Pinus: a model group for unlocking the secrets of alien plant invasions?

Borovice jako klíč k záhadám rostlinných invazí?

David M. Richardson

Dedicated to Marcel Rejmánek

Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa, e-mail: rich@sun.ac.za

Richardson D. M. (2006): *Pinus*: a model group for unlocking the secrets of alien plant invasions? – Preslia 78: 375–388.

The global-scale natural experiment created by the widespread dissemination of most of the 111 species of pines (genus *Pinus*, family *Pinaceae*) has shed light on many aspects of plant invasion ecology. Introductions and the fate of alien pines have been well documented worldwide, facilitating the accurate labelling of species as "naturalized", "invasive", or "non-invasive" using objective criteria. Thirty species are naturalized and 21 are invasive. Three life-history traits that clearly separate invasive from non-invasive taxa define the inherent ability of species to disperse over long distances, win in competition against other plants, and to survive or proliferate under a range of disturbance regimes. The realization of colonization opportunities for potentially invasive pines is determined by extrinsic factors, especially those that mediate seedling establishment. Meta-analysis of many introduction/invasion events revealed the interplay of factors. Detailed studies of pine invasions have elucidated the roles of long-distance seed dispersal and propagule pressure in driving invasions. Enhanced understanding of the ecology of pine invasions has improved our ability to manage these invasions. No other speciose genus of plants has yielded important insights on so many facets of invasion ecology.

Keywords: biological invasions, invasibility, invasiveness, model genus, natural experiments, plant invasion ecology, tree invasions

Introduction

More than a century ago pioneering naturalists such as Charles Darwin and Joseph Hooker made astute contributions to the understanding of plant invasions. At that time plants thriving outside their natural range were a curiosity and not a serious environmental problem. Until the middle of the 20th century, invasions were mostly documented on a case-by-case basis; there was no theoretical framework for the systematic study of the phenomenon. The book "The ecology of invasions by animals and plants" by the British zoologist Charles Elton (1958) launched the new discipline of invasion ecology. In it, Elton proposed a series of bold generalizations to explain the invasions of many types of alien species that were increasing in importance at that time. The growth of invasion ecology was slow at first, but the field exploded in the 1980s, largely due to the rapid upsurge of invasions as a crucial environmental problem – the legacy of a wave of introductions a century or more earlier – and the need to manage some species. Concurrent with the increasing abundance of alien organisms in many areas, the dramatic increase in the modification of ecosystems, as humans cemented their domination of the planet, provided many opportunities for alien species to invade. The increased interest in the formal study of invasions coincided with a general move in ecology from working only in natural systems (where the influences of humans could be discounted and therefore did not provide noise in the study system) to the current situation where ecologists intentionally include anthropogenic factors as crucial components in most studies (Mooney 1998).

An important impetus for the increased scientific rigour in invasion ecology was the international programme on biological invasions that ran under the auspices of SCOPE (the Scientific Committee on Problems of the Environment of UNESCO) in the second half of the 1980s. The SCOPE programme set out to revisit some key assumptions and generalizations proposed in Elton's book, and to review the current status of invasions in many parts of the world. It called on some of the world's top ecologists to apply their minds to the problems and challenges relating to biological invasions. Progress in invasion ecology has, however, been hampered by a range of conceptual road blocks, and advances have been erratic. In this paper I provide a personal and selective review of perspectives on alien plant invasions that have emerged from the study of pines. I contend that pines (genus *Pinus*; family *Pinaceae*) are an exceptionally useful group of plants for this purpose.

Facets of plant invasion ecology

Invasion ecology addresses all issues relating to the introduction of species and their fate in the new region. Figure 1 shows the various major barriers that an introduced plant must overcome to become naturalized or invasive (sensu Richardson et al. 2000b, Pyšek et al. 2004). Human-aided transport allows the species to reach a region that is outside its normal dispersal range. Once there, the alien species must cope with fundamental environmental conditions, including the climate and soil. If able to deal with these conditions, the alien species can survive and grow. Many alien species move no further along the "naturalization-invasion continuum" (Richardson & Pyšek 2006) and remain in the new region for their lifespan or as long as humans re-introduce individuals of the species. Such species are termed "casual aliens" and are of little concern to biogeographers and conservationists. The next major hurdles involve reproduction and dispersal. Many plants can reproduce asexually and disperse without the help of animal partners. Most plants, however, need animal pollinators and seed dispersers (Richardson et al. 2000a). Introduced species with highly specialized pollination and seed-dispersal systems are at a disadvantage, since the required partners are much less likely to be present outside their natural ranges. Introduced species that reproduce regularly in the new region are termed "naturalized"; species that proceed no further along the naturalization-invasion continuum do not assume the status of major pests. The ability to disperse freely from introduction sites separates naturalized species from invasive species (Richardson et al. 2000b, Pyšek et al. 2004). Once able to disperse from the confines of the immediate environment to which it was introduced, an alien species can reach additional environments where it faces a new series of hurdles, but also more opportunities to invade. It is useful to separate the challenges and opportunities that await the alien in sites affected by human-caused disturbance, from those that exist in natural conditions. Many alien species are able to deal superbly with the challenges and opportunities in disturbed sites but are totally unable to penetrate habitats unmodified by human activities. These species may become "pests" or "weeds" of human-modified systems such as agricultural land. Only a few introduced species have the capacity to deal with all the aforementioned barriers as well as those in intact natural systems. They interact with indigenous species in many ways. Such interactions cause the impacts that make invasive species of most concern to conservationists, by threatening biodiversity and disrupting the functioning of ecosystems. Invasion ecologists are most interested in understanding the reasons for the proliferation of such species.

Many options are available for uncovering the importance of different barriers and the role of associated processes for different species, in different areas, or the combined effect of barriers for a particular region in shaping the success of introduced species. Much of our current understanding of invasion ecology is derived from “natural experiments” rather than formal manipulative experiments. Natural experiments are those where the experimenter does not apply manipulations but seizes opportunities where manipulations have already taken place (Richardson et al. 2004). The intentional or accidental movement of thousands of species to areas outside their natural range at different times, in different numbers and various mixtures, accompanied by a radical array of changes to every conceivable feature of the environments in which the alien species find themselves provides a natural experiment at a grand scale.

Manipulative experiments offer more power to control for extraneous factors and to focus in on selected aspects. They are practical for gaining insights for a few species, over small areas, and there is some scope for applying results to different areas or for scaling up results to gain insights at larger spatial scales. However, such experiments are generally practical only for species with short life cycles, such as herbaceous plants. Many of the world’s most serious invasive plants are, however, trees and shrubs, whose long life cycles usually make manipulative experiments untenable. Natural experiments are particularly appealing and necessary for gaining information on the ecology of tree invasions for at least the following reasons:

1. Trees are long lived; events at many stages of their life cycle affect the likelihood of recruitment, establishment and persistence, and thus the impact that the species potentially has as an invader. Some of these events are rare occurrences (occurring less frequently than the average lifespan of a plant) that have profound implications for populations over longer time scales. Manipulative experiments required to obtain sufficient data on the range of factors that potentially affect different stages in the development of the plant are virtually impossible.

2. Some tree species are very widely used by humans, and have been introduced, planted, and managed in many parts of the world, allowing them to sample a very wide range of habitats and be exposed to many extrinsic and stochastic factors that (potentially) affect their ability to reproduce and spread from sites of cultivation.

3. Because of their size and conspicuousness, and since most alien tree invasions occur in short vegetation, trees are relatively easy to map using various remote-sensing methods (e.g. historical photographs, aerial photography, satellite imagery). Accurate spatial data are thus easy to acquire, even for large geographical areas. Geographic information systems and newly developed statistical tools facilitate analysis of such data at many geographical scales. Since different processes drive invasions at different spatial scales, multi-scale assessments are crucial for uncovering the full complexity of invasions (Rouget & Richardson 2003).

4. Tree distribution and abundance, and trajectories of change can often be inferred from historical documents, cultural evidence, and a range of palaeoecological methods to provide important demographic perspectives, also from the early stages of invasions.

Many alien trees are planted over large areas. Events and conditions in different parts of the range may effect populations differently. Information from many localities greatly improves our knowledge of the factors that drive invasions. Only natural experiments can yield information at such large spatial scales.

***Pinus* as a model genus**

Pines are very useful and important for the study of alien plant invasions for at least the following reasons:

1. The genus *Pinus* contains a large number of species (about 111; Price et al. 1998). All pines are trees (some with shrubby forms) that are mostly confined to fairly harsh sites in their natural ranges. That they can grow well in much more productive environments (Richardson 1998a, Rundel & Richardson 2004) points to the crucial role of biotic influences in mediating range limits.
2. The genus displays a very wide range of ecological adaptations, for example reflected in the diversity of features for coping with fire, and for seed dispersal. These features afford different species varying inherent capacities in several core areas that are especially relevant in the context of biological invasions – e.g. the ability to survive in small populations and the facility for rapid population growth.
3. Various features of pines make them useful to humans and many species are widely planted and managed in many parts of the world. Especially important is their usefulness for plantation forestry (Richardson 1998b). The demand for products supplied by pines has driven of the rapid expansion in the area planted to pines in many parts of the world, bringing pines into contact with organisms and environments with which they have had no prior experience. Pines have been widely planted for centuries, both within and well outside their natural ranges.
4. Where pines have been planted outside their natural range, the introductions and the fate of planting are generally well documented. This makes it possible to evaluate successes and failures reasonably accurately – much more so than for most introduced species.
5. A few pine species are among the most widely used forestry species worldwide and have been planted in massive numbers in large plantations in widely separated situations where contrasting conditions has exposed them to a wide range of potential habitats.
6. Human activities in some parts of the natural range of pines have allowed some species to expand their ranges, leading to “natural invasions” that are useful for comparing with invasions in foreign regions.
7. Pines are intensively managed in many parts of the world. Silviculture is directed very largely at improving productivity of plantations, but some facets of management have potentially important implications for invasions. For example, the last decade has seen an upsurge of interest in genetic transformation of pines to improve productivity and pest resistance. This has potentially profound implications for pines as invasive species (Richardson & Petit 2006).

A recent global survey, applying objective criteria for categorizing species, found that 30 species of pines are known to be naturalized only (9 species) or invasive (21 species) (Table 1). The list includes representatives from most taxonomic and ecological groups in the genus. Several species are major invaders.

The elements of invasiveness

Pines are an excellent group for exploring the factors that separate invasive from non-invasive plant species. As discussed above, many species of pines have been introduced to many areas and widely planted, giving them opportunities over decades or longer to sample many potentially invasible habitats. Sufficient opportunity and time to invade is a crucial requirement for the objective labelling of introduced taxa as "invasive" or "non-invasive" (Richardson 2004). The clear-cut evidence for success or failure in pines is unique among large groups of closely related plants.

Rejmánek & Richardson (1996) selected 24 pine species – half of them invasive and half non-invasive. Both sets of species had experienced similar levels of dissemination and thus opportunities to invade over at least a century. They collated data on a large number of biological features of the 24 species and used discriminant analysis to determine the set of traits that best separated invasive from non-invasive species. The most robust discriminant function they found required only three factors to consistently separate the two groups in samples of species other than the 24 from which the function was derived. The factors were mean seed mass (M; in mg), minimum juvenile period (J, in yr – the time between germination and the attainment of reproductive maturity), and the mean interval between large seed crops (S, in yr). The mathematical function is: $Z = 19.77–0.51\sqrt{M} – 3.14\sqrt{J} –1.21S$, where Z (hereafter the Z score) is a measure of invasiveness.

The function accurately predicts invasiveness in other coniferous trees and even in woody angiosperms (Rejmánek et al. 2005). This has been one of the most robust, albeit surprisingly simple, predictive frameworks to emerge in plant invasion ecology. Is there something special about pines that made it easier to identify the traits associated with invasiveness than for other groups of plants? Why should the model be transferable to a much wider group of plants? I suggest that the robustness of the simple predictive framework based on pines is partly because pines have fairly simple regeneration requirements. The set of traits described above together define the inherent ability (i.e. without aid from mutualists) of species (at least woody species) to disperse over long distances, win in competition against other plants, and to survive (or proliferate) under local disturbance regimes. Overall, pines are less reliant on mutualists than are most other woody plants. Pine pollen is very abundant and very widely distributed by wind. Seeds of most pine species are dispersed by wind, and barriers to invasion through the absence of appropriate mycorrhizal fungi which existed prior to European colonization in many parts of the southern hemisphere have largely been overcome (Richardson et al. 1994, 2000a). Being unburdened with inherent constraints on colonizing ability (unlike most other plants; Richardson et al. 2000a), I suggest that invasiveness, and the potential range of pines with life-history traits encapsulated in high *Z* scores is very largely determined by biotic and abiotic limiting features. The realization of colonization opportunities for these species is determined largely by extrinsic factors (see below). Therefore, I suggest, weedy pines provide a benchmark against which to evaluate "inherent invasiveness" in other groups of plants.

The method described above provides a unique, quantitative measure of potential invasiveness. Several studies have sought mechanistic explanations for the score. For example, Grotkopp et al. (2002) conducted a detailed study of 29 pine species. They found a positive correlation between invasiveness (high *Z* scores) and the relative growth rate of seedlings, as well as Specific Leaf Area (leaf area/unit mass of leaf) and Leaf Area Ratio

Table 1. – *Pinus* species known to be naturalized or invasive (sensu Pyšek et al. 2004). Updated from Richardson & Higgins (1998) and Richardson & Rejmánek (2004). Nomenclature follows Richardson (1998a). Widely separated localities within countries are viewed as separate regions (e.g. Western Australia and South Australia; Tasmania and mainland Australia). Records for contiguous political entities within countries are scored as a single region.

Species	Naturalized	Invasive	Number of regions (naturalized/invasive)
P. banksiana	Belarus, Poland, Russia, USA (New York)	Lithuania, New Zealand	4/2
P. brutia	Australia (WA,SA)	–	1/0
P. canariensis	Australia (WA, SA)	South Africa	2/1
P. caribaea	Hawaii, Puerto Rico, Venezuela	Australia (WA,SA), New Caledonia	3/3
P. contorta	Argentina, Russia	Australia (NSW), Chile, Great Britain, Ireland, New Zealand, Sweden	2/6
P. clausa	–	USA (Florida and other SE states)	0/1
P. elliotti	New Zealand	Argentina, Australia (NSW), Brazil, Hawaii, South Africa	1/5
P. halepensis	USA (California)	Argentina, Australia (SA, Vic), Israel, New Zealand, South Africa	1/5
P. jeffreyi	Hawaii	Australia	1/1
P. kesiya	Brazil, South Africa	–	2/0
P. koraiensis	–	Japan	0/1
P. luchuensis	–	Japan (Bonin Islands)	0/1
P. monticola	Argentina	–	1/0
P. mugo	Great Britain, Lithuania, USA (New England states), Russia	New Zealand	4/1
P. muricata	Great Britain	New Zealand	1/1
P. nigra	Czech Republic, Lithuania, Russia, USA (New England states)	Australia (NSW, Vic, SA), France, Great Britain, Hungary, New Zealand, USA (Michigan)	4/6
P. patula	Hawaii, Madagascar, New Zealand	Malawi, South Africa, Zimbabwe	3/3
P. peuce	Finland, Russia, Slovakia	–	3/0
P. pinaster	La Réunion	Australia (SA, Vic, NSW, TAS), Chile, Great Britain, Hawaii, New Zealand, South Africa, Uruguay	1/8
P. pinea	Australia (NSW), Mediterranean Basin (many places, e.g. Italy), USA (Santa Cruz Island, CA)	South Africa	3/1
P. ponderosa	Russia	Argentina, Australia (SA), Chile, New Zealand	1/4
P. radiata	Great Britain	Australia (WA, SA, Qld, NSW, Vic, TAS), Chile, Hawaii, New Zealand, South Africa, Spain	1/8
P. rigida	Italy	–	1/0
P. roxburghii	South Africa	–	1/0
P. strobus	Belorussia, Bulgaria, Great Britain, Poland, Russia, Ukraine (former USSR))	Czech Republic, Germany, Hungary, New Zealand	6/4

P. sylvestris	Argentina, Ireland, USA (New England states, NE USA, New York, SE USA)	Canada (Ontario), Chile, New Zealand	3/3
P. taeda	New Zealand	Argentina, Australia (NSW, Qld), Brazil, Hawaii, South Africa	1/5
P. thunbergii	China, USA (New England states)	–	2/0
P. uncinata	New Zealand	–	1/0
P. virginiana	USA (Missouri)	–	1/0

(leaf area/unit mass of plant). Intriguingly, invasiveness was also found to be negatively associated with genome size, i.e. the amount of DNA in one basic (monoploid) set of unreplicated chromosomes (Grotkopp et al. 2002). Such findings greatly improve our ability to construct a causal network of all relevant variables contributing to plant invasiveness (Rejmánek et al. 2005). With further work, such phylogenetically controlled analyses of invasiveness will improve our ability to predict invasiveness.

What makes habitats susceptible to pine invasions?

The above section has shown that many pines are inherently well equipped to be invasive (with some better equipped than others). Invasion is, however, only manifested once an introduced pine has successfully negotiated numerous barriers in the new environment (Fig. 1). Two studies capitalized on the natural experiment of widespread pines invasions in many parts of the world to derive an improved understanding of the many factors that regulate plant invasions, and some of the interactions between these factors (Richardson & Bond 1991; Richardson et al. 1994). Some points to emerge from these studies were:

1. The invasion process is dynamic and stochastic. Some species that at one time or place are non-invasive or casual can become invasive due to climatic fluctuations (e.g. periods of above- or below-average rainfall), increases in propagule pressure (e.g. by an increase in the area planted or the time since planting), changed disturbance regimes, or the introduction of other species that might facilitate their expansion. Figure 2 gives an example of the complex web of interactions between factors at one site and underscore the huge importance of biotic interactions in facilitating or limiting invasion.

2. Disturbances that increase the supply of limiting resources create opportunities for establishment of seedlings, thus triggering invasion, provided enough seeds are available. It is difficult to identify the exact processes responsible for triggering and/or sustaining invasion in any given case because of the complex interactions involved, especially between environmental and biotic constraints. However, meta-analysis drawing on a large number of case studies is useful for cutting through the noise (Richardson et al. 2004).

3. Disturbance can both facilitate and limit invasions. Fire is often implicated, and has many roles in triggering, sustaining, or halting pine invasions. Invasions are favoured by the presence of fires in some cases but by the suppression of fires in others. Fire can facilitate invasions indirectly by reducing biotic pressures including competition and herbivory. Fires prevent invasions where they occur too frequently, killing regenerating trees before they have produced seeds.

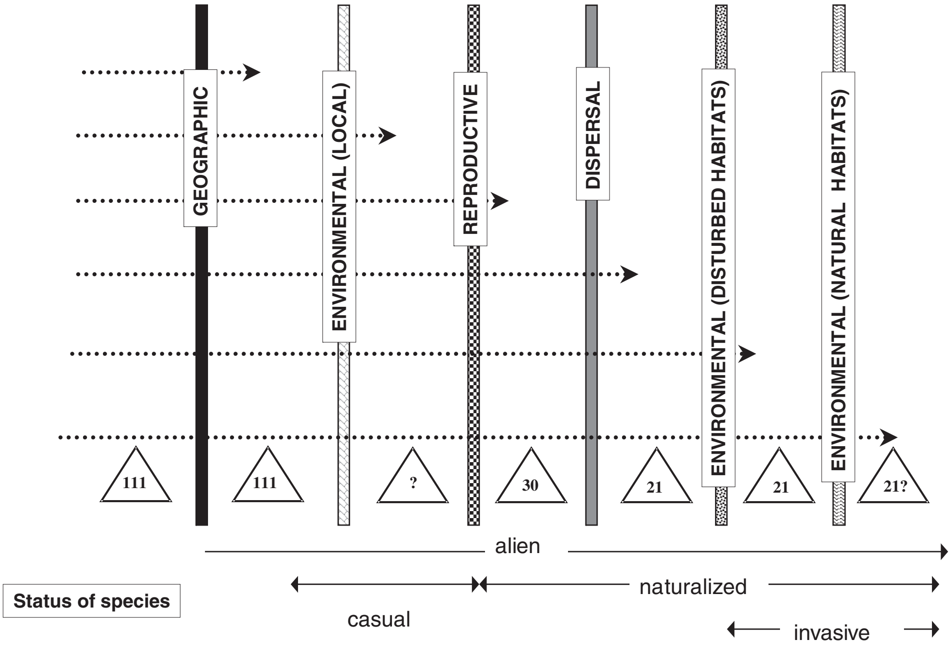

Fig. 1. – A conceptualization of the naturalization-invasion process, showing successive barriers (or invasion windows) that an introduced species has to negotiate to become naturalized or invasive (modified from Richardson et al. 2000). Numbers in triangles indicate the number of *Pinus* species: all 111 *Pinus* species have been moved by humans to areas far removed from their natural ranges; 30 species reproduce regularly in alien environments, but only 21 species are classified as invasive (see Table 1).

4. Grazing, browsing, and deforestation due to logging or fuelwood cutting are also important categories of disturbance implicated in pine invasion, especially in the Northern Hemisphere.

5. Abiotic and especially biotic processes (e.g. competition from vigorous plants and herbivory) that influence the fate of seeds and/or early seedling survival are crucial in determining the success of invasion.

6. Broad vegetation types can be ranked according to their susceptibility to invasion. Bare ground is most invasible, followed by vegetation dominated by grasses or shrubs; tree-dominated vegetation is least susceptible to invasion by pines.

7. Insights from range expansions and contractions within the natural range of pines were useful for elucidating the dynamics of invasions of pines in foreign environments, and vice versa.

Such insights proved very useful in conceptualizing the many dimensions of pine invasions and facilitated the development of a mechanistic model of pine invasions. In a series of studies by Steven Higgins and collaborators, this model framework was parameterized with data from real invasions in South African fynbos to provide a spatially-explicit model which could be tested and validated through its application in other situations (Higgins et al. 1996, 2000). To further explore the interactions between life-history traits and distur-

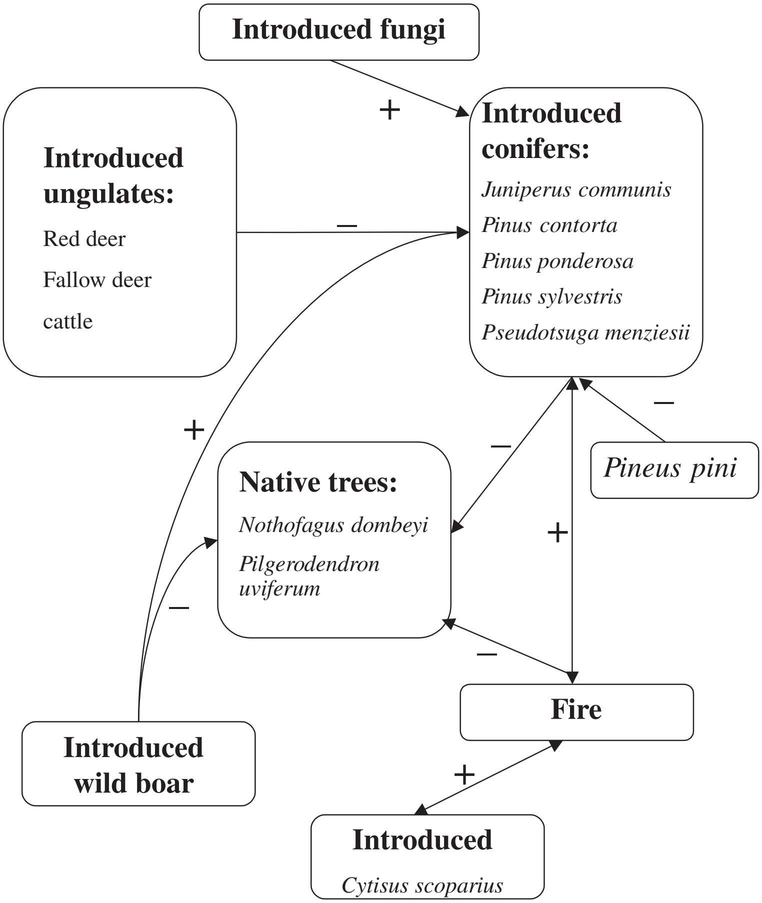

Fig. 2. – An example illustrating the complex interaction between biotic factors in mediating the fate of introduced pines. The diagram summarizes interactions between introduced pines and key components of the community at Isla Victoria (Nahuel Huapi National Park, Argentina), a large island dominated by native *Nothofagus* and *Austrocedrus* forest, with old plantations of many introduced tree species. Alien pines benefit from introduced fungi, wild boar, and fire (whose occurrence is favoured by another introduced plant). Pine regeneration is limited by introduced ungulates and the introduced insect pest *Pineus pini*. The introduced conifers have a negative impact on native tree species (modified from Simberloff et al. 2003).

bance in different vegetation types, Higgins & Richardson (1998) modelled invasions of two hypothetical pine “species” in three idealized vegetation types – grassland, shrubland, and forest. The “species” were built using sets of traits characteristic of species at the two extremes of “weediness” in the genus; the species may be termed “weedy pine” and “non-weedy pine”. The response of these two “species” to increasing levels of modification of the natural disturbance regime was studied using simulations. Results showed that: rates of invasion generally increased as disturbance levels increased; grasslands and shrublands are more open than forests to invasion; and that the weedy pine is generally much more invasive than the non-weedy pine, except in grassland at levels of disturbance high enough to exclude fire. More importantly, the simulations confirmed that interactions between environmental factors, disturbance regime, and life-history traits are crucial, often as important as the main effects. Also, some interactions produce outcomes that are counter intuitive, emphasizing the extreme complexity of spatially-explicit predictions in invasion ecology (Higgins & Richardson 1998).

The development of spatially-explicit models of pine invasion also led to the first analytical demonstration of the disproportionate importance of rare, long-distance seed dispersal events in driving population growth and spatial expansion in invasive species (Higgins & Richardson 1999). The models showed that even in single-vector dispersal systems, as in most pines, spread is the product of several dispersal processes. For pines, dispersal was best modelled when dispersal units (seeds) were divided into three "populations", each with different dispersal properties, rather than using the long-tailed seed-dispersal curve traditionally applied in such models. The fact that different processes are involved for local and for long-distance dispersal events means that central tendency varies independently of the tail of a dispersal curve. This greatly complicates the parameterization of the model from real seed-dispersal data. Insights on long-distance dispersal gleaned from work on pine invasions in fynbos have been widely applied in ecology and conservation biology (e.g. Trakhtenbrot et al. 2005).

Propagule pressure is intuitively a crucial factor in invasions: increased availability of propagules (e.g. seeds), both in total number and over time, must increase the chances of establishment, persistence, naturalization, and invasion. Put simply, it should be possible to dampen the limiting effects of various barriers to invasion (see Fig. 1) by flooding a site with propagules. Colautti et al. (2006) have suggested that propagule pressure should be a null model for biological invasions. They suggest that only once propagule pressure has been accounted for can we sensibly seek more basic explanations for differences in invasiveness between taxa and invasibility between areas – see also Lonsdale (1999) and Chytrý et al. (2005). Evidence for the role of propagule pressure has emerged from correlative studies in many parts of the world (also for pines; see above), but had never been tested analytically beyond the scale of small experimental plots. One way to do this is to determine whether the presence of dense nodes of invaders (with the highest abundance of propagules) is more influential in driving invasions than would be predicted if spread from such nodes was to occur simply according to the environmental preferences of the invader. Natural experiments of pine invasions in the fynbos also provided a superb opportunity to test the power of propagule pressure as a driver of invasive spread at the regional scale. The distribution of woody invasive species, including *Pinus pinaster*, was mapped at very fine resolution for the entire Agulhas Plain (2016 km^2 in extent) at the southern tip of Africa. The contribution of propagule pressure in structuring the distribution of *P. pinaster* in the region was determined by comparing actual (mapped) distribution patterns with distribution patterns simulated using correlative models using geology, climate, land use, and topography, and a semi-mechanistic model that incorporated propagule pressure and environmental heterogeneity. Results showed that the model incorporating propagule pressure was substantially better than those that simulated spread using only environmental preferences (Rouget & Richardson 2003). This suggests that once invasions "get going" they build up considerable momentum which can be a more potent driver of further spread than other factors known to play a role (see a further application and additional discussion in Foxcroft et al. 2004).

Although alien pines have become naturalized and invasive in many parts of the world, in a very wide range of habitat types, there are some parts of the world that seem to be resistant to pine invasions (references in Richardson & Rejmánek 2004: 327, Mortensen & Mack 2006). The failure of introduced pines to invade is especially striking in North America. Evidence assembled by Mortensen & Mack (2006) suggests that the most plausible explanation for the failure of introduced pines to invade in the USA is the low propagule pressure (small size of founder populations), but the other factors reviewed in the above sections (and interactions between them) are probably also implicated.

Towards improved management of pine invasions

Many of the results of research on pine invasions have been applied to guide management of these invasions. Most work in this area has been done in South Africa. For example, insights on the current and potential distribution of invasive pines and other woody invaders in the Cape Floristic Region have been incorporated in systematic conservation planning (Rouget et al. 2003). Invasive pines present a special challenge for management, since most of the invasive species are commercially-important forestry trees that form that foundation of South Africa's forestry enterprise. New legislation allows for such species to be grown in demarcated zones of the country under conditions specified in a permit. Recently acquired knowledge of the invasion ecology of pines facilitates the objective demarcation of such zones (Rouget et al. 2002). Our understanding of links between traits of pines and features of the environment in mediating invasiveness is also useful for considering the implications of genetic engineering of pines. The alteration of traits could make pines more invasive, but there is also considerable potential for using molecular biology to reduce invasiveness, for example by inducing reproductive sterility (Richardson & Petit 2006).

Conclusions

General answers, i.e. those that explain patterns across a wide range of systems, to the key questions in invasion ecology have been elusive. Some researchers have argued that because invasions are so complex there are no generalizations to be made, other than trivial correlations that are of limited use to managers (Crawley 1986). However, studies on pines, perhaps more so than any other plant genus, have been extremely informative, shedding much light on fundamental questions in invasion ecology. To a surprising degree, many of the insights to emerge from studies of pine invasions appear to be transferable to other plant groups. In the preface to the book "Ecology and biogeography of *Pinus*" I argued that *Pinus* seemed "…to be the model genus for exploring all sorts of fascinating ecological and evolutionary questions" (Richardson 1998a: xvi). In this paper, I hope I have shown that pines are a model group for unlocking the secrets of alien plant invasions – perhaps the *Drosophila* of plant invasion ecology? No other speciose genus of plants has yielded important insights on so many facets of invasion ecology. Of course, the work reviewed here has raised many additional questions, and much more work is needed. For example, the role of factors shown to be important mediators of pine invasions from correlative results, such as browsing and various types of disturbance that influence levels of competition with regenerating seedlings, needs to be explored in manipulative experiments. So, too, the role of mycorrhizal fungi. Advances in molecular techniques offer exciting opportunities to explore many crucial aspects of pine ecology relevant to invasions (Petit et al. 2004). The biggest challenge we face is to meld our increasing understanding of the ecology of pine invasions into practical ways of managing pines, both in alien and native contexts, in our rapidly changing world.

Acknowledgements

Many colleagues and friends have shared ideas on plant invasions with me over the past two decades. I was particularly lucky to have met Marcel Rejmánek in the late 1980s, early in my career and near the beginning of my fascination with pines. His encyclopaedic knowledge of natural history, enthusiasm, energy, and generosity have been truly inspiring and it has been a privilege to work with him. We have spent many memorable hours pondering aspects of pine ecology, in the field, laboratories, and herbaria, in various parts of the world. Others who have collaborated with me directly in research dealing with pines include William Bond, Pat Brown, Richard Cowling, Greg Forsyth, Steven Higgins, Richard Hobbs, Fred Kruger, David Le Maitre, Sue Milton, Mathieu Rouget, Brian van Wilgen and Peter Williams. Petr Pyšek is thanked for many discussions and interactions on a wide range of invasion-related projects over the years. I thank Martin Nuñez and Claire Williams for comments on a draft of the MS.

Souhrn

Přírodní experiment spočívající v rozšiřování většiny ze 111 druhů borovic (rod *Pinus*) po celém světě pomohl osvětlit mnohé aspekty invazní ekologie. Introdukce a následné zplaňování a případné šíření borovic je dobře dokumentováno, což umožňuje objektivně vymezit, které druhy jsou v jednotlivých oblastech naturalizované či invazní. Celkem 30 druhů je v různých částech světa naturalizovaných a 21 invazních. Pomocí tří vlastností, jež diferencují invazní a neinvazní druhy, je možno vymezit vrozenou schopnost některých druhů šířit se na velké vzdálenosti, uspět v kompetici s ostatními rostlinnými druhy a přežít či prosperovat v širokém rozmezí disturbančních režimů. Úspěšná kolonizace nových území závisí na vnějších faktorech, zejména těch, jež ovlivňují uchycení semenáčků. Detailní studie jednotlivých případů invazí borovic ukázují, že klíčovou roli hraje dálkové šíření semen a tlak propagulí. Lepší pochopení mechanismů invazí borovic výrazně zlepšilo možnosti jejich kontroly a managementu. Studie žádného jiného druhově bohatého rostlinného rodu neposkytlo tak významné poznatky o tolika okruzích invazní ekologie.

References

Chytrý M., Pyšek P., Tichý L., Knollová I. & Danihelka J. (2005): Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. – Preslia 77: 339–354.

Colautti R. I., Grigorovich I. A. & MacIsaac H. J. (2006): Propagule pressure: a null model for biological invasions. – Biol. Invas. 8: 1023–1037.

Crawley M. J.: (1986): The population biology of invaders. – Phil. Trans. R. Soc. Lond. B 314: 711–731.

Elton C. S. (1958). The ecology of invasions by animals and plants. – Methuen & Co., London.

Foxcroft L. C., Rouget M., Richardson D. M. & MacFadyen S. (2004): Reconstructing fifty years of *Opuntia stricta* invasion in the Kruger National Park: environmental determinants and propagule pressure. – Diversity Distrib. 10: 427–437.

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 – Amer. Natur. 159: 396–419.

Grotkopp E., Rejmánek M., Sanderson M. J. & Rost T. L. (2004): Evolution of genome size in pines (*Pinus*) and its life-history correlates: supertree analyses. – Evolution 58: 1705–1729.

Higgins S. I. & Richardson D. M. (1996): A review of models of alien plant spread. – Ecol. Model. 87: 249–265.

Higgins S. I. & Richardson D. M. (1998): Pine invasions in the Southern hemisphere: modelling interactions between organism, environment and disturbance. – Plant. Ecol. 135: 79–93.

Higgins S. I. & Richardson D. M. (1999): Predicting plant migration rates in a changing world: the role of long-distance dispersal. – Amer. Natur. 153: 464–475.

Higgins S. I., Richardson D. M. & Cowling R. M. (1996): Modelling invasive plant spread: the roles of plant-environment interactions and model structure. – Ecology 77: 2043–2054.

Higgins S. I., Richardson D. M. & Cowling R. M. (2000): Validation of a spatial simulation model of a spreading alien plant population. – J. Appl. Ecol. 38: 571–584.

Higgins S. I., Richardson D. M., Cowling R. M. & Trinder-Smith T. H. (1999): Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. – Conserv. Biol. 13: 303–313.

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

Mooney H. A. (1998): The globalization of ecological thought. – Ecology Institute, Oldendorf/Luhe.

Mortensen S. G. & Mack R. N. (2006): The fate of alien conifers in long-term plantings in the USA. – Diversity Distrib. 12: 456–466.

Petit R. J., Bialozyt R., Garnier-Géré P. & Hampe A. (2004): Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. – For. Ecol. Manage. 197: 117–137.

Price R. A., Liston A. & Strauss S. H. (1998): Phylogeny and systematics of *Pinus*. – In: Richardson D. M. (ed.), Ecology and biogeography of *Pinus*, p. 49–68, Cambridge Univ. Press, Cambridge.

Pyšek P., Richardson D. M., Rejmánek M., Webster G., Williamson M. & Kirschner J. (2004): Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. – Taxon 53: 131–143.

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

Rejmánek M., Richardson D. M., Higgins S. I., Pitcairn M. J. & Grotkopp E. (2005): Ecology of invasive plants: state of the art. – In: Mooney H. A., Mack R. N., Mc Neely J. A., Neville L., Schei P. J. & Waage J. (eds.), Invasive alien species: A new synthesis, p. 104–161, Island Press, Washington, DC.

Richardson D. M. (ed.) (1998a): Ecology and biogeography of *Pinus*. – Cambridge Univ. Press, Cambridge.

Richardson D. M. (1998b): Forestry trees as invasive aliens. – Conserv. Biol. 12: 18–26.

Richardson D. M. (2004): Plant invasion ecology – dispatches from the front line. – Diversity Distrib. 10: 315–319.

Richardson D. M., Allsopp N., D'Antonio C. M., Milton S. J. & Rejmánek M. (2000a): Plant invasions: The role of mutualisms. – Biol. Rev. 75: 65–93.

Richardson D. M. & Bond W. J. (1991): Determinants of plant distribution: Evidence from pine invasions. – Amer. Natur. 137: 639–668.

Richardson D. M. & Higgins S. I. (1998): Pines as invaders in the southern hemisphere. – In: Richardson D. M. (ed.), Ecology and biogeography of *Pinus,* p. 450–473, Cambridge Univ. Press, Cambridge.

Richardson D. M. & Petit R. (2006): Pines as invasive aliens: Outlook on transgenic conifers in the Southern Hemisphere. – In: Williams C. (ed.), Landscapes, genomics and transgenic conifer forests, p. 169–188, Springer, Dordrecht.

Richardson D. M. & Pyšek P. (2006): Plant invasions: Merging the concepts of species invasiveness and community invasibility. – Progr. Phys. Geogr. 30: 409–431.

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

Richardson D. M. & Rejmánek M. (2004): Invasive conifers: A global survey and predictive framework. – Diversity Distrib. 10: 321–331.

Richardson D. M., Rouget M. & Rejmánek M. (2004): Using natural experiments in the study of alien tree invasions: Opportunities and limitations. – In: Gordon M. S. & Bartol S. M. (eds), Experimental approaches to conservation biology, p. 180–201, Univ. California Press, Berkeley.

Richardson D. M., Williams P. A. & Hobbs R. J. (1994): Pine invasions in the Southern Hemisphere: determinants of spread and invadability. – J. Biogeogr. 21: 511–527.

Rouget M. & Richardson D. M. (2003): Inferring process from pattern in alien plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. – Amer. Natur. 162: 713–724.

Rouget M., Richardson D. M., Cowling R. M., Lloyd J. W. & Lombard A. T. (2003): Current patterns of habitat transformation and future threats to biodiversity in the Cape Floristic Region, South Africa. – Biol. Conserv. 112: 63–85.

Rouget M., Richardson D. M., Nel J. A. & van Wilgen B. W. (2002): Commercially-important trees as invasive aliens: Towards spatially explicit risk assessment at a national scale. – Biol. Invas. 4: 397–412.

Rundel P. W. & Richardson D. M. (2004): Pines. – In: Burley J., Evans J. & Youngquist J. A. (eds.), Encyclopedia of forest sciences. Vol. 3, p. 1430–1441, Elsevier, Oxford.

Simberloff D., Relva M. A. & Nuñez M. (2003): Introduced species and management of a *Nothofagus*/*Austrocedrus* forest. – Environm. Manage. 31: 263–275.

Trakhtenbrot A., Nathan R., Perry G. & Richardson D. M. (2005). The importance of long-distance dispersal in biodiversity conservation. – Diversity Distrib. 11: 173–181.

Received 6 June 2006
Revision received 2 August 2006
Accepted 2 August 2006