Plant invasions: merging the concepts of species invasiveness and community invasibility

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Abstract: This paper considers key issues in plant invasion ecology, where findings published since 1990 have significantly improved our understanding of many aspects of invasions. The review focuses on vascular plants invading natural and semi-natural ecosystems, and on fundamental ecological issues relating to species invasiveness and community invasibility. Three big questions addressed by the SCOPE programme in the 1980s (which species invade; which habitats are invaded; and how can we manage invasions?) still underpin most work in invasion ecology. Some organizing and unifying themes in the field are organism-focused and relate to species invasiveness (the tens rule; the concept of residence time; taxonomic patterns and Darwin's naturalization hypothesis; issues of phenotypic plasticity and rapid evolutionary change, including evolution of increased competitive ability hypothesis; the role of long-distance dispersal). Others are ecosystem-centred and deal with determinants of the invasibility of communities, habitats and regions (levels of invasion, invasibility and propagule pressure; the biotic resistance hypothesis and the links between diversity and invasibility; synergisms, mutualisms, and invasional meltdown). Some theories have taken an overarching approach to plant invasions by integrating the concepts of species invasiveness and community invasibility (a theory of seed plant invasiveness; fluctuating resources theory of invasibility). Concepts, hypotheses and theories reviewed here can be linked to the naturalization-invasion continuum concept, which relates invasion processes with a sequence of environmental and biotic barriers that an introduced species must negotiate to become casual, naturalized and invasive. New research tools and improved research links between invasion ecology and succession ecology, community ecology, conservation biology and weed science, respectively, have strengthened the conceptual pillars of invasion ecology.

Key words: biological invasions, biotic resistance, invasibility, invasiveness, long-distance dispersal, naturalization, phenotypic plasticity, plant invasions, propagule pressure, rapid evolution, residence time, taxonomic patterns, tens rule.

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I Introduction

Invasion ecology is the study of the human-mediated introductions of organisms, especially to areas well outside their potential range as defined by their natural dispersal mechanisms and biogeographic barriers. The field covers all aspects relating to the introduction of organisms, their capacity to naturalize and invade in the target region, their interactions with resident biota and, increasingly, the consideration of costs and benefits of their presence and abundance with reference to human value systems. Biological invasions have been chronicled for centuries, but Charles Elton's (1958) book *The ecology of animal and plant invasions* was the starting point of what has come to be known as invasion ecology (Rejmánek *et al.*, 2005a).

This paper considers some of the most significant developments in the field of plant invasion ecology, with emphasis on work published since 1990 – after the publication of the global synthesis volume from the SCOPE programme on biological invasions (Drake *et al.*, 1989). We have selected for discussion issues where there has been intense research interest and where new findings have significantly improved our understanding of invasions. Our focus is on vascular plants invading natural and semi-natural ecosystems, and on fundamental ecological issues relating to invasiveness and invasibility, rather than those relating to impacts and specific management concerns.

II Background

Interest in biological invasions has exploded in the past two decades. The SCOPE programme of the 1980s (Drake *et al.*, 1989) set the scene by revisiting some key assumptions and generalizations put forward by Elton (1958), reviewing the current status of invasions in many parts of the world, and calling on some of the world's top ecologists to apply their minds to the problems and challenges regarding biological invasions. The SCOPE programme addressed three fundamental questions: which species invade; which habitats are invaded; and how can we manage invasions? (Drake *et al.*, 1989). Phase 1 of the Global Invasive Species Programme (GISP; Mooney, 1999) primarily sought practical solutions to the rapidly escalating problems, while realizing the need for improved understanding of some fundamental ecological aspects. The three big questions from the SCOPE programme still underpin most work in invasion ecology. The past decade has, however, seen considerable activity on numerous fronts, as the extent and impacts of invasive species have increased. Attempts have been made to strengthen the conceptual pillars of invasion ecology; these include moves to bridge the gap between the study of invasions and succession ecology, community ecology, conservation biology, and weed science. Many thorough studies have profiled key invaders and invaded systems (Weber, 2003), facilitating better generalizations. New approaches and technologies have been applied in addressing crucial issues; for example, molecular techniques, remote sensing, and advanced spatial analysis tools are shedding light on issues and processes that were out of reach of earlier researchers. Since humans cause and interpret invasions, there have been increased inputs from social scientists and economists, and social concerns are increasingly shaping research agendas. The increasing urgency in the search for unifying concepts has led to the generation of new hypotheses and generalizations. Our aim here is to review such organizing and unifying themes in the field, to evaluate these, and to suggest some challenges for the future.

Given the many interlinked elements of invasion ecology, there is no single ideal structure for a broad review such as the one we attempt here. Each part of the story demands a link to several others. The headings below start with an emphasis on general and overarching aspects, and move through organism-focused to ecosystem-centred considerations. The terminology used in the paper (following Richardson *et al.*, 2000b; Pyšek *et al.*, 2004b) is outlined in Figure 1.

A
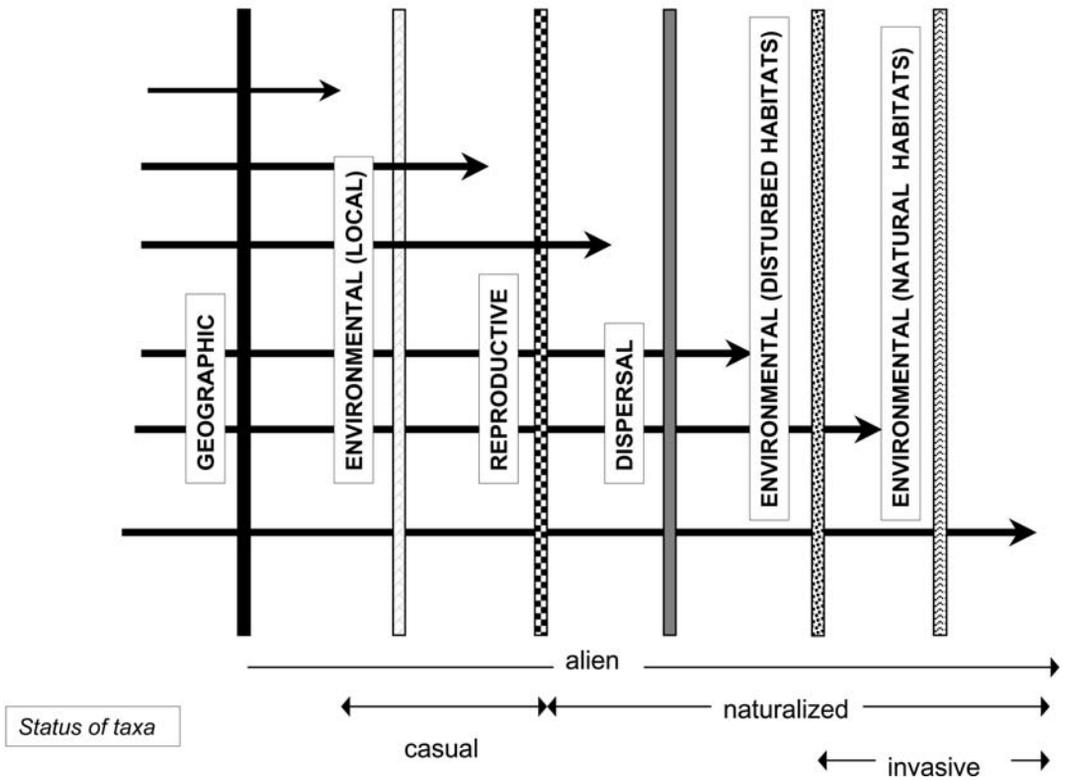
Figure 1 The 'naturalization-invasion continuum' (panel **A**) conceptualizes the various barriers that a plant must overcome to become alien, casual, naturalized or invasive in a new environment (adapted from Richardson *et al.*, 2000b). The scheme also provides a framework for the objective definition of categories of alien plants (Pysek *et al.*, 2004b). **Alien** plants are those whose presence in an area is the result of human-mediated transport. **Casual alien** plants are alien plants that may flourish and even reproduce occasionally outside cultivation but that eventually die out because they do not form self-replacing populations; they rely on repeated introductions for their persistence. **Naturalized** plants are those aliens that form self-replacing populations for at least 10 years without direct intervention by people (or despite human intervention) by recruitment from seeds or ramets capable of independent growth. **Invasive** plants are a subset of naturalized plants that produce reproductive offspring, often in large numbers, at considerable distances from parent plants, and thus have the potential to spread over a large area. Understanding of the dynamics of plant invasions requires insights on traits of the plant (elements of species invasiveness) and features of the environment (components of community invasibility), but neither aspect can be fully evaluated without reference to the other (panel **B**). Invasions are context specific, and invasiveness only materializes when certain environmental requirements are met. Boxes in panel **B** list the key concepts addressed in this paper
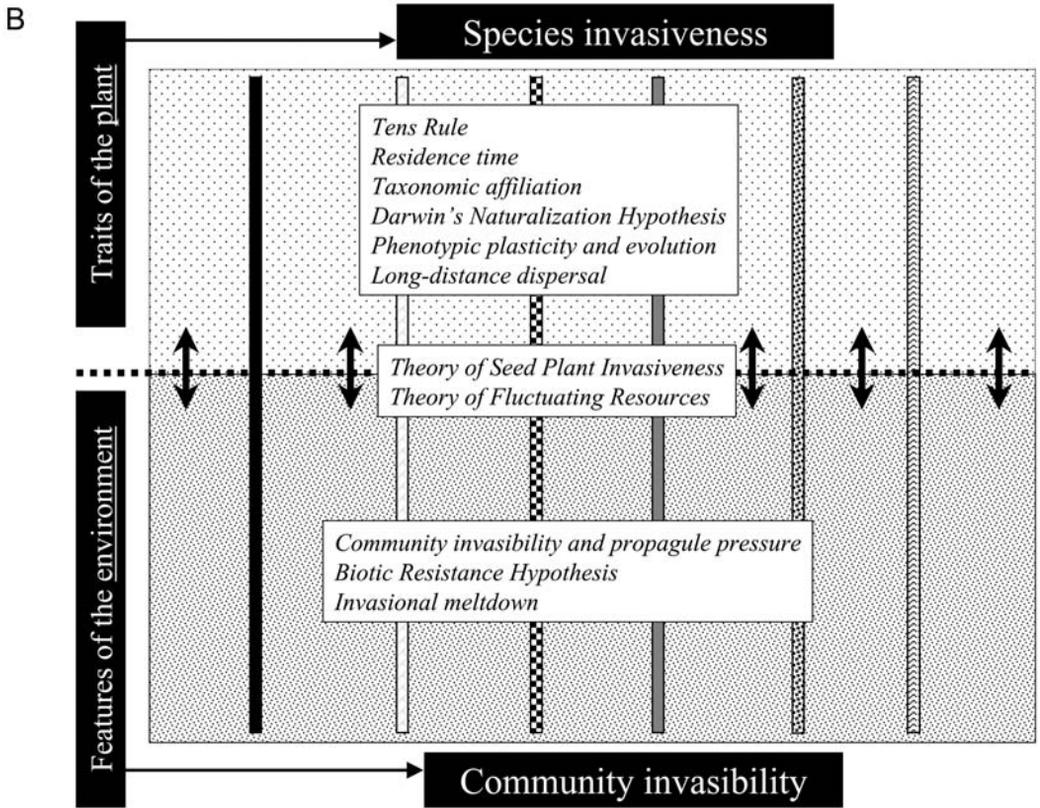
Figure 1 *Continued*

III How many invaders? The tens rule

The tens rule (originally the ten-ten rule; Williamson and Brown, 1986) was proposed as a quantitative estimate of the proportion of introduced species that become pests (Williamson, 1993; Williamson and Fitter, 1996). It is a probabilistic assessment of the proportion of species that reach particular stages in the invasion process. It predicts that 10% of imported species escape to become casual, 10% of casuals become naturalized (*sensu* Richardson *et al.*, 2000b), and 10% of naturalized species become pests (*sensu* Pyšek *et al.*, 2004b). The rule was derived from European plant data but the general principle that successful invasions are rare (the rule predicts that alien pests comprise very roughly only 1% of the introduced

species found casual) holds for other regions and across many taxa of plants and animals (Williamson, 1996). The tens rule received considerable reaction, but has also been widely misinterpreted, mostly when applied directly to numbers of 'invasive' species. The reasonably constant proportion of alien taxa that invade across a wide range of systems is, at least partly, a result of the similar residence times (see section IV) of species in different alien floras (Rejmánek *et al.*, 2005b). In other words, the tens rule is largely an artifact of the particular stage of invasions worldwide and this will change over time (Figure 2).

Despite the wide limits, the many exceptions (Williamson, 2000), and the caveats mentioned above, the tens rule is a useful generalization that can be used as a
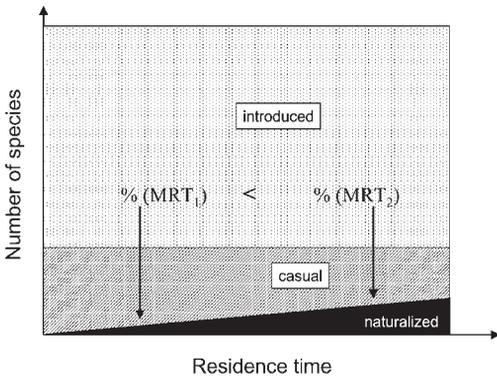
Figure 2 The effect of residence time (MRT; see text) on the second transition of the tens rule (from casual to naturalized stage; see Figure 1). Even if the number of introduced and casual species remains stable over time, the proportion of casual species that become naturalized increases because increasingly more species have enough time to adapt or encounter suitable symbionts, climatic events or chance factors that potentially trigger invasion. The reasonably constant proportion of alien taxa across a wide range of systems is partly a result of the similar residence times of species in different alien floras. The proportion of naturalized species therefore depends on the date of assessment; it will be higher at MRT_2 than at MRT_1

benchmark to which real data can be related; deviations indicate taxa with higher or lower invasiveness and regions/habitats with lower or higher invasibility (Williamson, 1996; Gaston *et al.*, 2003).

The tens rule also provides some basis for estimating the global number of naturalized species. Had all 260,000 of the world's vascular plant species been transported to regions remote from their native ranges (which is clearly an overestimated assumption as many rare species never get introduced), then the tens rule predicts 2600 naturalized species

worldwide. Taking into account that the rule is supposed to hold within a statistically derived range of *c.* 5–20%, allowing for biological variation and different approaches to the classification of species among researchers (Williamson, 1996), this gives for the two transitions an estimate of 13,000–52,000 casuals and 650–10,400 naturalized species globally. This seems a more reasonable estimate (for now at least) than Rapoport's (1991) suggestion that at least 10% of the world's vascular plant species are potential invaders. The figure derived from the tens rule has some support from real data, eg, from numbers of naturalized plant species estimated for Europe (1568; Weber, 1997) or New Zealand (2319; Randall, 2002).

Despite efforts to create lists of invasive alien species for different regions and for the whole world (Weber, 2003; see http://invasivespecies.nbii.gov/as/DraftIASDBs.htm), we clearly have insufficient information on which species can objectively be classified as 'naturalized' or 'invasive' (*sensu* Richardson *et al.*, 2000b; Pyšek *et al.*, 2004b). This is hindering our ability to develop sound generalizations on the correlates and determinants of invasiveness and invasibility. Accurately compiled lists and alien floras (using objective criteria) are essential for future progress in this respect (Binggeli, 1996; Richardson *et al.*, 2000b; Pyšek *et al.*, 2002b; 2004b).

IV Time changes everything – the role of residence time

Stochastic factors, including initial inoculum size, residence time, propagule pressure, and chance events, are crucial for determining of whether (or when) a species will invade (Rejmánek *et al.*, 2005a). One of the most robust emerging generalizations in invasion biology is that the probability of invasion increases with the time since the introduction (residence time). As it is mostly not known exactly when a taxon was introduced, the term 'minimum residence time' (MRT) has been proposed (Rejmánek, 2000). A positive relationship between MRT and current

distribution of alien species is evident for several regional floras (Crawley *et al.*, 1996; Wu *et al.*, 2003; 2004; Rejmánek *et al.*, 2005a; see Pyšek and Jarošik, 2005, for a review), and for individual species at different scales (Richardson and Higgins, 1998; Müllerová *et al.*, 2005). MRT explains not only the range and frequency of current distributions but also the invasion status of a species. In the Czech Republic casual species have significantly shorter mean MRT than naturalized and invasive aliens (Pyšek and Jarošík, 2005). Residence time integrates aspects of propagule pressure: the longer the species is present in the region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and the founding of new populations (Rejmánek *et al.*, 2005a). The effect on the invaded community also increases with residence times (Collier *et al.*, 2002). In Europe, the effect of residence time is still obvious after several millennia of plant invasions. Those archaeophytes (*sensu* Preston *et al.*, 2004; Pyšek *et al.*, 2004c) that invaded soon after the beginning of Neolithic agriculture are more common and have wider distribution ranges than those that arrived later (Pyšek and Jarošík, 2005). Residence time also affects the ecology of weed communities on arable land where both groups of aliens distinguished in Europe according to the time of introduction meet; archaeophytes are more common in old crops such as cereals than in more recently introduced crops, where neophytes are most numerous (Pyšek *et al.*, 2005).

MRT is a crucial consideration in studies evaluating determinants of invasiveness; an analysis of naturalized neophytes of the Czech flora showed that MRT was more important than selected species traits for explaining their current distribution (Pyšek and Jarošik, 2005). This suggests that unbiased evaluation of factors affecting invasiveness of alien species can be only obtained if the confounding effect of MRT is factored out. Since many species have not been present for long enough to naturalize and become invasive, the importance of any particular plant trait in determining the success or failure of invasion is discernible only after the species has either established or failed in a new region (Williams *et al.*, 2002). Residence time must also be considered when labelling species as invasive or non-invasive in different parts of the world – an important step in most screening protocols where the performance of a species elsewhere (invasive or not) is often used (often uncritically) as a crucial input. MRT is closely associated with the lag phase (also termed 'latency period') that often precedes invasions of alien species – the delay between the start of invasion and the typical phase of exponential increase (Baker, 1965; Kowarik, 1995). The phenomenon of lag phases has important implications for the tens rule (see section III), because the considerable lags preceding invasions mean that the patterns we observe today are largely the net result of introductions and prevailing conditions and processes from over a century ago (Hulme, 2003). A practical implication of this is that, because of the lag phase, biological invasions have a built-in inertia – the number of naturalized and invasive species will increase in the future even if no additional introductions are made (Kowarik, 1995; Figure 2). Preventive measures need to address not only precluding further introductions of high-risk species, but also screening and monitoring of already introduced species, some of which are 'sleeper weeds' (*sensu* Groves *et al.*, 2003).

V Born under a bad sign – taxonomic patterns in alien plant invasions

Not all species/genera/families have been moved around to the same extent, so opportunities to become naturalized and invasive are not even among taxa. Even with the caveat that the large-scale natural experiment of human-mediated rearrangement of regional floras is imperfect, it is clear that invasive alien plants are non-randomly distributed within higher taxonomic groups,

whether considered globally (Daehler, 1998; Pyšek, 1998), continentally (Weber, 1997), or regionally (Williams *et al.*, 2002; Wu *et al.*, 2004; Pauchard and Alaback, 2004; Villasenor and Espinoza-Garcia, 2004). This pattern has a phylogenetic background. When related to the global species pool, families with a disproportionally high representation of invasive aliens are concentrated within the classes Asteridae, Caryophyllidae and Commelinidae (Pyšek, 1998). At the family level, Amaranthaceae, Brassicaceae, Convolvulaceae, Malvaceae, Poaceae, Papaveraceae, and Polygonaceae are consistently over-represented in invasive-alien floras, and Fabaceae are highly successful as invaders of natural areas (Weber, 1997; Daehler, 1998; Pyšek, 1998; Wu *et al.*, 2004). Many families of aquatic or sub-aquatic (Alismataceae, Hydrocharitaceae, Nymphaeaceae, Potamogetonaceae, Typhaceae; Daehler, 1998) and woody plants (Myrtaceae, Rosaceae, Salicaceae, and Tamaricaceae; Williams *et al.*, 2002) are over-represented among high-impact invaders. There are very few invasive aliens in the Orchidaceae and Rubiaceae (Daehler, 1998; Pyšek, 1998). The non-random distribution is also reflected in differences in naturalization rates of particular families. In New Zealand, Juncaceae, Poaceae and Salicaceae are several times more likely to naturalize than the average (Williams *et al.*, 2002).

Evidence for invasiveness being phylogenetically related also at lower taxonomic levels comes from a study of gymnosperms. Twenty-eight of the 36 gymnosperms known to be invasive worldwide (78%) belong to one family (Pinaceae) and 21 of these belong to the genus *Pinus* (Richardson and Rejmánek, 2004). Using an index of invasiveness, defined as the number of invasive species/number of rare or threatened species within a family, Richardson and Rejmánek (2004) concluded that, despite being often portrayed as less successful in an evolutionary sense, some groups of conifers have similar or higher levels of invasiveness as highly invasive

angiosperm families comprising predominantly woody taxa, eg, Sapindaceae, Betulaceae, Eleagnaceae and Salicaceae.

VI Family ties – Darwin's naturalization hypothesis

De Candolle (1855) noted that naturalized species are more likely to recruit from genera with no native species in a given region. Darwin (1859) used this observation to support his theory of intense competition between congeners leading to easier naturalization of species from non-allied genera. Darwin's naturalization hypothesis (DNH) has attracted renewed interest recently as lists of naturalized plants become available for more regions of the world (Daehler, 2001). Two studies (Mack, 1996; Rejmánek, 1996) provided support for the hypothesis. Rejmánek (1996) determined that in three families (Asteraceae, Fabaceae, and Poaceae) European species naturalized in California are statistically more likely to belong to alien (non-American) genera than expected from a random pool of European species. The same pattern was found in the Australian flora (Rejmánek, 1999). Daehler (2001) pointed out that if the phenomenon proved to be universal, it could potentially lead to statistically based rules that could help to understand the assembly of invaded communities. To test the validity of the hypothesis he undertook the most rigorous study to date, examining 20 plant families in Hawaii. Interestingly, he also considered residence time (see section III), to see whether alien species once naturalized, hence present in the flora, become honorary natives and influence the naturalization success of late arrivals. He found no support for DNH. Indeed, for some families the pattern was opposite to that predicted by DNH. The same result emerged for the naturalized flora of New Zealand (Duncan and Williams, 2002). This suggests that for an introduced plant, the advantages of having close relatives, on average, outweigh the drawbacks (Williams, 1951) and that alien species from native genera have better chances of

naturalizing because they share with their congeners some level of preadaptation to the conditions of the invaded region – a notion originally articulated by Darwin (1859). Daehler (2001) suggested that the contrasting results in previous studies may be due to differences between families and regions, or because island and mainland communities are possibly regulated by different factors. DNH clearly does not hold in all situations, but the concept has stimulated some informative research and drawn attention to key aspects of naturalization in invasive plants.

VII Getting ready for the conquest – phenotypic plasticity and/or rapid evolution?

For an introduced plant species to invade a new region (ie, establish and proliferate across a range of environmental conditions) two basic options are available: either the plant must possess sufficiently high levels of physiological tolerance and plasticity, or it must undergo genetic differentiation to achieve required levels of fitness. The options are not mutually exclusive. A 'general-purpose genotype' (*sensu* Baker, 1965) facilitates spread of populations founded by small numbers of individuals through reproductive systems such as autogamy (selfing) that do not promote genetic exchange but do provide reproductive assurance. If an introduced species does not have a general-purpose genotype, it will be confined to a restricted area until genetic alteration, through recombination, introgression or mutation, allows it to grow and flourish across a wider range of sites. Much research in the past decade has explored the relative importance of plasticity versus rapid evolution across a wide range of systems and many taxa (Reznick and Ghalambor, 2001; Bossdorf *et al*., 2005). Phenotypic plasticity is undoubtedly important for many invasive species from many taxonomic groups and in diverse habitats. A few examples where this has been demonstrated are: *Alliaria petiolata* in New Jersey (Byers and Quinn, 1998), *Bunias orientalis* in Germany (Dietz *et al*.,

1999), *Carpobrotus* spp. in coastal California (Weber and D'Antonio, 1999), *Clidemia hirta* in Hawaii (DeWalt and Hamrick, 2004), *Pennisetum setaceum* in Hawaii (Williams *et al*., 1995), and *Verbascum thapsus* in California (Parker *et al*., 2003). Daehler (2003) reviewed case studies available and showed that invasive species have greater phenotypic plasticity than co-occurring native species.

Evolution can serve as another potential explanation for invasion success. Evolution can be rapid and is relevant to ecological studies (Thompson, 1998). Invasive plants may evolve by genetic drift and inbreeding in founder populations, by intra- and interspecific hybridization in the introduced range creating novel genotypes, and by drastic changes in selection regimes imposed by novel environments that may cause adaptive evolutionary change (Bossdorf *et al*., 2005). Hybridization can lead to adaptive evolution in a number of ways, including fixed heterozygosity via polyploidy (Ellstrand and Schierenbeck, 2000; Clements *et al*., 2004). Polyploids have many characteristics that allow them to maintain higher levels of genetic diversity, compared to diploids, and therefore to cope with problems of a small founder population (Soltis and Soltis, 1993; Levin, 2002). Hybridization has been shown an important mechanism of evolution of invasive species (Ellstrand and Schierenbeck, 2000; Vila *et al*., 2000; Daehler and Carino, 2001) and many widespread and successful invaders are recently formed allopolyploid hybrids (Abbott, 1992; Lee, 2002). Building on the work of Baker (1965) and Stebbins (1985), much recent research has explored the role of the evolution of polyploidy in facilitating invasions – eg, for Brassicaceae (Hurka *et al*., 2003), *Impatiens glandulifera* (Kollmann and Banuelos, 2004), *Rubus alceifolius* (Amsellem *et al*., 2001), and *Senecio cambrensis* (Abbott and Lowe, 2004). Increased performance of hybrid taxa or genotypes has been documented for a number of species (Vila *et al*., 2000; Pyšek *et al*., 2003b; Mandák *et al*., 2004).

Many studies have found at least partial support for the 'evolution of increased competitive ability' (EICA) hypothesis which predicts that plants introduced into an environment that lacks their usual herbivores will experience selection favouring individuals that allocate less energy to defence and more to growth and reproduction (eg, Blossey and Nötzold, 1995; Leger and Rice, 2003; Siemann and Rogers, 2003; Jakobs *et al.*, 2004; Maron *et al.*, 2004; Rogers and Siemann, 2004). Other studies found no support for EICA (eg, Willis *et al.*, 2000; Thébaud and Simberloff, 2001; Bossdorf *et al.*, 2004) or the opposite of what EICA predicts (Wolfe *et al.*, 2004). However, only a few studies provided a full test of the EICA hypothesis by addressing both growth and defence in the same species (Bossdorf *et al.*, 2005). Elegant evidence for the EICA hypothesis was recently provided by Zangerl and Berenbaum (2005). By examining herbarium specimens of alien *Pastinaca sativa* in North America over 152 years, they revealed phytochemical shifts towards increased toxicity coincident with the accidental introduction of a major herbivore from its native range. Overall, there is reasonable empirical evidence that genetic differentiation through rapid evolutionary change plays an important role in plant invasions (Bossdorf *et al.*, 2005). Nevertheless, available evidence suggests that some invaders are 'born' (released from fitness constraints), and some are 'made' (they evolve invasiveness after colonization) (*sensu* Ellstrand and Schierenbeck, 2000), and that the relative importance of ecological and evolutionary forces seems to be unique to each plant invasion episode.

VIII Go far away and multiply – long-distance dispersal

Observed rates of spread vary greatly among invasive plants in different habitats and regions and many invasions show extremely fast spread rates. The comparative analysis of the spatiotemporal dynamics of over 100 taxa from studies undertaken worldwide (Pyšek and Hulme, 2005) indicates that average rates of local spread of invasive species range from $2 \, m \, yr^{-1}$ to $370 \, m \, yr^{-1}$ but average rates of long-distance dispersal are at least two orders of magnitude greater than estimates of local dispersal, with the highest value of $167 \, km \, yr^{-1}$ recorded for *Wedelia trilobata* over a 15-year period (Batianoff and Franks, 1997). However, the maximum values recorded are many times higher than the mean. For example, over a period of 50 years, one population of *Opuntia stricta* spread up to 18.5 km from its origin, an average rate of $370 \, m \, yr^{-1}$ (Foxcroft *et al.*, 2004). But even in the first two years outlying populations were established up to 14 km away. Estimates of the area occupied through local spread have sometimes been drawn from aerial photographs and maximum recorded values range between 1100 and $2000 \, m^2 \, yr^{-1}$ (for *Rhododendron ponticum*, *Heracleum mantegazzianum* and the alga *Caulerpa taxifolia*; Pyšek and Hulme, 2005). For long-distance spread, most studies indicate 3 to $500 \, km^2 \, yr^{-1}$, but indirect estimates drawn from distribution maps can give much higher values up to $5000 \, km^2 \, yr^{-1}$ for *Bromus tectorum* (Mack, 1989). These examples indicate that invasions are often faster than most natural migrations, for example following deglaciation (Clark, 1998).

The past decade has seen considerable advances in the study of dispersal. A hierarchy of processes operating at different temporal and spatial scales determines the dynamics of biological invasions. Long-distance dispersal events (LDD; dispersal beyond the local patch or cluster of conspecifics) may occur during periods of negligible population increase and appear to bear little relationship to population size. Invasive species rarely move across the landscape as a continuous front and both local and long-distance dispersal determine spatial patterns (Pyšek and Hulme, 2005). The recognition of the important role of long-distance dispersal has changed the way ecologists view species dynamics (Nathan, 2005). For instance, it now appears that traits typically associated

with 'normal' dispersal capacity (eg, seed mass and morphology) are inappropriate for predicting the potential spread dynamics of a species. Infrequent, long-distance dispersal events, often via non-standard means of dispersal (Higgins *et al.*, 2003) ultimately control the rate of spread (Higgins and Richardson, 1999). Increasingly, post introduction dispersal by human agency (intentional or accidental) is probably the most significant driver of many plant invasions (Hodkinson and Thompson, 1997). One implication of this is that modelling the spread of alien species assuming 'normal' dispersal is likely to produce marked underestimates of spread rates, certainly at scales beyond the landscape (Pyšek and Hulme, 2005; Rejmánek *et al.*, 2005a). The underlying assumption that seed dispersal follows a diffusion process led to the formulation of 'Reid's paradox of rapid plant migration' since the rates of spread predicted by such models are much slower than those observed for the postglacial advance of trees (Clark *et al.*, 1998). LDD is extremely difficult to measure so a large proportion of variation remains unexplained in such studies, although significant correlates are found. Alien plants often produce more propagules in their introduced ranges (eg, Hönig *et al.*, 1992), which makes LDD more likely than in their native ranges, accounting, at least in part, for their invasive behaviour. This has profound implications for the capacity of alien species to spread across fragmented landscapes (Richardson *et al.*, 2000b; With, 2004) and, ultimately, for their capacity to respond to changing environmental conditions. This is one reason why alien plant species are likely to become increasingly dominant as global change forces range shifts. LDD is potentially an important unifying theme for linking invasion ecology with other fields such as conservation biology, with the realization that limited LDD is a key factor for consideration in the management of rare species, whereas excessive LDD is the major driver of biological invasions (Trakhtenbrot *et al.*, 2005).

IX Traits do matter – a theory of seed plant invasiveness

Many studies have attempted to profile successful invaders, starting with the work of Baker (1965) on identifying the traits of the 'ideal weed', an idea now considered simplistic (Perrins *et al.*, 1993). Subsequent studies have identified characteristics associated with reproductive potential, vegetative reproduction and dispersal as important correlates of invasiveness (eg, Forcella *et al.*, 1986; Noble, 1989; Roy, 1990; Richardson and Cowling, 1992; Thompson *et al.*, 1995; Crawley *et al.*, 1996). A limitation of such studies is, however, the lack of relevant information for most plant species. Good data are available for plant height, growth form, seed mass and (apparent) dispersal syndrome, but data on growth rates, palatability, seed production, and many other traits that are crucial for invasion success (Pyšek *et al.*, 2004a; Rejmánek *et al.*, 2005b) are, in many cases, lacking or of dubious quality. It has become obvious that finding a set of traits associated with invasiveness that applies to all vascular plants is an unrealistic aim (Williamson, 1999). Consequently, the focus has shifted to exploring the components of invasiveness at a finer taxonomic scale or for particular life forms. For example, Rejmánek and Richardson (1996) were able to explain invasiveness in *Pinus* species using only three traits (seed mass, length of juvenile period and interval between seed mast years). They defined a discriminant function that successfully separated invasive and non-invasive species. This framework was expanded, by adding considerations relating to dispersal by vertebrates and characteristics of fruits, and successfully applied to predict invasiveness in other gymnosperms and woody angiosperms (Rejmánek and Richardson, 1996; Richardson and Rejmánek, 2004).

Marcel Rejmánek's 'theory of seed plant invasiveness' is the most ambitious attempt to date to synthesize available knowledge into a unified scheme (Rejmánek, 1996; 2000; Rejmánek *et al.*, 2005a; 2005b). It highlights a

low nuclear amount of DNA as a result of selection for the short generation time, membership to alien genera (but see section VI), and primary latitudinal range as major factors contributing to the invasiveness of seed plants. Large geographical range is often among the best predictors of invasion success (Goodwin *et al.*, 1999; Scott and Panetta, 1993; Rejmánek, 1995). Widespread species are more likely to be dispersed because they occur in more locations and have higher chances to be dispersed, and they are more likely to be adapted to wider range of conditions (Booth *et al.*, 2003). Although there are exceptions to this rule reported for individual species (Richardson and Bond, 1991), it seems that the same traits that allow a species to be widespread in the native range are also favourable for a successful invasion (Booth *et al.*, 2003). An additional study identified RGR as the most important predictor of invasiveness in disturbed habitats and related invasiveness to physiological measures (Grotkopp *et al.*, 2002).

When analysing large comparative data sets, potentially confounding effects of phylogenetic relatedness should be taken into account to distinguish between ecological and evolutionary explanations (Harvey and Pagel, 1991; Westoby *et al.*, 1995). Only a few studies looking at traits associated with invasiveness have applied phylogenetic correction, either by employing phylogenetically independent contrasts (Crawley *et al.*, 1996; Pyšek, 1997; Grotkopp *et al.*, 2002; Kühn *et al.*, 2004; Rejmánek *et al.*, 2005a), or by comparing each naturalized species with a closely related non-naturalized (Goodwin *et al.*, 1999). Using the former approach, Crawley *et al.* (1996) found invasiveness in British plants to be associated with tall stature, large seed size, pattern of dormancy, mode of pollination and time of flowering (see also Pyšek *et al.*, 2003c). Compared to native, alien plants seem to 'try harder', exhibiting more extreme features (being either very small or very big, flowering very early or very late, non-dormant or with long dormancy). This indicates that they may occupy vacant niches at both ends of the spectrum (Crawley *et al.*, 1996).

X Owls are not what they seem – level of invasion, invasibility and propagule pressure

Variations in the level/extent of invasion among recipient communities could be simply due to differences in the number of aliens arriving in the community (Williamson, 1996; Lonsdale, 1999; Hierro *et al.*, 2005; Chytrý *et al.*, 2005). To know whether a region, community or habitat is more invasible we need to ask not only whether it has more alien species, but whether it is intrinsically more susceptible to invasions (Lonsdale, 1999). Intrinsic invasibility can only be determined if processes of immigration and extinction are taken into account. Most invading species fail to establish (see section III), so the number of alien species in a region (community, habitat) is the product of the number of alien species introduced S and their survival rate I in the new environment. It is useful to break down both parameters further – the number of introduced species into accidental and intentional introductions, and survival rate into losses attributable to competition, herbivory, chance, pathogens, and maladaptations associated with release of a species into unsuitable environment (Lonsdale, 1999). Clearly, 'more invaded' does not necessarily mean 'more invasible' and real differences in invasibility can only be assessed by analysing residuals from the relationship between invasion success and propagule pressure (Williamson, 1996), which determines S in Lonsdale's equation.

That propagule pressure, both in space (by widespread dissemination, abundant plantings) and/or time (by long history of cultivation) can fundamentally influence the probability of invasions by alien species has been convincingly demonstrated (Mulvaney, 2001; Kowarik, 1995; Crooks and Soulé, 1999; Richardson, 1999; Rejmánek, 2000; Kolar and Lodge, 2002; Williams *et al.*, 2002; Rouget and Richardson, 2003; Brown and

Peet, 2003, Kühn *et al.*, 2004; Foxcroft *et al.*, 2004). This finding corroborates growing evidence that plant populations are seed limited (Turnbull *et al.*, 2000; Parker, 2001; Seabloom *et al.*, 2003). When studying invasibility at the scale of large areas (habitats, communities, regions), propagule pressure is extremely difficult to measure. Various quantitative surrogates for propagule pressure including the number of visitors to nature reserves (Lonsdale, 1999; McKinney, 2002), human population size or density (Pyšek *et al.*, 2002a; 2003a; McKinney, 2001; 2002; Taylor and Irwin, 2004), the amount of trade and tourism (Thuiller *et al.*, 2005) or economic activity (Taylor and Irwin, 2004) have been used with reasonable success.

Models incorporating propagule pressure are proving markedly superior to those invoking only environmental parameters for explaining distribution patterns and abundance of invaders at a regional scale. Attempts to model ongoing and predict future invasions must therefore incorporate propagule pressure (Rouget and Richardson, 2003). While adding more propagules to sites increases establishment success, the relative importance of propagule pressure compared with that of other factors such as disturbance and resource supply is not well understood (Hierro *et al.*, 2005). Once propagule pressure of invaders is factored out, both physical and biotic factors determining the outcome of plant invasion can be studied (Chaneton *et al.*, 2002), but controversy persists over which prevail (Tilman, 1997; Levine and D'Antonio, 1999; Naeem *et al.*, 2000; see section VII). Carefully designed factorial field experiments in which a range of propagule pressures are crossed with different levels of the other influential factors could improve our understanding of invasion mechanisms (Hierro *et al.*, 2005). Studies are also needed to determine the extent to which propagule pressure can compensate for low inherent species invasiveness (Richardson and Rejmánek, 2004) and/or low intrinsic community invasibility (D'Antonio *et al.*,

2001). The issue of propagule pressure is closely related to ecological resistance which is determined by both biotic (see section XI) and abiotic factors. A simple conceptual framework of how variation in propagule pressure interacts with abiotically determined ecological resistance was suggested by D'Antonio *et al*. (2001). When resistance is low, few propagules are needed for an invader to establish in a community and the rate of invasion is fast. High resistance can be overcome only if the rate of propagule supply is high or if invaders themselves alter the resistance of the community.

Lonsdale's concept of invasibility has proved extremely useful in emphasizing the role of propagule pressure and pointing out the difference between invasibility (or vulnerability to invasion) of a region, community or habitat and a simple number of invasive species it harbours; for the latter the term 'level of invasion' (Hierro *et al.*, 2005; Chytrý *et al.*, 2005) seems to be more appropriate. Yet many studies label sites with higher numbers of invasive species as being more invasible (eg, Planty-Tabacchi *et al.*, 1996; Naiman and Decamps, 1997; Hood and Naiman, 2000). The concept also drew attention to determinants of alien species' survival in a new region, which can be tested experimentally, and stimulated analyses aimed at disentangling the effect of particular factors determining invasibility (Chown *et al.*, 1998; McKinney, 2001; 2002; Pyšek *et al.*, 2002a; 2005). To compare the invasibility of plant communities or vegetation types, factors potentially biasing differences in their intrinsic invasibility such as area, climate, and soil need to be controlled (Pyšek *et al.*, 2002a).

Global-scale studies focused on habitat-related correlates of invasibility and/or the level of invasion have made it possible to sketch the 'big picture' and to evaluate hypotheses generally accepted but rarely rigorously tested before (Lonsdale, 1999). Robust geographical patterns have emerged, confirming among other things that islands are more invasible than mainland (Darwin,

1845, cited by Cassey, 2003; Rejmánek, 1996; Lonsdale, 1999; Denslow, 2003), temperate agricultural or urban sites are the most invasible biomes, and that the New World is more invasible than Old World (but only if a surrogate for habitat diversity is factored out; Lonsdale, 1999). Invasibility increases with latitude on mainland but not on islands (Lonsdale, 1999), and tropical areas are less invaded than extratropical regions (Rejmánek, 1996), but species naturalized in tropics have larger geographical ranges (Sax, 2001). The number of naturalized species is negatively correlated and geographical range size is positively correlated with latitude (Rapoport's rule; Sax, 2001). On mainlands, ranges of alien species rarely exceed the lower latitudinal limit of their native ranges, but on islands they do because of reduced biotic pressure (Sax, 2001). The inherent superiority, acquired through evolutionary time, of dominant mainland species from species-rich regions has been suggested as one factor contributing to the high invasibility of islands, and as an explanation for the apparent paradox that introduced species can displace native species that are, presumably, well adapted to their native environment (Sax and Brown, 2000). Similarly, global reviews of the performance of selected taxa in a wide range of localities, differing in the level of disturbance, shed new light on habitat invasibility (Richardson and Bond, 1991).

XI Diversity and invasibility – the illusive link
Principles of the biotic resistance hypothesis (also termed the 'diversity resistance hypothesis' or the 'species richness hypothesis') were raised by Elton (1958) who suggested a negative relationship between native species diversity and community invasibility. Numerous studies have indeed found species-rich communities to be less invasible (eg, Rejmánek, 1989; Tilman, 1997; 1999; Knops *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Dukes, 2002; Kennedy *et al.*, 2002), but others found areas with a high species

diversity to harbour more alien species (Timmins and Williams, 1991; Lonsdale, 1999; Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1999; Lonsdale, 1999; Stadler *et al.*, 2000; Pyšek *et al.*, 2002a; McKinney, 2001). Empirical tests of the effects of species richness on invasibility have produced unambiguous results (Levine and D'Antonio, 1999). Most of the evidence for biotic resistance, ie, the negative relationship, comes from experimental work using synthetic assemblages that vary in diversity, while large-scale observational studies have mostly shown a positive correlation between diversity and invasibility (Levine, 2000; Naeem *et al.*, 2000; Levine *et al.*, 2002; Hierro *et al.*, 2005). This discrepancy is mostly due to the spatial scale of observation (Fridley *et al.*, 2004; Herben *et al.*, 2004) and can be explained by covarying external factors (Shea and Chesson, 2002). At the large scale, the same abiotic conditions that promote high diversity of native species (climate, substrate, habitat heterogeneity, etc) also support diverse alien floras; in other words, what is good for natives is good for aliens too.

Elton's hypothesis rests on the theoretical notion that, in less diverse communities, intraspecific interactions are weaker because more empty niches are available (MacArthur, 1972; Crawley, 1987). Reduced resource uptake in species-poor communities (Tilman *et al.*, 1996; Hooper and Vitousek, 1998), leading to more free resources, renders species-poor communities more invasible than species-rich communities (Hierro *et al.*, 2005). Where competition-driven extinction dominates, leading to resource complementarity or space limitation (particularly likely at small scales owing to direct interactions between species; Huston, 1999) we should expect a negative correlation between diversity and invasibility (Brown and Peet, 2003). However, competitive interactions alone are unlikely to explain the observed patterns; there appear to be only few 'super-invaders' that have universal superior performance over co-occurring native species. Based on 79 case

studies of competition between native and invasive species, Daehler (2003) found that alien invaders were not statistically more likely to be competitively superior, but rather that the relative performance of invaders and co-occurring natives was context-dependent. Moreover, in 55 situations when data on pairs of aliens and native exposed to various growing conditions (resource availability, disturbance regimes) are available, the performance of natives was superior to that of aliens at least for some key performance in some of the growing condition (Daehler, 2003). Models of competition predict and field experiments have confirmed that higher diversity leads to higher primary productivity; the relationship results both from the sampling effect and niche differentiation effect and leads to more complete utilization of limiting resources at higher diversity (Tilman, 1999). The low invasibility of high diversity communities thus results from the uniformly low levels of resources that occur in these communities (Tilman, 1999; 2004; Fargione *et al.*, 2003).

Species-rich communities occur in habitats with high levels of heterogeneity in terms of climate, soil and topography. Alien species are more likely to find suitable habitats to invade in more heterogeneous habitats than in less heterogeneous habitats (Huston and De Angelis, 1994). If factors amenable to high species diversity also lower invasion resistance, the positive relationship between both variables observed on broad spatial scales is explained. At finer scales, for fixed extrinsic conditions, a negative pattern of invasibility as a function of species diversity is predicted. The broad-scale positive relationship is then the outcome of combining data from a series of negative relationships where each negative relationship comes from different extrinsic conditions (Shea and Chesson, 2002). The positive correlation between alien and native plant diversity found in most large-scale studies therefore occurs because native plant diversity is a proxy variable for habitat diversity (Lonsdale, 1999; Pyšek *et al.*, 2002a; McKinney, 2002).

Most studies exploring the effects of species diversity on invasibility focus simply on the number of species but community composition and species identity have been shown to be important for the interpretation of observed effects, which may not be due to richness itself but to the overriding effect of keystone species (Booth *et al.*, 2003). Crawley *et al.* (1999) found species identity to be more important in determining both the number of invading species and the total biomass of invasives than species richness *per se*. Assemblages with more species are more likely to have some members able to thwart invading species (Grime, 1997; Hooper and Vitousek, 1998; Lepš *et al.*, 2001). Furthermore, simulation models suggest that processes regulating species richness in resident communities crucially affect the pattern of invasibility along species richness gradients (Moore *et al.*, 2001) and that the diversity-invasibility relationship depends on the size of the species pool (Herben *et al.*, 2004; Herben, 2005). This suggests that the focus of research in this area should shift from considering species richness as a synthetic variable to an approach that recognizes the importance of species identities and mechanisms of coexistence.

Species richness may be simply too broad a factor to explain observed differences in community invasibility (Levine and D'Antonio, 1999). Other factors such as disturbance, nutrient availability, climate and propagule pressure can covary with species richness; by exerting different effects on invasive and resident species (Siemann and Rogers, 2003; Leishman and Thomson, 2005), they can affect the relationship between species richness and invasibility in numerous ways (Levine and D'Antonio 1999; Levine, 2000; Naeem *et al.*, 2000; Shea and Chesson, 2002). Generally, in disturbed environments, abiotic factors seem to be more pivotal as determinants of invasibility than biotic factors (Richardson and Bond, 1991; Hood and Naiman, 2000). Recent studies have also found little general support for the role of

biotic resistance in determining geographical patterns of establishment of introduced species but have found evidence for a dominant effect of climate matching (Lodge, 1993; Chown *et al.*, 1998; Gaston *et al.*, 2003; Thuiller *et al.*, 2005). One factor known to facilitate invasibility at larger spatial scales is resource availability (Hobbs and Huenneke, 1992; Davis *et al.*, 2000; Davis and Pelsor, 2001); this sometimes explains more variance in invasibility than species richness (Foster *et al.*, 2002). Given that resource supply and diversity of natives, when considered separately, appear to have opposite effects on invasion resistance, the critical issue is how these factors interact to mediate community invasibility (Hierro *et al.*, 2005). To better understand the relationship between species richness and invasibility, species richness must be manipulated in situ in order to separate its effects from covarying factors (Foster *et al.*, 2002; Von Holle, 2005). However, obtaining a more general picture is complicated by the fact that it is difficult to extend the results of biodiversity-manipulation experiments to argue that diverse communities in nature are inherently less invasive than species-poor ones (Naeem *et al.*, 2000). Also, as pointed out by Hierro *et al.* (2005), correlative large-scale observational studies have not controlled for extrinsic factors known to covary with diversity and that also may influence invasibility, such as propagule pressure, disturbance, resource availability and consumers (Levine and D'Antonio, 1999; Shea and Chesson, 2002). Experimental studies, on the other hand, have controlled for these factors essentially by ignoring them. This limits our understanding of how diversity interacts with processes that vary over broader spatial scales (Hierro *et al.*, 2005).

XII Catch if catch can – fluctuating resources, fluctuating invasibility

Besides the insights on invasibility from correlative studies (reviewed above), numerous recent studies have explored the determinants of invasibility (the capacity or susceptibility of a community to accept new members) from a more mechanistic perspective. Most results from such studies are context-specific with little potential for generalization. Among the various attempts at unifying the many factors potentially influencing invasibility we find four particularly useful: Alpert *et al.* (2000), Davis *et al.* (2000), D'Antonio *et al.* (2001) and Huston (2004). All of them integrate, to various levels and in different ways, the roles of disturbance, competitive release, resource availability, and propagule pressure. The most widely embraced of these has been the 'fluctuating resources theory of invasibility' (Davis *et al.*, 2000) which posits that invading species must have access to available resources, eg, light, nutrients, and water, and that an invading species will be more successful at invading a community if it does not encounter intense competition for these resources from resident species. By using insights from experiments and long-term monitoring studies, the theory identifies fluctuation in resource availability as the key factor controlling invasibility (Davis *et al.*, 2000). There is good evidence that intermittent resource enrichment or release (often due to disturbance) increases community susceptibility to invasions, and that invasions occur if this coincides with availability and arrival of suitable propagules. Many studies attest to invasion being facilitated by increasing water or nitrogen availability (eg, Seabloom *et al.*, 2003). Experimental evidence has confirmed that the larger the difference between gross resource supply and resource uptake, the more susceptible the community to invasion, and that a short fluctuation in resource availability had a long-term impact on the outcome of an invasion (Davis and Pelsor, 2001).

XIII Bitches' brew – synergisms, mutualisms, ecosystem engineers and invasional meltdown

Until recently, research on the interactions between invasive species and other resident species in the invaded range dealt largely with

the harmful effects of the invaders. This trend, of greater emphasis on negative than on positive or facilitating interactions, has been evident throughout ecology (see discussion in Richardson *et al.*, 2000a). In the past decade or so, more attention has been given to positive interactions in ecology (Bruno *et al.*, 2003) and work on invasive species has been enlightening in this regard. In many cases, the success of an alien species (ie, its ability to overcome various barriers in the new environment) depends on the presence of other species (native or alien) already resident in the area (Richardson *et al.*, 2000a). Such interactions may counter, and potentially override, any inherent biotic resistance – a fact that is generally overlooked in discussions of biotic resistance (eg, Levine *et al.*, 2004). The presence of alien species is making some areas more susceptible to invasion by other alien species (Richardson *et al.*, 2000a). Sometime this process may produce entirely novel ecosystems dominated by a suite of species other than those native to the site (Hobbs *et al.*, 2006). Simberloff and Von Holle (1999) introduced the term 'invasional meltdown' to describe such synergistic interactions among invaders that accelerate invasions and amplify their effects on native communities. The term, now widely applied in the invasion literature (>120 citations in five years), is, however, often used with reference to any escalation in the net effects of invasive organisms at a site, rather than true synergistic effects. Dramatic evidence has emerged recently regarding the potentially facilitative effects of soil biota for invading plants. Positive interactions with soil biota have been shown to facilitate invasions for some plant species (Richardson *et al.*, 2000a; Klironomos, 2002; Reinhart *et al.*, 2003; Callaway *et al.*, 2004). Some studies have identified switches from negative plant-soil community feedback in native ranges to positive plant-soil community feedback in the adventive ranges (Callaway *et al.*, 2004). Such positive feedbacks point to 'invasional meltdown'.

The concept of invasional meltdown is also closely linked to that of 'ecosystem engineers' – organisms that affect resource availability, directly or indirectly, by altering abiotic or biotic features of an ecosystem (Jones *et al.*, 1994). Many invasive plant species qualify as ecosystem engineers (Crooks, 2002), though not all invaders alter habitats in such a way as to facilitate further invasions. Where alien plant ecosystem engineers most clearly drive invasional meltdown is where the initial invasion totally alters ecosystem processes such as the fire regime. Probably the best example of this is the 'grass-fire cycle' in which invasive alien grasses change the distribution and abundance of fine fuels, resulting in more frequent fires (and in some cases introducing regular fires to non fire-prone ecosystems). This profound alteration of ecosystem functioning, which often favours further invasion of fire-tolerant alien species, has had radical effects on biodiversity in many semi-arid systems (D'Antonio and Vitousek, 1992). Similar effects are evident for plants other than grasses. For example, invasion of South African fynbos by serotinous trees and shrubs disrupts the prevailing non-equilibrium condition of cyclical replacement of native shrubs, instituting a depauperate steady-state system which favours a suite of aliens including *Hakea* and *Pinus* species (Richardson and Cowling, 1992).

XIV Conclusions

Exciting progress has been made in all of the facets of plant invasion ecology reviewed in this paper. Advances are partly attributable to the fact that good research has been done at multiple levels and scales and that the conceptualization of processes mediating invasions has helped to focus efforts on elucidating factors responsible for key phase-transitions. The lack of standardized categorization of alien plants in different parts of the world is a problem. The adoption of a global standard would facilitate improved generalizations concerning levels of invasiveness and invasibility. The large number of good case studies undertaken

recently has improved our ability to make robust generalizations and move towards mechanistic and predictive models. Models are starting to embrace both species invasiveness and community invasibility, providing a measure of integration. The stage is set for further advances. Molecular ecology has huge scope for shedding light on crucial gaps in our knowledge. For example, since seed dispersal, and especially rare long-distance dispersal events, is difficult to measure in the field, insights from molecular studies are needed to unravel key unknowns in invasion dynamics. Many of the concepts reviewed here are amenable to testing in manipulative experiments; increased robustness of generalizations and theories can be expected through experimentation. Improved integration of perspectives from all fields of research is needed to improve our ability to manage invasions.

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