed to allow rigorous testing of mechanistic hypotheses that have been advanced to explain exotic plant success. Plants that become superabundant only in the introduced range must be ‘doing something different’ in recipient communities that enables them to attain such dominance. In this paper, we review the hypotheses that attempt to explain why exotics are able to attain spectacularly higher density in recipient vs. native communities and suggest how more rigorous testing could be achieved. We also touch upon some issues in invasion ecology that do not require an explicit biogeographical perspective, but where new approaches might be beneficial, and highlight how an increased mechanistic understanding of invasions can shed light on how native ecological systems function.

### Patterns in invasion biology

A common assumption about invasions is that exotic organisms occur at much greater densities and have greater performance in their introduced than native ranges (Crawley 1987; Noble 1989; Blossey & Nötzold 1995). While general observations suggest that this is

often true, quantitative data are surprisingly scarce and can be contradictory. We currently do not know what percentage of exotic plants occur at dramatically higher densities in their introduced vs. native range; however, considering Williamson’s tens rule (Williamson 1996; Williamson & Fitter 1996), it is probably small. Surely many exotics must occur at similar or even lower densities in recipient communities compared with their native range. For these ‘weak invaders’, the processes that regulate population numbers in their native and introduced range may be similar. Without empirical estimates, however, it is difficult to generalize about the overall success of exotics or determine how widely various mechanisms for exotic success might apply. Just as ecologists have long sought to understand what the distribution of interaction strengths might be for members of a community, it would be of great value to determine how the magnitude difference in population size between plants in their native and introduced range is distributed across exotic species.

Based on information published in European and North American floras, Crawley (1987) was one of the first researchers to quantify sizes of organisms in both ranges, showing that exotics often were larger than their native conspecifics. More recently, a similar pattern has been found for marine invertebrates by Grosholz & Ruiz (2003). In a survey of 46 native and 45 introduced populations of *Solidago gigantea* Ait., Jakobs *et al.* (2004) found that total plant biomass was larger among exotic vs. native plants. Thébaud & Simberloff (2001), however, found no consistent evidence for increased size among exotics. Height and biomass were also found to be similar in five native and six introduced populations of *Lythrum salicaria* L. (Edwards *et al.* 1998), despite this being the species that inspired the formulation of the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold 1995). Similarly, Paynter *et al.* (2003) reported that *Cytisus scoparius* (L.) Link does not grow faster or taller in recipient communities compared with native communities. *Cytisus scoparius* was first reported to live longer on average in introduced than native communities (Rees & Paynter 1997), but a recent study showed no differences in maximum plant ages between native and exotic populations of this species (Paynter *et al.* 2003). The fecundity of *Chrysanthemoides monilifera* (L.) T. Nord, *Acacia longifolia* (Andr.) Willd. (Weiss & Milton 1984, as cited in Noble 1989), and *C. scoparius* (Rees & Paynter 1997) has been shown to be higher in introduced regions when compared with native ones, but no differences between regions were found for *Echium plantagineum* L. (Grigulis *et al.* 2001). Populations of *L. salicaria* growing in nutrient-rich habitats were significantly more fecund in the introduced range, but fecundity was similar between ranges for populations growing in nutrient-poor and intermediate habitats (Edwards *et al.* 1998). Recently, Buckley *et al.* (2003) compared seed size between native and exotic populations of *C. scoparius* and *Ulex europaeus* L. They found that *C. scoparius* seeds were significantly heavier in the

introduced range compared with the native range, but that there were no differences between ranges in the seed size of *U. europaeus* (Buckley *et al.* 2003). Given the sampling design and impressive array of locations worldwide, Buckley *et al.*'s study is the most comprehensive evaluation for a single species' trait in both ranges, and should serve as a model for future investigations.

Comparisons of the traits of species in their introduced and native range are important, but comparative demographic studies of exotics at home and abroad will ultimately be far more informative for establishing the fundamental patterns of distribution and abundance that are requisite for evaluating hypotheses for invasive success. For exotics that clearly attain higher population sizes in the introduced than in the native range, understanding the demographic forces that lead to this difference is a necessary first step towards understanding the mechanisms by which some species invade.

To date, only a few studies have taken a comparative biogeographical approach to demography and these have been illuminating. Studies of Scotch broom in Europe and Australia have revealed that *C. scoparius* does not recruit beneath dense stands of conspecifics in the native range (Paynter *et al.* 1998), yet where it is exotic in Australia seedlings readily establish under monocultural stands of conspecifics (Sheppard *et al.* 2000). Grigulis *et al.* (2001) compared the demography of *E. plantagineum* between native sites in southern Portugal and introduced sites in south-eastern Australia. They found that, although values of many demographic transitions were similar between the native and introduced range, seedling establishment and rates of incorporation of seeds into the seedbank were two to five times higher in Australia than Portugal. This result, which would be obscure in the absence of such careful demographic investigation, clearly highlights the importance of establishment limitation in capping the size of populations in the native range (Eriksson & Ehrlén 1992) and suggests where to focus experimental work.

The next step, coupling manipulative experiments of competitors or enemies with demography, is a powerful approach to understanding not only how population processes may differ between ranges but also the mechanisms responsible for population release. For example, the poor success of weed biocontrol, in cases where biocontrol agents establish, often stems from biocontrols attacking weeds at life-history stages that are not demographically important (Shea & Kelly 1998; McEvoy & Coombs 1999). Comparative demographic studies of weeds would not only suggest what life history transition most limits population growth but it would also provide clues as to what factors might control population size in the native range.

Observations of exotic plants growing in disturbed areas are common (Elton 1958; Crawley 1987; Mack 1989; Rejmánek 1989; D'Antonio *et al.* 1999). Disturbance-adapted or ruderal species are often short-lived, fast growing and have high fecundity (Grime 1974, 1977;

Bazzaz 1979) and, over time, these species are thought to be replaced by late successional species (Bazzaz 1979; Glenn-Lewin & van der Maarel 1992). However, the post-disturbance response of many exotics seems to differ from natives in that exotics can create stable and long lasting monocultures after disturbance. One way to distinguish between this and the alternative that exotic and native colonizers do not behave differently (Davis *et al.* 2001) is to initiate comparative long-term successional studies in both distributional ranges. Although noticeably rare even in introduced ecosystems (D'Antonio *et al.* 1999; Davis *et al.* 2001), such studies could be accomplished through parallel field experiments where disturbance type and intensity are crossed with seed additions of the focal plant and changes in plant composition are documented through time. Alternatively, establishment of permanent plots in the native and introduced ranges in recently disturbed fields containing a high abundance of the target species would allow documentation of successional trends.

### Hypotheses for invasion success

Several hypotheses have been postulated to explain the success of species that are superabundant as exotics (Mack *et al.* 2000; Table 1, notably hypotheses 1–4), but few have received rigorous tests (Shea & Chesson 2002).

#### THE NATURAL ENEMIES HYPOTHESIS

One of the oldest and most widely cited hypothesis attributes success to the fact that many exotics, upon introduction, are liberated from their specialist herbivores and pathogens (Darwin 1859; Williams 1954; Elton 1958). Exotics are thought to gain a substantial advantage both because their populations are no longer directly suppressed by specialist enemies and also because they obtain a competitive advantage over natives that may disproportionately suffer from native enemy attack. The fundamental assumption is that release from strong suppression by enemies in their native range enables plants to attain higher densities in their introduced range. While native herbivores and pathogens can be quite damaging (Burdon 1987; Crawley 1989, 2002; Burdon & Leather 1990; Bever *et al.* 1997; van der Putten & Peters 1997; Klironomos 2002; Callaway *et al.* 2004), our understanding of the strength and pervasiveness of population-level control of plants by their enemies is surprisingly poor. In fact, many ecologists assert that the relative impact of enemies on *populations* of native plants is 'minimal' (Crawley 1989). Even in the context of biological control, detailed demographic data demonstrating strong population-level suppression of exotics are scarce and estimates of how commonly biocontrol agents actually limit the population size of their targets vary widely and are often based on qualitative accounts rather than hard data. Explicit comparisons of the effects of enemies in the native and introduced range are crucial for testing the natural enemies hypothesis.

**Table 1** Major hypotheses for the success of exotic plants in recipient communities. Hypotheses 1–4 require an explicit comparison between native and introduced ranges to be critically evaluated. Hypotheses 5–7 can be assessed by studying exotics only in their introduced range

Hypothesis name	Definition	References
(1) Natural enemies	Exotics are released from natural enemies that control their population growth	Darwin (1859), Williams (1954), Elton (1958)
(2) Evolution of invasiveness	Exotics experience rapid genetic changes linked to new selection pressures in the novel environment	Blossey & Nötzold (1995), Lee (2002), Stockwell <i>et al.</i> (2003)
(3) Empty niche	Exotics utilize resources unused by the locals	Elton (1958), MacArthur (1970)
(4) Novel weapons	Exotics bring novel ways of biochemical interaction to recipient communities	Callaway & Aschehoug (2000), Bais <i>et al.</i> 2003
(5) Disturbance	Exotics are adapted to disturbances' type and intensity that are novel to natives	Gray (1879), Baker (1974)
(6) Species richness	Species-rich communities are more resistant to invasion than species-poor communities	Elton (1958), MacArthur (1970, 1972)
(7) Propagule pressure	Variations in levels of invasion among recipient communities are due to differences in the number of exotics arriving in the community	di Castri (1989), Williamson (1996), Lonsdale (1999)

Although researchers have compared levels of pathogen (Mitchell & Power 2003) or herbivore (Memmot *et al.* 2000; Wolfe 2002; Jakobs *et al.* 2004) attack on native and exotic conspecifics or of herbivore damage on exotics and ecologically equivalent natives in recipient communities (Agrawal & Kotanen 2003; Siemann & Rogers 2003c), such studies provide only limited insight into the importance of enemy escape. Differences in consumer pressure between plants in their native and introduced range do not necessarily translate to meaningful differences in plant performance (Siemann & Rogers 2003b). Studies that actually compare the impact of enemies on plant performance in native and introduced ranges have produced mixed results. Reinhart *et al.* (2003) showed that *Prunus serotina* Ehrh. (black cherry) invasion into Europe is facilitated by soil microbes, whereas in its native range *P. serotina* is inhibited by soil pathogens. Callaway *et al.* (2004) compared the effects of soil microbes collected from four populations of *C. maculosa* in its native range in western Europe and six populations in the north-western USA, where it has invaded. On average, sterilization of European soils caused a 166% increase in the total biomass of *C. maculosa* compared with a 24% increase when North American soils were sterilized. Depending on the population and rhizosphere, sterilization of European soils improved *C. maculosa* growth from as little as 31% to over 900%, whereas the effects of sterilizing North American soils ranged from a 24% decrease in *C. maculosa* growth (suggesting a positive effect of microbes) to a 59% increase. The stronger suppressive effects of European soil biota lend experimental support to earlier demonstrations of much higher fungal and viral infection on plant species in their home ranges than in invaded ranges. In contrast, Beckstead & Parker (2003) showed that the impacts of soil pathogens on dune grass, *Ammophila arenaria* (L.) Link, were of equally strong magnitude in the introduced and native range.

Without knowing whether negative impacts of herbivore or pathogen attack actually limit the abundance of plants in their native range, it is difficult to evaluate the ecological significance of escape from enemies. Studies are needed that both quantify the population-level impact of specialist enemies in the native and introduced range and determine how competitive interactions between natives and exotics may be affected by altered enemy pressure. To date, only DeWalt *et al.* (2004) have taken this approach. They demonstrated that herbivores and fungal pathogens reduce the survival of *Clidemia hirta* (L.) D. Don in understory habitats, and thus limit its distribution to open habitats in its native range (Costa Rica), but lack of enemy pressure has apparently allowed forest invasion where it is an exotic (Hawaii).

#### THE EVOLUTION OF INVASIVENESS HYPOTHESIS

Some species may attain dominance in introduced ranges because they experience rapid genetic changes linked to new selection pressures in the novel environment (Carroll & Dingle 1996; Sakai *et al.* 2001; Hänfling & Kollman 2002; Lee 2002; Stockwell *et al.* 2003; Maron *et al.* 2004). Various studies have identified both biotic and abiotic factors as important selective forces in the new environment (see Lee 2002 and Stockwell *et al.* 2003 for reviews). Among biotic agents, rapid evolution can occur not only in response to the presence of a new set of organisms but also in response to their absence. The evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold 1995) argues that exotics long liberated from their specialist enemies should lose costly traits that confer resistance to their native specialist enemies. Exotics can reallocate resources from the maintenance of resistance to traits, such as size or fecundity, that might be under greater

selection in the introduced range. Thus, EICA predicts that liberation from natural enemies should result in exotics evolving in ways that enhance their performance in recipient communities. Testing for genetically based changes in phenotype between exotic and native conspecifics requires growing plants from both ranges together in common gardens and, to date, such tests have produced mixed results. Siemann & Rogers (2003b) showed that in a glasshouse, generalist grasshoppers preferred exotic over native genotypes of *Sapium sebiferum* (L.) Roxb. (Chinese Tallow Tree) seedlings. Daehler & Strong (1997) showed that specialist planthoppers (*Prokelisia marginata* Van Duzee) were more damaging to exotic *Spartina alterniflora* Loisel. (cordgrass) that had little history of planthopper herbivory compared with either native or exotic genotypes that were used to attack. Siemann & Rogers (2001, 2003c) found that exotic genotypes of *S. sebiferum* were larger and more fecund than native genotypes. Leger & Rice (2003) found that introduced *Eschscholzia californica* Cham. (California poppy) from Chile were larger and more fecund than native Californian conspecifics in common gardens, but only in the absence of competition. On the other hand, Willis *et al.* (2000) grew four species of plants collected from their native European and introduced ranges in a common garden in Britain and found no evidence that exotic plants had evolved increased size. Based on common gardens in Washington, California, Sweden and Spain, Maron *et al.* (2004) found no evidence that exotic genotypes of *Hypericum perforatum* L. (St John's Wort) were larger or more fecund than native genotypes, although they had lower pathogen resistance and reduced defensive chemistry (Maron *et al.* 2005).

Reciprocal common garden studies should be conducted in both the native and introduced range, using plants from multiple populations that are sampled widely across each range. If possible, plants collected as seed from natural populations should be grown in a common environment and the progeny of these individuals should be used in common garden experiments to control for potential maternal effects. In addition, individuals used in common gardens should be genotyped so that invasion history can be inferred and the possibility that any differences are simply due to exotic populations being founded by a small and unrepresentative subset of native genotypes ruled out.

Crossed common garden experiments offer the most complete assessment of evolutionary hypotheses, but they present important ethical and logistic problems. Foremost is the risk of novel genotypes being introduced into new regions. We cannot over-emphasize that extreme caution and close follow-up is required, with seeds harvested before dispersal and all plants destroyed after research is completed. In addition, to minimize opportunities for gene flow, plants should not be grown in areas immediately adjacent to extant populations of the same species. The logistic difficulties in the implementation of common gardens in different parts of the world are substantial and can only be solved by

developing strong international collaborations among scientists. A less powerful alternative is to perform genotypic comparisons in growth chambers where climates from different regions can be simulated. These studies, however, are more limited in reality and replication than field experiments.

So far, tests of the EICA hypothesis have generally compared the phenotypes of natives and exotics that have been grown together in a single glasshouse (Daehler & Strong 1997; Siemann & Rogers 2003b) or in a common garden in the introduced range (Siemann & Rogers 2003c). Environmental conditions in the introduced range might, however, be less favourable to native genotypes and, in a single garden, it is impossible to rule out genotype by environment interactions, leading to greater performance for certain genotypes only in some environments. This point has been well illustrated for work done on St John's wort, a plant native to Europe but introduced into North America, Australia, New Zealand and other locales. Based on a limited sample of plants from Europe and North America that were grown in a single common garden in the UK, Pritchard (1960) reported that exotic genotypes were more robust than natives. More recently, although Maron *et al.* (2004) obtained a similar result after exotic and native genotypes of St John's Wort were grown for 2 years in a common garden in Washington, this pattern disappeared after a further year, and there was no evidence that exotic genotypes were larger or more fecund than natives when grown in California, Sweden and Spain.

#### THE EMPTY NICHE HYPOTHESIS

Although by definition a niche can only exist in the presence of an organism, this hypothesis refers to the possibility that certain exotics may be successful because they have access to resources in the introduced community that no local species utilize (Elton 1958; MacArthur 1970; Levine & D'Antonio 1999; Mack *et al.* 2000; but see Herbold & Moyle 1986). Because species-rich communities are thought to have a more complete use of resources, the lack of empty niches would also explain why they are more resistant to invasion (Elton 1958; MacArthur 1970; Levine & D'Antonio 1999). The related hypothesis of ecological opportunity, stating that extinctions, and in consequence the creation of 'empty' niches, promote the establishment of exotic species, has been proposed to explain successful fish (Christie 1974) and bird (Diamond & Veitch 1981) introductions, as well as the asymmetrical exchange of marine biota following the disappearance of major barriers to biological dispersion (Vermeij 1989, 1991a,b). The theory of fluctuating resource availability, similarly argues that the susceptibility to invasion of a community increases whenever the amount of unused resources in that community is enhanced (Davis *et al.* 2000).

Some exotic plants certainly appear to take advantage of empty niches in the communities they invade.

The success of *Centaurea solstitialis* L. in dominating annual grasslands in California, for example, has been proposed to be due to the presence of unused water below 60 cm in the soil profile resulting from a combination of shallow root systems and early senescence of annual grasses (Borman *et al.* 1992; Holmes & Rice 1996; Dyer & Rice 1999). By having an extensive and deep root system, *C. solstitialis* has the potential to exploit this resource (Roché *et al.* 1994). In an experiment assessing the invasibility of several plant functional groups to *C. solstitialis*, Dukes (2001) concluded that by reducing the availability of soil moisture in the summer, functionally diverse communities and monocultures of native *Hemizonia congesta* DC., which like the exotic is a deep-rooted late-season annual herb, provided more resistance to invasion than communities without summer-active deep-rooted species. A related study similarly revealed that communities of perennial grasses were less susceptible to invasion than those of annual grasses (Dukes 2002). It is puzzling, however, why deep-rooted natives fail to dominate these grasslands given that they have access to such a rich resource (but see Dyer & Rice 1999).

Although exclusive study of introduced communities can certainly provide some evidence that exotics gain access to 'free' or unused resources, parallel studies in both the native and introduced range would offer a far more convincing evaluation of this hypothesis because it would enable one to demonstrate not only that a successful exotic benefits from accessing unused resources in the recipient community, but also that these resources are utilized by other plants in the original community (or in areas of the introduced range where the exotic fails to achieve community dominance). To our knowledge, no work of this kind has been performed. The presence of an empty niche can be inferred by measuring the availability of resources such as light, water and nutrients in locations suspected to have unused resources and where the niche is thought to be occupied, followed by the determination that those available resources are being used by the target species. Experimentally, plant communities resembling those encountered by an exotic in its native and recipient community can be assembled with the goal of determining how resource availability and use varies between assemblage types. In addition, indirect measurements of resource complementarity, such as relative yield totals (Harper 1977) and proportional deviation of a mixture from its expected productivity (Wardle *et al.* 1997; Loreau 1998) can be used to evaluate whether resource partitioning between the study plant and other members of the assemblage is occurring (e.g. Dukes 2002).

#### THE NOVEL WEAPONS HYPOTHESIS

A recent hypothesis emphasizes the importance of allelopathy (*sensu* Muller 1969) in the invasion process and proposes that some exotic plants may succeed because they bring novel ways of interaction to natural

plant communities (Callaway & Aschehoug 2000; Bais *et al.* 2003). Specifically, the novel weapons hypothesis argues that exotics exude allelochemicals that are relatively ineffective against well-adapted neighbours in origin communities, but highly inhibitory to naïve plants in recipient communities. Strong tests of this hypothesis must of course involve a comparative biogeographical component. In the first assessment of the novel weapons hypothesis, Callaway & Aschehoug (2000) compared the inhibitory effects of *Centaurea diffusa* Lam., an invasive Eurasian herb in North America, on three bunchgrass species that coexist with it in Eurasia with those on three North America bunchgrasses matched with the Eurasian species for genus (or nearly congeneric), morphology and size. *Centaurea diffusa* had much stronger negative effects on North American species unless activated carbon was added to ameliorate the action of allelochemicals, when Eurasian species were more affected. The overall effect of activated carbon on North American species was positive, but it reduced dramatically the biomass of all Eurasian grass species growing with *C. diffusa*. These results suggest that *C. diffusa* produces chemicals that long-term and familiar Eurasian neighbours have adapted to, but its new North American neighbours have not. Biogeographical differences in the resistance or susceptibility of plant communities to *C. diffusa* were further explored by establishing microcosms in which North American and Eurasian plant communities were established in both North American and Eurasian soils (Vivanco *et al.* 2004). The regional source of the plant community was by far the most important factor in resistance to *C. diffusa*; Eurasian communities were much more resistant to invasion.

Similar biogeographical comparisons have been performed with the closely related *C. maculosa*. By integrating ecological, physiological, biochemical signal transduction and genomic approaches, Bais *et al.* (2003) were able to isolate a chemical, (-)-catechin, produced by *C. maculosa* roots that has phytotoxic properties, to determine that the concentration of (-)-catechin is about twice as high in soils occupied by *C. maculosa* in North America than in similar habitats in Europe and to demonstrate that germination and growth of European grasses are more resistant to (-)-catechin than those of North American counterparts.

Using a similar approach to the one employed by Callaway & Aschehoug (2000), Prati & Bossdorf (2004) tested allelopathic effects of *A. petiolata*, an aggressive invader of the understorey of forests in North America, on germination of two congeneric species that co-occur with *Alliaria* in the field, the American *Geum laciniatum* Murray and the European *G. urbanum* L. They also investigated whether the allelopathic potential of *A. petiolata* varied between native European and exotic North American populations of the weed. They found that exotic North American populations of *A. petiolata* significantly reduced the germination of 'naïve' North American *G. laciniatum* seeds, but had no effects on

'experienced' European *G. urbanum* seeds. Native European *A. petiolata*, on the other hand, significantly reduced seed germination of both North American *G. laciniatum* and European *G. urbanum* in similar proportions. These results partially support the novel weapons hypothesis and suggest that North American *A. petiolata* has lost its detrimental effects on its former European neighbour.

The general picture emerging from research on invasive *Centaurea* species and *A. petiolata* is that chemicals exuding from their roots may disrupt naïve communities in ways that do not occur in their communities of origin. Clearly, it is not possible to explore the novel weapons hypothesis without integrating biogeography into experimental designs. So far, experiments have only been conducted in the glasshouse or *in vitro*, but, as likely allelopathic agents for many invasive species have been identified and are commercially available, it should be relatively simple to apply them in the field at natural concentrations. It may be more difficult, however, to assess the effects of allelochemicals while maintaining appropriate residence times, realistic rates of release or renewability and accounting for the effects of microbial communities.

### Other research needs in plant invasion biology

Several mechanisms have been proposed to explain the variation in community susceptibility to invasion (see Lonsdale 1999; Mack *et al.* 2000; Sakai *et al.* 2001; Table 1, hypotheses 5–7). There are a number of issues here whose further examination can be accomplished by studying exotics only in their introduced range.

### THE DISTURBANCE HYPOTHESIS

As exotics that invade disturbed communities are, in general, ruderal species (*sensu* Grime 1974), it is not surprising that they flourish under such conditions. Moreover, according to plant strategy theory, it is expected that exotic *ruderals* will outperform native *competitors* and *stress-tolerants* in early successional stages (Grime 1979; Huston & Smith 1987). What is unclear, though, is why ruderals native to the system are not able to colonize disturbed areas as successfully as exotic ruderals. The disturbance hypothesis argues that differences exist because native ruderals have not experienced the type and intensity of disturbances to which exotics are adapted (Gray 1879; Baker 1974; Mack *et al.* 2000). A puzzling aspect of this proposition, however, is that exotics often thrive even in areas altered by natural disturbances. A longer history with humans and, in consequence, with severe disturbances might have enabled some exotics to gain tenure under a larger suite of disturbed conditions. The disturbance hypothesis is long standing (Gray 1879), but it has received poor examination and further understanding could be obtained by implementing factorial field experiments with treatments mimicking disturbances within local vegetation and adding seeds of both resident and exotic ruderals.

Even better, but perhaps unrealistic for exotic species, would be to simulate disturbances to which both native and exotic ruderals are and are not adapted.

### THE SPECIES RICHNESS HYPOTHESIS

Elton (1958) first proposed the notion that more diverse communities might be more resistant to invasion than species-poor communities. This idea has been supported by theoretical arguments that lower diversity communities have weaker interspecific interactions and more 'empty niches' (MacArthur 1970; MacArthur 1972; Post & Pimm 1983; Crawley 1987; Drake 1990). As resource uptake is reduced in species-poor communities (Crawley 1987; Tilman *et al.* 1996; Hooper & Vitousek 1998), the presence of more 'free' resources might render species-poor communities more invisable than species-rich communities.

Empirical tests of the effects of species richness on invasibility have produced mixed results (see review by Levine & D'Antonio 1999). Large-scale observational studies have shown a positive correlation between diversity and invasibility, with more diverse communities being more heavily invaded (Kruger *et al.* 1989; Knops *et al.* 1995; Planty-Tabacchi *et al.* 1996; Wisser *et al.* 1998; Lonsdale 1999; Smith & Knapp 1999; Stohlgren *et al.* 1999; Stadler *et al.* 2000; Foster *et al.* 2002). In contrast, experiments using synthetic assemblages that vary in diversity have usually shown the opposite pattern, with more diverse assemblages being less invisable (Knops *et al.* 1999; Naeem *et al.* 2000; Hector *et al.* 2001; Dukes 2002; Stachowicz *et al.* 2002; but see Palmer & Maurer 1997). Part of this discrepancy is clearly scale related (Tilman 1999). Beyond this, however, large-scale observational studies have been correlative, and have not controlled for extrinsic factors such as propagule pressure, disturbance, resource availability and consumers, factors known to covary with diversity and that also may influence invasibility (Levine & D'Antonio 1999; Shea & Chesson 2002). Experimental studies, on the other hand, have controlled for these factors essentially by ignoring them, thereby limiting our understanding of how diversity interacts with processes that vary over broader spatial scales.

One factor known to play a key role in influencing invasibility at larger spatial scales is resource availability. Increasing water or nitrogen availability often facilitates invasion (Aerts & Berendse 1988; Bobbink 1991; Hobbs & Mooney 1991; Hobbs & Huenneke 1992; Milchunas & Lauenroth 1995; Maron & Connors 1996; Wedin & Tilman 1996; Davis & Pelsor 2001; Siemann & Rogers 2003a). Foster *et al.* (2002) found that more diverse grassland plots were more heavily invaded and that resource availability explained a greater percentage of the variance in invasibility than did species diversity. Given that resource supply and native diversity appear to have opposite effects on invasion resistance in isolation, a critical issue becomes how these factors interact to influence community invasibility. Does resource

supply have primacy over native diversity in influencing invasion resistance? Can any negative diversity–invasibility relationship be fundamentally changed by increasing resource availability? Future studies that examine interactions between different components of native species richness and extrinsic factors such as resource availability or disturbance would yield rich dividends (e.g. Von Holle 2005).

#### THE PROPAGULE PRESSURE HYPOTHESIS

Several authors have pointed out that variations in the level of invasion among recipient communities could simply be due to differences in the number of exotics arriving in the community (Williamson 1996; Lonsdale 1999; Mack *et al.* 2000). Evidence for this assertion comes mainly from studies that relate the number of exotics in a region with isolation from main shipping routes (di Castri 1989; Lonsdale 1999; Mack *et al.* 2000). A growing number of studies also show that seed limitation is common (see reviews by Eriksson & Ehrlén 1992; Turnbull *et al.* 2000), suggesting that propagule pressure can also fundamentally influence the probability of invasion by new species. Yet, while it is clear that adding more seeds to sites can affect establishment success, it is not well understood how the relative importance of propagule pressure compares with that of other processes such as disturbance and resource supply. As such, carefully designed factorial field experiments are needed in which a range of propagule pressures are crossed with different levels of other factors thought to influence invasion. Such experiments would have the added benefit of shedding light on processes that influence the early life-history stages, rather than the adult–adult or seedling–adult interactions that are the focus of many invasion studies.

#### Implications for understanding the nature of native systems

Beyond simply understanding why exotics succeed in recipient communities, the study of exotic species could shed new light on several fundamental issues in basic ecology. Species introductions are grand-scale ‘experiments’ where the abiotic and biotic background and co-evolutionary history of interacting species are manipulated, providing an opportunity to tease apart how such factors might influence population abundance of particular species. If appropriately designed biogeographical experiments consistently find evidence for release from natural enemies as the driver for successful invasions, then top-down effects in natural communities would appear to have been substantially underestimated. If studies of invaders in their origin and invaded communities show that empty niches are crucial for invasion, then the composition and function of natural communities must be remarkably limited by regional species pools, local adaptation must be overrated and the diversity–invasion resistance hypothesis would gain mechanistic

credibility. Finally, contrasting allelopathic interactions among plants from different biogeographical regions have profound implications for plant community theory. Plant communities are widely thought to be ‘individualistic’, composed primarily of species that have similar adaptations to a particular physical environment. This traditional view downplays any persistent and powerful role of co-evolution in shaping the structure of interactions, and does not account for facilitation between species. However, if some exotic plants succeed because they bring novel mechanisms of interaction to natural plant communities, then natural plant communities may be more tightly knit than generally thought. Continuing with this line of thought, novel weapons suggest that interactions among plant species may drive natural selection in communities and imply that natural biological communities may evolve in some way as functionally organized units.

Whilst a greater emphasis on biogeographical comparisons will yield invaluable information on invasion processes, perhaps the potential for supporting or challenging general ecological paradigms is even more important. As for fundamental questions about community theory raised by invasions themselves, the few experiments conducted with explicit biogeographical treatments have raised questions about general community theory, provided insight into the nature of trophic interactions in ecosystems, elucidated the role of soil microbes in population regulation and suggested that co-evolutionary processes may be important for the organization of natural communities. This may be only the beginning.

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