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Plant Invasions and Invasibility of Plant Communities

Marcel Rejmánek[1], David M. Richardson[2] and Petr Pyšek[3]

[1]University of California Davis, USA
[2]Stellenbosch University, South Africa
[3]Academy of Sciences of the Czech Republic, Czech Republic

13.1   Introduction

Historically, plant taxa have always been migrating and spreading. Colonization of deglaciated areas has been very well illustrated by many examples. For obvious reasons, less documented are plant migrations via the Bering landbridge and the Central American landbridge. Occasional long-distance dispersal events have been fundamental for assembling the floras of many islands. For example, while New Zealand is often characterized as a sort of living museum of late Gondwanan vegetation, most of the predecessors of the New Zealand flora arrived by long-distance dispersal. Transoceanic dispersal events have been apparently more frequent than we thought only 10 years ago. Nevertheless, we should note that associated time scales have been enormous: thousands to millions of years.

Currently, however, the rate of human-assisted migrations (i.e. invasions *sensu* Pyšek *et al*. 2004) of plants is several orders of magnitude higher. In California, for example, more than 1300 alien plant species, introduced either intentionally or accidentally, have established self-sustaining populations over the past 250 years. About half of them are spreading to some extent. Throughout the three million year history of the Galápagos Islands, only one new vascular plant species arrived with birds or sea currents approximately every 10 000 years on average. Over the past 470 years, however, the human-assisted introduction rate has been about 1.2 established species per year – about 13 000 times the background rate (Tye 2006). In light of these numbers, and for other reasons discussed later, human-mediated plant invasions are radically different from natural long-distance dispersal events.

Most human-introduced species stay in disturbed areas or are incorporated into resident plant communities and have no noticeable or measurable impact. A small percentage of introduced plants do have substantial environmental and/or economic impacts. This is the main reason for the explosion of research interest in biological invasions.

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 plant invaders?

13.2   Definitions and major patterns

Unlike **natives** (taxa that evolved in the region or reached it without help from humans from another area where they are native), **aliens** ('exotic', 'introduced', or 'non-native') owe their presence to the direct or indirect activities of humans. Most aliens occur only temporarily and are not able to persist for a long time without human-assisted input of propagules; these are termed **casual**. **Naturalized taxa** form sustainable populations without direct human help but do not necessarily spread; the ability to spread characterizes their 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 – the last-mentioned should rather be called alien **weeds**, alien **pest plants** or **transformer species** (Richardson *et al.* 2000b; Pyšek *et al*. 2004). It is important to stress that the ecological definition of 'invasive' that we advocate is not universally accepted. For example, managers, particularly in the USA, define as invasive only those alien taxa that cause environmental or economic damage.

Weeds comprise both native and alien species and the relative contribution of alien species in weed floras varies across the world. Most weedy taxa in Europe, Malaysia, Mexico and Taiwan are native, whereas in Australia, Chile, Hawaii, New Zealand and South Africa weed floras are overwhelmingly dominated by non-natives. 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 be recognized on other continents (Rejmánek 1996; Lonsdale 1999). For instance, areas with mediterranean-type climates (with the exception of the Mediterranean Basin itself) seem to be more vulnerable, and the tropics probably 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*, *Melinis minutiflora* and *Urochloa mutica,* while similar tropical habitats in Africa and Asia are dominated by
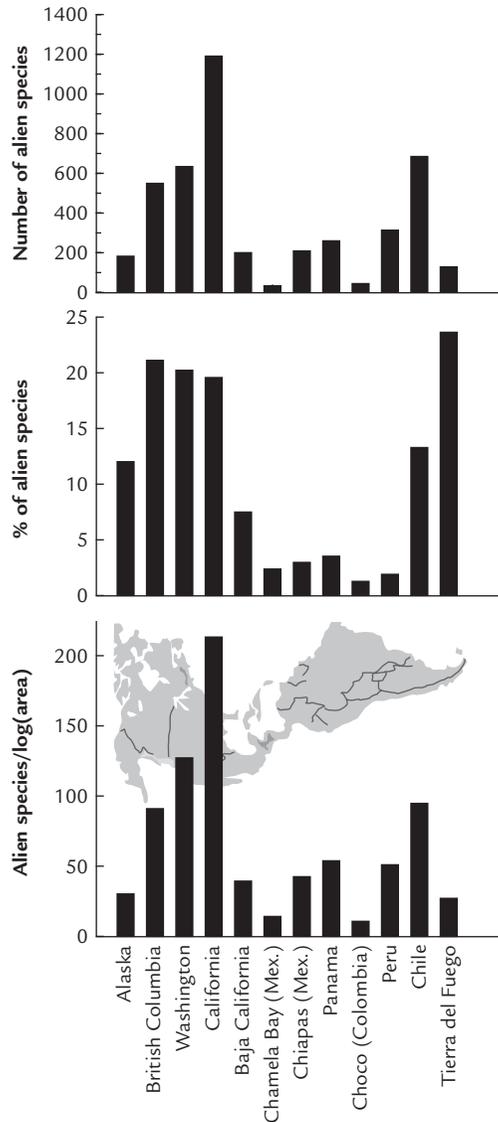
Fig. 13.1 Total number of alien plant species, percentage of alien plant species, and number of alien plant species per log(area) along the Pacific coast of Americas. 'Alien species' here are plants growing in individual areas without cultivation. Not all of them are fully naturalized and even fewer 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).

Neotropical woody plants, e.g. *Lantana camara* and *Opuntia* spp. (Foxcroft *et al.* 2010). The absolute number of alien species, therefore, is not necessarily the best indicator of ecosystem invasibility, at least at this scale (Stohlgren *et al*. 2011). Undisturbed tropical forests, however, harbour only very small numbers of alien plant species and most of them do not spread beyond trails and gaps. 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 (Rejmánek 1996).

At the regional scale, enormous differences in the presence and abundance of invaders among different communities (ecosystems) within one area seem to be the rule. An overview is now available for several areas in Europe (Fig. 13.2, Table 13.1). Alien species are concentrated mostly in vegetation of deforested
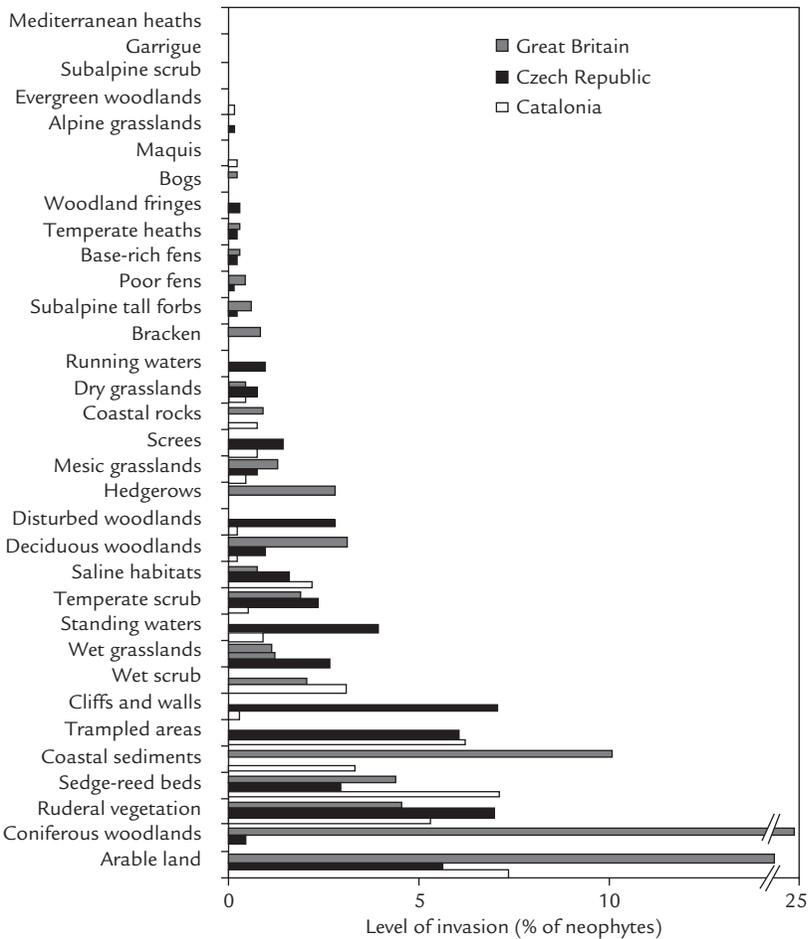

Fig. 13.2 Proportions of neophytes (species introduced after AD 1500) occurring in vegetation plots in different habitats in Catalonia, Czech Republic, and Great Britain. (Based on Chytrý *et al.* 2008.)

Table 13.1 Numbers of alien species, classified according to the time of introduction into archaeophytes and neophytes, in representative vegetation alliances of the Czech Republic.

Vegetation group[a]	No. of archaeophytes	No. of neophytes	% of invasive among neophytes
Ruderal vegetation			
Sisymbrion officinalis (tall-herb communities of annuals on nitrogen-rich mineral soils)	96	106	9.4
Aegopodion podagrariae (nitrophilous fringe communities)	16	76	36.8
Arction lappae (nitrophilous communities of dumps and rubbish tips)	36	45	31.1
Balloto–Sambucion (shrub communities of ruderal habitats)	18	34	41.2
Matricario–Polygonion arenastri (communities of trampled sites)	20	20	15.0
Potentillion anserinae (communities of salt-rich ruderal habitats)	12	20	10.0
Convolvulo–Agropyrion (communities of field margins and disturbed slopes)	24	16	31.3
Onopordion acanthii (thermophilous communities of village dumps and rubbish tips)	34	8	12.5
Weed communities of arable land			
Veronico–Euphorbion (weed communities of root crops on basic soils)	47	28	21.4
Panico–Setarion (weed communities of root crops on sandy soils)	28	15	40.0
Caucalidion lappulae (thermophilous weed communities on base-rich soils)	79	11	0.0
Aphanion (weed communities on acid soils)	41	8	12.5
Sherardion (weed communities of cereals on medium base-rich soils)	47	7	14.3
Grasslands			
Arrhenatherion (mesic *Arrhenatherum* meadows)	15	56	25.0
Festucion valesiacae (narrow-leaved dry grasslands)	12	12	0.0

(*Continued*)

Table 13.1 (*Continued*)

Vegetation group[a]	No. of archaeophytes	No. of neophytes	% of invasive among neophytes
Bromion erecti (broad-leaved dry grasslands)	6	8	0.0
Nardion (subalpine *Nardus* grasslands)	0	1	0.0
Helianthemo cani–Festucion pallentis (rock-outcrop vegetation with *Festuca pallens*)	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
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 naturally 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	–

[a]Within each vegetation group, alliances are ranked according to the decreasing total number of alien species.
Data from Pyšek *et al*. (2002b).

mesic habitats with frequent disturbance (Pyšek *et al*. 2002a, b). Native forests generally 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 are 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. 13.3) 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. It is important to stress, however, that the actual level of invasion may be mostly correlated with, but need not necessarily always correspond to, invasibility (see Section 13.3) of particular communities or habitats. To determine the invasibility of different communities, we need to factor out the effects of confounding variables such as propagule pressure and climate on the level of invasion (Chytrý *et al*. 2008; Eschtruth & Battles 2011).

Data from California (Fig. 13.3) suggest that the proportions of alien species numbers are reasonably well correlated with their dominance (cover). This is probably attributable to a simple sampling effect: with an increasing proportion of alien species, there is an increasing chance that one or more of them will dominate the community. While there seems to be a general agreement between the proportion of alien species numbers and their actual importance (cover and biomass), some exceptions are very noteworthy. Whereas the number of alien species in European *Chelidonio–Robinion* woodland is not exceptionally high (Table 13.1), the dominant *Robinia pseudoacacia* is an alien tree from North America. On the other hand, while there are many alien species in some grassland communities (*Festucion valesiaceae*, *Bromion erecti*), the dominants are all native and aliens are rarely invasive.

13.3   Invasibility of plant communities

Can we say anything conclusive about differences in invasibility (susceptibility to invasions) of particular ecosystems? Analyses of ecosystem invasibility based just on one-point-in-time observations (*a posteriori*) are usually unsatisfactory (Rejmánek 1989; Chytrý *et al*. 2008). In most cases we know nothing about the quality, quantity and regime of introduction of alien propagules. Nevertheless, available evidence indicates that only a 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 years of uninterrupted secondary succession (Fig. 13.4), or over longer periods of primary successions. However, some *r*-strategists are shade-tolerant, for example *Acer platanoides*,
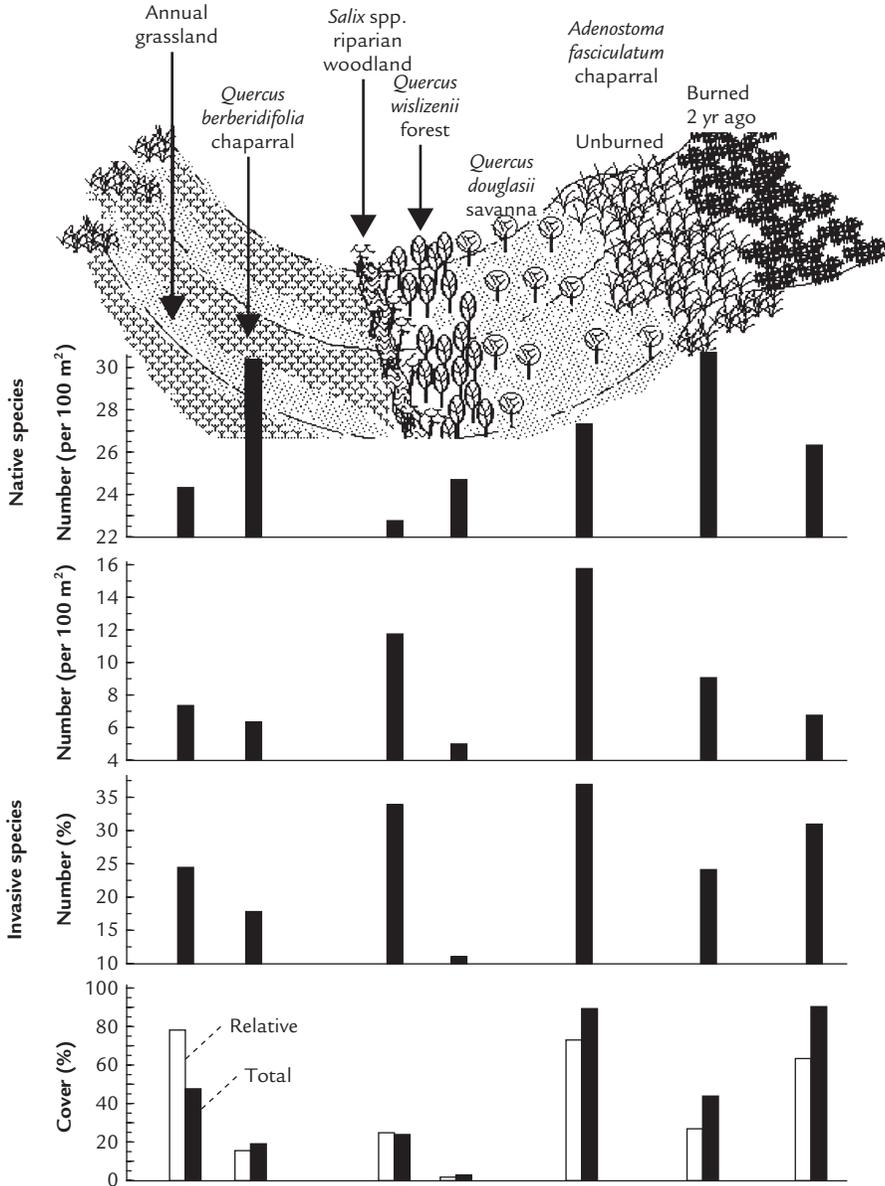
Fig. 13.3 Native and invasive species in seven plant communities of the Stebbins Cold Canyon Reserve, North Coast Ranges, California (150–500 m a.s.l.). Each column represents a mean from three 100-m^2 plots. 'Relative cover' of invaders is their cover with respect to the cumulative vegetation cover 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 ($r = 0.75$; $n = 7$; $p = 0.05$). (M. Rejmánek, unpublished data.)
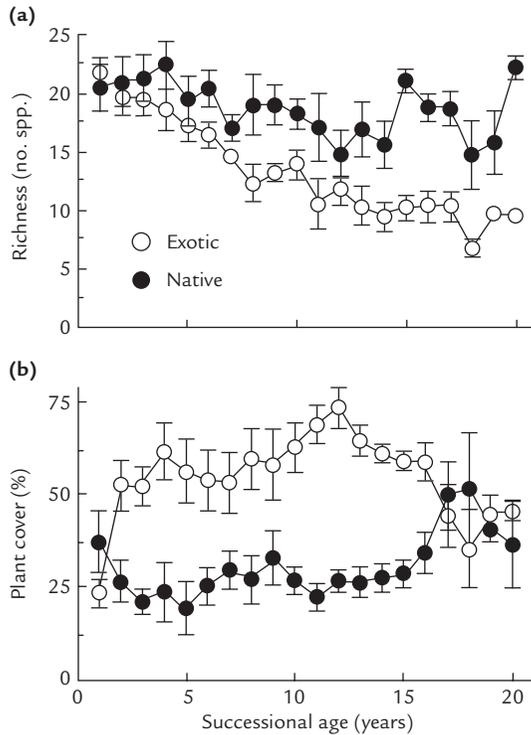
Fig. 13.4 Effect of time since abandonment on the mean species richness (a) and cover (b) of native and alien (non-native) species over 20 years of old-field succession in Argentina (Tognetti *et al*. 2010). Data points show means and vertical bars show SE for plots reaching a given age in different years. Decline of the mean percentage of alien species richness is even more dramatic. Mean relative cover of alien species usually temporarily increases during the first 10 years of succession. See also Meiners *et al.* (2002), Rejmánek (1989), and Schmidt *et al.* (2009).

Alliaria petiolata, *Microstegium vimineum* and *Triadica sebifera* (= *Sapium seb-iferum*). Such species can invade successionally advanced plant communities and, therefore, represent a special challenge to managers of protected areas (Martin *et al*. 2009).

   Plant communities in mesic environments seem to be more invasible than those in extreme terrestrial environments (Rejmánek 1989). Xeric environments are much less 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 species (biotic resistance). We have to be cautious, however, in interpretating 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 invasions following introductions of *Brassica tournefortii* and *Pennisetum ciliare*.

Open water is notoriously known as vulnerable to invasions of all kinds of non-native aquatic plants. Disturbance, nutrient enrichment, slow recovery rate of resident vegetation and fragmentation of successionally advanced communities generally promote plant invasions (Rejmánek 1989; Hobbs & Huenneke 1992; Cadenasso & Pickett 2001; but see Moles *et al.* 2012). In addition, increasing CO_2 levels will probably accelerate invasions in arid ecosystems (Smith *et al.* 2000; Dukes *et al.* 2011).

A general theory of invasibility was put forward 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 the 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. 13.5) and expressed more rigorously by Shea & Chesson (2002). Davis & Pelsor (2001) experimentally manipulated resources and competition in an herbaceous community to show 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. Not all field experiments, however, support this theory (Walker *et al.* 2005; Maron & Marler 2008).
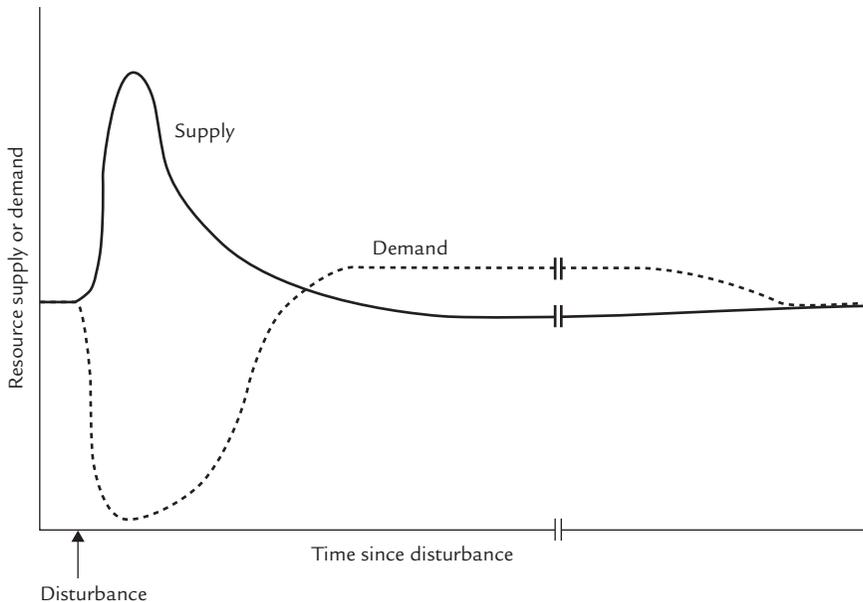

Fig. 13.5 Changes in supply and demand of resources after disturbance in terrestrial ecosystems. Resource availability is generally at its maximum shortly after disturbance, although conditions of bare ground can inhibit seedling establishment in some sites. (Modified from Vitousek & Walker 1987.)

Experiments on invasibility of different types of ecosystems have been gaining momentum in recent years (Fargione *et al*. 2003; Roscher *et al*. 2009; Petermann *et al*. 2010). The notion that there is a causal connection between invasibility of a plant community and the number of species present in that community (biotic invasions' resistance due to species richness) is usually attributed to Charles Elton (Fridley 2011). However, Crawley *et al*. (1999), Davis *et al*. (2000), and Schamp & Aarssen (2010), among others, pointed out that there is not necessarily any unambiguous relationship between these two phenomena. Other studies show that such a relationship exists: positive at the landscape scale (e.g. Stohlgren *et al*. 1999; Davies *et al*. 2011) and negative at scales usually of $1\,m^2$ or smaller (neighbourhood scales). This fact is sometimes called the 'invasion paradox' (Fridley *et al*. 2007). Many recent, well-designed experimental studies confirmed a negative relationship between resident plant species richness and invasibility in small (Fargione & Tilman 2005; Maron & Marler 2008; Fig. 13.6) and even in somewhat larger plots ($4\,m^2$; Petermann *et al*. 2010). 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 most plausible explanation of low invasibility of highly diverse communities at this scale is not the effect of diversity *per se*, but rather species complementarity in the use of resources and their uniformly low levels in high-diversity communities (Tilman 2004).

In this context, it is not surprising that some studies concluded that it is not necessarily the diversity of taxa, but that of functional groups (guilds; see Chapter 12), that makes communities in small plots more resistant to invasion (Symstad 2000; Lanta & Lepš 2008; Hooper & Dukes 2010). On the other hand, dominant species identity (Emery & Gross 2007) and/or intraspecific genetic diversity of dominant species may also contribute to invasion resistance (Crutsinger *et al*. 2008).

The experimental studies just mentioned usually relate the number of resident plant species to the number and/or 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 as, 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*. 2000a). Experiments by Klironomos (2002) on species from Canadian old-fields and grasslands showed that rare species of native plants accumulate soil plant pathogens rapidly, while invasive species do not. This plant-soil feedback and similar findings of other authors (Callaway *et al*. 2004; Inderjit & van der Putten 2010) have potentially important consequences for community invasibility.
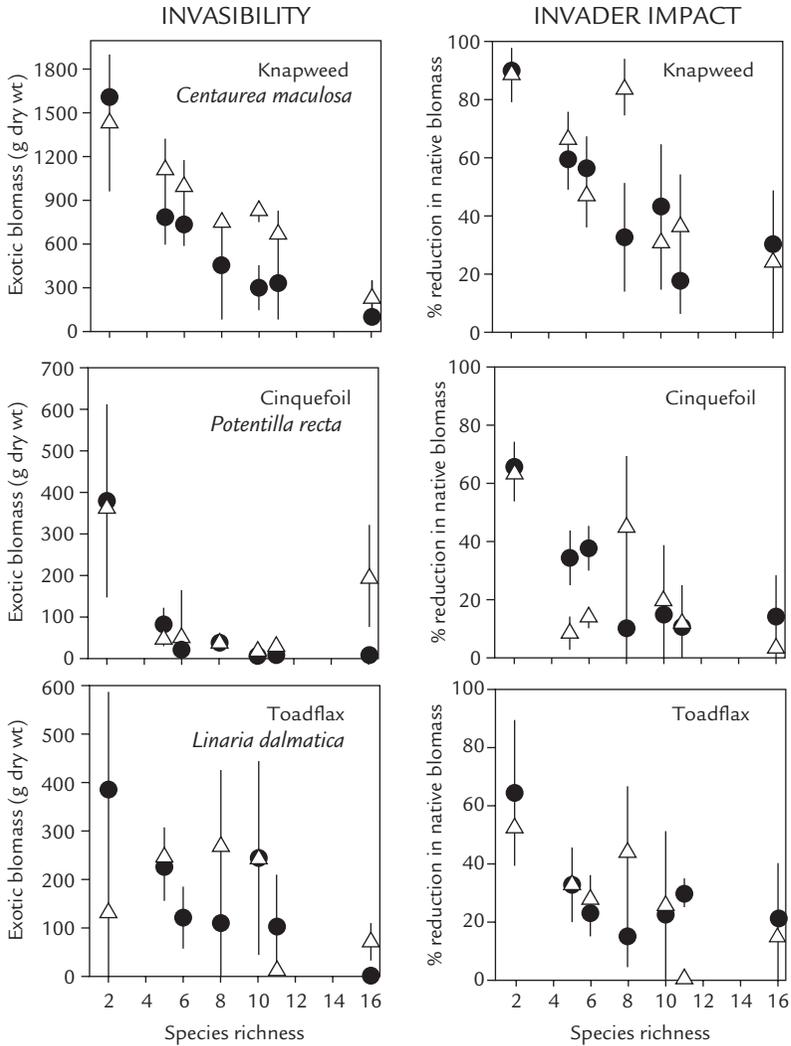
Fig. 13.6 Effect of native species richness on invasibility (left panel), quantified as mean (±SE) above-ground biomass of invaded non-natives, and invader impact (right panel), quantified as mean (±SE) per cent reduction in above-ground biomass of native plants. Circles, dry treatments; triangles, wet treatments. (Maron & Marler 2008.)

When introduced outside of their native territories, plants are often liberated from their enemies, including soil pathogens. This should be a clear advantage that would make natives and aliens, at least temporarily, different. However, the evidence is mixed. The recent meta-analysis by Chun *et al.* (2010) showed that non-native plant species may not always experience enemy release and that enemy release may not always result in greater plant performance. In their

meta-analysis of the role of biotic resistance in invasions of non-native plants, Levine *et al.* (2004) concluded that biotic interactions rarely enable communities to resist invasion, although they do very often constrain the abundance of invasive species once they have successfully established.

A conceptual cause–effect diagram (Fig. 13.7) captures all the fundamental components of the current debate on the issue of invasibility. The fact that both invasibility and species diversity of residents are 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 a positive correlation between numbers of native and non-native species when several different communities or areas are compared (Tilman 2004; Davies *et al.* 2005; Stohlgren *et al.* 2006). Fast post-disturbance recovery of residents (native and already established non-native species) may be a key factor making the wet tropics more resistant to plant invasions – measured as the 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. 13.7). Is this why islands are more vulnerable and Eurasia least vulnerable to invasions? Is instability of so many artificial 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 conducted to resolve this question. Artificial experimental plant communities that are so often used for invasibility experiments have a clear advantage of homogeneous substrata and microclimates. However, assembly processes in such communities are very short and/or artificially directed via arbitrary species pool selection, weeding, reseeding, etc. The existence of well-established 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. In this context, the size and composition of alien species pools (Fig. 13.7) play an important role. Such pools determine the traits and identity of invading alien species, as well as the composition of all communities in the landscape.

First, the size: size of the species pool ultimately determines the range of trait variation of the available species. It is more likely that some better competitors and species better adapted to the local environment will exist in large species pools. Island communities represent limited samples of potential species matching their habitats. Therefore, invasibility of islands should be studied in terms of the differences in species pools, not local differences in the species richness of invaded communities (Herben 2007). Also, it has been proposed that species in larger and diverse regions are 'more advanced' by a greater diversity and intensity of competition to match a wider range of both abiotic and biotic challenges. Floras consisting of such species should be less invasible because of their greater evolutionary advancement (Fridley 2011). This seems to be in agreement with a recent analysis of plant communities in the Netherlands which showed
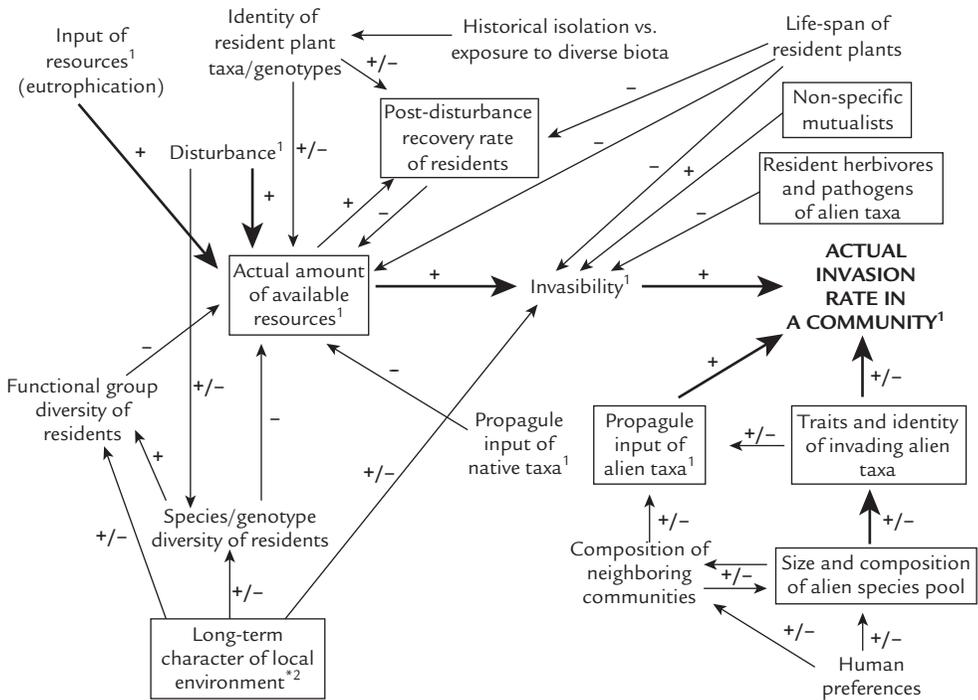
Fig. 13.7 Causal relationships between factors and processes that are assumed responsible for invasions of alien species into plant communities. The most important relationships are indicated by thick arrows. *, spatial heterogeneity, (micro)climate, and long-term regime of available resources and toxic compounds. Time scale: 1, days–years; 2, years–centuries. The key components are in boxes.

that phylogenetically less diverse communities are invaded by more alien species (Gerhold *et al.* 2011).

Second, phylogenetic relatedness clearly matters. The recent study by Davies *et al.* (2011) demonstrated that at both small (16 m^2) and large (10 816 m^2) scales, native and alien plant species in Californian grasslands are more distantly related than expected from a random assemblage model. Alien species closely related to those already present are excluded. Therefore, even communities that appear unsaturated still can be structured by biotic resistance. This is in agreement with the so-called Darwin's naturalization hypothesis: introduced species that are phylogenetically distant from their recipient communities should be more successful invaders than closely related introduced species (Rejmánek 1999; Proches *et al.* 2008; Parker *et al.* 2012).

Third, introduced species are not random samples from donor floras. Particularly, intentional introductions are heavily biased toward potentially invasive species: '. . . a useful exotic pasture species is almost certain to become a weed in some circumstances' (Lonsdale 1994). Fast-growing plantation trees with

short juvenile periods and ornamental woody species with showy fleshy fruits are other examples. Moreover, due to the nursery's cultivation experience, plant species that have been sold more recently are more likely to naturalize than those sold earlier (Pemberton & Liu 2009). Obviously, biases in introduction pools make often an *a priori* trait difference between introduced non-native and native 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. This is essentially identical to the idea proposed by Bruun & Ejrnaes (2006) that a community's invasibility is positively influenced by the turnover rate of reproductive genets in the community, which they call the 'community-level birth rate'.

13.4   Habitat compatibility

The identity of non-native taxa (Fig. 13.7) 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 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. Hejda *et al*. 2009b; Petipierre *et al*. 2012). In North America, for example, latitudinal ranges of naturalized European plant species from the Poaceae and Asteraceae are on average 15° to 20° narrower than their native ranges in Eurasia and North Africa (Rejmánek 2000). These differences essentially reflect the differences in the position of corresponding isotherms and major biomes in Eurasia and North America. Knowledge of species or genotype tolerance limits (Richards & Janes 2011) and habitat compatibility is essential for predictions of the potential distribution of invasive species (Gallien *et al*. 2010; Franklin 2010).

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 used 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. The combination of Ellenberg indicator values (Ellenberg *et al*. 1992) with Grime's functional types (strategies) (Grime *et al*. 2007) especially can be a powerful tool for predictions of habitat compatibility of European species. The strength of affiliation with phytosociological syntaxa 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. Also, 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, *Acacia* and *Pinus* species in South African fynbos shrublands, many Cactaceae species in arid regions of the Palaeotropics, *Rhizophora mangle* (mangrove) in treeless coastal marshes of Hawaii, and the tree *Cinchona pubescens* (Rubiaceae) in mountain shrublands 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; Hooper & Dukes 2010; Petermann *et al*. 2010).

13.5   Propagule pressure and residence time

Invasions result from an interplay between habitat compatibility and propagule pressure (Fig. 13.7). 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. 13.8). This example 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 increases outside or within such areas, invasions could well start or increase (Foster 2001; Duncan 2011; but see Nunez *et al*. 2011). Estimates of propagule pressure are essential for distinguishing between the extent of invasion and invasibility of biotic communities (Eschtruth & Battles 2011). A highly relevant aspect is the propagule pressure of native species: if propagules of natives are not available, as for instance around abandoned fields in California, the 'repairing' function of ecological succession (Fig. 13.4) 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 seldom know exactly when taxa are introduced, we use 'minimum residence time' (MRT) based on herbarium specimens or reliable records. Nevertheless, the number of discrete localities of naturalized species is significantly positively correlated with MRT (Fig. 13.9). There is usually longer MRT for naturalized species compared with casual species and even longer MRT for invasive species. However, transformers may have their MRT even shorter than other invasive species (Fig. 13.10). MRT is an important factor explaining the extent of invasion of alien plants at a regional scale (Wilson *et al*. 2007; Pemberton & Liu 2009).
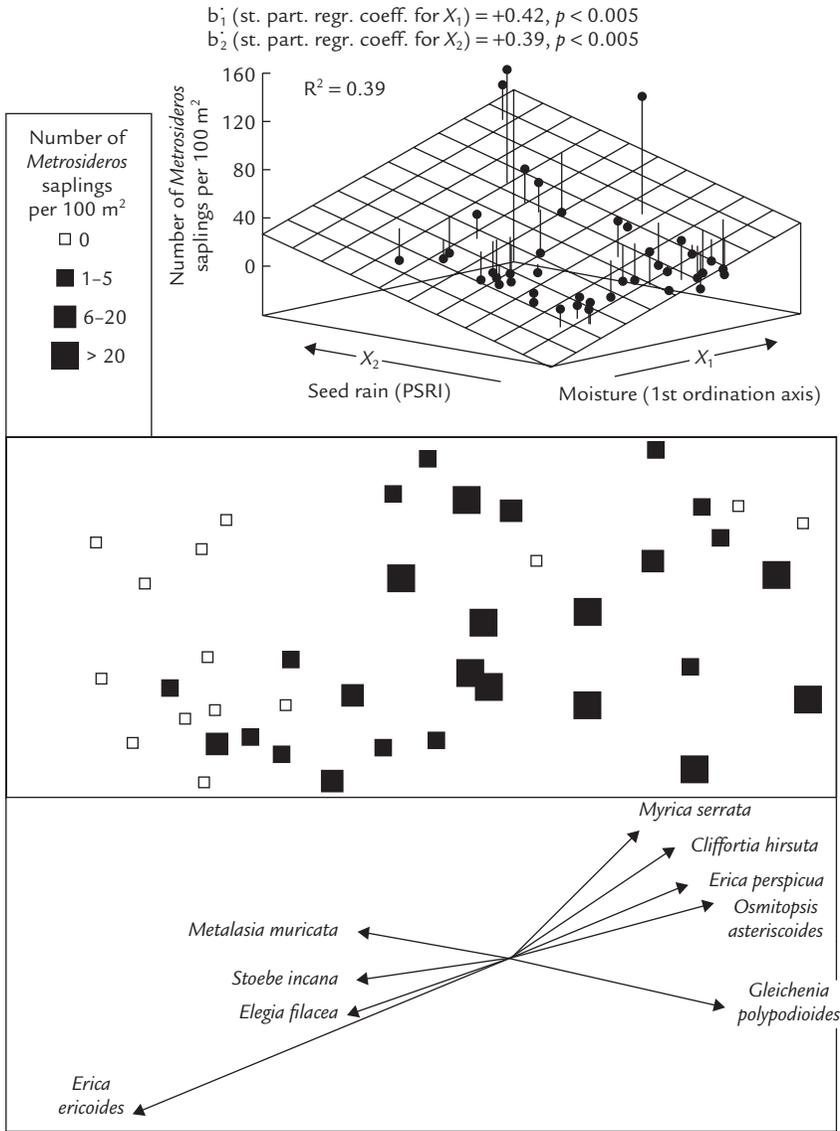
Fig. 13.8 The dependence of the sapling density of *Metrosideros excelsa* on potential seed rain index (PSRI) and moisture in fynbos of the Western Cape, South Africa. PSRI = SUM($1/d_i$), where d_i is distance to the i-th mature tree in metres within the radius 300 m. The first ordination axis (below) serves as a surrogate for moisture gradient. Standardized partial regression coefficients 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.)
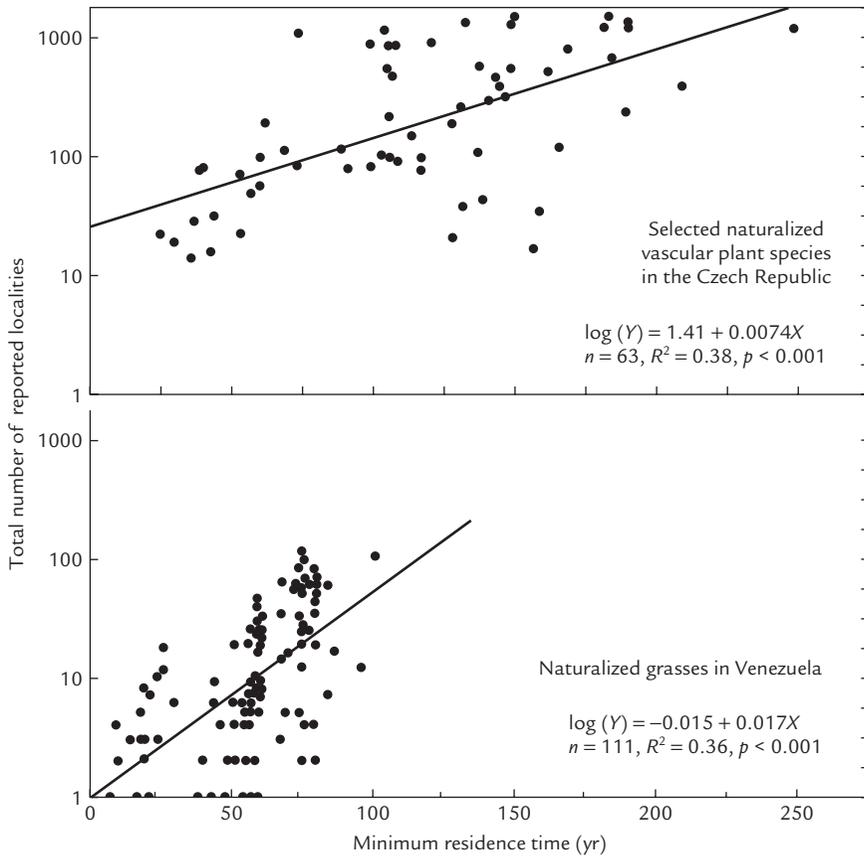
Fig. 13.9 The dependence of the total number of reported localities on the minimum residence time (years since the first record) of selected naturalized species in the Czech Republic and Venezuela. (P. Pyšek & M. Rejmánek, unpublished data.)

13.6 What are the attributes of successful invaders?

The identity of introduced species certainly matters (Fig. 13.7). One of the basic questions is whether some taxa are more invasive than others and if so, which biological attributes are responsible for that difference. The current consensus is that plant species are not equal in their invasiveness; however, different biological attributes may be important in different life-forms of plants and in different environments. Many other factors, namely propagule pressure (introduction effort) and residence time, often mask differences in invasiveness that are due to biological attributes.

Several prerequisites and stages of biological invasions are usually recognized: (1) selection of species and genotypes → (2) transport → (3) introduction → (4) establishment (consistent reproduction) = naturalization → (5) spread (invasion
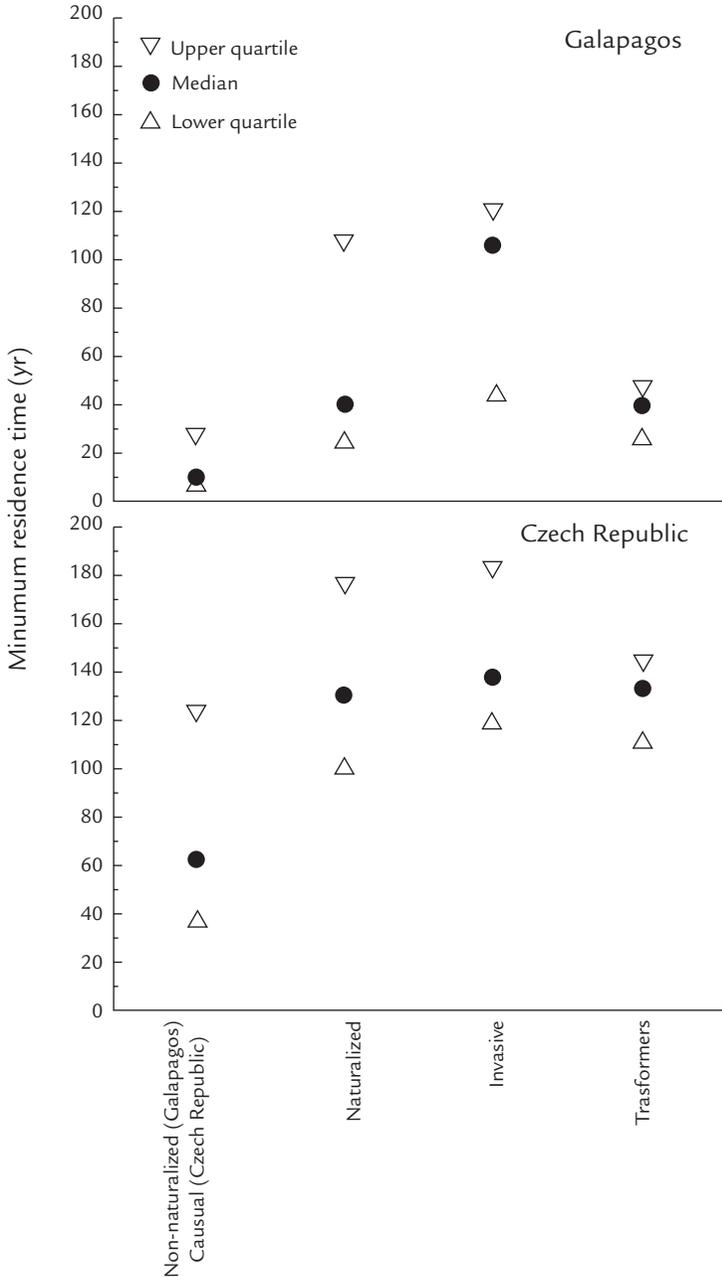
Fig. 13.10 Medians and interquartile ranges of minimum residence times for alien plant species categories in Galapagos and the Czech Republic. The subset of 'Invasive' is excluded from 'Naturalized', and the subset 'Transformers' is excluded from 'Invasive'. (Based on Trueman *et al*. 2010 and P. Pyšek, unpublished data.)

sensu stricto) → (6) environmental and/or economic impact. Obviously, very different factors may be important at each stage (Dawson *et al*. 2009). The first three steps entail intentional or unintentional human assistance. The remaining steps are spontaneous but may still be assisted by human activities. The first three steps determine the species pool of potential invaders. Species that are invasive may be introduced due to different selection processes operating during these stages. Here we will focus on step 5 (spread), which implicitly includes step 4 (reproduction). It is conceptually useful to distinguish between steps 4 and 5, but they are tightly interconnected. For a species to be invasive, it has to reproduce (establish), successfully disperse (spread) and reproduce (establish) again in new locations, and so on.

Extrapolations based on previously documented invasions are fundamental for predictions in invasion ecology. With the development of relevant databases – see, for example, Richardson & Rejmánek (2011) for invasive trees and shrubs – this approach should lead to immediate rejection of imports of many taxa known to be invasive in similar habitats elsewhere (prevention) and prioritized control of those that are already established. Such transregional, taxon-specific extrapolations are very useful in many situations, but our lack of mechanistic understanding makes them intellectually unsatisfying. Understanding how and why certain biological characters promote invasiveness is extremely important, since even an ideal whole-Earth database will not cover all (or even most) 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.

Basic taxonomic units used in plant invasion ecology are usually species or, much less often, subspecific taxa. However, genera are certainly worth considering. Plant species belonging to genera notoriously known for their invasiveness or 'weediness' (e.g. *Amaranthus*, *Cuscuta*, *Echinochloa*, *Ehrharta*, *Myriophyllum*) should all be treated as high risk. However, a continuum from invasive to non-invasive species is also common in some genera (*Acer*, *Amsinckia*, *Centaurea*, *Eichhornia*, *Pinus*). Which pattern is more typical should be rigorously tested. Naturally, attention has been paid to taxonomic patterns of invasive plants. In terms of relative numbers of invasive species, some plant families are consistently over-represented: Amaranthaceae, Brassicaceae, Chenopodiaceae, Fabaceae, Gramineae, Hydrocharitaceae, Papaveraceae, Pinaceae, and Polygonaceae. Among large families, the only conclusively under-represented one is Orchidaceae (Daehler 1998; Pyšek 1998).

Assuming abiotic environment compatibility, five biological attributes are, to different degrees, responsible for invasiveness of all kinds of organisms: (a) population fitness homeostasis, (b) population fitness, (c) minimum generation time, (d) rate of population expansion, and (e) organismal competitiveness and/ or self-suitable modification of the environment (Fig. 13.11).

The relative importance of these attributes varies depending on the amount of critical resources, disturbance regimes and spatial heterogeneity of the environments. Their components are not necessarily compatible and may be important under different circumstances. For example, the ability to use available
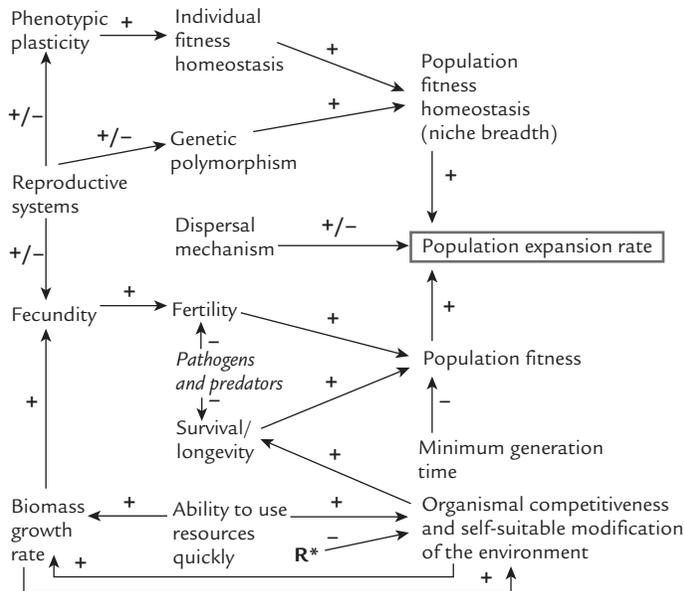
Fig. 13.11 Positive (+) and negative (−) causal relationships among biological attributes responsible for species invasiveness. R* is the level to which the amount of the available form of the limiting resource is reduced by a monoculture of a species once that monoculture has reached equilibrium (i.e. once it has attained its carrying capacity). (Modified from Rejmánek 2011.)

resources quickly is important in disturbed habitats, while the ability to reduce the amount of critical resources (lower R*) is important when invading successionally advanced communities. Also, short minimum generation time (positively influencing fitness) is usually associated with short longevity (negatively influencing fitness).

(a) *Population fitness homeostasis* (PFH) means consistent fitness at a population level over a broad range of environments. PFH is determined by individual fitness homeostasis and genetic polymorphism. Individual fitness homeostasis (IFH), or Herbert Baker's (1965) *general purpose genotype*, is the ability of an individual to maintain consistent fitness across a range of conditions through phenotypic plasticity. Phenotypic plasticity is responsible for both IFH and PFH of many plant invaders with little or no genetic diversity (e.g. *Alternanthera philoxeroides* in Asia, *Arundo donax* and *Hieracium aurantiacum* in North America, *Clidemia hirta* and *Pennisetum setaceum* in Hawaii). However, our current understanding of the role of phenotypic plasticity is far from conclusive (Davidson *et al*. 2011). On the other hand, there is abundant evidence for local adaptations through selection acting on population genetic diversity of introduced plant species (e.g.

Escholzia californica in Chile, *Hypericum perforatum* in North America, *Phyla canescens* in Australia). In this context, polyploidy, as a source of genetic diversity, can be a particularly important factor (te Beest *et al.* 2012). One important source of genetic diversity within invasive species is their repeated introduction from multiple sources (Novak 2011). Multiple introductions often transform among-population variation in native ranges to within-population variation in introduced areas. High PFH of a species translates into its broader ecological niche. It is reasonable to expect that a wide native habitat range of a species is a good indicator of its high PFH and therefore high invasiveness.

(b) *Actual level of population fitness in particular environments* is the key component of all invasions. Unfortunately, fitness quantified as finite rate of population increase (λ) is only rarely properly measured and comparisons of fitness between invasive and non-invasive species are almost non-existent. In an exceptional study, Burns (2008) found that invasive plant species in the family Comelinaceae had significantly larger λ values than non-invasive ones, but only under high-nutrient conditions. More often, fitness is just estimated on the basis of its components: fertility or fecundity. A positive correlation between individual plant biomass and seed production per plant is one of the most robust generalizations of plant ecology. Therefore, higher values of relative growth rates (RGR) in plants may often indicate higher fitness and invasiveness (Grotkopp *et al.* 2002, 2010). The recent meta-analysis of all available studies by van Kleunen *et al.* (2010) revealed that both growth rates and fitness-related attributes are significantly higher for invasive plant species when compared with either non-invasive or native plant species. However, there are trade-offs between biomass growth rate and survival – another component of fitness. There are both benefits and costs to fast living. For example, because RGR of plants is usually negatively related to water-use efficiency, fast growth is not the best strategy for perennial plant invaders in arid environments. Based on their studies in resource-poor habitats in Hawaii, Funk & Vitousek (2007) showed that invasive plant species were generally more efficient than native species at using limited light, water and nitrogen.

Last but not least, fecundity depends on reproductive systems. The consistent production of offspring 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. lycopsoides*, *A. menziesii*) 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.

Vegetative reproduction can compensate more than sufficiently for sexual reproduction in some invasive plant species. Water hyacinth (*Eichhornia crassipes*) and infertile hybrid giant salvinia (*Salvinia molesta*) are well-known examples. The ability to allocate energy to different modes of reproduction depending on environmental conditions is one type of phenotypic plasticity and increases IFH and PFH. Apomictic plants (like

dandelions) have an advantage, at least initially, as a single individual can establish a population (Koltunow *et al*. 2011).

(c) *Short minimum generation time*, also called juvenile period, is an obvious advantage for invasive species. Not surprisingly, substantial proportions of non-native floras in temperate zones are annual species. Short minimum generation time is usually a prominent attribute used for identification of (potentially) invasive woody species. Invasiveness of woody taxa in disturbed landscapes is associated with short juvenile period (<10 years), small seed mass (<50 mg), and short intervals between large seed crops. Differences between invasive and non-invasive pine (*Pinus*) species served as the first illustration of such regularities (Fig. 13.12; Rejmánek & Richardson 1996). The three attributes, listed above, contribute, directly or indirectly, to higher values of three parameters 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 $\sqrt{(\text{seed mass})}$. Because of the trade-off between seed number and mean seed mass, small-seeded taxa usually produce more seeds per unit biomass. Invasions of woody species with very small seeds (<3 mg), however, are limited to wet and preferably mineral substrates (Fig. 13.13). 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.

(d) *Fast dispersal of propagules* is another crucial component of plant invasiveness. Rate of dispersal always depends on two species-specific characteristics: fertility and efficiency of dispersal mechanism. This is also the substance of Fisher–Kolmogorov's classic formulation of population rate of expansion of the population front (how many metres a constant population density can propagate in one dimension in one year) in a homogeneous environment: $2\sqrt{(rD)}$, where r is the intrinsic rate of population increase (fertility minus mortality, i.e., individual/individual/year) and D is the diffusion coefficient ($m^2 yr^{-1}$). The first term is directly related to population fitness: $r = \ln \lambda$.

The most important long-distance dispersal agents for plants are people, other vertebrates (mostly birds), water, and wind. Plants have many different adaptations or preadaptations for dispersal by these vectors. Plant species with seeds without any dispersal-promoting appendages are usually less invasive (*Eucalyptus* spp.). However, because increasing volumes of soil are moved around by people (in topsoil, in mud on cars, with horticultural stock), plant species with numerous, dormant, soil-stored seeds are preadapted for this kind of dispersal (Hodkinson & Thompson 1997; Von der Lippe & Kovarik 2007).

Seed dispersal by vertebrates is responsible for the success of many invaders in disturbed as well as 'undisturbed' habitats (Aslan & Rejmánek 2010;
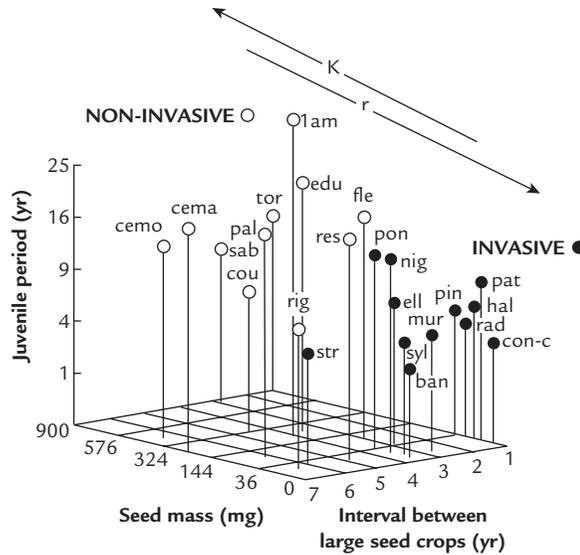
Fig. 13.12 Distribution of 23 frequently cultivated *Pinus* species in a space created by three biological variables critical in separating invasive and non-invasive species. The *K-r* selection continuum running from the upper left to the lower right corner of the diagram also represents the direction of the discriminant function (Z) separating non-invasive and invasive *Pinus* species. $Z = 23.39 - 0.63\sqrt{M} - 3.88\sqrt{J} - 1.095S$, where M = mean seed mass (in milligrams), J = minimum juvenile period (in years), and S = mean interval between large seed crops (in years). 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, *elliotii*; 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*.

Richardson & Rejmánek 2011). Even some very large-seeded alien species like mango (*Mangifera indica*) or avocado (*Persea americana*) can be dispersed by large mammals. Assessment of whether there is an opportunity for vertebrate dispersal is an important component of the screening procedure for woody plants (Fig. 13.13).

(e) *Undisturbed (natural and semi-natural) plant communities* in mesic environments are more likely invaded by tall plant species. The most prominent examples are new, taller, life-forms (*Acacia* spp. and *Pinus* spp. in South African fynbos, *Cinchona pubescens* in shrub and fern/grassland communities of the Galapagos highlands). Undisturbed plant communities in *semiarid* habitats seem to be invasible especially by environmentally compatible species that rapidly develop deep root systems (e.g. *Bromus tectorum* or *Centaurea solstitialis*). In short, in undisturbed plant communities, efficient competitors for limiting resources will very likely be successful invaders and the worst environmental weeds. Theoretically, given a set of R_i^* values
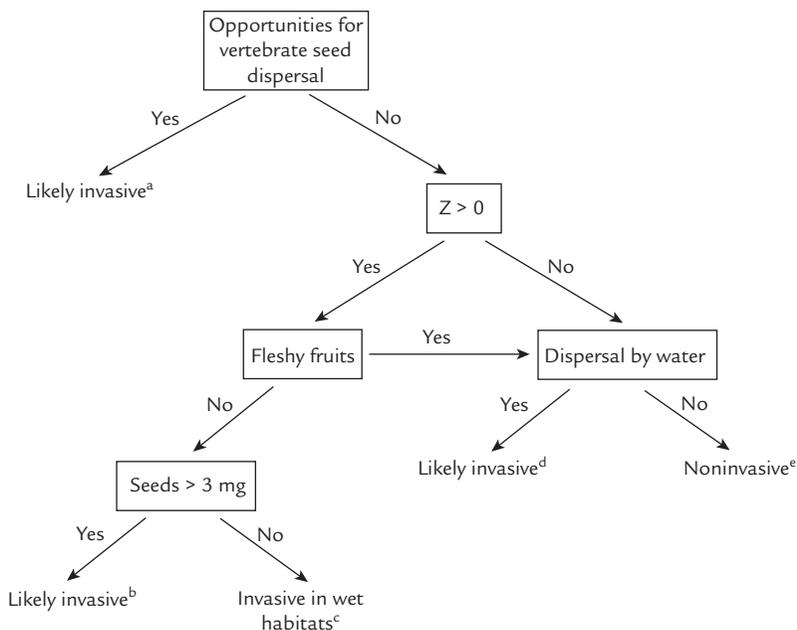
Fig. 13.13 Decision tree for detection of invasive woody seed plants based on values of the discriminant function Z*, seed mass values and presence or absence of opportunities for vertebrate dispersal (derived from Table 6.1 in Rejmánek *et al*. 2005). *$Z = 23.39 - 0.63\sqrt{M} - 3.88\sqrt{J} - 1.09S$, where M = mean seed mass (in milligrams), J = minimum juvenile period (in years), and S = mean interval between large seed crops (in years). This discriminant function (Z) was derived on the basis of differences between invasive and non-invasive pine (*Pinus*) species. Positive Z indicates invasive species; negative Z indicates non-invasive species. The function was later successfully applied to other gymnosperms and, as a component of broader frameworks, to woody angiosperms. 'Opportunities for vertebrate seed dispersal' mean that plant species are producing fruits attractive for vertebrates, usually fleshy fruits or nuts, and that at least one member of the local vertebrate fauna is can serve as a dispersal agent.
[a]Examples of invasive species in this group are many fleshy-fruiting species with small seeds: *Berberis* spp. *Clidemia hirta, Lantana camara, Ligustrum* spp., *Lonicera* spp., *Muntingia calabura*, *Passiflora* spp., *Pittosporum undulatum*, *Psidium guajava*, *Rosa* spp., *Rubus* spp., *Solanum* spp. Species with seeds possessing large arils (*Acacia saligna*) or with seeds coated with a wax (*Triadica sebifera*) are dispersed by birds. Even some large-seeded species may be dispersed by some vertebrates: *Pinus pinea* and *Melia azedarach* in South Africa, *Olea europaea* in Australia, *Juglans regia* and *Quercus rubra* in Europe, *Mangifera indica* in the Neotropics, and *Persea americana* in Galapagos.
[b]Mainly wind- and ant-dispersed species, e.g. *Acer platanoides, Ailanthus altissima*, *Clematis vitalba, Cryptomeria japonica, Cytisus scoparius, Pinus radiata, Pseudotsuga menziesii, Robinia pseudoacacia, Tecoma stans, Ulex europaeus*.
[c]Examples of these are *Alnus glutinosa* and *Salix* spp. in New Zealand, *Eucalyptus camaldulensis* in South Africa, *Melaleuca quinquenervia* in southern Florida, *Tamarix* spp. in the south-western US, and *Baccharis halimifolia* in Australia. If species in this category reproduce only by seeds, they need wet mineral substrata for their establishment. Some species in this category can also propagate vegetatively: viable branches of *Salix* spp. and *Populus* spp. can be dispersed by water in streams and rivers over a long distance.
[d]*Nypa fruticans* spreads along tidal streams in Nigeria and Panama, *Thevetia peruviana* can be dispersed over short distances by rain-wash in Africa.
[e]Examples of non-invasive species are *Aesculus hippocastanum, Araucaria araucana*, *Bertholletia excelsa, Camellia* spp., *Fagus* spp., *Pinus lambertiana, Tilia* spp. Some fleshy-fruiting species with $Z > 0$ may be locally non-invasive if opportunities for vertebrate dispersal are not present: *Acca sellowiana*, *Rhaphiolepis indica*, *Pyrus calleryana*, and *Nandina domestica* are frequently cultivated but non-invasive species in California because very few vertebrates eat their fruits; *N. domestica*, however, is dispersed by birds and water in the south-eastern USA.

(R_i^* is a level of resource below which an *i*-th species cannot survive), for a pool of potential invaders, it should be possible to predict the average likely success of each invading species in undisturbed communities (Tilman 1999; Shea & Chesson 2002). However, if seasonality, senescence, or even very low levels of natural disturbance allow establishment of shade-intolerant taxa that are taller than resident vegetation at maturity, then such taxa can still be very successful and influential invaders in spite of their high R^* for light.

The ability to use available resources quickly is an attribute of many successful plant invaders in disturbed habitats. Obviously, there is a trade-off between this kind of strategy and possession of low R^*. Whether some species can quickly use resources and also reduce their levels below those tolerable by resident species remains to be seen. Such species would be the most successful invaders.

Recently, there has been a renewal of interest in the role of allelopathy in plant invasions. It seems that some chemical substances released from the living or decaying biomass of non-native species can inhibit the growth of native plants and/or soil micro-organisms. This can increase the invasiveness of such species. However, with the exception of some consistent effects (e.g. juglone released by walnuts, *Juglans* spp.), results are highly inconsistent, depending on climate and soil properties (Blair *et al.* 2006; Inderjit *et al.* 2006; Callaway 2011). Allelopathic substances are potentially more influential in soils with low organic content and in habitats with low precipitation.

In general, reducing the amount of critical resources below the level needed by resident species or release of chemicals inhibiting growth of residents by non-native species are examples of 'niche constructions' accelerating plant invasions, particularly in undisturbed environments. Some invasive grasses (e.g. *Andropogon gayanus*, *Bromus tectorum*, *Hyparrhenia rufa*) can initiate and maintain a positive grass-fire feedback and transform whole ecosystems to their benefit (Foxcroft *et al.* 2010; Mack 2011).

Long-term population invasiveness, however, does not depend only on organismal anatomical or physiological properties treated above, but on relationships between population fitness values of invaders and residents and the degree of niche overlap between invaders and residents (Fig. 13.14). As Chesson (1990) and more recently MacDougall *et al.* (2009) showed, there are essentially three possible invasion outcomes for all possible combinations of niche and fitness differences: (1) when fitness of residents > fitness of invader and niche overlap is large, residents will repel the potential invader; (2) when there is either no difference in fitness, or niche overlap is small, invader and residents can co-exist; (3) when fitness of invader > fitness of residents and niche overlap is large, the invader can exclude residents. High PFH may contribute to the third outcome. In general, successful invasion can result from either fitness differences that favour the dominance of invader, or niche differences that allow the invader to establish despite lower population fitness. However, the outcomes of invasion will differ. Only the former leads to displacement of resident species. The latter leads to co-existence and not to local extinctions of residents. This model
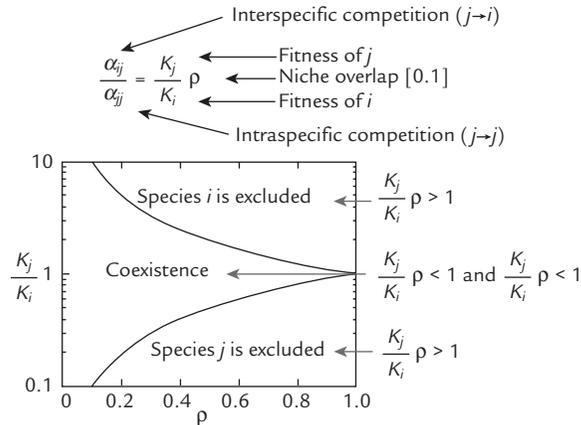
Fig. 13.14 According to Robert MacArthur's consumer-resource model, the ratio of interspecific (between species, a_{ij}) and intraspecific (within species, a_{jj}) competitive effects can be expressed in terms of population fitness (k_j and k_i) of species j and i and resource-use (niche) overlap (ρ) between those species. Species j competitively excludes species i if the ratio is greater than one. In general, when $\rho = 1$ (niche overlap is complete), the species with the larger population fitness excludes the other. However, niche overlap less than 1 constrains the fitness differences compatible with coexistence. This model provides a theoretical framework for potential outcomes of interactions between invading and resident species. (Derived from Chesson 1990; Chesson & Kuang 2008.)

explicitly connects two major topics of invasion biology that are often treated independently: species invasiveness and invasibility of biotic communities. Even though quantifications of both fitness and niche overlap are far from simple measurements, this model provides a useful theoretical framework that will very likely guide research on biological invasions in years to come.

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

Many invasive taxa have transformed the structure and function of ecosystems by, for example, changing disturbance- or nutrient-cycling regimes (Ehrenfeld 2010). In many parts of the world, impacts have clear economic implications for humans, for example as a result of reduced stream flow from watersheds in South African fynbos following alien tree invasion, or through disruption to fishing and navigation after invasion of aquatic plants such as *Eichhornia crassipes*.

It is important to stress, however, that the impacts of invasive plants on biodiversity are generally less dramatic than the impacts of non-native pathogens, herbivores or predators. It seems that most naturalized/invasive plant species have hardly any detectable effect on biotic communities (Williamson & Fitter

1996; Meiners *et al*. 2001). There are at least 3000 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 non-native 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 non-native plant species on the landscape scale can be interpreted as a lack of mechanisms for competitive exclusion of native plants by non-native ones. Nevertheless, we should be careful with conclusions – many invasions are quite recent and extinction takes a long time.

While there has been substantial progress in understanding the plant attributes responsible for or, at least, correlated with successful reproduction and the spread of invasive plant species, our ability to predict their impacts, or even measure their impact using standardized methods, is still very rudimentary. This fact is very important in the context of the ongoing discussion about the possible overestimation of negative impacts of non-native species (Simberloff *et al*. 2011). Several meta-analyses of published data on the ecological impacts of invasive plant species have been published recently (e.g. Powell *et al*. 2011; Vilà *et al*. 2011). In general, they conclude that many alien plants have a statistically significant negative effect on native plant abundance, fitness and diversity. However, at least 80% of over 1000 field studies included in these meta-analyses were based on a 'space-for-time-substitution' approach. Particular examples of results obtained this way are presented in Fig. 13.15 and Table 13.2. However, without pre-invasion data from the invaded and non-invaded sites, conclusions may be
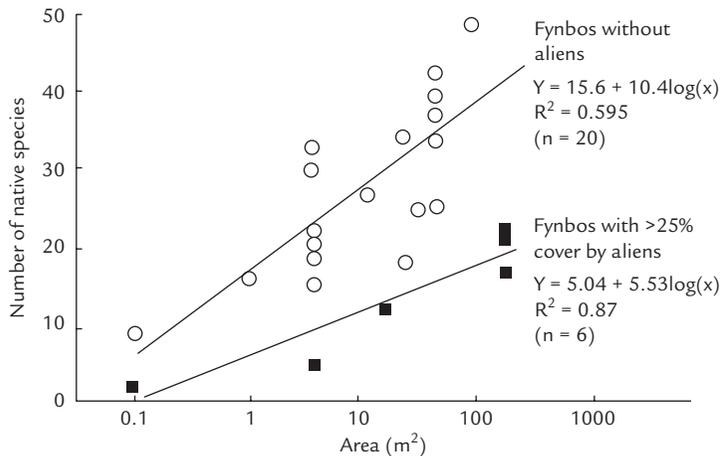

Fig. 13.15   Species–area relationships for native vascular plant species in South African fynbos areas densely infested (squares) by alien woody plants and in uninfested areas (circles). Elevations of the two regression lines are significantly different (*p* < 0.001). Sources of the data are acknowledged in Richardson *et al*. (1989).

Table 13.2   Impact of 12 invasive plant species on species richness of invaded plots.

Species	Cover range (%)	Species number[a]		Impact (%)
		Uninvaded	Invaded	
Fallopia sachalinensis	70–100	13.3 ± 4.9	1.8 ± 1.6	86.4***
F. japonica	100	12.1 ± 3.5	3.3 ± 2.8	73.0**
F. x bohemica	40–100	14.8 ± 7.3	5.4 ± 5.0	65.9*
Heracleum mantegazzianum	90–100	16.7 ± 4.5	7.4 ± 3.1	52.6**
Rumex alpinus	75–100	12.6 ± 2.5	7.7 ± 2.4	39.1***
Aster novi–belgii	60–90	14.1 ± 4.8	8.9 ± 6.3	38.7
Helianthus tuberosus	50–100	12.7 ± 6.5	8.0 ± 4.9	33.7
Rudbeckia laciniata	80–100	10.6 ± 2.6	6.9 ± 3.0	29.8
Solidago gigantea	70–100	16.4 ± 6.7	12.0 ± 6.3	25.5
Imperatoria ostrunthium	50–80	14.3 ± 5.6	9.9 ± 2.6	21.4
Lupinus polyphyllus	60–95	21.1 ± 2.3	16.4 ± 3.8	21.2
Impatiens glandulifera	60–90	10.9 ± 1.8	9.5 ± 2.6	12.3

[a]Species numbers are expressed as mean ± SD per $16\,m^2$, $n = 10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
From Hejda *et al.* (2009a).

misleading. For example, invaded sites that have lower species richness than non-invaded sites in the post-invasion condition may suggest that non-native species negatively affected diversity of native species. An alternative interpretation is that invaded sites could have had lower species richness than the non-invaded ones prior to invasion. This is possible if, for example, invaded sites had lower habitat heterogeneity and/or other environmental conditions that limit numbers of both native species and non-native species. Another possibility is that non-native species invaded less rich sites because of lower biotic resistance. Thus, one cannot determine whether the non-native species really had a negative impact on diversity of native species.

Although the time approach (comparisons of sites in pre- and post-invasion situations) is apparently the only option for resolving the above limitations and serves the purpose of measuring the real impact of non-native species, it can nonetheless also produce mistaken conclusions. Without data from equivalent non-invaded habitats in pre- and post-invasion situations, one may not estimate the direction of the effects of non-native species, nor their magnitudes. Such sources of confusion (see also Thiele *et al.* 2010) could be resolved by testing the effects of non-native species through experiments in conditions that are as realistic as possible.

Competition experiments that are usually limited just to pairs of species represent one option (Vilà & Weiner 2004). Responses to invaders in multispecies communities can be evaluated in invader addition experiments (Maron & Marler 2008; see Fig. 13.6), invader removal experiments (Schutzenhofer & Valone 2006) and experiments where passive colonization of invader monocultures is analysed (Hovick *et al.* 2011). Preferably, in all situations the multiple mechanisms of impacts of invasive species should be anticipated and

systematically tested (Bennett *et al*. 2011). Demographic matrix models are an increasingly standard method for quantitative evaluation of invader's impacts on endangered plant species (Thomson 2005).

Invasiveness and impact are not necessarily positively correlated. Some fast-spreading species, such as *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).

There is a need for universally acceptable, and objectively applicable, procedures for the assessment of influential invasive plant taxa within given regions, or globally. Some attempts in this direction (Magee et al. 2010; Thiele *et al*. 2011) are more promising than others. A potentially useful term to use in this regard is 'transformer species' (Richardson *et al*. 2000b). 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 is an important prerequisite for excessive transpiration; *Andropogon gayanus* inhibits soil nitrification and thereby depletes total soil nitrogen from nitrogen-poor soils and promotes fire-mediated nitrogen loss;

2   Donors/enhancers of limiting resources: nitrogen – *Acacia* spp., *Lupinus arboreus*, *Morella* (*Myrica*) *faya, Robinia pseudoacacia, Salvinia molesta*; phosphorus – *Buddleja davidii, Centaurea maculosa, Solidago gigantea*;

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

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

5   Erosion promotors: *Andropogon virginicus* in Hawaii*, 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 the vegetation structure of the forest, and *Lythrum salicaria* and *Impatiens glandulifera* can have negative impacts on the pollination and

reproductive success of co-flowering native plants (Grabas & Laverty 1999; Chittka & Schürkens 2001). A meta-analysis recently published by Morales and Traveset (2009) demonstrated the predominant detrimental impact of alien plants on the pollination and reproduction of natives. Morover, hybridization with native congeners may be the most important permanent impact of some invaders (Mercure & Bruneau 2008; Hall & Ayers 2009).

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 the 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.

It follows from the discussion on impacts of non-native plants that careful prioritization is needed before starting often very expensive and time-consuming eradication projects. Maintenance of biodiversity is dependent on the mainte-nance of ecological processes. Our priority should be the 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. Non-native taxa with large-scale environmental impacts (transform-ers) 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 wide-spread 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 Agricul-ture on 18 species and 53 separate infestations targeted for eradication in 1972–2000 (Table 13.3), it is shown that professional eradication of non-native

Table 13.3 Areas of initial gross infestations (at the beginning of eradication projects) of exotic weeds in California, numbers of eradicated infestations, numbers of ongoing projects, and mean eradication effort for five infestation area categories.[a]

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

[a]The data include 18 noxious weedy species (2 aquatic and 16 terrestrial) representing 53 separate infestations.
From Rejmánek & Pitcairn (2002).

weed infestations smaller than 1 ha is usually possible. In addition, about one third of infestations between 1 and 100 ha and a quarter of infestations between 101 and 1000 ha have been eradicated. However, the 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 13.3).

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 (Panetta *et al.* 2011). 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 a non-native 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 (Van Driesche *et al.* 2008).

Finally, it is important to stress that many large-scale invasive plant management efforts have had only moderate restoration success. One of the major reasons has been only the limited focus on revegetation with natives after invasive control or eradication (Kettenring & Adams 2011).

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

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