



Residence time and potential range: crucial considerations in modelling plant invasions

John R. U. Wilson¹, David M. Richardson^{1*}, Mathieu Rouget², Şerban Procheş¹, Mao A. Amis¹, Lesley Henderson³ and Wilfried Thuiller⁴

¹Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa; ²South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa; ³ARC-Plant Protection Research Institute, c/o South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa; and ⁴Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France

ABSTRACT

A prime aim of invasion biology is to predict which species will become invasive, but retrospective analyses have so far failed to develop robust generalizations. This is because many biological, environmental, and anthropogenic factors interact to determine the distribution of invasive species. However, in this paper we also argue that many analyses of invasiveness have been flawed by not considering several fundamental issues: (1) the range size of an invasive species depends on how much time it has had to spread (its residence time); (2) the range size and spread rate are mediated by the total extent of suitable (i.e. potentially invasible) habitat; and (3) the range size and spread rate depend on the frequency and intensity of introductions (propagule pressure), the position of founder populations in relation to the potential range, and the spatial distribution of the potential range. We explored these considerations using a large set of invasive alien plant species in South Africa for which accurate distribution data and other relevant information were available.

Species introduced earlier and those with larger potential ranges had larger current range sizes, but we found no significant effect of the spatial distribution of potential ranges on current range sizes, and data on propagule pressure were largely unavailable. However, crucially, we showed that: (1) including residence time and potential range always significantly increases the explanatory power of the models; and (2) residence time and potential range can affect which factors emerge as significant determinants of invasiveness. Therefore, analyses not including potential range and residence time can come to misleading conclusions. When these factors were taken into account, we found that nitrogen-fixing plants and plants invading arid regions have spread faster than other species, but these results were phylogenetically constrained. We also show that, when analysed in the context of residence time and potential range, variation in range size among invasive species is implicitly due to variation in spread rates, and, that by explicitly assuming a particular model of spread, it is possible to estimate changes in the rates of plant invasions through time.

We believe that invasion biology can develop generalizations that are useful for management, but only in the context of a suitable null model.

Keywords

Biological invasions, range size, invasive species, rates of spread, residence time, South Africa.

*Corresponding author. David M. Richardson, Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa.
Tel.: +27 21 8083711; Fax: +27 21 8082995;
E-mail: rich@sun.ac.za

INTRODUCTION

Many factors have been postulated to influence invasiveness (the extent to which an introduced species is able to overcome various biotic and abiotic barriers, establish, proliferate, and disperse in a new environment) and invasibility (the susceptibility of an assemblage, ecosystem, or region to invasion by introduced species).

Many hypotheses have been tested, but usually using only a few species or in particular settings, making it difficult to draw general conclusions. Different approaches to the problem have yielded different levels of success in explaining patterns of invasiveness and invasibility (review in Richardson & Pyšek, 2006). At broad spatial scales, we can explain the species richness of invasive alien plants by invoking human-disturbance and

environmental factors (Thuiller *et al.*, 2006) and/or species richness of native plants (Stohlgren *et al.*, 2003; Richardson *et al.*, 2005; Stark *et al.*, 2006). Similarly, recent studies of invasiveness have highlighted the importance of propagule pressure (i.e. the amount, frequency, and timing of reproductive material reaching a new area and disseminating within it) (Lockwood *et al.*, 2005).

We concur with Colautti *et al.* (2006) that propagule pressure must be viewed as a null model for explaining differences in invasion success among sets of introduced species. For plants, the length of time that a species has been in its introduced range ('residence time') is a particularly important factor (Rejmánek, 2000; Pyšek *et al.*, 2004b; Castro *et al.*, 2005; Hamilton *et al.*, 2005). Residence time integrates a suite of factors (some of them directly affecting propagule pressure) that potentially affect the success of an alien species, including the likelihood of an alien species becoming naturalized, occupying a large adventive range, and overcoming a lag phase (Richardson & Pyšek, 2006). When trying to understand the importance of biological traits and anthropogenic factors in determining invasiveness, residence time is an obvious confounding factor. Strangely, the significance of this factor has been ignored in many analyses (but see Castro *et al.*, 2005 and Hamilton *et al.*, 2005).

Just as propagule pressure 'should form the basis of a null model for invasion studies' (Colautti *et al.*, 2006), we argue that any attempt to explain the differential levels of 'success' of invasive species (e.g. using area invaded) must, intuitively, consider the effects of residence time and potential range. The observed range of a spreading invasive species will increase with time until it reaches all areas that are suitable [or rather until it occupies a distribution of the suitable sites, with the suitability of sites fluctuating with climate and the occupancy of those sites changing with extinction-colonization dynamics (Gaston, 2003)]. The observed range of an invasive species will also be highly dependent on the size of the climatically suitable range and the spatial configuration of that range. If suitable sites are widely separated, it should take longer for a species to fill its range. When these factors are not taken into consideration, comparative studies run the risk of either missing important explanatory variables or coming to misleading conclusions (Fig. 1).

We test the importance of this idea using a set of invasive alien plant species in South Africa. South Africa is an interesting place to study invasive plants because: there are good data on current distributions; there are several types of biomes and climatic conditions; there is a long and fairly well-documented history of introductions (Fig. 2); the introduced plant species vary markedly in the size and the spatial arrangement of their potential range (Rouget *et al.*, 2004); and plants have been introduced, used, and disseminated for many reasons and at different intensities (Henderson, 2001). We drew on a large database of invasive plant species distributions to explore which factors determine the broadscale distribution of the major invasive plants in South Africa. The aim was neither to provide a predictive framework for all species nor to completely evaluate the myriad of factors used to explain invasiveness. Instead, we want to assess the importance of 'null' factors (e.g. potential

range and residence time) that may confound (and may have confounded) attempts to explore the role of biotic and social factors in plant invasions.

By comparing species on the basis of how quickly they have filled up their potential ranges, we are implicitly comparing rates of spread. If (in addition to having information on the potential range, residence time, and current range of each species) we assume a particular model of spread, it may be possible to estimate the rate of spread for each species. Our second aim was to examine the estimates of spread rates across the same set of species. We focused on logistic growth in the number of occupied quarter-degree grid cells, as logistic growth has been shown to be an appropriate model for data on plant invasions at a coarse scale (Salisbury, 1961; Forcella, 1985; Shigesada & Kawasaki, 1997; Barney, 2006). Our expectation was that the rate of spread of invasive species has increased over the past two to three centuries as human populations have grown and land has become increasingly degraded and invaded.

METHODS

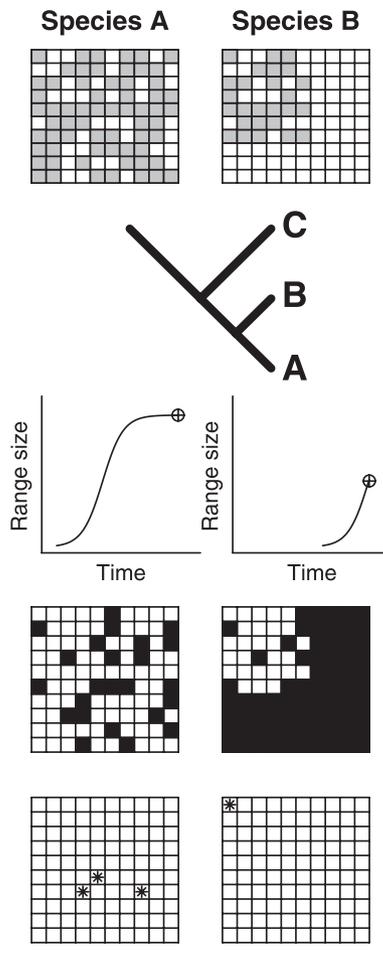
SAPIA database

Data on the distribution of invasive alien plants in South Africa were compiled in the Southern African Plant Invaders Atlas (SAPIA) (Henderson, 2001). This database contains presence and absence records for over 500 species at a resolution of a quarter degree (one quarter-degree grid cell (QDGC) \approx 630–710 km² at the latitude of South Africa). There are 2014 QDGCs in South Africa, Lesotho, and Swaziland, but we excluded the 70 QDGCs in Lesotho and Swaziland as these countries have been less well surveyed.

Only alien species invading natural or seminatural habitats are listed in SAPIA (species invading only agricultural lands and urban systems are not included). We considered all species in SAPIA to be naturalized or invasive (Pyšek *et al.*, 2004a). SAPIA is biased in favour of woody species, mainly for reasons of field identification, and invasive alien grasses and other herbaceous taxa are underrepresented. This is not a major problem, as most of the invasive alien plants that have had substantial impacts in South Africa are woody species (Richardson & van Wilgen, 2004), and these species are well covered in SAPIA. Also, we make no claims that our findings necessarily apply to the full suite of invasive plants in South Africa.

Estimating climatically suitable potential range

Matching the climate of the native range of a species to non-native areas has provided very valuable information as to potential risks of establishment and spread. However, such an approach assumes that the same interactions between biotic factors and climatic factors that limit range size in the native range operate in the introduced range. This assumption is highly suspect given that invasive species are a particular subset of non-native species, and invasive species are often much more abundant in their introduced range than their native range (i.e. it



The invasive alien plant species A is more widely distributed than the invasive alien plant species B (presence is denoted by shaded cells).

Species A and species B are sister taxa, and share many traits, except that species A is bird dispersed. Therefore, a researcher may hypothesize that seed dispersal by birds, in this example, is a **trait** that promotes **invasiveness**

But, species A may have been introduced earlier than species B, i.e. have a different **residence time**, and therefore species A has simply had more time to reach potentially invasible sites ...

... or more sites may be potentially suitable for species A, i.e. species A has a larger **potential range** ...

... or species A could have been introduced more times and/or in greater numbers (**propagule pressure**), or to sites closer to the centre of the species' potential range (**position of founder population**), or have a more contiguous potential range (**spatial distribution of potential range**).

Figure 1 Factors confounding the determination of traits associated with invasiveness in alien plants. Any of these factors on their own could explain the greater adventive range of species A. The basic concepts are scale independent, but the likely contribution of each factor will vary at different spatial scales, particularly in relation to dispersal rates, the stage of invasion, and the criterion used to define invasiveness (distribution based on presence/absence here, and local abundance in other cases).

is clear that the interactions between biotic factors and climatic factors in the native range are different in the introduced range). If a species has had sufficient time to sample a wide variety of habitats in its introduced range, at least for the purposes of this work, it is preferable to estimate potential range based on current

distribution in the introduced range. This does not assume, however, that the species are in 'equilibrium' with the environment. If the species used in the analysis had not had sufficient time to sample a representative range of climates, then there may be a relationship between residence time and potential range size (which did not exist, see Results).

There are different niche-based models that can be used to estimate the potential range of a species based on a set of environmental variables (e.g. climatic (Guisan & Thuiller, 2005)). In this study, we drew on previous work that estimated the potential range of invasive plants from their current distribution in South Africa (Rouget *et al.*, 2004). Three climatic indices were calculated from a principal component analysis on seven climatic variables (growth days per year, minimum soil water stress, frost duration, growth temperature, mean temperature of the hottest month, mean temperature of the coldest month, and mean annual precipitation; see Rouget *et al.*, 2004 for further details). Oblique ellipse models were then fitted to the current distribution of each species, and Mahalanobis distances were calculated (Farber & Kadmon, 2003; Rouget *et al.*, 2004). Mahalanobis distances indicate how 'far' the climate at a given location is from optimal conditions. As in Rouget *et al.* (2004), 'climatic suitability' was defined by a Mahalanobis distance of 2.5 or less.

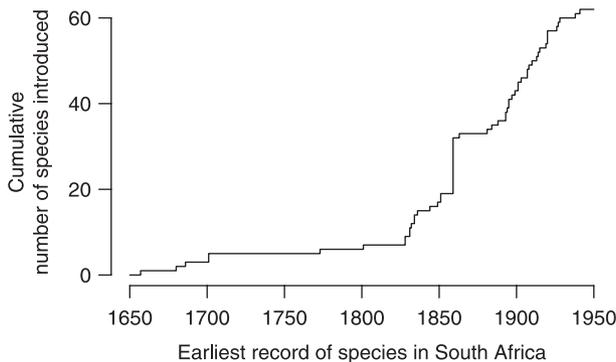


Figure 2 Dates of introduction for the 62 species used in the analysis. A detailed list of plants in the Cape Town Botanic Garden was compiled by McGibbon in 1858; and this date is the earliest known presence in South Africa for 11 of the species.

Testing the effect of the spatial configuration of the potential range

Six measures were used to define the spatial configuration of the potential range. The simplest measure was calculated by drawing a box with the edges defined by the maximum and minimum latitudes and longitudes of a species' potential range. The number of climatically suitable QDGCs was then divided by the area of the box and was log transformed. This gave an idea of how compact the potential ranges were, although no correction for box size was made. The second measure was the ratio of perimeter to area, equivalent to the average number of unsuitable grid cells that border a suitable grid cell. The third measure was the join count statistic (Dale *et al.*, 2002). A distribution of expected perimeter to area ratio values was calculated for each species by randomly sampling South African QDGCs a thousand times, the size of each sample being determined by the species' potential range. The join count statistic for each species was then calculated as (observed – mean of expected)/(standard deviation of expected). The final measures were based on the distance between grid cells. The Euclidian distance between each pair of climatically suitable grid cells was calculated and a distribution of distances was formed, from which the mean, coefficient of variation, and skewness were calculated. The ability of these statistics to explain the observed range sizes was explored.

Species selection

Our analysis required species for which we could obtain a reliable spatial distribution, a reliable first record of occurrence in South Africa, and an estimate of potential range size. Because we estimated a species' potential range size based on its current distribution in South Africa, our study was limited to those species that have had sufficient time to sample different climates in South Africa. Therefore, our analysis focused on 'major invaders' (Nel *et al.*, 2004), that are recorded in more than 20 QDGCs, and that have been in the country for more than 50 years. We also excluded taxa that are difficult to identify to species level in the field (e.g. *Casuarina* and some *Eucalyptus* species) and aquatic species (as their distribution is dependent on the presence of water much more than on broadscale climatic factors).

Sixty-two species were suitable for the analysis. The earliest date on which a given species was recorded in South Africa was obtained from the literature and specimen records in the Pretoria National Herbarium. For each species, we explored a large list of factors that have been evoked at some point to explain invasiveness: habitat (biome) invaded; dispersal mechanism; human use; seed production; seed size; presence and type of asexual reproduction; location of native range; age at first sexual reproduction; and nitrogen fixation (Dean *et al.*, 1986; Richardson *et al.*, 1997; Henderson, 1998; Henderson, 2001).

Analysis

All analyses were conducted in the open source R software version 2.10 (R Development Core Team, 2005).

The response variable was the number of QDGCs occupied by the species in 2000. This variable was log transformed, as the number of QDGCs occupied was mostly a small fraction of the area of South Africa (the most widespread species, *Opuntia ficus-indica*, was found in 43% of South African QDGCs, while the rest were present in fewer than 30%).

Dates of introduction were converted to residence times and were log transformed to create a more even spread of dates, so that each datum would have a more similar influence in the analysis. The effect of potential range on range size was analysed using the logit-transformed percentages of South African QDGCs that were estimated to be climatically suitable (i.e. potential range). Because the estimated climatically suitable potential range was calculated from the current range, and current range is expected to vary with residence time, the aim of the first analysis was to check whether there was a correlation between potential range and residence time. Such a relationship could be explained by recently introduced species having smaller potential ranges, or, perhaps more likely, that current range size (and ergo residence time) biases the estimation of potential range size.

The different measures of spatial arrangement were then tested to see how much extra variation was explained when compared with a basic model including only residence time and potential range. As none of the spatial variables had a statistically significant effect (or explained much variation), these variables were not included in the model.

Four scenarios were then created to approximate different approaches to the comparative analysis. The first was simply testing the individual effect of biogeographical, anthropogenic, and biotic variables on current range size. The second and third included residence time or potential range in the analysis, and the final scenario tested the significance of the proposed variables in the context of both residence time and potential range. In each case, the maximal model, including all interactions, was fitted, and terms were dropped in a stepwise manner. The *P*-value obtained by dropping each biogeographical, anthropogenic, and biotic variable is presented.

Within each scenario the false detection rate test (*fdr* option, *p.adjust* function in R) was used to correct for multiple comparisons. The uncorrected significance values for each variable (as would have been produced if each variable were considered in isolation) are presented in Table 1, with those that were significant at a level of $\alpha = 0.05$ after correction (as would have been produced by an evaluation of several variables) highlighted.

If species with an observed trait share evolutionary history, then species may not be independent with respect to that trait. As yet, there is no phylogeny available that covers all the species in the data set. Because an ultrametric tree could not be created, some of the more sophisticated methods for phylogenetic analyses could not be used. Therefore, to test for phylogenetic constraints, sister clade comparisons were made. For each clade (regardless of clade age) that contained species with and without a given trait, the residual deviances from the model were compared. A sign test was used to determine whether the direction of change in the residuals of the model at the branching of informative clades was consistent. For example, the closest relative in the phylogeny

Table 1 Residence time and potential range are vital components in modelling plant invasions. We considered four modelling scenarios: (1) current range size ~ residence time (rt) + potential range (pr) + variable (var); (2) range ~ rt + var; (3) range ~ pr + var; and (4) range ~ variable. For each variable for each scenario, the adjusted r^2 of that model is presented. In addition, ANOVAs were used to compare linear regression models with and without each biogeographical, anthropogenic or biotic variable, i.e. range ~ pr + rt + var was compared to range ~ pr + rt. The probability that a variable significantly improved the fit of the model is shown. For variables that are factors with two levels, the number of species in each factor level is shown, as is the direction of the relationship: a (+) under bird dispersal indicates that bird-dispersed species were more widely distributed than non-bird dispersed species. Effects that were significant after correcting for multiple comparisons are shown in bold (false detection rate test conducted separately for each scenario, $P < 0.05$). There are two points to note: (1) including residence time and potential range always significantly increases the fit of the models (ANOVA of models with and without residence time or potential range, $P < 0.05$; the r^2 values shown increase from right to left, the trends are similar for AIC and log likelihoods); and (2) potential range and residence time can affect which anthropogenic and biological variables are found to significantly influence invasiveness (the P -values change between columns to the extent that the statistical significance of factors and/or the direction of the relationship changes)

Biological/ environmental/ or anthropogenic factor used to explain invasiveness		No. of species		Four comparative analysis scenarios							
				r^2 of model				P -value that variable significantly improves the fit of the model			
				yes	no	rt + pr + var	rt + var	pr + var	var	rt + pr + var	rt + var
Principal dispersal agent	Bird, mammal, water, wind	NA	NA	0.566	0.224	0.397	0.047	0.095	0.209	0.065	0.124
Dispersal agent	Bird	23	39	0.533	0.199	0.339	-0.007	0.488 (+)	0.384 (+)	0.590 (+)	0.454 (+)
	Mammal	16	46	0.534	0.199	0.345	-0.009	0.429 (-)	0.399 (+)	0.410 (-)	0.510 (+)
	Water	26	36	0.567	0.219	0.394	0.032	0.027 (+)	0.135 (+)	0.022 (+)	0.088 (+)
	Wind	22	40	0.569	0.235	0.378	0.030	0.023 (-)	0.065 (-)	0.058 (-)	0.093 (-)
Seed production	Yes/no	57	5	0.533	0.189	0.338	-0.004	0.420 (+)	0.963 (+)	0.691 (-)	0.390 (-)
Seed size	Very small, small, medium to large*	NA	NA	0.557	0.142	0.421	0.032	0.151	0.425	0.032	0.510
Asexual reproduction	Any mechanism	44	18	0.540	0.211	0.339	-0.008	0.272 (+)	0.200 (+)	0.674 (+)	0.468 (+)
	Coppice	36	26	0.566	0.196	0.349	-0.017	0.030 (+)	0.471 (+)	0.323 (+)	0.994 (+)
	Sucker	17	45	0.554	0.217	0.372	0.023	0.087 (+)	0.149 (+)	0.084 (+)	0.123 (+)
	Division	11	51	0.545	0.192	0.357	-0.014	0.141 (-)	0.614 (+)	0.167 (-)	0.711 (+)
Minimum generation time	A continuous variable	NA	NA	0.540	0.193	0.343	-0.008	0.230 (-)	0.596 (+)	0.452 (-)	0.470 (+)
Nitrogen fixation	Yes/no	16	46	0.587	0.203	0.407	0.003	0.006 (+)	0.315 (+)	0.010 (+)	0.277 (+)
Region	Africa, Asia, Australia, NA Central America, North America, South America, Europe	NA	NA	0.597	0.176	0.420	-0.054	0.035	0.668	0.052	0.820
Climate	Arid	25	37	0.581	0.487	0.402	0.315	0.009 (+)	< 0.001 (+)	0.011 (+)	< 0.001 (+)
	Humid	16	46	0.529	0.240	0.348	0.005	0.915 (+)	0.051 (-)	0.373 (+)	0.262 (-)
	Mesic	35	27	0.529	0.198	0.341	-0.014	0.868 (+)	0.404 (-)	0.531 (+)	0.721 (-)
Biome	Forest	27	35	0.531	0.207	0.341	0.009	0.508 (-)	0.255 (-)	0.420 (-)	0.214 (-)
	Fynbos	24	38	0.530	0.204	0.365	-0.007	0.778 (-)	0.301 (-)	0.085 (+)	0.445 (+)
	Grassland	31	31	0.529	0.291	0.337	0.093	0.831 (+)	0.005 (+)	0.812 (+)	0.009 (+)
	Karoo	13	49	0.550	0.401	0.358	0.204	0.078 (+)	< 0.001 (+)	0.127 (+)	< 0.001 (+)
	Savanna	34	28	0.531	0.228	0.344	0.011	0.549 (-)	0.091 (+)	0.389 (-)	0.203 (+)
	Subtropical thicket	20	42	0.548	0.341	0.380	0.192	0.100 (+)	< 0.001 (+)	0.038 (+)	< 0.001 (+)
Reason for introduction	Agricultural, barrier, NA cover, fodder, no reason, ornamental, silviculture	NA	NA	0.529	0.151	0.390	-0.051	0.505	0.882	0.125	0.202
Current usage	Agricultural	16	46	0.533	0.194	0.349	-0.004	0.440 (-)	0.536 (-)	0.298 (+)	0.381 (+)
	Barrier	36	26	0.529	0.193	0.337	-0.014	0.803 (+)	0.590 (-)	0.745 (+)	0.688 (-)
	Cover	12	50	0.529	0.248	0.342	0.010	0.998 (-)	0.035 (-)	0.429 (+)	0.206 (-)
	Fodder	10	52	0.541	0.250	0.375	0.096	0.218 (+)	0.033 (+)	0.058 (+)	0.008 (+)
	None	3	59	0.559	0.190	0.391	-0.009	0.052 (-)	0.811 (-)	0.020 (-)	0.497 (-)
	Ornamental	49	13	0.568	0.208	0.365	-0.005	0.025 (+)	0.236 (+)	0.110 (+)	0.403 (+)
	Silviculture	13	49	0.529	0.198	0.337	-0.011	0.895 (+)	0.416 (-)	0.740 (+)	0.574 (-)

*(Dean *et al.*, 1986).

to *Macfadyena unguis-cati* is *Jacaranda mimosifolia*. While *M. unguis-cati* can reproduce by suckers, *J. mimosifolia* cannot; and so this species pair was used to evaluate how the presence of suckers affects invasiveness.

Estimating the rate of spread using the logistic model

The logistic model was rearranged to give the rate of spread in terms of the initial introduction and carrying capacity:

$$r = \frac{1}{t} \cdot \ln \left[\frac{N_t \cdot (K - N_0)}{N_0 \cdot (K - N_t)} \right] \quad (1)$$

where N_t , the number of QDGCs where the plant species was found as of 2000, was estimated from SAPIA; N_0 , the number of QDGCs in South Africa to which the plant was introduced, was initially assumed to be 1; t , the number of years since the earliest record of the plant in the country, was calculated from herbarium records; and K , the number of QDGCs that are climatically suitable for the species, was calculated from climatic modelling (Rouget *et al.*, 2004). This calculation was performed for each species. The estimated rates of spread were then regressed against the log residence time. Sensitivity analysis was conducted on both the size of the initial introduction (N_0) and the carrying capacity (K).

RESULTS

As expected, species introduced earlier were present in more QDGCs (Fig. 3a; $F_{1,60} = 16.5$, $P < 0.01$, $r^2 = 0.22$), and occupied a greater proportion of their suitable range (Fig. 3b; $F_{1,60} = 25.0$, $P < 0.01$, $r^2 = 0.29$). The basic model including residence time and potential range as additive effects had an r^2 of 0.54 ($F_{2,59} = 36.32$; $P < 0.01$) and there was no interpretable pattern in the residuals (Appendix S1 in Supplementary Material). The interaction between residence time and potential range was not significant ($F_{1,59} = 0.36$, $P = 0.55$), and this interaction made little difference to the fit of the model ($r^2 = 0.55$). There was no significant correlation between residence time and potential range size (Pearson's correlation: $r = 0.04$, $t_{60} = 0.32$, $P = 0.75$).

None of the measures of the spatial structure of the potential range caused a large increase in the amount of variation explained (r^2 of the maximal model was increased from 0.55 to at most 0.60), nor did they have a significant effect (the statistic with the highest significance was the mean Euclidian distance between grid cells $F_{3,59} = 1.31$, $P = 0.27$). No significant interaction was found between the spatial arrangement of the potential range and an anthropogenic or biological factor.

As 29 anthropogenic and biological factors were tested (Table 1), the analysis was expected to contain several false positives. After correcting for multiple comparisons, the model with just residence time as an explanatory variable showed that species invading arid climates, the karoo, and the subtropical thicket biomes were present in more QDGCs than expected. If the model only included potential range, or included both potential range and residence time, then no effects were significant after correction. However, this correction probably produced several false negatives as there was a gross overrepresentation of

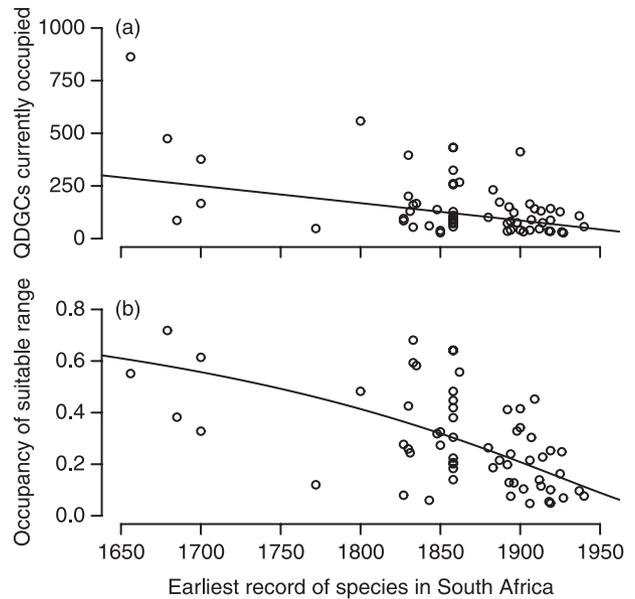


Figure 3 How residence time affects the range size of invasive plants. (a) The relationship between range size [number of quarter-degree grid cells (QDGCs)] and time since introduction, $\log(\text{current range}) \sim 0.975 \cdot \log(\text{residence time}) - 0.0382$, $r^2 = 0.22$; (b) the proportion of the potential range that was occupied in 2000, $\text{logit}(\text{occupancy}) \sim 1.42 \cdot \log(\text{residence time}) - 7.89$, $r^2 = 0.29$.

uncorrected probability values (seven of 31 uncorrected probability values are below 0.05). The multiple-comparison test assumes that factors have high tolerances, but many of our factors had low tolerances (i.e. were highly intercorrelated). None of the wind-dispersed plants in our data set were bird dispersed, and the main dispersal mechanism used by a species was clearly not independent of whether an organism used a specific dispersal mechanism. Therefore, there is insufficient resolution in the data to tease apart the myriad of hypotheses used to explain invasiveness.

However, if the model included potential range and residence time, species in arid regions and nitrogen fixers were much more widely distributed than expected (uncorrected $P = 0.009$ and 0.006, respectively), and we would argue that these effects were statistically significant. There was also a trend, but a much weaker one, for wind-dispersed species to be less widespread; water-dispersed species, ornamental species, and species that coppice to be more widespread; and the range size of a species to be affected by the region of origin (Table 1, uncorrected P -values between 0.01 and 0.05). Invasive plants from Australia were more widespread (mostly legumes), and species from Europe and South America were less widespread. While these patterns were not entirely conclusive, they may provide a focus for future work and comparisons with other geographical regions.

In no cases did sister clade comparisons show a significant pattern, but this test had very low power. At least six comparisons are required before a sign test can produce a probability of less than 0.05, and at most 14 sister-clade comparisons were possible (Fig. 4).

Assuming a logistic model of spread from a single-point introduction, more recent introductions apparently spread faster

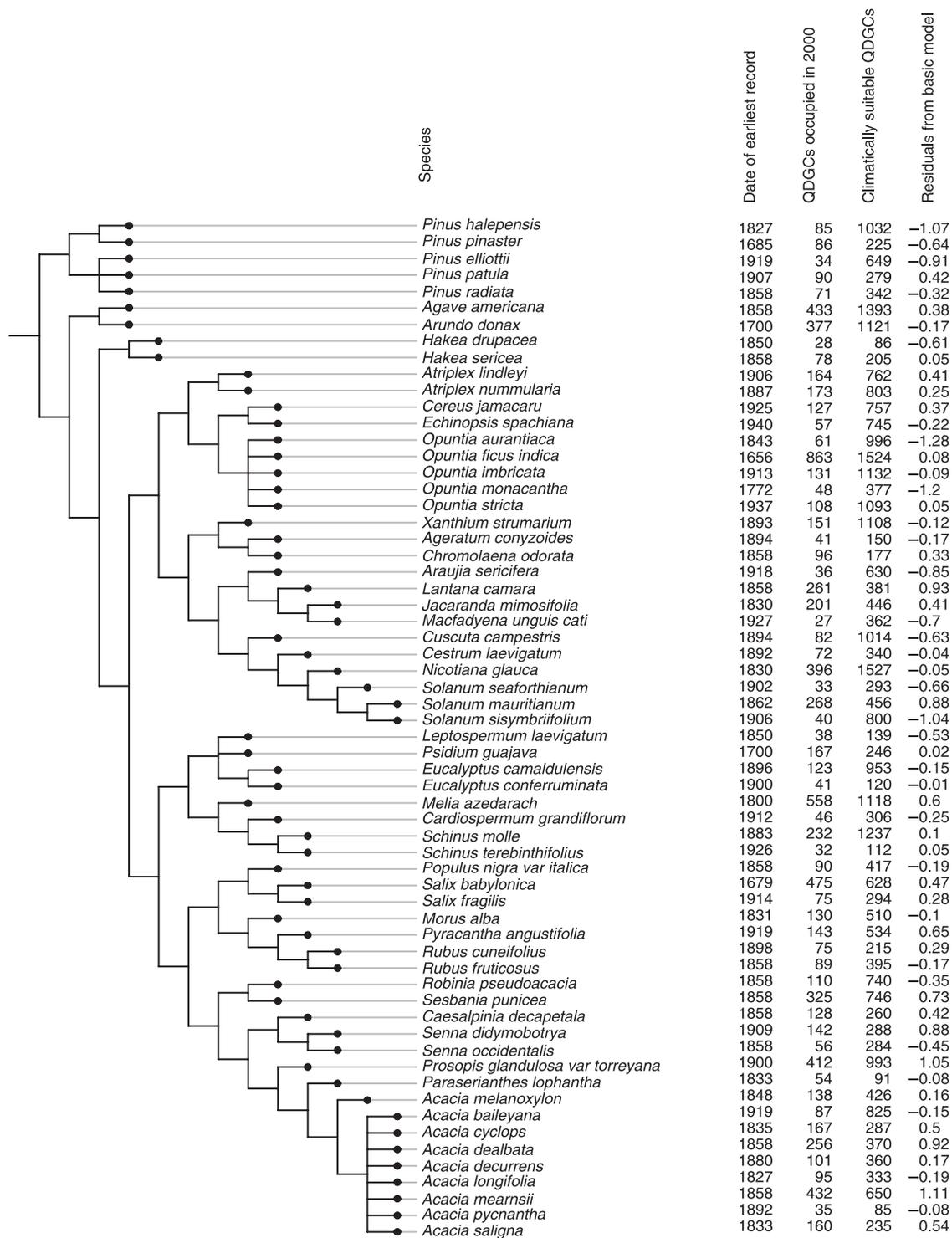


Figure 4 Phylogenetic relationships of the examined species. The residuals shown are from the model that incorporates residence time and potential range, i.e. $\text{range} \sim \text{pr} + \text{rt}$. Negative values for the residuals imply that the observed range of a species is smaller than expected. QDGCs, quarter-degree grid cells. For details of the phylogeny see Thuiller *et al.* (2006).

than less recent ones (Fig. 5). A linear regression of log residence time against rate of spread has a slope significantly different from zero ($t_{60} = -11.7$, $P < 0.01$), and any realistic values for (N_0) and (K) also produced significant (and large) negative relationships. However, the relationship is highly constrained (Fig. 5).

DISCUSSION

Potential range and residence time affected whether variables had a significant effect on invasiveness (Table 1). Therefore, if a comparison was made without considering potential

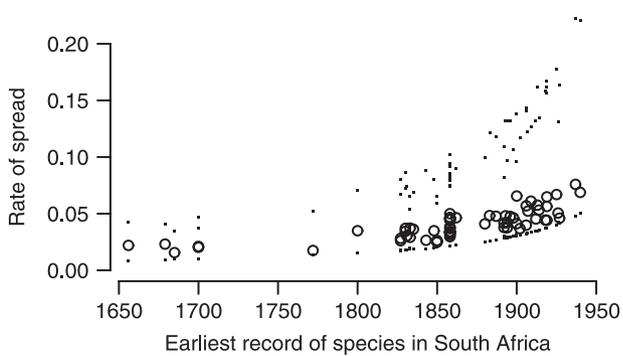


Figure 5 Change in rate of spread through time. Each circle represents an individual species and shows the estimated intrinsic rate of spread for each species assuming logistic growth [quarter-degree grid cells (QDGCs) occupied per QDGC per year after an initial introduction]; $r \sim -0.0276 \cdot \log(\text{residence time}) + 0.175$, $r^2 = 0.70$. The lower dots show the minimum possible rate of spread; and the upper dots the maximum possible rate of spread. Assuming a logistic growth in the number of QDGCs occupied creates a constrained pattern whereby recently introduced species appear to have spread faster than species introduced earlier.

range and residence time, it could easily come to misleading conclusions.

Climate and biome

If the model only included residence time, then the results were significantly affected by climate and biome invaded (Table 1). Because most of South Africa is covered by grassland, karoo, and savanna, species suited to these biomes can potentially occupy many more QDGCs than those suited to other biomes (Fig. 6). However, species in arid environments were still found in more QDGCs than expected even after considering potential range size (Table 1). We hypothesized that this was due to the spatial arrangement of the range (Fig. 6). A plant species invading arid regions should be able to spread in more directions (and so potentially quicker) than in humid or mesic regions, as the arid areas of South Africa are more contiguous than the humid and mesic areas. This explanation would mean that a statistic describing the spatial arrangement of the potential range should explain a significant amount of the variation in current range, but none did. Alternatively, arid environments may be less competitive than humid ones (Maestre & Cortina, 2004), and the lower abundance of indigenous species may allow invasive species to spread faster. Arid regions are typically more open and exposed. It would be interesting to test whether highly invasive species are likely to spread faster in arid regions than in wetter areas in other regions in the world, especially given different spatial arrangements of the range.

Other factors associated with invasiveness

The only other factor that showed a strong effect on current range size was nitrogen fixation. Nitrogen fixers were found to

have larger ranges than expected. It is difficult to say whether nitrogen fixation per se facilitates a greater rate of spread, but many introduced nitrogen fixers have certainly become invasive in many parts of the world (Paynter *et al.*, 2003; Weber, 2003). However, nitrogen fixation in our data set is completely phylogenetically constrained (only legumes) and largely biogeographically constrained (10 of 18 species are Australian acacias), with South Africa and Australia sharing similar habitats and climates. All nitrogen-fixing plants in this data set are also used for ornamental purposes and none are wind dispersed. However, nitrogen fixation in our data set is not significantly correlated with presence in arid environments, and so these two results can be viewed as independent.

The role of other factors is less clear, but some trends were apparent. There is some suggestion that plants used as ornamentals have spread faster. If a plant is a suitable ornamental, then it will be disseminated rapidly to many disparate locations, and certainly some of the world's worst weeds are ornamentals (Reichard & White, 2001). Ornamental species may also have an advantage in invasions due to selective breeding or hybridization in the cultivation process. Ornamental species are often characterized by a continual introduction of new genetic material. This may aid invasions by providing genetic diversity, or may slow invasions by continually diluting adaptations to the new environment. Wind-dispersed plants, however, tended to be much less widespread. The spread of wind-dispersed species is highly dependent on wind patterns and directions (e.g. Buckley *et al.* (2005)), and a species may only spread quickly if it is up-wind of its potential range. Most other reproductive parameters (e.g. seed size, the presence and method of asexual reproduction) showed no trends.

What is most evident is that, given phylogenetic constraints and strong correlations between variables, the results of comparative analyses concentrating on a few factors will lack generality. A larger data set is required to obtain full resolution of the many possible factors that could be correlated with invasiveness. However, there may be significant management benefits to establishing rules of thumb. Even if the reason for ornamental species being more widely distributed is due to a preference for ornamentals with a particular biological trait as opposed to being due to the trade of ornamental plants per se, clearly such an analysis as presented here can be used to derive testable mechanistic hypotheses and to inform any application of the precautionary principle.

Rate of spread

Many types of models have been used to describe how invasive species spread through a landscape (Higgins & Richardson, 1996; Hastings *et al.*, 2005), at different spatial scales, and including different levels of complexity (With, 2002). They range from relatively simple differential equations to mechanistic simulations that incorporate sophisticated wind-flow models (Nathan *et al.*, 2005). By analysing the range size of invasive species in the context of potential range and residence time, we examined the variation in rates of spread between species without modelling

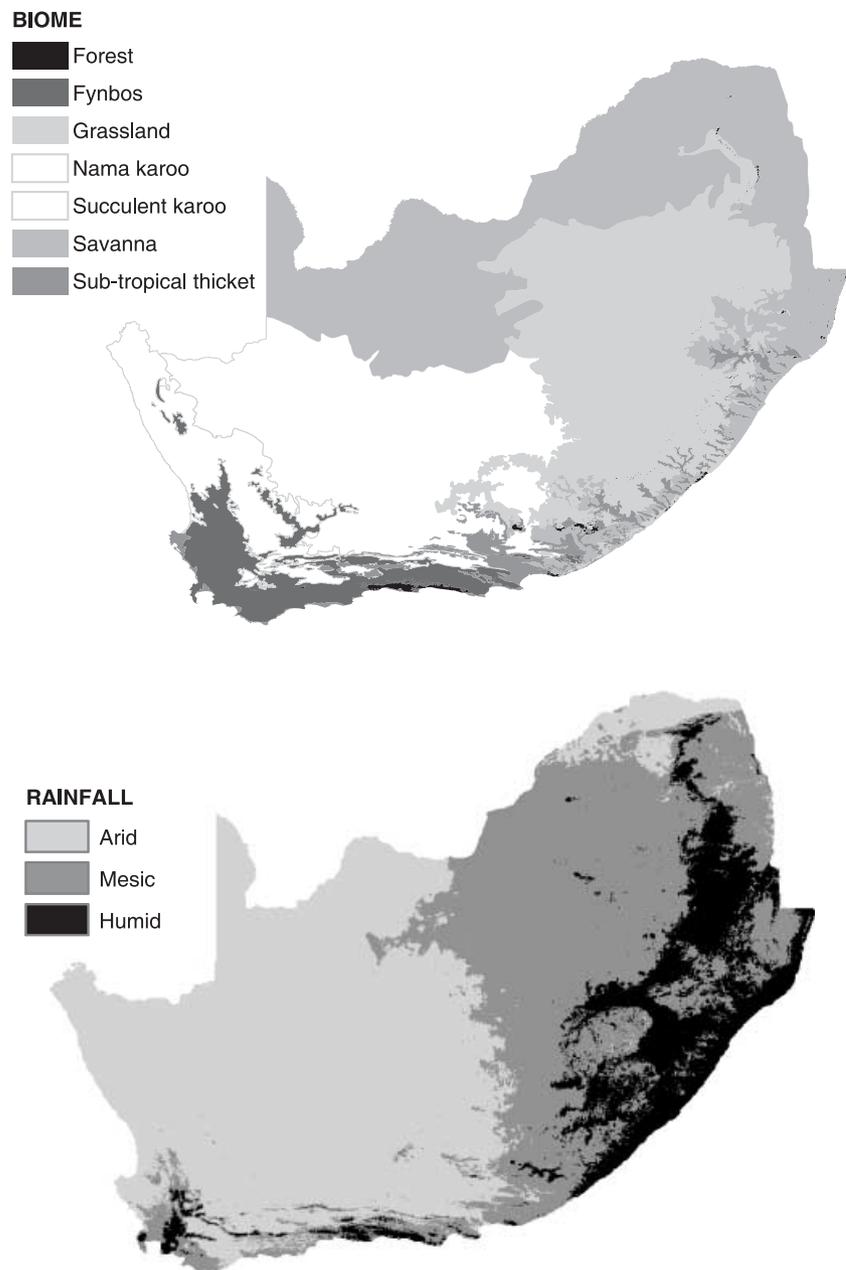


Figure 6 South African biomes and rainfall. Biome distribution data are from Low & Rebelo (1998), and rainfall data from Schultze (1997). In the analysis, Nama karoo (the eastern section of the karoo) and succulent karoo (the coastal/western section) are combined as karoo. Mean annual precipitation for arid < 425 mm; mesic 425–750 mm; and humid > 750 mm. See Rouget *et al.* (2004) for examples of species' potential ranges.

individual species and without making assumptions as to which dispersal mechanisms are operating. This allowed us to directly assess the role of humans in moving introduced species, an analysis that should be independent of trends in invasive spread through time, in particular as none of the biological or anthropogenic factors showed a significant interaction with residence time.

The alternative of assuming a single model of spread is beset by problems and constraints on the relationship. While the data are highly suggestive that the rate of invasive spread has increased through time, this conclusion rests on the appropriateness of the logistic model; the assumption of a single-point introduction; the suitability of fitting discrete data to a continuous model; and non-independence in the selection of the 62 species

(recent invaders will have had to spread fast for inclusion in the analysis, whereas older invaders could have spread slower).

Future directions

Processes affecting invasion success have been shown to operate at several different spatial scales. Dispersal ability, ecological suitability of habitat, and biotic and abiotic barriers all interact to constrain naturalization in and spread across different spatial scales (Hobbs & Humphries, 1995; Rejmánek *et al.*, 2005; Pyšek & Richardson, 2006). In particular, the spatial resolution of the data in this study (quarter-degree grid cells) may be too coarse to reveal the effect of spatial arrangement of the range. There are many

other factors not explored here that are known to be important in certain cases — e.g. the presence of a suitable pollinator or a co-evolved dispersal agent (Stout *et al.*, 2002) and sufficient genetic diversity (Shigesada & Kawasaki, 1997; Novak & Mack, 2005) — and a different set of factors may influence the *likelihood of establishment* of new invasive species. Although these are all important considerations, we stress that an evaluation of these factors needs to be placed in the context we have outlined.

It would also be interesting to explore how the importance of these factors varies with the stage of invasion. Clearly, for a new emerging invasion, propagule pressure and residence time may be expected to have much higher proportional effects than for an invasive species that has been established and spreading for a long time. In contrast, the distribution of a widespread invader may be more influenced by potential range (and any control measures implemented); and its pattern of spread may be more characterized by ‘filling in’ currently unoccupied sites than broadscale range expansion.

The selection of species in the study was somewhat limited. Our analysis only considers highly invasive species that have already attained fairly large adventive distributions, and, more particularly, relatively large, conspicuous plants with reliable dates of introduction. However, species with smaller potential distributions would likewise be restricted by the suitability of range and how much time they had to spread. There could, however, be a problem when examining less-conspicuous plants as there may be a strong correlation between the ability to detect a species and a trait of invasiveness, e.g. invasive grasses arriving in contaminated fodder may be present and invasive for a significant period of time before detection when compared to a showy ornamental plant with detailed importation and invasion records. The relationship between factors determining invasiveness and detectability is of great interest, particular for management. While none of the biological or anthropogenic factors examined here showed a significant interaction with residence time, this is an interesting area for future research.

Effective control measures and quarantine can reduce the abundance of a species in a given area, and slow the spread of a plant species (Lonsdale, 1993; Mack *et al.*, 2000). However, control measures rarely if ever eradicate a weed from an area the size of a QDGC (Rejmánek & Pitcairn, 2002; but see Simberloff, 2003). Regardless of the relative scale or impact, a better understanding of how invasive plants spread can inform control strategies (Moody & Mack, 1988) and address fundamental ecological questions (Rejmánek, 2005). Rules governing quarantine have certainly become stricter in recent years (Shine *et al.*, 2000), and many quarantine services do an excellent job at preventing new invasions. However, more legislative and other control measures are required to slow the spread of invasive plants within a region (Perrings *et al.*, 2005). A distinction also needs to be made between presence and impact. Although invasive species may spread faster in arid regions of South Africa than in other biomes such as fynbos, the conservation implications of this must be weighed against the value placed on the land. Conservation planners understandably focus on conserving global hotspots of biodiversity like the Cape Floristic Region (Cowling *et al.*, 2003).

Residence time and potential range also affect, to differing degrees, the invasion dynamics of other taxa of alien species. For birds and mammals, invasion success for individual species is less influenced by residence time and more by the initial number of individuals, the number of separate introduction events, the spatial distribution of these introductions, and the size of the climatically suitable potential range (Duncan *et al.*, 2001; Forsyth *et al.*, 2004; Lockwood *et al.*, 2005). Similarly, propagule pressure has been shown to be an important consideration in invertebrate invasions, at least when releasing classical biological control agents (Shea & Possingham, 2000; Memmott *et al.*, 2005). The degree to which these effects apply to invasive alien microorganisms has been less studied, but it will have incredibly important biosanitary implications.

CONCLUSIONS

Invasiveness is influenced by many factors: life-history traits, socioeconomic factors, and environmental variables all affect the spatial distribution of invasive species (Thuiller *et al.*, 2006). However, we show here that there are several fundamental considerations that explain much of the variation in the range size of individual highly invasive plant species: in particular climatically suitable potential range and residence time. While we could not obtain data on the distribution of propagule pressure in space and time, we would argue that these are also important considerations. By first considering these fundamental factors, we believe that general rules governing invasions can emerge.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Conditioning plot showing that the residuals of the basic model ($\text{range} \sim \text{rt} + \text{pr}$) are randomly distributed.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1366-9516.2006.00302.x>

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