

## Alien tree invasions in South Africa: pulling together pieces of the puzzle from natural experiments

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**Summary** Alien trees have been introduced and widely planted in South Africa since the 17th century. Self-sown stands of alien trees cover very large areas of natural and semi-natural vegetation in many parts of the country.

The configuration of alien tree plantings – many species planted in a wide range of habitats, subject to many types, intensities and combinations of disturbance – provides a natural experiment with considerable potential for deriving useful insights on the roles of different factors in driving invasions.

This paper focuses on approaches used for identifying elements of invasiveness, inferring process from pattern, and deriving spatially-explicit explanation and predictions

**Keywords** Biological invasions, correlative models, *Eucalyptus*, mechanistic models, *Metrosideros excelsa*, *Pinus*, quasi-mechanistic models, tree invasions.

### INTRODUCTION

The study of the dynamics of long-lived organisms like trees presents special challenges to ecologists. Events at many stages of a tree's life cycle affect the likelihood of recruitment, establishment, persistence and reproduction. Some events are rare (occurring less frequently than the average lifespan of an individual tree), but may have profound implications for populations over longer time scales. Some events affect only a part of the population in a given area, but may shed light on the dynamics of the species over larger parts of its range. This paper deals with the challenges associated with gaining an understanding of invasive alien trees.

Most of the body of theory on invasion ecology has emerged from the study of typical 'weedy' or 'ruderal' organisms, i.e. short-lived species associated with disturbed sites. Trees are generally not considered typical weedy plants, but many species are invasive aliens in many parts of the world. Among the most invasive/best studied genera are: *Acacia* (Fabaceae), *Ailanthus* (Simaroubaceae), *Elaeagnus* (Oleaceae), *Pinus* (Pinaceae), *Melaleuca* (Myrtaceae), *Miconia* (Melastomataceae), *Mimosa* (Fabaceae), *Myrica* (Myricaceae), *Pittosporum* (Pittosporaceae), *Robinia*

(Fabaceae), *Prosopis* (Fabaceae), *Sapium* (Euphorbiaceae), *Schinus* (Anacardiaceae) and *Tamarix* (Tamaricaceae). Most of this taxonomically disparate assemblage are useful to humans and have therefore been moved around the world and cultivated to varying degrees. Partly because of their large size, but also due to special features such as the ability to fix atmospheric nitrogen (many legumes), those trees that have become important invasive species have had disproportionately large impacts, e.g. *Acacia* and *Pinus* species in South Africa, *Melaleuca quinquinerva* in Florida, *Miconia calvescens* in Tahiti, *Mimosa pigra* in northern Australia, *Myrica faya* in Hawaii, *Prosopis* species in arid parts of South Africa, and *Schinus terebinthifolius* and *Tamarix* species in parts of North America.

Most of the above mentioned tree taxa are relatively long lived, and ecologists need to use various short cuts to obtain sufficient information to understand the dynamics of invasive trees. Managers generally use only snippets of information on the dynamics of invading trees on which to base their planning and management actions. South Africa, probably invaded by alien trees to a greater extent than any other part of the world, has many 'natural experiments' in place with considerable scope for deriving a more comprehensive understanding of the many factors that drive alien tree invasions.

Scientists in many disciplines rely on 'natural experiments' (i.e., where the experimenter does not apply manipulations but selects sites or other entities where manipulations have already taken place) for deriving insights that could not be obtained from more formal (i.e., laboratory or field) experiments for ethical and/or practical reasons. Natural experiments are a rich source of knowledge in ecology. Much of our understanding of biological invasions is based on insights from natural experiments, and only recently have manipulative experiments been applied to address certain aspects of invasions.

Natural experiments are particularly appealing (and necessary) for gaining information on tree invasions for at least the following reasons:

- Trees are long-lived organisms and manipulative experiments required to obtain sufficient data on

the range of factors that potentially affect different stages in the development of the plant tend towards the impossible.

- Some species of trees 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 very many extrinsic factors that (potentially) mediate the ability of these species to reproduce and spread from sites of cultivation.
- 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. Accurate spatial data for very large geographical areas is thus relatively easy to acquire. GIS and geostatistical tools facilitate analysis of such data at many geographical scales.
- Tree distribution/abundance and trajectories of change can often be inferred from historical documents, cultural evidence and a range of paleoecological methods to provide important demographic perspectives, also from the early stages of invasions.
- Many alien trees are planted over large areas. Events and conditions at different parts of the advective range may affect populations in different ways. Information from many localities greatly improves our knowledge of the factors that drive invasions. Only natural experiments can yield information at such large geographical and spatial scales.

This paper presents a broad overview of some approaches taken in South Africa to improve our understanding of such central concepts such as propagule pressure, and for inferring process from pattern using different methods. Further details are given in Richardson *et al.* (in press).

#### INFERRING PROCESS FROM PATTERN

**Propagule pressure** Propagule pressure is an intuitive determinant of invasibility – the greater the number and higher the rate of introductions, the better the chance of establishment and invasion. A quantitative description of its role in invasions has, however, remained illusive. Observed patterns of invasion (or non-invasion) of introduced Myrtaceae in South Africa provide intriguing opportunities for exploring the role of propagule pressure.

About 100 species of *Eucalyptus* have been introduced to South Africa where they have been cultivated at different levels of intensity in commercial plantations, arboreta and as amenity plantings for a variety of uses. Surprisingly, given their abundant cultivation

and long residence time in the country, eucalypts have fared poorly as invaders, for example compared with pines that have had similar opportunities to invade. Unlike for the pines, we have been unsuccessful in separating the few invasive species of eucalypts from non-invasive congeners based on any life-history traits, or any other feature of biology. However, if we regress the number of records of spontaneous regeneration (from published sources and an intensive review of herbarium specimens) against a crude index of propagule pressure (the number of plantations), we see that the extent of spontaneous regeneration (naturalisation/invasion) is positively correlated with the number of records of planting (Rejmánek *et al.* in press). A very similar pattern is emerging from a global review of the extent of spontaneous regeneration (from published reports, herbarium specimens and our observations in many parts of the world for over a decade) for eucalypts introduced to many countries (our primary data base contains information on 62 eucalypt species planted outside their natural range in Australia, South Africa, California, Florida, New Zealand, the Mediterranean Basin and Hawaii; M. Rejmánek and D.M. Richardson, unpublished data).

Much work remains to be done to explain why eucalypts, so spectacularly successful in a wide range of habitats in their native range in Australia, and so widely transplanted across the world, perform so poorly as invaders outside Australia. The fact that propagule pressure is clearly an important driver of invasions (much more so than with pines) suggests that the answer lies in the specialised regeneration requirements of eucalypts. Natural experiments can thus identify crucial questions that can direct manipulative experiments.

Another myrtaceous tree, *Metrosideros excelsa*, which is widely planted as an ornamental tree and hedge plant in the Western Cape of South Africa, provided the opportunity to explore the role of propagule pressure more quantitatively. This species is highly invasive in one small region of the Cape Floristic Region. We mapped all source trees and the entire invasive population in an area of approximately 5 km<sup>2</sup>. We could distinguish, on the basis of native indicator plant species, two distinct habitat types which displayed different invasion patterns – one of these (the 'wet' habitat) was clearly much more suitable for establishment of *M. excelsa* than the other (shown by the much greater number of seedlings). Regressions of the number of *Metrosideros* saplings on a potential seed rain index (PSRI) revealed that 'wet' habitats are almost exactly 10 times more invasible than 'dry' habitats (respective regression coefficients are 16.36 and 1.59) (Rejmánek *et al.* in press).

**Getting spatial** Invasions are spatial phenomena, and plant invasion ecology must strive for spatially-explicit explanations and predictions. Spatial dimensions can be effectively added to predictive models using information from natural experiments in various ways. ‘Correlative’, ‘quasi-mechanistic’ and ‘mechanistic’ approaches are feasible, and offer useful insights, in different situations.

*Correlative models* Many studies that address the determinants of plant distribution use correlative methods in which environmental factors (climate, topography, vegetation type, etc) are assumed to be important drivers of distribution. Invasive spread from plantations of alien trees into natural ecosystems provides wonderful opportunities to investigate the environmental correlates of invasion success. Each invasive tree or stand can be considered as a replicate. If ‘treatments’ occur over a large area relative to the region under consideration, we can assume that the whole range of environmental conditions has been sampled. Using this approach we have studied the determinants of invasive alien trees as different spatial scales in South Africa. We have used regression-tree analysis as this technique is highly suited to the study of distributions and yields better estimates than other classical methods. Regression trees revealed that soil pH and vegetation structure were the key determinants of invasive pine distribution at the landscape scale ( $10^3$  ha) in the Kango Valley in the Western Cape (Figure 1) (Rouget *et al.* 2001). A study using a similar approach for the entire Cape Floristic Region ( $10^7$  ha) revealed a different suite of factors (mainly vegetation type and climatic factors) to be the main determinants of distribution of invasive trees (Figure 1) (Rouget *et al.* in press). Correlative methods such as these are useful for using with GIS to produce layers of ‘potential distribution’, which indicate other areas which share the features found to best discriminate invaded from non-invaded sites. For example, for the Cape Floristic Region, such an approach suggests that 30% of the area of remaining untransformed land in the region is invisable.

*‘Quasi-mechanistic’ models* Correlative approaches assume that plants and environment are in equilibrium. This is problematic where introductions and/or invasions are relatively recent, since such species will have had insufficient time to sample all potentially suitable sites. ‘Quasi-mechanistic’ models, which retain biological attributes but also utilise the correlative approach, are more appropriate in some situations. For the Agulhas Plain ( $2160 \text{ km}^2$ ) in the Cape Floristic Region, we used very detailed maps of the current distribution of 36 alien woody plant species to explore determinants of distribution and

spread rates of invasive species. Correlative models proved of little value in this situation because of the relatively homogenous environment and the recent invasion history of many species.

Our model starts by considering only propagule pressure, by exploring the relationship between the distance to source populations (the densest/oldest stands) as a predictor of the distribution and abundance of alien species. We then analyse the role of environmental factors in explaining the residuals between actual and modelled distributions for all species based on propagule pressure. Spread rate was generally higher in natural areas and lower in cultivated land. Topography was also a key factor for adjusting the spread rate. In the case of *Pinus pinaster*, the model accurately predicted 85% of the presence/absence and 70% of the species density.

Such models are potentially very attractive as they bridge the gap between the complexity of pure mechanistic models and the lack of biological attributes in correlative models. Quasi-mechanistic models are relatively simple to compute and offer reasonable estimates of the invasion process because the key biological attribute – dispersal – is accounted for. Such models highlight the importance of plant-environment interactions in determining the trajectory of invasions.

*Mechanistic models* Over small spatial scales ( $10^0$ – $10^1$  ha), biological attributes of the invader are of overriding importance and need to be included to model distribution and spread rates. At this scale, models need to simulate the entire life cycle of the invasive plant, and thus mechanistic models become more tractable. This approach integrates space, ecological processes and stochasticity into a single framework. Mechanistic models can also trace the spatial locations of modelling entities so that the model predictions can be linked to a GIS for further analysis. Importantly, these models can be parameterised, calibrated and validated using information from natural experiments. Individual-based simulation models were built to simulate the spread of alien pine trees from established plantations in natural fynbos ecosystems (Higgins and Richardson 1998). The mean spread rate was about  $10 \text{ m y}^{-1}$ . Results show strong interactions among the ecological processes investigated and emphasised the importance of dispersal ability.

Using information from natural experiments in a variety of ways to model spatial patterns of alien plant invasions has greatly improved our understanding of plant-environment interactions in the invasion process. Most of the studies on the distribution of plant species (including invasive alien plants) have focused on the ecological process and environmental correlates

of importance. However, the different approaches outlined above suggest that the spatial scale strongly influences the type of models that can be used, and the outcome of the modelling. Correlative models are well suited for application at the scale of landscapes, regions or countries, but lose their predictive power at smaller spatial scales. Mechanistic models become more tractable and appropriate at smaller spatial scales (Rouget and Richardson, in press). Insights derived at one spatial scale are usually NOT applicable at larger spatial scales. In our studies, both correlative and mechanistic models yielded non-consistent results when the resolution of the spatial grain was changed. This is partly because of the different processes that operate at different scales, but also due to features of the accuracy and precision of available data. Further studies are needed to determine the thresholds of applicability of the different models.

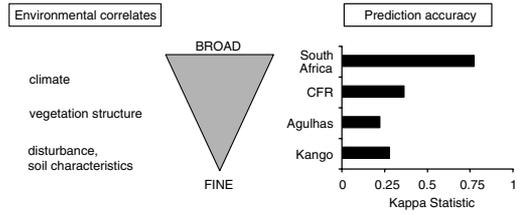
These studies show that the recent development of new computational techniques, together with the increased availability of geo-referenced data in Geographic Information Systems, have paved the way for new research on ways to better utilise the many opportunities afforded by natural experiments.

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**Figure 1.** Effects of spatial scale on predicting the distribution of invasive alien trees in South Africa. The main environmental factors used are shown on the left, and the accuracy of the modelling prediction on the right. Correlative models were developed for South Africa (1 250 000 km<sup>2</sup>), the Cape Floristic Region (CFR; 88 000 km<sup>2</sup>), the Agulhas Plain (2160 km<sup>2</sup>), and the Kango Valley (25 km<sup>2</sup>). The Kappa statistic compares the agreement against that which might be expected by chance. Kappa ranges from -1 (complete disagreement) through 0 (no agreement above that expected by chance) to 1 (perfect agreement) (Richardson *et al.* in press).

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