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Plant invasions and invasibility of plant communities

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13.1 Introduction

Some 2500 yr ago, Heraclitus of Ephesus said that 'All things change . . . and you cannot step twice into the same stream'. Today, ecologists would not only say the same about streams but also about vegetation. Plant communities change with time due to changes in the environment (Chapter 7), biotic interactions (Chapter 9) and invasions of alien species and genotypes, introduced intentionally or accidentally by humans. Invasions have received detailed attention only recently. There have always been migrating taxa, but now the rate of human-assisted introductions of new taxa is several orders of magnitude higher. In California, for example, more than 1000 alien plant species were intentionally or non-intentionally introduced and established viable populations over the last 250 yr. In the Galápagos Islands, over 3 million yr of their history, only one new plant species arrived with birds or sea currents every 10,000 yr. However, over the last 20 yr the introduction rate has been *c.* 10 species per yr, or some 100,000 times the natural arrival rate (Tye 2001).

Three basic questions arise:

1. What kind of ecosystems are more (or less) likely to be invaded by alien plants?
2. What kind of plants are the most successful invaders and under what circumstances?
3. What is the impact of the plant invaders?

13.2 Definitions and major patterns

Unlike **natives** (taxa that evolved in the region or reached it from another area where they are native without help from humans), **aliens** ('non-native' or 'exotic') owe their presence to direct or indirect activities of humans. Most of them occur only temporarily and are not able to persist for a long time without human-assisted input of diaspores; these are termed **casual**. **Naturalized** taxa form sustainable populations without direct human help but do not necessarily spread; the ability to spread characterizes a subset termed **invasive** taxa. This distinction is critical because not all naturalized taxa reported in floras and checklists are invasive. Not all naturalized plant taxa, and not even all invaders, are harmful invaders – the last-mentioned should

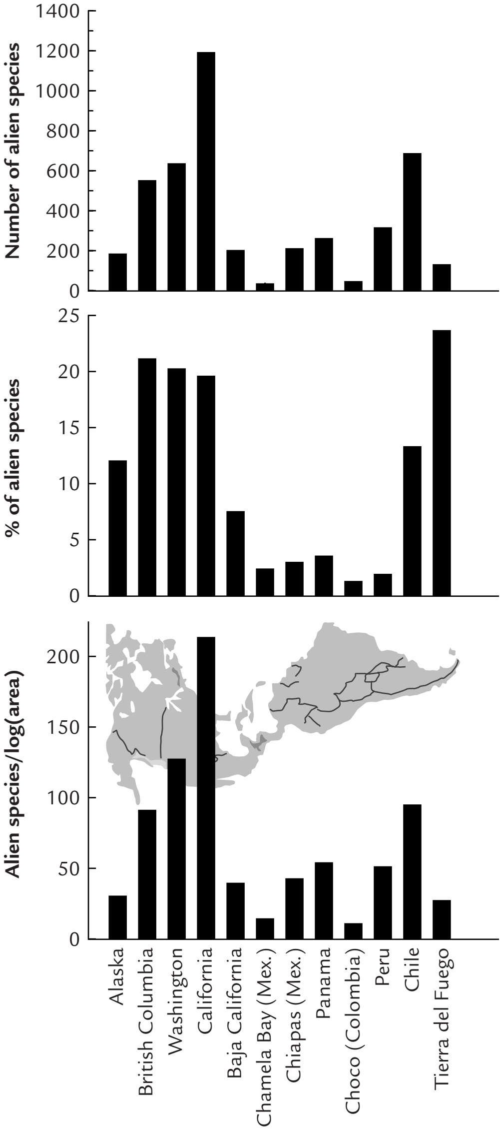

Fig. 13.1 Total number of alien plant species, percentage of alien plant species, and number of alien plant species per log(area) along the Pacific coast of Americas. 'Alien species' here are plants growing in individual areas without cultivation. Not all of them are fully naturalized and even fewer are invasive. Nevertheless, numbers of naturalized and invasive species are proportional to numbers of 'alien species' in this diagram. Primary data or references are in Kartesz & Meacham (1999) and Vitousek *et al.* (1997).

rather be called exotic *weeds* or exotic pest plants (Booth *et al.* 2003; Richardson *et al.* 2000a).

Weeds are both native and alien and the alien element in weed floras varies over the world. Most weedy taxa in southern Europe, Malaya, Mexico or Taiwan are native, whereas most weedy taxa in Australia, the USA, Chile, South Africa, New Zealand, Hawai'i, and many other islands are non-native. There may be inherent differences in invasibility of different parts of the world. Uneven representation of alien, mostly naturalized, plant species in regional floras along the Pacific shore of the Americas illustrates this point (Fig. 13.1). These differences are certainly partly due to the history of human colonization and trade. Nevertheless, similar patterns can also be recognized on other continents (Rejmánek 1996; Lonsdale 1999). For instance, areas with mediterranean climates (with the exception of the Mediterranean Basin itself) seem to be more vulnerable and the tropics appear more resistant to plant invasions. This should not be generalized, however. Savannas and especially disturbed deforested areas in the Neotropics are very often dominated by African grasses such as *Hyparrhenia rufa* and *Melinis minutiflora*, while similar tropical habitats in Africa and Asia are dominated by Neotropical woody plants, e.g. *Lantana camara* and *Opuntia* spp. The absolute number of alien species, therefore, is not necessarily the best indicator of ecosystem invasibility, at least at this scale. Undisturbed tropical forests, however, harbour only a very small number of alien plant species and most of them do not spread beyond trails and gaps (Rejmánek 1996). It is probably not the extraordinary species diversity of tropical forests that is important but simply the presence of fast-growing multilayered vegetation that makes undisturbed tropical forests resistant to invasions.

At the regional scale enormous differences in presence and abundance of invaders among different communities (ecosystems) within one area seem to be the rule. An overview is now available for Central Europe (Table 13.1). Alien species are concentrated mostly in vegetation of deforested mesic habitats with frequent disturbance (Pyšek *et al.* 2002a,b). In general, native forests harbour a low number and proportion of both archaeophytes (introduced before 1500) and neophytes (introduced later); alien species are completely missing from many types of natural vegetation, e.g. bogs, natural *Picea abies* forest, and rare in many natural herbaceous communities. Herbaceous communities of extreme habitats and/or with strong native clonal dominants (*Nanocyperion flavescentis*, *Phragmition*, *Nardion*) seem to be most resistant to invasions of both archaeophytes and neophytes. In general, Californian lowland communities (Fig. 13.2) are more invaded than corresponding communities in Europe. However, there are some important similarities. Open and disturbed communities are more invaded, while undisturbed forests are less invaded.

Data from California (Fig. 13.2) suggest that proportions of alien species numbers are reasonably well correlated with their dominance (cover). This is probably attributable to a simple sampling effect: with increasing proportion of alien species, there is an increasing chance that one or more of them will dominate the community. While there appears to be a general agreement between the proportion of alien species numbers and their actual importance (cover and biomass), some exceptions are quite remarkable. While alien species number in *Chelidonio-Robinion* woodland is certainly not exceptionally high (Table 13.1), the dominant *Robinia pseudoacacia* is an alien

Table 13.1 Numbers of alien species, classified according to the time of introduction into archaeophytes and neophytes, in representative plant communities of the Czech Republic on the phytosociological alliance level. Within each vegetation group, alliances are ranked according to decreasing total number of alien species. Data from Pyšek *et al*. (2002a).

	Number of archaeophytes	Number of neophytes	% invasive among neophytes
Ruderal vegetation			
Sisymbrion officinalis tall-herb comm. of annuals on nitrogen-rich mineral soils	96	106	9.4
Aegopodion podagrariae nitrophilous fringe comm.	16	76	36.8
Arction lappae nitrophilous comm. of dumps and rubbish tips	36	45	31.1
Balloto-Sambucion shrub comm. of ruderal habitats	18	34	41.2
Matricario-Polygonion arenastri comm. of trampled sites	20	20	15.0
Potentillion anserinae comm. of salt-rich ruderal habitats	12	20	10.0
Convolvulo-Agropyrion comm. of field margins and disturbed slopes	24	16	31.3
Onopordion acanthii thermophilous comm. of village dumps and rubbish tips	34	8	12.5
Weed communities of arable land			
Veronico-Euphorbion weed comm. of root crops on basic soils	47	28	21.4
Panico-Setarion weed comm. of root crops on sandy soils	28	15	40.0
Caucalidion lappulae thermophilous weed comm. on base-rich soils	79	11	0.0
Aphanion weed comm. on acid soils	41	8	12.5
Sherardion weed comm. of cereals on medium base-rich soils	47	7	14.3
Grasslands			
Arrhenatherion mesic meadows	15	56	25.0
Festucion valesiacae narrow-leaved dry grasslands	12	12	0.0
Bromion erecti broad-leaved dry grasslands	6	8	0.0
Nardion subalpine grasslands	0	1	0.0
Helianthemo cani-Festucion pallentis rock-outcrop vegetation	2	0	–
Forests			
Alnion incanae ash-alder alluvial forests	4	15	40.0
Carpinion oak-hornbeam forests	6	14	14.3
Chelidonio-Robinion plantations of *Robinia*	5	10	60.0
Genisto germanicae-Quercion dry acidophilous oak forests	1	11	36.4
Tilio-Acerion ravine forests	5	8	37.5
Luzulo-Fagion acidophilous beech forests	0	4	50.0
Quercion pubescenti-petraeae thermophilous oak forests	1	2	0.0
Quercion petraeae acidophilous thermophilous oak forests	0	2	50.0
Salicion albae willow-poplar forests of lowland rivers	0	2	50.0

Table 13.1 (*cont'd*)

	Number of archaeophytes	Number of neophytes	% invasive among neophytes
Alnion glutinosae alder carrs	0	2	0.0
Fagion beech forests	0	1	100.0
Betulion pubescentis birch mire forests	0	0	–
Piceion excelsae spruce forests	0	0	–
Aquatic and wetland vegetation			
Lemnion minoris macrophyte vegetation of eutrophic and mesotrophic still waters	0	3	0.0
Cardamino-Montion forest springs without tufa formation	0	2	50.0
Phragmition reed beds of eutrophic still waters	1	1	0.0
Magnocaricion elatae tall-sedge beds	0	1	0.0
Nanocyperion flavescentis annual vegetation on wet sand	1	0	–

tree from North America. On the other hand, there are many alien species in some grassland communities (*Festucion valesiaceae*, *Bromion erecti*), but dominants are exclusively native and aliens are rarely invasive.

13.3 Invasibility of plant communities

Can we say anything conclusive about differences in invasibility (vulnerability to invasions) of particular ecosystems? Analyses of ecosystem invasibility based just on one-point-in-time observations (*a posteriori*) are usually unsatisfactory (Rejmánek 1989). In most of the cases we do not know anything about the quality, quantity and regime of introduction of alien propagules. Nevertheless, available evidence indicates that only very few non-native species invade successionally advanced plant communities (Rejmánek 1989; Meiners *et al.* 2002). Here, however, the quality of common species pools of introduced alien species – mostly rapidly growing and reproducing *r*-strategists – is probably an important part of the story. These species are mostly not shade-tolerant and many of them are excluded during the first 10 or 20 yr of uninterrupted secondary succession (Fig. 13.3), or over longer periods of primary successions. However, some *r*-strategists are shade-tolerant. e.g. *Alliaria petiolata*, *Microstegium vimineum* and *Sapium sebiferum*. Such species can invade successionally advanced plant communities and, therefore, represent a special challenge to managers of protected areas.

Plant communities in mesic environments seem to be more invasible than communities in extreme terrestrial environments (Rejmánek 1989). Apparently xeric environments are not favourable for germination and seedling survival of many introduced species (abiotic resistance) and wet terrestrial habitats do not provide resources – mainly light – for invaders because of fast growth and high competitiveness of resident

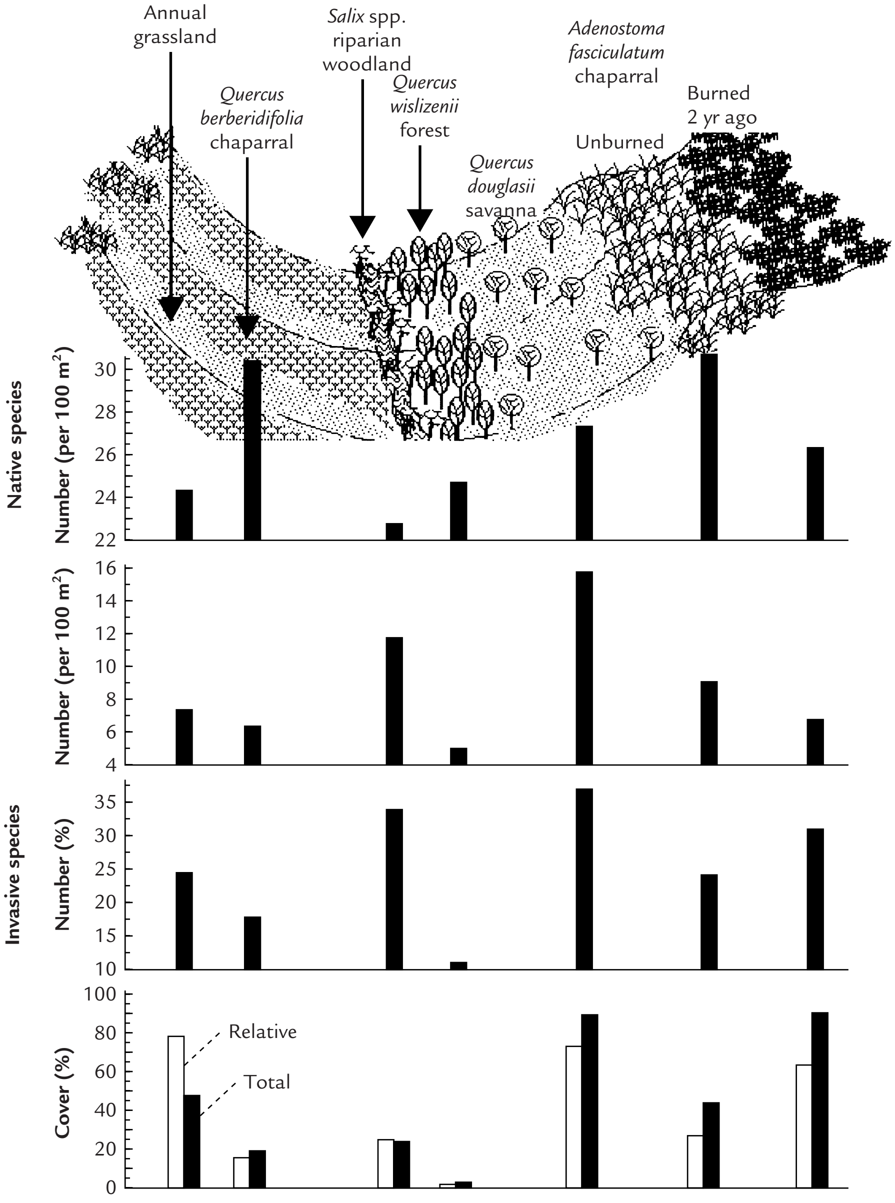

Fig. 13.2 Native and invasive species in seven plant communities of the Stebbins Cold Canyon Reserve, North Coast Ranges, California (150–500 m above sea level). Each column represents a mean from three 100-m^2 plots. 'Relative cover' of invaders is their cover with respect to the cumulative vegetation cover in all strata (herbs, shrubs and trees). Comparing means for individual vegetation types, the only significant correlation is between percentage of invasive species and total cover of invasive species ($r = 0.75$; $n = 7$; $p = 0.05$). Rejmánek (unpublished data).

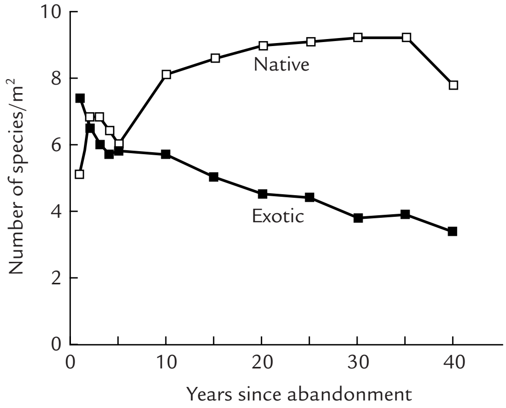

Fig. 13.3 Effect of time since abandonment on the mean species richness of native and exotic species over 40 yr of old-field succession in New Jersey (Meiners *et al.* 2002). Decline of the mean percentage of exotic species is even more dramatic, decreasing from 58 to 28%. Total and relative cover of exotic species declines significantly as well, but there can be a temporary increase during the first 5 or 10 yr of succession; see also Rejmánek (1989).

species (biotic resistance). We have to be cautious, however, in the interpretation of these patterns. When the 'right' species are introduced, even ecosystems that have been viewed as invasion-resistant for a long time may turn out to be susceptible, for instance the Mojave and Sonoran deserts are facing recent invasions by *Brassica tournefortii* and *Pennisetum ciliare*. Open water is notoriously known as open to all kinds of exotic aquatic plants. In general, disturbance, nutrient enrichment, slow recovery rate of resident vegetation, and fragmentation of successionally advanced communities promote plant invasions (Rejmánek 1989; Hobbs & Huenneke 1992; Cadenasso & Pickett 2001). In addition, the increasing CO_2 level will probably accelerate invasions in arid ecosystems (Smith *et al.* 2000).

A general theory of invasibility was put forward recently by Davis *et al.* (2000): intermittent resource enrichment (eutrophication) or release (due to disturbance) increases community susceptibility to invasions. Invasions occur if/when this situation coincides with availability of suitable propagules. The larger the difference between gross resource supply and resource uptake, the more susceptible the community to invasion. This was anticipated by Vitousek & Walker (1987) (Fig. 13.4) and expressed more rigorously by Shea & Chesson (2002). Davis & Pelsor (2001) experimentally manipulated resources and competition in a herbaceous community, and showed that fluctuations in resource availability of as little as one week in duration could greatly enhance plant invasion success (survival and cover of alien plants) up to one year after such events.

Experiments on invasibility of different types of ecosystems have been gaining momentum in recent years (Hector *et al.* 2001; Fargione *et al.* 2003). Crawley *et al.* (1999) and Davis *et al.* (2000) suggested that there is no necessary relationship between invasibility of a plant community and number of species present in that community.

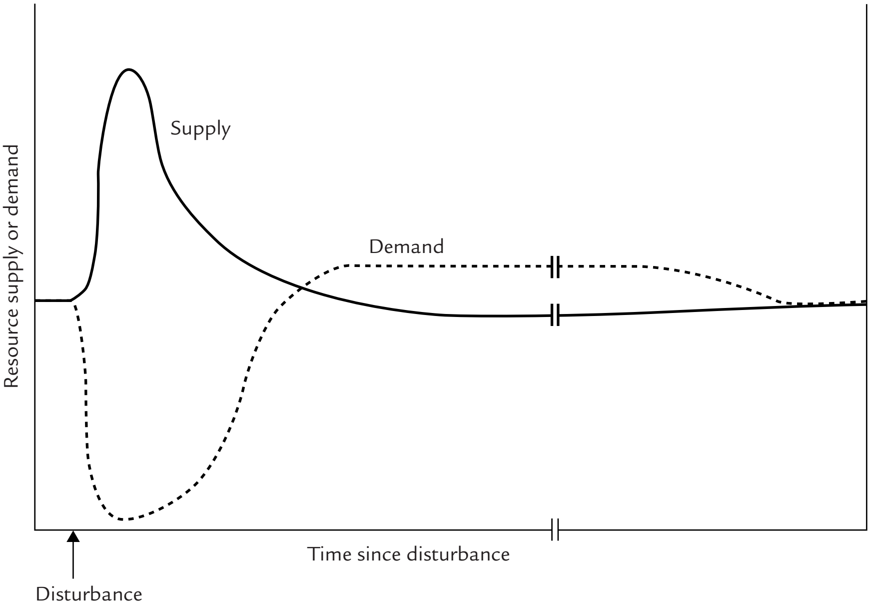

Fig. 13.4 Changes in supply and demand of resources after disturbance in terrestrial ecosystems. Resource availability is generally at its maximum shortly after disturbance, although conditions of bare ground can inhibit seedling establishment in some sites. Modified from Vitousek & Walker (1987).

Other studies show that such a relationship exists: positive at the landscape scale (e.g. Stohlgren *et al.* 1999; Sax 2002) and negative at scales of $< 1\ \mathrm{m}^2$ (neighbourhood scales *sensu* Levine 2000). Wardle (2001) provided a valuable methodological criticism of many of these studies. Nevertheless, Kennedy *et al.* (2002) concluded that in herbaceous communities neighbourhood species richness (within 5–15 cm radius) represents 'an important line of defence against the spread of invaders'. Hubbell *et al.* (2001) found that in an undisturbed forest in Panama neighbourhood species richness (within 2.5–50 m radius) had a weak but significantly negative effect on focal tree survival. Is there a generalization emerging from studies on neighbourhood scales? This would not be surprising as vascular plants are sedentary organisms and actual interactions are occurring among neighbouring individuals.

The experimental studies mentioned above relate the number of resident plant species to the number and abundance of alien plant species that establish or become invasive. But, the diversity of organisms at other trophic levels in the receiving environment may well be as important, if not more important, than the number of plant species. We can expect that diverse assemblages of mutualists (pollinators, seed dispersers, microbiota that form symbioses with plant roots) would promote invasibility (Simberloff & Von Holle 1999; Richardson *et al.* 2000b). Recent experiments by Klironomos (2002) on species from Canadian old-fields and grasslands showed that native rare plant species accumulate soil plant pathogens rapidly, while invasive species do not. This result has potentially very important consequences. When introduced

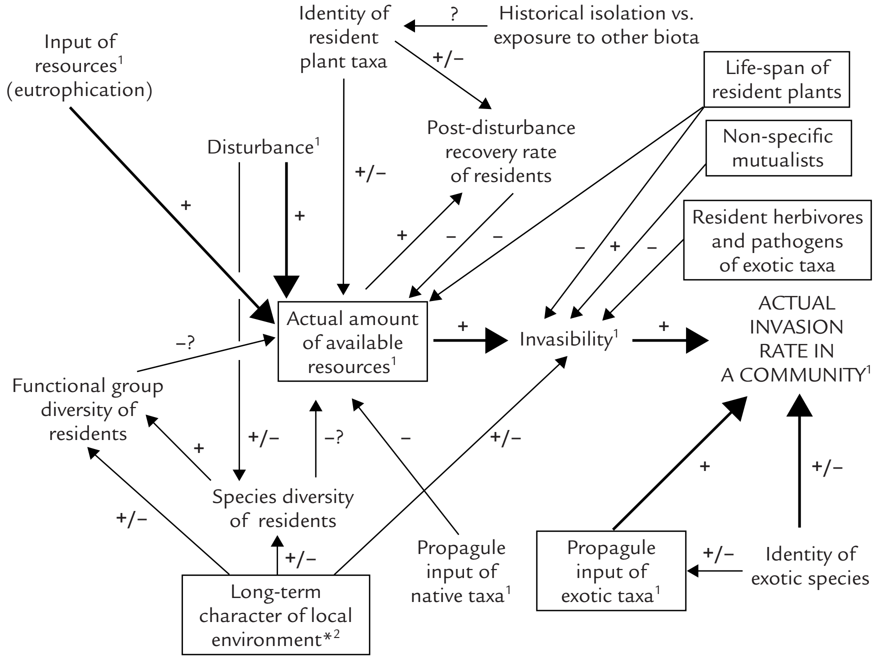

Fig. 13.5 Causal relationships between factors and processes which are assumed responsible for invasions of exotic species into plant communities. The most important relationships are indicated by thick arrows. * = Spatial heterogeneity, (micro)climate and long-term regime of available resources and toxic compounds. 1 = Time scale: days–years. 2 = Time scale: years–centuries. The key components are in boxes.

outside of their native territories, plants are often liberated from their enemies, including soil pathogens. This is a clear advantage that makes natives and aliens, at least temporarily, different (but see Colautti *et al.* 2004). At the same time, however, as many mycorrhizal fungi can associate with a broad range of plant taxa, root beneficial symbionts are likely to be always available to many alien plants.

A conceptual cause-effect diagram (Fig. 13.5) captures all the fundamental aspects of the ongoing debate on the issue of invasibility. The fact that both invasibility and species diversity of residents is regulated in a similar way by the same set of factors – (micro)climate, spatial heterogeneity, long-term regime of available resources – explains why there are so many reports of positive correlation between numbers of native and non-native species when several different communities or areas are compared. Fast post-disturbance recovery of residents may be a key factor making the wet tropics more resistant to plant invasions – measured as number of invading species per log(area) (Rejmánek 1996).

However, there is very likely one extra factor that is currently poorly understood: the historical and prehistoric degree of exposure of resident taxa to other biota (Fig. 13.5). Is this the reason why islands are more vulnerable and Eurasia least vulnerable to invasions? Is instability of so many man-made monocultures a result of the 'lack of any significant history of co-evolution with pests and pathogens' (May 1981)? Actual species richness may not be as important as the complexity of assembly history. In addition to mathematical models and computer simulations (Law 1999) relevant experiments with plant communities will have to be designed. Artificial experimental plant communities that are so often used for invasibility experiments have a clear advantage of homogeneous substrata and microclimates. However, assembly processes here are very short and/or artificially directed via arbitrary species pool selection, weeding, reseeding, etc. The existence of well-established phytosociological associations and the fact that plant species are combined in highly non-random patterns within their natural communities (Gotelli & McCabe 2002) indicate that historical assembly processes cannot be substituted by arbitrary mixtures of species.

Finally, longevity/persistence of resident plants is a distinct component of resistance to invasions (Von Holle *et al.* 2003), especially in forest communities, resulting in 'biological inertia', including allelopathic chemicals produced by living or dead residents.

13.4 Habitat compatibility

Identity of exotic taxa (Fig. 13.5) is important for two reasons. First, they may or may not survive and reproduce in habitats where they are introduced. Second, they may or may be not spread and become invasive. Recipient habitat compatibility is usually treated as a necessary condition for all invasions. The match of primary (native) and secondary (adventive) environments of an invading taxon is not always perfect but usually reasonably close (e.g. Beerling *et al.* 1995; Rejmánek 2000; Widlechner & Iles 2002). In North America, for example, latitudinal ranges of naturalized European plant species from the Poaceae and Asteraceae are on average 15–20° narrower than their native ranges in Eurasia and North Africa. These differences essentially reflect the differences in the position of corresponding isotherms and major biomes in Eurasia and North America. Major discrepancies between primary and secondary ranges have been found for aquatic plants where secondary distributions are often much less restricted than their primary distributions. Vegetative reproduction of many aquatic species seems to be the most important factor. Obviously, secondary ranges, if already known from other invaded continents, should be employed in any prediction of habitat compatibility.

As for plants introduced (or considered for introduction) from Europe, several useful summaries of their 'ecological behaviour' are available. Especially the combination of Ellenberg indicator values (Ellenberg *et al.* 1992) with Grime's functional types (strategies) (Grime *et al.* 1988) can be a powerful tool for predictions of habitat compatibility of European species. The strength of affiliation with phytosociological syntaxa (section 1.4.2) is well known for almost all European taxa. Environmental conditions (climate, soil, disturbance, management) of all syntaxa are available and potential habitat compatibility of taxa can be extracted from the European literature. Knowledge of this 'phytosociological behaviour' of taxa allows predictions about compatibility with analogous (vicarious) vegetation types, even if these will not always be correct.

‘Open niches’, habitats that can support life forms that are not present in local floras for historical and/or evolutionary reasons, deserve special attention. Dramatic invasions have occurred in such habitats, e.g. *Ammophila arenaria* (a rhizomatous grass) in coastal dunes in California, *Lygodium japonicum* (a climbing fern) in bottomland hardwoods from Louisiana to Florida, *Pinus* spp. and *Acacia* spp. in South African shrubby fynbos, *Opuntia* spp. (Cactaceae) in East African savannas, *Rhizophora mangle* (mangrove) in tree-less coastal marshes of Hawai’i, and the tree *Cinchona pubescens* (Rubiaceae) in mountain shrub communities on Santa Cruz Island, Galápagos. The explanation of such invasions is confirmed by experiments showing that the competitive inhibition of invaders increases with their functional similarity to resident abundant species (Fargione *et al.* 2003).

13.5 Propagule pressure and residence time

The notion of habitat compatibility includes all factors embraced in the concept of habitat. Most effort in assessments of habitat compatibility has been devoted to climatic and substrate compatibility, although it is well known that many other factors influence range limits. Invasions result from an interplay between habitat compatibility and propagule pressure (Fig. 13.5). This is illustrated by the invasion dynamics of the New Zealand tree *Metrosideros excelsa* (Myrtaceae) in South African fynbos (details in Richardson & Rejmánek 1998). Multiple regression of the number of *Metrosideros* saplings on a potential seed rain index (PSRI) and soil moisture revealed that, in this case, both factors are about equally important (Fig. 13.6). This example clearly shows that classification of habitats or communities into ‘invasible’ and ‘non-invasible’ cannot be absolute in many situations. Habitats that are currently unaffected (or only slightly affected) by plant invasions may be deemed resistant to invasion. However, as populations of alien plants build up and propagule pressure (Foster 2001) increases outside or within such areas, invasions could well start or increase. Another aspect is the propagule pressure of native species: if propagules of natives are not available, as for instance on abandoned fields in California, the ‘repairing’ function of ecological succession (Fig. 13.3) does not work.

Residence time – the time since the introduction of a taxon to a new area – represents another dimension of propagule pressure. As we usually do not know exactly when a taxon was introduced, we use a ‘minimum residence time’ based on herbarium specimens or reliable records. Nevertheless, the number of discrete localities of naturalized species is significantly positively correlated with minimum residence time (Fig. 13.7). One trivial but important conclusion is that the earlier an exotic pest plant taxon is discovered, the better is the chance of its eradication.

13.6 What are the attributes of successful invaders?

The identity of introduced species certainly matters (Fig. 13.5). Extrapolations based on previously documented invasions are fundamental for predictions in invasion ecology. With the development of relevant databases, this approach should lead to

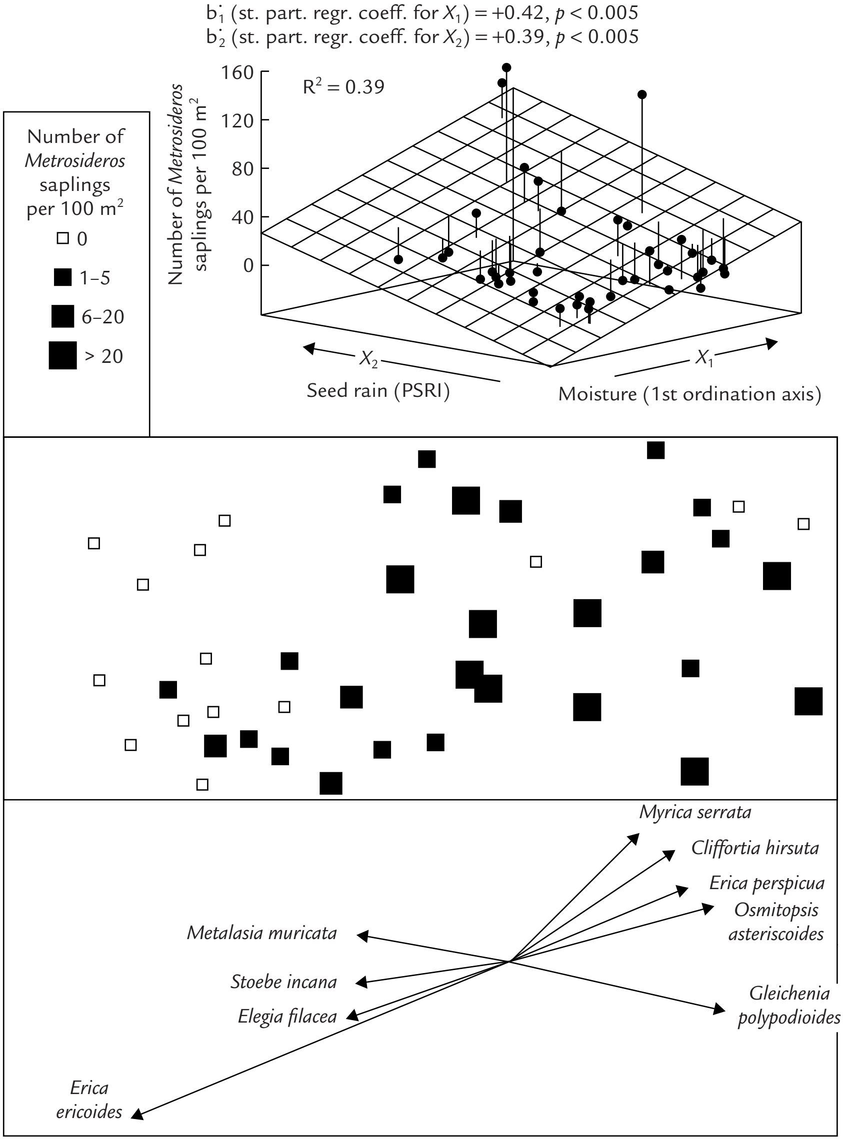

Fig. 13.6 The dependence of the sapling density of *Metrosideros excelsa* on potential seed rain index (PSRI) and moisture in fynbos of the Western Cape, South Africa. PSRI = SUM($1/d_i$), where d_i is distance to the i-th mature tree in metres within the radius 300 m. The first ordination axis (below) serves as a surrogate for moisture gradient. Standardized partial regression coefficients (st. part. regr. coeff.) of the multiple regression are almost identical. Therefore, both independent variables – environment and propagule pressure – are equally important in this case. M. Rejmánek & D.M. Richardson (unpublished data).

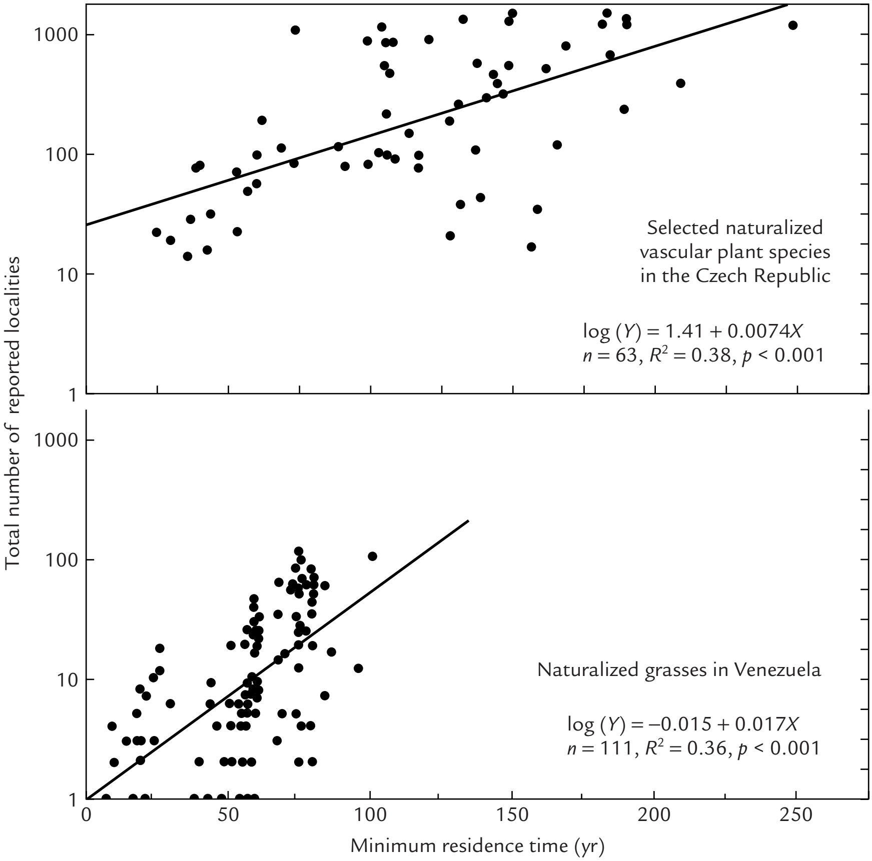

Fig. 13.7 The dependence of the total number of reported localities on the minimum residence time (yr since the first record) of selected naturalized species in the Czech Republic and Venezuela. P. Pyšek & M. Rejmánek (unpublished data).

immediate rejection of imports of many invasive taxa (prevention) and prioritized control of those that have already been established. Such transregional, taxon-specific extrapolations are very useful in many situations, but our lack of understanding makes them intellectually unsatisfactory. Understanding how and why certain biological characters promote invasiveness is very important since even a global database will not cover all potentially invasive taxa. In New Zealand, for example, Williams *et al.* (2001) reported that 20% of the alien weedy species collected for the first time in the second half of the 20th century had never been reported as invasive outside New Zealand. For these reasons, several attempts have been made to find differences in biological characteristics of non-invasive and invasive taxa or, at least, between native taxa and non-native invasive taxa in particular floras. Major predictions made by an emerging theory of plant invasiveness were summarized recently by Booth *et al.* (2003), Myers & Bazely (2003) and Rejmánek *et al.* (2004):

1 Fitness homoeostasis (the ability of an individual or population to maintain relatively constant fitness over a range of environments) promotes invasiveness.
2 Genetic change can facilitate invasions, but many species have sufficient phenotypic plasticity to exploit new environments.
3 Several characters linked to reproduction and dispersal are key indicators of invasiveness.
4 Seed dispersal by vertebrates is implicated in many plant invasions.
5 Low relative growth rate of seedlings and low specific leaf area are good indicators of low plant invasiveness in many environments.
6 Large native range is an indicator of potential invasiveness. However, several important exceptions are known (*Impatiens parviflora*, *Pinus radiata*).
7 Vegetative reproduction is responsible for many plant invasions, especially in aquatic and wetland environments.
8 Alien taxa are more likely to invade a continental area if native members of the same genus (and family) are absent, partly because many herbivores and pathogens cannot switch to phylogenetically distant taxa (Agrawal & Kotanen 2003; Mitchell & Power 2003). However, invaders on islands seem to exhibit the opposite tendency (Duncan & Williams 2002).
9 The ability to utilize generalist mutualists greatly improves an alien taxon's chances of becoming invasive.
10 Efficient competitors for limiting resources are likely to be the best invaders in natural and semi-natural ecosystems (Tilman 1999; Shea & Chesson 2002).
11 Characters favouring passive dispersal by humans greatly improve an alien plant taxon's chance of becoming invasive.

Points 3, 4 and 5 are particularly relevant. Reproduction and dispersal are key issues. Consistent seed production in new environments is usually associated with rather simple or flexible breeding systems. For example, rare and endangered taxa in the genus *Amsinckia* (e.g. *A. furcata*, *A. grandiflora*) are heterostylic, while derived invasive taxa (*A. menziesii*, *A. lycopsoides*) are homostylic and self-compatible. Self-pollination has been consistently identified as a mating strategy in colonizing species. Nevertheless, not all sexually reproducing successful invaders are selfers. Pannel & Barrett (1998) examined the benefits of reproductive assurance in selfers versus outcrossers in model metapopulations. Their results suggest that an optimal mating system for a sexually reproducing invader in a heterogeneous landscape should include the ability to modify selfing rates according to local conditions. In early stages of invasions, when populations are small, plants should self to maximize fertility. However, later, when populations are large and pollinators and/or mates are not limiting, outcrossing will be more beneficial, mainly due to increasing genetic polymorphism.

Invasiveness of woody taxa in disturbed landscapes is associated with small seed mass (< 50 mg), a short juvenile period (< 10 yr), and short intervals between large seed crops (1–4 yr) (see Fig. 13.8 and Rejmánek & Richardson 1996, 2003). These three attributes contribute, directly or indirectly, to higher values of three parameters which are critical for population expansion: net reproduction rate, reciprocal of mean age of reproduction, and variance of the marginal dispersal density. For wind-dispersed seeds, the last parameter is negatively related to terminal velocity of seeds which is positively related to √(seed mass) (Rejmánek *et al.* 2004). Because

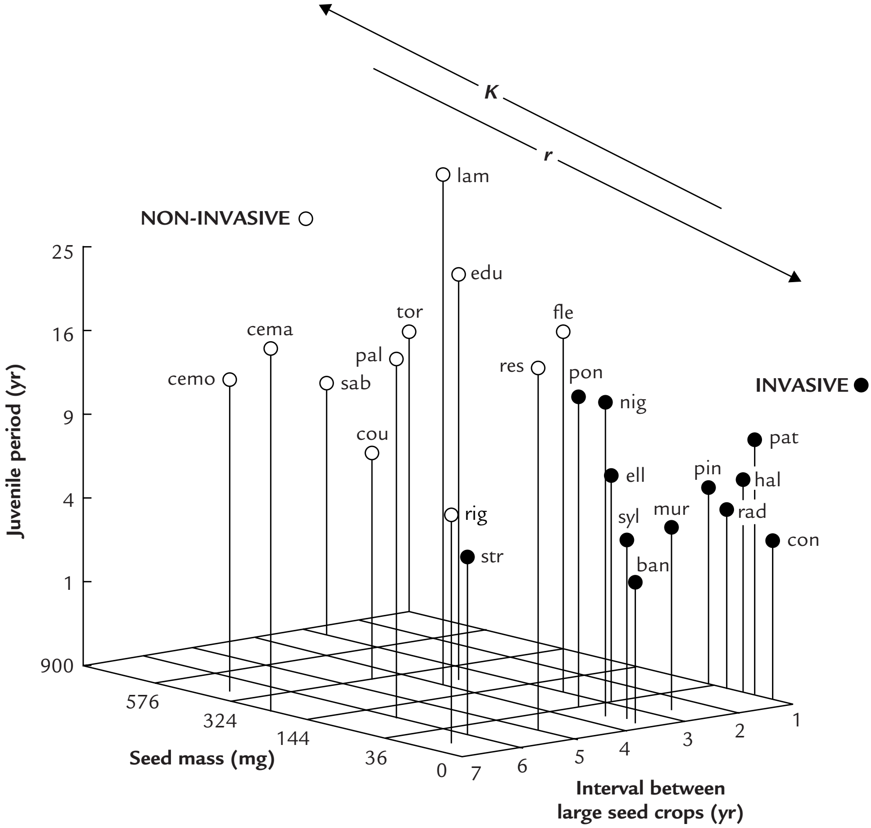

Fig. 13.8 Distribution of 23 frequently cultivated *Pinus* species in a space created by three biological variables critical in separating invasive and non-invasive species. The *K*–*r* selection continuum running from the upper left to the lower right corner of the diagram also represents the direction of the discriminant function (Z) separating non-invasive and invasive *Pinus* species. $Z = 23.39 - 0.63\sqrt{M} - 3.88\sqrt{J} - 1.09S$, where M = mean seed mass (in mg), J = minimum juvenile period (in yr), and S = mean interval between large seed crops (in yr). Pine species with positive Z scores are invasive and species with negative Z scores are non-invasive. Species abbreviations: ban = *banksiana*; cema = *cembra*; cemo = *cembroides*; con = *contorta*; cou = *coulteri*; edu = *edulis*; ell = *elliottii*; eng = *engelmannii*; fle = *flexilis*; hal = *halepensis*; lam = *lambertiana*; mur = *muricata*; nig = *nigra*; pal = *palustris*; pat = *patula*; pin = *pinaster*; pon = *ponderosa*; rad = *radiata*; res = *resinosa*; sab = *sabiniana*; str = *strobus*; syl = *sylvestris*; tor = *torreyana*.

of the trade-off between seed number and mean seed mass, small-seeded taxa usually produce more seeds relative to biomass. Invasions of woody species with very small seeds (< 3 mg), however, are limited to wet and preferably mineral substrata (Rejmánek & Richardson 1996). Based on invasibility experiments with herbaceous species, it seems that somewhat larger seeds (3–10 mg) extend species habitat compatibility (Burke & Grime 1996). As seed mass seems to be positively correlated with habitat shade, large-seeded aliens may be more successful in undisturbed, successionally more mature plant communities.

Seed dispersal by vertebrates is responsible for the success of many invaders in disturbed as well as 'undisturbed' habitats (Binggeli 1996; Rejmánek 1996; Richardson *et al*. 2000b; Widlechner & Iles 2002). Even some very large-seeded alien species like *Mangifera indica* can be dispersed by large mammals. The proportion of naturalized plant species dispersed by vertebrates seems to be particularly high in Australia: over 50% (Tables 2.1 and 7.3 in Specht & Specht 1999). The assessment of whether there is an opportunity for vertebrate dispersal is an important component of the screening procedure for woody plants (Table 13.2). However, vertebrate seed dispersal in relation to invasions is complicated (Richardson *et al*. 2000b).

Table 13.2 General rules for detection of invasiveness of woody seed plants based on values of the discriminant function Z^*, seed mass values, and presence or absence of opportunities for vertebrate dispersal. Modified from Rejmánek & Richardson (1996).

		Opportunities for vertebrate dispersal	
		Absent	***Present***
$Z > 0$	Dry fruits and seed mass > 3 mg	Likely[1]	Very likely[2]
	Dry fruits and seed mass < 3 mg	Likely in wet habitats[3]	Likely in wet habitats[3]
	Fleshy fruits	Unlikely[4]	Very likely[5]
$Z < 0$		Not unless dispersed by water[6]	Possibly[7]

*$Z = 23.39 - 0.63\sqrt{M} - 3.88\sqrt{J} - 1.09S$; where M = mean seed mass (mg); J = minimum juvenile period (yr); S = mean interval between large seed crops (yr). Z was derived on the basis of *a priori* defined groups of invasive and non-invasive *Pinus* species. The function was later successfully applied on other gymnosperms and, as a component of this table, even on woody angiosperms. Note that parameters in this discriminant function are somewhat different from those in Rejmánek & Richardson (1996). This is due to exclusion of *Pinus caribaea* from the data set used for estimation of the parameters. This species, that is in general non-invasive in many countries, is highly invasive in New Caledonia.

[1] For example *Acer platanoides, Cedrela odorata*, *Clematis vitalba*, *Cryptomeria japonica, Cytisus scoparius, Pinus radiata*, *Pittosporum undulatum*, *Pseudotsuga menziesii, Robinia pseudoacacia, Senna* spp., *Tecoma stans.*

[2] Species with large arils (*Acacia cyclops*) are dispersed by birds.

[3] For example *Alnus glutinosa* in New Zealand, *Eucalyptus globulus* in California, *Melaleuca quinquenervia* in southern Florida, *Tamarix* spp. in the south-western USA, *Cinchona pubescens* in Galápagos and *Baccharis halimifolia* in Australia.

[4] *Feijoa sellowiana* and *Nandina domestica* are frequently cultivated but non-invasive species in California. The second species, however, is dispersed by birds and water in the south-eastern USA.

[5] *Berberis* spp., *Clidemia hirta, Crataegus monogyna, Lantana camara, Lonicera* spp., *Myrica faya, Passiflora* spp., *Psidium guajava*, *Rubus* spp., *Schinus terebinthifolius, Solanum mauritianum.*

[6] *Nypa fruticans* is spreading along tidal streams in Nigeria and Panama. *Thevetia peruviana* can be dispersed over short distances by surface run-off in Africa.

[7] Examples of invasive species in this group are *Pinus pinea, Melia azedarach*, and *Maesopsis eminii* in Africa, *Quercus rubra* in Europe, *Mangifera indica* in the Neotropics, and *Persea americana* in Galápagos.

Table 13.3 Differences between means of growth related variables for non-invasive, unclassified and invasive *Pinus* species. Same superscript letters for each variable denote means that are not significantly different ($p > 0.05$, Scheffé test). From Grotkopp *et al.* (2002).

Variable	**Non-invasive**	**Unclassified**	**Invasive**
	$n = 8$	$n = 8$	$n = 8$
Relative growth rate (RGR, $\mathrm{mg \cdot g^{-1} \cdot d^{-1}}$)	23^{a}	33^{b}	37^{b}
Net assimilation rate (NAR, $\mathrm{mg \cdot cm^{-2} \cdot d^{-1}}$)	0.505^{a}	0.559^{a}	0.572^{a}
Leaf area ratio (LAR, $\mathrm{cm^{2} \cdot g^{-1}}_{\mathrm{plant}}$)	50^{a}	67^{b}	73^{b}
Specific leaf area (SLA, $\mathrm{cm^{2} \cdot g_{leaf}}$)	79^{a}	101^{b}	111^{b}
Relative leaf production rate ($\mathrm{leaf \cdot leaf^{-1} \cdot d^{-1}}$)	0.014^{a}	0.022^{b}	0.024^{b}

Many ecologists assume that a high relative growth rate should be an important characteristic of invasive plant taxa in disturbed or open areas, especially in resource-rich environments. Only a few studies have demonstrated this experimentally (Pattison *et al.* 1998; Grotkopp *et al.* 2002). An analysis of seedling growth rates for 29 *Pinus* species (Table 13.3) revealed that: (i) relative growth rate (RGR) of invasive species is significantly higher than that of non-invasive species; (ii) differences in RGR are primarily determined by leaf area ratio (LAR; leaf area per plant biomass); and (iii) LAR is primarily determined by specific leaf area (SLA; leaf area per leaf biomass). Consequently, invasive species have significantly higher specific leaf area. Moreover, there is a highly significant ($R^2 = 0.685$; $p < 0.001$) positive relationship between RGR and invasiveness of the *Pinus* species (Fig. 13.8, Table 13.2). Identical results were obtained using phylogenetically independent contrasts (Grotkopp *et al.* 2002). High SLA was implied as an important factor associated with invasiveness of grasses and other plants. In general, SLA $< 90\ \mathrm{cm^2 \cdot g^{-1}}$ (dry leaf mass) seems to be a good indicator of non-invasive or, at least, less-invasive evergreen woody plants and SLA $< 150\ \mathrm{cm^2 \cdot g^{-1}}$ probably means the same for other vascular plant taxa.

Basic taxonomic units used in plant invasion ecology are usually species or subspecies. However, genera are certainly worth considering as well. Species belonging to genera notorious for their invasiveness or 'weediness', e.g. *Amaranthus*, *Echinochloa*, *Ehrharta*, *Myriophyllum*, should be treated as highly suspicious. On the other hand, a continuum from highly invasive to virtually non-invasive species is also common in many genera, e.g. *Acer*, *Centaurea*, *Pinus*. Recently, some attention has been paid to taxonomic patterns of invasive plants (Daehler 1998; Pyšek 1998; Rejmánek & Richardson 2003). In terms of relative numbers of invasive species, some families seem to be over-represented: Amaranthaceae, Brassicaceae, Chenopodiaceae, Fabaceae, Gramineae, Hydrocharitaceae, Papaveraceae, Pinaceae and Polygonaceae. Among the larger families, the Orchidaceae is the only under-represented one.

13.7 Impact of invasive plants, justification and prospects of eradication projects

Numerous studies have documented the wide range of impacts caused by invasive plants. Many invasive taxa have transformed both the structure and function of ecosystems by, for example, changing disturbance- or nutrient-cycling regimes (D'Antonio *et al.* 1999). In many parts of the world, impacts have clear economic implications for humans, e.g. as a result of reduced stream flow from watersheds in South African fynbos following alien tree invasions (Van Wilgen *et al.* 2001), or through disruption to fishing and navigation after invasion of aquatic plants such as *Eichhornia crassipes*.

It is important to stress, however, that the impact of invasive plants on biodiversity is much less dramatic than impact of exotic pathogens, herbivores or predators. It seems that most of the naturalized/invasive plant species have hardly detectable effects on biotic communities (Williamson & Fitter 1996; Meiners *et al.* 2001). There are at least 2000 naturalized plant species in North America and more than 1000 of them are invasive. However, not a single native plant species is known to have been driven to extinction due to interactions with alien plants alone. Even on islands, where numbers of exotic plant species are often increasing exponentially, extinctions of native plant species cannot be attributed to plant invasions *per se* (Sax *et al.* 2002). Also, the often reported correlation between numbers of native and exotic plant species on the landscape scale can be interpreted as a lack of mechanisms for competitive exclusion of native plants by exotic ones. Nevertheless, we should be careful with conclusions – many invasions are quite recent and extinction takes a long time.

Considerable progress has recently been made in developing methodologies for making biological, ecological and economic assessments. In attempting to quantify the value of ecosystem services of South African fynbos systems and the extent to which these values are reduced by invasions, Higgins *et al.* (1997) showed that the cost of clearing alien plants was very small (< 5%) as compared to the value of services provided by these ecosystems. Their conclusion was that pro-active management could increase the value of these ecosystem services by at least 138%. The most important ecosystem service was water, and much work has been done on developing models for assessing the value (in monetary terms) of allocating management resources to clearing invasive plants from fynbos watersheds. Among the most dangerous invaders in riparian areas within the USA are species of the Old World genus *Tamarix* (salt cedar). An instructive economic evaluation of *Tamarix* impacts is provided by Zavaleta (2000).

As we showed earlier, the most reliable predictions based on biological characters are limited to invasiveness (likelihood of species establishment and spread). Predictions of potential impacts will always be less reliable. Because decline in native species richness is dependent on cover of invaders (Fig. 13.9; Richardson *et al.* 1989; Meiners *et al.* 2001), indices based on a ratio of cover to frequency should be tested as impact predictors for individual taxa. Other obvious impact indicators may be biological characters of plants that are known to have ecosystem consequences (e.g. high transpiration rates or nitrogen fixation).

Invasiveness and impact are not necessarily positively correlated. Some fast-spreading species, like *Aira caryophyllea* or *Cakile edentula*, exhibit little (if any) measurable environmental or economic impact. On the other hand, some relatively slowly spreading species, e.g. *Ammophila arenaria* or *Robinia pseudoacacia*, may have far-reaching environmental effects (stabilization of coastal dunes in the first case and nitrogen soil enrichment in the second).

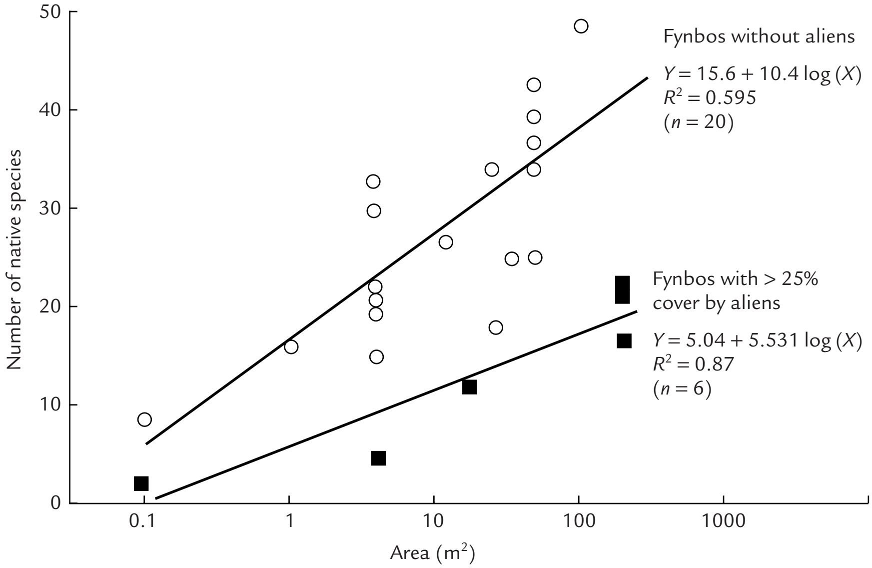

Fig. 13.9 Species-area relationships for native vascular plant species in South African fynbos areas densely infested (squares) by alien woody plants and in uninfested areas (circles). Elevations of the two regression lines are significantly different ($p < 0.001$). Sources of the data are acknowledged in Richardson *et al.* (1989).

There is a need for a universally acceptable, and objectively applicable, term for the most influential invasive plant taxa within given regions, or globally. A potentially useful term to use in this regard is 'transformer species' (Richardson *et al.* 2000a). Such species, comprising perhaps only about 10% of invasive species, have profound effects on biodiversity and clearly demand a major allocation of resources for containment/control/eradication. Several categories of transformers may be distinguished:

1 Excessive users of resources: water – *Tamarix* spp., *Acacia mearnsii*; light – *Pueraria lobata* and many other vines, *Heracleum mantegazzianum*, *Rubus armeniacus*; water and light – *Arundo donax*; light and oxygen – *Salvinia molesta*, *Eichhornia crassipes*; high leaf area ratio, LAR, of many invasive plants (discussed earlier) is an important prerequisite for excessive transpiration;

2 Donors of limiting resources: nitrogen – *Acacia* spp., *Lupinus arboreus*, *Myrica faya, Robinia pseudoacacia, Salvinia molesta*;

3 Fire promotors/suppressors: promotors – *Bromus tectorum*, *Melaleuca quinquenervia*, *Melinis minutiflora*; suppressors – *Mimosa pigra*;

4 Sand stabilizers: *Ammophila* spp., *Elymus hymus* spp.;

5 Erosion promotors: *Andropogon virginicus* in Hawai'i, *Impatiens glandulifera* in Europe;

6 Colonizers of intertidal mudflats – sediment stabilizers: *Spartina* spp., *Rhizophora* spp.;

7 Litter accumulators: *Centaurea solstitialis*, *Eucalyptus* spp., *Lepidium latifolium*, *Pinus strobus*, *Taeniatherum caput-medusae*;

8 Soil carbon storage modifiers: promotor – *Andropogon gayanus*; suppressor – *Agropyron cristatum*;

9 Salt accumulators/redistributors: *Mesembryanthemum crystallinum, Tamarix* spp.

The potentially most important transformers are taxa that add a new function, such as nitrogen fixation, to the invaded ecosystem (Vitousek & Walker 1989). Many impacts, however, are not so obvious. For example, invasive *Lonicera* and *Rhamnus* change vegetation structure of the forest, affecting nest predation of birds (Schmidt & Whelan 1999), and *Lythrum salicaria* and *Impatiens glandulifera* can have negative impacts on pollination and reproductive success of co-flowering native plants (Grabas & Laverty 1999; Chittka & Schürkens 2001).

It follows from the discussion on impacts of exotic plants that careful prioritization is needed before starting often very expensive and time-consuming eradication projects. Maintenance of biodiversity is dependent on the maintenance of ecological processes. Our priority should be protection of ecological processes. Attempts to eradicate widespread invasive species, especially those that do not have any documented environmental impacts (including suppression of rare native taxa), may be not only useless but also a waste of time and resources. Exotic taxa with large-scale environmental impacts (transformers) are usually obvious targets for control and eradication. But when is complete eradication a realistic goal?

There are numerous examples where small infestations of invasive plant species have been eradicated. There are also several encouraging examples where widespread alien animals have been completely eradicated. Can equally widespread and difficult alien plants also be eradicated? On the basis of a unique data set on eradication attempts by the California Department of Food and Agriculture on 18 species and 53 separate infestations targeted for eradication in the period 1972–2000 (Table 13.4), it is shown that professional eradication of exotic weed infestations smaller than 1 ha is usually possible. In addition, about 1/3 of infestations between 1 and 100 ha and 1/4 of infestations between 101 and 1000 ha have been eradicated. However, costs of eradication projects increase dramatically. With a realistic amount of resources, it is very unlikely that infestations larger than 1000 ha can be eradicated (Table 13.4).

Table 13.4 Areas of initial gross infestations (at the beginning of eradication projects) of exotic weeds in California, numbers of eradicated infestations, numbers of on-going projects, and mean eradication effort for five infestation area categories. The data include 18 noxious weedy species (two aquatic and 16 terrestrial) representing 53 separate infestations. From Rejmánek & Pitcairn (2002).

Initial infestation (ha)	< 0.1	0.1–1	1.1–100	101–1000	> 1000
No. of eradicated infestations	13	3	5	3	0
No. of on-going projects	2	4	9	10	4
Mean eradication effort per infestation (work hours)					
Eradicated	63	180	1496	1845	–
On-going	174	277	1577	17,194	42,751

Early detection of the presence of an invasive harmful taxon can make the difference between being able to employ offensive strategies (eradication) and the necessity of retreating to a defensive strategy that usually means an infinite financial commitment. Nevertheless, depending on the potential impact of individual invaders, even infestations larger than 1000 ha should be targeted for eradication effort or, at least, substantial reduction and containment. If an exotic weed is already widespread, then species-specific biological control may be the only long-term effective method able to suppress its abundance over large areas (Myers & Bazely 2003).

Regardless of their environmental and/or economical effects, plant invasions provide unique chances to understand some basic ecological processes that are otherwise beyond the capacity or ethics of standard ecological experiments. We are just beginning to fully appreciate these opportunities. However, we have a long way to go to achieve a more complete understanding and more rational decision making.

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References

Agrawal, A.A. & Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controled experiment. *Ecology Letters* **6**, 712–715.

Beerling, D.J., Huntley, B. & Bailey, J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science* **6**, 269–282.

Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science* **7**, 121–124.

Booth, B.D., Murphy, S.D. & Swanton, C.J. (2003) *Weed Ecology in Natural and Agricultural Systems*. CABI Publishing, Wallingford.

Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology* **77**, 776–90.

Cadenasso, M.L. & Pickett, S.T.A. (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* **15**, 91–97.

Chittka, L. & Schürkens, S. (2001) Successful invasion of a floral market. *Nature* **411**, 653.

Colautti, R.I., Ricciard, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, in press.

Crawley, M.J., Brown, S.L., Heard, M.S. & Edwards, G.G. (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* **2**, 140–148.

Daehler, C. (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation* **84**, 167–180.

D'Antonio, C.M., Dudley, T.L. & Mack, M. (1999) Disturbance and biological invasions: direct effects and feedbacks. In: *Ecosystems of the World: Ecosystems of Disturbed Ground* (ed. L.R. Walker), pp. 413–452. Elsevier, Amsterdam.

Davis, M.A. & Pelsor, M. (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* **4**, 421–428.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**, 528–534.

Duncan, R.P. & Williams, P.A. (2002) Darwin's naturalization hypothesis challenged. *Nature* **417**, 608–609.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **18**, 1–248.

Fargione, J., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 8916–8920.

Foster, B.L. (2001) Constrains on colonization and species richness along a grassland productivity gradient: the role of propagule availability. *Ecology Letters* **4**, 530–535.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* **83**, 2091–2096.

Grabas, G.P. & Laverty, M. (1999) The effect of purple loosestrife (*Lythrum salicaria* L.; Lythraceae) on the pollination and reproductive success of sympatric co-flowering wetland plants. *EcoScience* **6**, 230–242.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*. Unwin Hyman, London.

Grotkopp, E., Rejmánek, M. & Rost, T.L. (2002) Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* **159**, 396–419.

Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Lawton, J.H. (2001) Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* **16**, 819–831.

Higgins, S.I., Turpie, J.K., Costanza, R., Cowling, R.M., Le Maitre, D.C., Marais, C. & Midgley, G.F. (1997) An ecologically-economic simulation model of mountain fynbos ecosystems: Dynamics, valuation and management. *Ecological Economics* **22**, 155–169.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity and invasion: implications for conservation. *Conservation Biology* **6**, 324–337.

Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R. (2001) Local neighborhood effects on long-term survival of individual trees in a Neotropical forest. *Ecological Research* **16**, 859–875.

Kartesz, J.T. & Meacham, C.A. (1999) *Synthesis of the North American Flora*. CD-ROM Version 1.0. North Carolina Botanical Garden, Chapel Hill.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002) Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–638.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **417**, 67–70.

Law, R. (1999) Theoretical aspects of community assembly. In: *Advanced Ecological Theory* (ed. J. McGlade), pp. 143–171. Blackwell Science, Oxford.

Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* **288**: 852–854.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536.

May, R.M. (1981) Patterns in multi-species communities. In: *Theoretical Ecology. Principles and Applications* (ed. R.M. May), pp. 197–227. Blackwell Scientific, Oxford.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* **24**, 633–644.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2002) Exotic plant invasions over 40 years of old field succession: community patterns and associations. *Ecography* **25**, 215–223.

Mitchell, C.E. & Power, A.G. (2003) Release of invasive plants from fungal and viral pathogens. *Nature* **421**, 625–627.

Myers, J.H. & Bazely, D.R. (2003) *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge.

Pannel, J.R. & Barrett, S.C.H. (1998) Baker's Law revisited: reproductive assurance in a metapopulation. *Evolution* **52**, 657–668.

Pattison, R.R., Goldstein, G. & Ares, A. (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rain forest species. *Oecologia* **117**, 449–459.

Pyšek, P. (1998) Is there a taxonomic pattern to plant invasions? *Oikos* **92**, 282–294.

Pyšek, P., Jarošík, V. & Kučera, T. (2002b) Patterns of invasion in temperate nature reserves. *Biological Conservation* **104**, 13–24.

Pyšek, P., Sádlo, J. & Mandák, B. (2002a) Catalogue of alien plants of the Czech Republic. *Preslia* **74**, 97–186.

Rejmánek, M. (1989) Invasibility of plant communities. In: *Biological Invasions. A Global Perspective* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 369–388. John Wiley & Sons, Chichester.

Rejmánek, M. (1996) Species richness and resistance to invasions. In: *Diversity and Processes in Tropical Forest Ecosystems*. (eds G.H. Orians, R. Dirzo & J.H. Cushman), pp. 153–72. Springer-Verlag, Berlin.

Rejmánek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology* **25**, 497–506.

Rejmánek, M. & Pitcairn, M.J. (2002) When is eradication of exotic plant pests a realistic goal? In: *Turning the Tide: The Eradication of Invasive Species* (eds C.R. Veitch & M.N. Clout), pp. 249–253. IUCN, Gland, Switzerland and Cambridge, UK.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology* **77**, 1655–1661.

Rejmánek, M. & Richardson, D.M. (2004) Invasiveness of conifers: extent and possible mechanism. *Acta Horticulturae* **615**, 375–378.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J. & Grotkopp, E. (2003) Ecology of invasive plants: State of the art. In: *Invasive Alien Species: Searching for Solutions* (eds H.A. Mooney, J.A. McNeelly, L. Neville, P.J. Schei & J. Waage), Island Press, Washington.

Richardson, D.M. & Rejmánek, M. (1998) *Metrosideros excelsa* takes off in the fynbos. *Veld & Flora* **85**, 14–16.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000b) Plant invasions – the role of mutualisms. *Biological Reviews of the Cambridge Philosophical Society* **75**, 65–93.

Richardson, D.M., Macdonald, I.A.W. & Forsyth, G.G. (1989) Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. *South African Forestry Journal* **149**, 1–8.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000a) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**, 93–107.

Sax, D.F. (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* **8**, 193–210.

Sax, D.F., Brown, J.H. & Gaines, S.D. (2002) Species invasions exceed extinctions on islands world-wide: a comparative study of plants and birds. *American Naturalist* **160**, 766–783.

Schmidt, K.A. & Whelan, C.J. (1999) Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conservation Biology* **13**, 1502–1506.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**, 170–176.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* **1**, 21–32.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seeman, J.R. & Nowak, R.S. (2000) Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature* **408**, 79–82.

Specht, R.L. & Specht, A. (1999) *Australian Plant Communities*. Oxford University Press, Oxford.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkham, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**, 25–46.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474.

Tye, A. (2001) Invasive plant problems and requirements for weed risk assessment in the Galapagos Islands. In: *Weed Risk Assessment* (eds R.H. Groves, F.D. Panetta & J.G. Virtue), pp. 153–175. CSIRO Publishing, Collingwood.

Van Wilgen, B.W., Richardson, D.M., Le Maitre, D.C., Marais, C. & Magadlela, D. (2001) The economic consequences of alien plant invasions: Examples of impacts and approaches for sustainable management in South Africa. *Environment, Development and Sustainability* **3**, 145–168.

Vitousek, P.M. & Walker, L.R. (1987) Colonization, succession and resource availability: ecosystem-level interactions. In: *Colonization, Succession and Stability* (eds A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 207–223. Blackwell Science, Oxford.

Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**, 247–265.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1–16.

Von Holle, B., Delcourt, H.R. & Simberloff, D. (2003) The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science* **14**, 425–432.

Wardle, D.A. (2001) Experimental demonstration that plant diversity reduces invasibility – evidence of a biological mechanism or a consequence of sampling effect? *Oikos* **95**, 161–170.

Widlechner, M.P. & Iles, J.K. (2002) A geographic assessment of the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture* **20**, 47–56.

Williams, P.A., Nicol, E. & Newfield, M. (2001) Assessing the risk to indigenous biota of plant taxa new to New Zealand. In: *Weed Risk Assessment* (eds R.H. Groves, F.D. Panetta & J.G. Virtue), pp. 100–116. CSIRO Publishing, Collingwood.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology* **77**, 1661–1666.

Zavaleta, E. (2000) Valuing ecosystem services lost to *Tamarix* invasion in the United States In: *The Impact of Global Change on Invasive Species* (eds H.A. Mooney & R.J. Hobbs), pp. 261–300. Island Press, Washington.