Macroecology meets invasion ecology: linking the native distributions of Australian acacias to invasiveness

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Running title: Linking geographic range size to invasiveness

Abstract

Aim Species' native ranges reflect the net outcome of interactions between life-history strategies and biotic and abiotic influences over evolutionary timescales. Differences in native ranges might be indicative both of relative historical performance, and adaptability to new conditions. Consequently, the native ranges of successful invaders might have distinctive biogeographical characteristics. We test this hypothesis by (i) quantifying macroecological patterns of the entire assemblage of native taxa in *Acacia* subgenus *Phyllodineae* in Australia, (ii) testing whether highly invasive taxa represent random samples from the patterns observed for the assemblage as a whole, and (iii) exploring the link between native geographic range and the position of species along the introduction-naturalisation-invasion continuum.

Location Australia and worldwide.

Methods Three distributional metrics representing particular biogeographical characteristics of species' native ranges—the logarithms of range size; percolation intercept; and percolation exponent—were calculated by fitting a revised alpha-hull to records from Australia's Virtual Herbarium. Randomization and cascaded tests were used to compare these metrics for species at different stages of invasion.

Results The macroecological patterns of the three distributional metrics displayed lognormal-like frequency distributions. Most invasive species had significantly lower percolation exponents and larger native ranges than expected from random draws from the entire assemblage of Australian acacias, but percolation intercepts were not significantly different. This can be explained by a selection bias at the early stages of invasion.

Main conclusions The outcome of the natural experiment of transplanting many Australian acacias into novel environments is not random. While invasive species have a particular macroecological pattern, this can be explained by the observation that species with large native ranges and low percolation exponents (i.e. high population increase rate) are most likely to have been introduced and naturalised. Whether this pattern is an artefact of human selection or reflects a human bias towards selecting invasive species remains to be seen.

Keywords
biological invasions, invasive plant, native geographical range, spatial scales, species-range size distribution, wattles

INTRODUCTION

Biological invasions are an important driver of biotic homogenization and biodiversity loss worldwide (McKinney & Lockwood, 1999; Olden *et al.*, 2005; Gaertner *et al.*, 2009). They also represent superb natural experiments in biogeography, with temporal and spatial dimensions that could never be achieved in formal manipulative experiments. A key question in invasion biology is why some introduced species are so much more successful than others in establishing, undergoing rapid population growth, and spreading in novel environments (e.g. Pyšek *et al.*, 2009). To rephrase the question, are successful invaders a random subset of native assemblages? Or are there particular features of species that equip them to become successful invaders?

Attempts to quantify species invasiveness have mainly focussed on evaluating the capacity of species to survive (e.g. physiological tolerance and niche generalism), reproduce (especially from small populations over short periods), and disperse (particularly the capacity for long-distance dispersal) (Williamson, 1999; Sakai *et al.*, 2001), after at least initial facilitation by humans (Kolar & Lodge, 2001). "Invasiveness" defines the ability of the species to successfully negotiate geographic, environmental and biotic barriers (Richardson *et al.,* 2000, 2011 p. 415). This suggests the existence of a cascaded framework for quantifying alien species along an introduction-naturalisation-invasion (INI) continuum (Richardson *et al.*, 2000; Blackburn *et al.*, 2011). Most case studies in invasion biology involve *a posteriori* assessments of the factors associated with successful invasions. For invasion science to provide a predictive understanding of assembly rules, the field needs to be able to make accurate *a priori* assessments of the probability of particular species becoming naturalised and invasive following introduction. Many studies have sought insights on invasiveness by examining features of species in their native ranges, but most results and predictive frameworks are highly context-specific (Richardson & Pyšek, 2006).

The native distribution range of a species reflects the accumulated outcome of the interplay between its life-history characteristics (reproduction, dispersal, physiology and phylogeny, etc.) and interactions with abiotic (topography, soil characteristics, land use and climate), and biotic factors (resource competition, predation, pollination, mutualism and parasitism) over evolutionary timescales (Gaston, 2003; Colwell & Rangel, 2009; Soberon & Nakamura, 2009). As such, the native range potentially provides a surrogate measure of all these factors, and therefore should be indicative of how populations will change in the future (e.g., Wilson *et al*., 2004). For example, the native range size of a species is a direct indicator of its ability to persist and is therefore used to define its conservation status (IUCN, 2001). Similarly, the commonness or rarity of a species is linked to life-history characteristics (e.g. the core-satellite hypothesis; Hanski & Gyllenberg, 1993). If the life-history characteristics responsible for performance in a species' native distributions have similar effects in foreign environments, then patterns of native species distributions (and their macroecological patterns) should designate invasiveness.

Considering this with reference to the INI continuum, we suggest: that introduced species should be a non-random draw from the total species pool; that they should differ from naturalized species; and that naturalised species should differ from invasive species in their observed macroecological characteristics. Should such relationships exist, this would provide ecologists with important additional metrics that could enhance their capacity for identifying potential invasive species *a priori* (e.g. Wilson *et al*., 2011).

Australian acacias or "wattles" (1,012 taxa in *Acacia* subgenus *Phyllodineae* native to Australia; see Miller *et al*., 2011 for discussion on taxonomic issues) have been widely planted outside their native ranges for a variety of purposes (e.g. for forestry and dune stabilisation). Although about a third of the group have been introduced to regions outside Australia (Richardson *et al*., 2011), only twenty-three are confirmed as invasive (Richardson & Rejmánek, 2011). We suggest that wattles provide a superb (probably the best possible) natural experiment for exploring whether one can detect a signal of invasiveness from macroecological patterns for an entire large species assemblage across an entire continent.

The observed variation in invasiveness of Australian acacias clearly depends on a complex interplay of factors, including functional traits, dispersal strategies, climate similarity between Australia and recipient areas, as well as numerous extrinsic factors (e.g. Thuiller *et al*., 2006; Richardson & Thuiller, 2007; Wilson *et al*., 2007; Castro-Díez *et al*. 2011; Gallagher *et al*., 2011; Gibson *et al*., 2011). In this paper, however, we focus on exploring whether macroecological patterns of acacia distribution in their native range could potentially provide a simple accumulated index that would assist in predicting the probability of them becoming invasive.

Species distributions are scale dependent (e.g. Gaston & Blackburn, 2000) because ecological processes (e.g. dispersal and soil nutrient dynamics) that affect distributions operate at different scales for different species, and the measurements of species distribution will change with spatial scale according to certain statistical and percolation processes (Hui *et al*., 2006). Importantly the scaling pattern of a distribution provides information on population-level processes, e.g. on the nature and likelihood of range expansion (Wilson *et al*., 2004), and can be used to estimate abundances (Hui *et al*., 2009). In this paper we quantify the native range size for Australian acacias at different scales to build three macroecological patterns: frequency distributions of species range size, percolation intercept, and percolation exponent. Species range size provides a baseline for comparison, whereas the two coefficients of percolation processes capture the essence of the scale dependence of a species' range — as the size of grain increases, adjacent range clusters merge into one larger cluster and thus increase the estimate of a species range size (Hui *et al*., 2010).

These macroecological patterns allow us to test whether introduced, naturalised and invasive species (sensu Pyšek *et al*., 2004) have particular distributional characteristics in their native range, as well as how geographical scale and reason for introduction affect the observed patterns for species along the INI continuum. The null hypothesis is that species reported as invasive or introduced represent a random sample of all species. In rejecting the null hypothesis, we would identify distributional characteristics associated with invasive Australian acacias, which could potentially be used to predict future invaders. Furthermore, by comparing the distributional characteristics of lists of introduced, naturalised or invasive species, we are able to test for a bias at each stage of invasion.

METHODS

Data

Over 220,000 herbarium records of Australian acacias were obtained from Australia's Virtual Herbarium (AVH: ersa.edu.au/avh) in June 2010. We limited the list to geographical records of *Acacia* subgenus *Phyllodineae* native to Australia that were sampled in Australia, removed all hybrids and sub-specific information, and edited the data set for synonyms (see Richardson *et al*., 2011, for further details regarding data sorting). While AVH records are available from across Australia, there is a sampling bias in favour of centres of human population and areas with high road density (Fig. 1a). Furthermore, some herbarium records are from cultivated samples, but this is not as yet dealt with consistently for all the herbaria. Several species have also expanded their ranges in Australia due to human-mediated movement, in particular some species native to Western Australia have become invasive in eastern Australia and vice versa. For 11 species with known invasive ranges within Australia (*A. baileyana*, *A. cyclops*, *A. dealbata*, *A. decurrens*, *A. elata*, *A. iteaphylla*, *A. longifolia*, *A. mearnsii*, *A. melanoxylon*, *A.*

pycnantha and *A. saligna*), we manually removed the invasive range records from our dataset. This treatment only affected species with discrete adventive ranges, not those that may have extended their range at the edge of their natural ranges.

This data editing resulted in a list of ~135,000 geo-referenced records for 1,012 species (Fig. 1a) which was used for quantifying macroecological patterns of Australian acacias within their native range. Because the number of records per species is highly skewed (median 49, range 1 to 2402, with 105 species having less than 10 records, see Fig. S1) estimates of these variables from low-number records could be problematic, especially for species occupying a large geographic extent. Although the use of these problematic estimates from a low number of records is not recommended for species-specific inference, the assemblage-level community (or macroecological) patterns are often reliable due to the law of large numbers (in this case of species). Consequently, we used the full data-set throughout.

To examine whether macroecological characteristics vary along the INI continuum, thirty lists of species with different compositions and representing different invasion stages were calibrated and examined: Richardson & Rejmánek's (2011) list of invasive species (R&R; 16 lists for different geographic regions and on different reasons for introduction); Castro-Díez *et al.*'s (2011) list of invasive Australian acacias for invasive potential greater than 0.5 and species with an invasive potential less than 0.1; European Invasive Alien Species Gateway (DAISIE; Europe-aliens.org); species recorded outside Australia in the Global Biodiversity Information Facility database (GBIF; data.gbif.org) and those recorded in more than 10 countries (GBIF>10); records of seeds dispatched internationally by the Australian Tree Seed Centre (ATSC; Griffin *et al.*, 2011); Kueffer *et al.*'s (2010) list of invasive species on Oceanic islands; Poynton's (2009) list of Australian *Acacia* species tested for forestry in southern Africa (survived, naturalised and invasives); species listed in Rod Randall's Global Compendium of Weeds (GCW; hear.org/gcw; also data available for Europe); species recorded in South African herbaria (H. Glen, unpubl. data); species listed in the Southern African Plant Invaders Atlas (SAPIA; agis.agric.z/wip). These lists are of considerable interest for exploring the makeup of species lists at different stages in the INI continuum. For instance, the R&R list includes 23 invasive Australian acacia species (Fig. 1b) sensu Pyšek *et al.* (2004), compared to the ATSC list that provides the records of *Acacia* seeds transferred globally (Griffin *et al.*, 2011) and Rod Randall's GCW list of species naturalized anywhere in the world, we used a total of 30 lists representing Australian acacias that are introduced, naturalised, and/or invasive. Moreover as the lists contain various additional information, we could test the link between macroecological patterns for different geographic areas and for species introduced for different purposes (Richardson & Rejmánek, 2011). For example, Poynton (2009) describes which Australian *Acacia* species were used in forestry trials in southern Africa and details the success of these trials; while the Global Compendium of Weeds (2010) lists which species are regarded as having becoming weedy anywhere in the world (i.e. species that presumably have naturalised), as well as those that have been described as invasive in a given location. The full lists and sources are described in Supplementary Table S3 and are collated in Richardson *et al.* (2011).

Parameters used to describe native ranges

When exploring macroecological patterns, presence-absence maps at a given spatial scale are often used to define species distributions. This enables one to measure the occupancy (i.e. the proportion of grid cells where the species is found) and the extent (i.e. the total area encompassed by observed presences) of a species' range (Gaston & Blackburn, 2000; Robertson *et al.*, 2010). However, three inherent problems bedevil such grid-based methods when using continental-scale herbarium records: (i) the records are collected in a haphazard fashion rather than through a systematic survey; (ii) areas with no records cannot be taken as true absences, as absence of data may simply reflect low sampling effort in less accessible areas; and (iii) accuracy of records can vary substantially, particularly records collected before GPS technology (e.g. Newbold, 2010).

The AVH herbarium records are presence-only data with biased sampling effort (Fig. 1a). Gaston & Fuller (2009) suggested three formal (non-grid-based) methods for estimating species ranges: convex hull, alpha hull and abundance interpolation. Given the scope of this paper and the data quality, the interpolation method is not feasible. The convex hull (Fig. 2a) is a standardized way to handle haphazard point records when measuring range sizes (e.g. Miller *et al*., 2007). Essentially a polygon (a hull) is drawn that encompasses all observations. The area of the hull is then taken to be the range size of the species. However, this approach is very sensitive to the location of points at the edge of a species' range (and therefore particularly sensitive to data errors). The convex hull was refined through the introduction of the α-hull methodology, where the hull is split to exclude large areas without presence records (i.e. where there is high uncertainty about presence) and is therefore much more robust against data bias (Edelsbrunner *et al.*, 1983; Okabe *et al.*, 2000; Burgman & Fox, 2003).

Burgman & Fox (2003) provide a four-step procedure for calculating α-hull for a given species: (i) all records are linked by non-intersecting triangles using Delaunay triangulation such that the minimum angles are maximised; (ii) the mean edge length (L) is measured; (iii) all edges longer than the mean edge length multiplied by α (i.e. $L_i > L \times \alpha$) are removed; and finally (iv) the total area of all remaining triangles is taken to be the range size. Therefore range size estimates are specific to a given value of α. Since the size of species geographic range estimated from the α-hull varies drastically with the increase of α due to the non-random sampling effort (e.g. intensive sampling of a specific area can reduce the mean edge length and thus the hull size for a given value of α), we revised step (iii). Instead of removing edges where $L_i > \alpha \times L$, we removed edges longer than a specific distance, d. We then calculated the range size for all 1012 *Acacia* species for seven different distances ($d = 2^i$ km, where $i = 3, 4, \ldots, 9$), arranged exponentially to linearize the scaling patterns of species distribution. It is worth noting that records more than d km apart either belong to separate clusters, or are connected to each other via intermediate records. As such, how range size increases with d depends on the spatial point pattern of records, and range sizes for large values of d will essentially become the same as for the convex hull. This means a smoother scaling pattern of range sizes is created that using an unmodified α-hull and a sensible estimation of distributional metrics can be obtained.

Three metrics describing characteristics of species distribution were measured for each species using the revised α-hull calculation. First, species range size (P) was measured at a scale of $d = 128$ km to yield the species-range size distribution (also known as the occupancy frequency distribution (Gaston & Blackburn, 2000). This represents an estimate of range size at a specific spatial scale. Preliminary tests using the convex hull method suggest that each record represents on average an area of 50×50 km^2 and a maximum area of 243×243 km^2. The choice of this specific distance (128 km) represents the range size at a moderate resolution for wattles in Australia. The following cross-scale metrics further ensure that the results are representative and robust to the specific choice of d.

The other two metrics of range are estimated by exploring how range size P varies with d. As the edge-length threshold d increases, the convex hull P_c of species range is gradually percolated (filled up) by an expanding α-hull P_d. This can be depicted by a percolation process,

$$\frac{P_d}{P_c} = 1 - \exp\left(-a \times d^b\right), \tag{1}$$

where a (percolation intercept) indicates the subtractive logarithm of the proportional area within the convex hull that is not covered by the α-hull when d = 1km, and b (percolation exponent) indicates how fast the α-hull approaches the convex hull with the increase of spatial scales. A higher percolation intercept indicates a species is found at many locations spread across its overall range (and so tends to be common throughout its range), whereas a higher percolation exponent indicates a species is found clustered at a few geographically distinct locations (and refers to species with a lower population increase rate and thus a lower resilience to perturbation) (Hui, 2011). For instance, Wilson *et al*. (2004) report that a higher percolation exponent entails a high likelihood of range retraction for British butterflies. Together, these three variables (P_{128}, a and b) capture the essence of species range size across scales, and, we suggest, a rigorous depiction of the types of native ranges exhibited by a given group of species (in this case Australian acacias). In the analyses these distributional metrics were log-transformed to reduce the skewness of the resulting frequency distributions.

Statistics

First, the frequency distributions of the above three variables for the native distribution of Australian acacias were calculated. Second, each species list was tested against random samples (of the same length) from the native species assemblage based on a randomisation test (namely the density probability plot; Jones & Daly, 1995). For instance, to test whether each of the 23 invasive species (Richardson & Rejmánek, 2011) has a larger native range than expected from random draws, we sorted these species according to their log-transformed ranges from low to high $\{x_1, x_2,\ldots, x_{23}\}$. In each of the 10000 runs of the randomisation test, we (i) randomly chose 23 species without replacement in the native species assemblage and (ii) sorted them from low to high according to their log-transformed range sizes $\{y_{1j}, y_{2j},\ldots, y_{23j}\}$ (j = 1, 2,…, 10000). The value y_{1j} was then considered a prediction of x_1 in this run, so did y_{2j} for x_2, and so on. In the density probability plot, a perfect linear relationship between x_i and y_{ij} (i.e. $y_{ij} = x_i$) would indicate that $\{ x_1, x_2,\ldots, x_{23}\}$ and $\{ y_{1j}, y_{2j},\ldots, y_{23j} \}$ were from a same density probability distribution of the log-transformed ranges. The above run was repeated for 10000 times so that each observed x_i has 10000 expected values from the randomisation test $\{y_{i1}, y_{i2},\ldots, y_{i10000}\}$. Statistical significance was tested by comparing x_i with the 0.95 quantiles of $\{y_{i1}, y_{i2},\ldots, y_{i10000}\}$. Randomization tests were applied to all 30 species lists to examine the difference of these macroecological characteristics for species at different geographical scales, regions, and invasion stages, as well as species initially introduced for forestry, dune stabilization, and ornament.

To explore how species resemble each other in terms of these distributional metrics, we performed a cluster analysis for the entire species assemblage (with Ward linkage and squared Euclidean distance). We selected Ward linkage and squared Euclidean distance because we consider these to be more efficient than other potential methods (e.g. single linkage); these procedures also create clusters of smaller size, thus reducing the Type I error for reporting potential invasive species. The 23 invasive Australian *Acacia* species on Richardson & Rejmánek's (2011) list were then plotted onto these clusters. This enabled us to identify clusters of species with a high proportion of invasives.

To examine the selection preference for introduced, naturalised and invasive acacias along the INI continuum, we compared these three distributional metrics using the unequal variance *t*-test (Ruxton, 2006) for three groups of cascaded (nested) species lists, representing a comparison between regional (native) species and introduced species, between introduced species and naturalised, and between naturalised species and invasive. Specifically, we compared native species with those known to have been distributed as seed (Griffin *et al*., 2011), those distributed as seed with those known to have also naturalised (Global Compendium of Weeds, 2010), and those distributed as seed and that have also naturalised with those that have also been recorded as invasive (Richardson & Rejmánek, 2011). We also looked at similar nested analyses for wattles recorded in herbaria outside Australia, and for wattle known to have been introduced to South Africa. These comparisons enable us to tease apart the contribution of distributional metrics to the success of species when crossing the geographic, establishment, and spread barriers on the INI continuum.

RESULTS

As shown in Figure 2, intermediate values of the α-hull provide a more sensible estimate of species distribution than the traditional estimate from convex hulls, although at low values of the distance threshold *d* the pattern becomes dependent on sampling intensity (Fig. 2b-d). Range sizes (P_{128}) of the 23 invasive species on Richardson & Rejmánek's (2011) list vary from *A. mangium* (28,000 km^2) to *A. victoriae* (1,360,000 km^2). Range size estimates for different edge-length threshold (d = 8, 16,…, 512 km) were well depicted by Eq. (1) (i.e. all 23 invasive Australian acacias on Richardson & Rejmánek's (2011) list have $R^2 \geq 0.98$, with the *t*-test $p < 0.05$ for a and $p < 0.01$ for b; see Table S1). The log-transformation of the three distributional metrics has largely reduced the skewness of the frequency distribution (Fig. 3), yet they are still significantly different from normal distributions (Kolmogorov-Smirnov test, $p < 0.01$).

The three variables formed a cone-shaped scatter of points (Animation S1), with the 23 invasive species located on the peak of the cone pointing towards the high value of P_{128}. Further tests revealed that these three variables were correlated ($\ln(P_{128})$~$\ln(a)$, r = 0.074, p = 0.02; $\ln(P_{128})$~$\ln(b)$, r = -0.33, p<0.01; $\ln(a)$~$\ln(b)$, r = -0.43, p<0.01). Although the observed range sizes ($\ln(P_{128})$) for these 23 invasive acacias were significantly higher than expected from random draws (the median of $x_i – y_{ij}$ is 2.4, 95% CI 0.76 ~ 5.62; Table S2), the other two variables showed no significant discrepancy ($\ln(a)$: median 0.26, 95%CI -4.57 ~ 6.46; $\ln(b)$: median -0.5, 95%CI -1.2 ~ 0.3).

At the species level, only three species out of the 23 invasive acacias showed a significant discrepancy in the percolation intercept (Fig. 4a), with *A. implexa* having a higher observed value and *A. auriculiformis* and *A. mangium* having lower observed values than expected from random draws. However, most invasive species had a significantly lower percolation exponent than expected from random draws (Fig. 4b). All species except *A. auriculiformis* had a significantly higher value of log range size than expected from random draws (Fig.4c). These results suggest that the range size and percolation exponent are strongly associated with invasiveness, whilst percolation intercept is poorly associated with invasiveness.

Based only on logarithmic range size and percolation exponent, a dendrogram was built for the entire assemblage of Australian acacias. For illustration purposes, only ten clusters are presented here (Fig. 5), with the 23 invasive acacias occurring in only four clusters, one of which contained 10 invasive species (16% of the 62 species in the cluster are invasive; Table S3). Detailed examinations of the species in this cluster further revealed other potential and claimed invasives (e.g. *A. ligulata* and *A. deanei*).

When the randomization test was performed for all 30 species lists (Table S2), there was no significant change in the size of the effect on logarithmic range size and percolation exponent across different geographic scales, or between different reasons for introduction (Fig. S2). However, invasive wattles in the Middle East and Atlantic islands tended to have the largest range sizes, whereas invasive acacias from the Atlantic, Indian Ocean and Pacific islands, as well as from North and South America had the lowest percolation exponents (Fig. S2).

The comparison of the three distributional metrics for the nested species lists revealed a strong selection bias during the early invasion stage and a weak selection during the late invasion stage (Fig. 6; see statistical results in Table S4). Species with large native range and low percolation exponent were significantly preferred during the introduction stage. Among the introduced species, species with larger native ranges were further selected during naturalisation for seed exportation and planting in foreign environments. Importantly, progression from naturalized to invasive is a random draw from the pool of naturalised species, *at least in terms of characteristics of the species' native range*. Comparing the cascaded tests for seed exportation and for the South African experiment (Fig. 6), we can see that the reason for introduction and the spatial extent of the experiment (global vs. regional) also affect the selection bias along the INI continuum. For instance, selection bias only exists at the introduction stage for South Africa, but not at the naturalisation stage as in the global experiment. Sixteen percent of Australian acacias have been introduced to at least one foreign region. Thirty-nine percent of introduced species have become naturalised and 37% of naturalised species have become invasive (i.e., 15% of introduced species become invasive).

DISCUSSION

Percolation & scales in macroecology

The inherent scale dependency of species distributions (Gaston & Fuller, 2009; Hui *et al*., 2010) can be appropriately described by the revised α-hull that resembles the proposed percolation process (Eq.(1)). With the increase of distance threshold *d*, distant points and clusters gradually become connected, forming larger clusters, and the new edges that are added could indicate potential dispersal pathways and barriers at the focal scales. Such a percolation process has been useful especially in quantifying distributions of plant species (Sole e*t al*., 2005), and holds promise in invasion ecology for identifying the source of introductions, dispersal pathways, and intra-limit range structures.

The lognormal-like shape of species-range size distribution (as shown in Fig. 3c) has been widely observed (e.g. Hui *et al*., 2009). Although mechanisms leading to these macroecological patterns are multiple and scale dependent (McGill *et al*., 2007; Hui *et al*., 2009), direct analysis and comparison of species distributional structure provides us with a simple and elegant alternative to the piecemeal linking of the complicated and interacting biotic and abiotic factors and processes that affect species performance in foreign environments (invasiveness) (Jenkins & Keller, 2011; Gallagher *et al*., 2011). Moreover, the observed distributional characteristics may represent an emergent property that can explain invasiveness (Fig. 6). The links between these macroecological characteristics and invasiveness needs to be explored in different taxonomic groups to determine whether the patterns revealed in this study apply universally. Should this be the case, macroecological metrics will have immediate application in risk assessment protocols.

Invasion ecology & macroecology

The 23 species of Australian acacias that have become invasive after human-mediated transfer to, and dissemination within, regions far removed from their natural range show macroecological signatures within the natural ranges that differ significantly from those of a random draw of species. This implies that invasiveness of Australian acacias is linked, to some degree, to the range of factors that have generated the macroecological patterns quantified in this study, particularly native range size and percolation exponent (a potential surrogate for population increase rate) (Figs. 2-5).

Acacias with large native ranges are more likely to become invasive. These results are consistent with Gravuer *et al*.'s (2008) findings for *Trifolium* introductions to New Zealand that large native range is strongly associated with invasion success at all stages, as well as Rejmánek's (1996) finding that native latitudinal range of herbaceous Asteraceae, Fabaceae and Poaceae is the best predictor of their invasiveness (also this relationship is much weaker for *Pinus spp.*; Procheş *et al.*, 2011). Species with large native ranges may be more invasive because (i) they are more likely to be encountered and used by people and thus introduced to other areas (Duncan *et al*., 2001); or (ii) large range could translate into large niche space and environmental tolerance (Brown, 1984; Gaston & Spicer, 2001), characteristics which may also be seen as desirable if species have been chosen for land rehabilitation projects. Our study corroborates previous work (providing the most robust test to date, using the largest number of species) for the link between native range size and invasiveness. Our approach adds additional power by elucidating the link between invasiveness and other components of native range dimensions, notably the selection for species with a lower percolation exponent (as a potential indicator of population increase rate) at the introduction and some of the naturalisation stages (Fig.6).

Widespread acacias with high rates of population increase are more likely to become invasive. This could be because widespread species which produce large amounts of seed are simply more likely to be favoured by seed collectors, leading to higher introduction effort and propagule pressure (Verling *et al*., 2005). Indeed, native range size ($\ln(P_{128})$) and introduction effort (as measured by the logarithmic of the number of seed lots distributed; Griffin *et al*., 2011) are significantly positively correlated ($r = 0.32$, $p < 0.01$). Moreover, species with high population increase rates can recover rapidly after perturbation and would also have shorter lag phases and faster spread rates, and so likely to be observed as invasive more rapidly than other species (Sakai *et al*., 2001).

Potential for risk assessment

The macroecological patterns observed also highlighted the potential for their use in risk assessment. We further compared the metrics seen here with a quantitative ranking of "invasiveness" by Castro-Díez *et al*. (2011). Their invasiveness score is not correlated with any of the three distributional metrics ($\ln(P_{128})$~logit(score), $r = 0.04$, $p = 0.69$; $\ln(a)$~logit(score), $r = 0.04$, $p = 0.75$; $\ln(b)$~logit(score), $r = -0.19$, $p = 0.08$). This is consistent with our result that successful invaders may represent a random draw from the pool of naturalised species at least in terms of species' distributional characteristics (Fig.6). However, the model scores on axis 1 of their principle component analysis of climate, life-history traits and human use of acacias correlate extremely well with the number seeds introduced (logit(score)~ln(seeds), $r = 0.71$, $p < 0.01$). This suggests that Castro-Díez *et al*.'s (2011) model score is a good indicator of propagule pressure, and that propagule pressure is a dominant component of species invasiveness (Colautti *et al*., 2006). Furthermore, it also suggests that acacias with a high population increase rate are more likely to be introduced (and also in a large quantity; $\ln(b)$~ln(seeds), $r = -0.17$, $p <0.01$), which further enhances the chance of being naturalised and the overall probability of invasion success (Fig.6).

More importantly, our results emphasize that the concept of "invasiveness" has several layers. Invasiveness has been defined as the capacity of an alien organism to overcome various barriers to invasion (Richardson *et al*., 2010). This can be interpreted as the conditional probability of a species, *once naturalised*, becoming invasive (the narrowest sense), or the compound probability of a species negotiating all barriers and stages in the INI continuum (the broadest sense). That different factors mediate these outcomes is not given sufficient cognisance in most studies of the determinants of "invasiveness" or "invasive success". For invasiveness in the broadest sense, species with large native ranges and high population increase rate are most likely to be become invasive (Fig. 3 and Fig. 4). However, this compound definition of invasiveness (or the likelihood of being invasive) is mediated by the selection bias only at the early stages of invasion (i.e. introduction and naturalisation). No selection bias was found to exist for the last stage of invasion (Fig. 6). In other words, species distributional characteristics were not found to contribute to invasiveness in the narrowest sense here. This supports Richardson *et al*.'s (2000) definition of the invasion process as a stochastic Markov chain where species from native assemblages cross different barriers to become introduced, then naturalised, then finally invasive. The different sets of species arising from this natural experiment of human-mediated transfers are nested in accordance with the introduction-naturalisation-invasion (INI) continuum construct. The problem remains, however with interpretation. Are those species that are most likely to show invasiveness in the narrowest sense (i.e. become invasive if given the chance) also those species that are most likely to have been selected by humans for introduction? Or are all species potentially invasive and the only pattern seen is due to introduction bias? The data on Australian acacias are consistent with both hypotheses (Wilson *et al*., 2011).

Conclusions

Overall, it is evident that the macroecological pattern of species' native distributions provides a strong signal of species invasiveness. Our results suggest that the performance of a species in its native range is indeed correlated with their potential success in new regions. An introduction-naturalisation-invasion continuum assessed according to species' native distributional characteristics exists and is consistent with the theoretical outline in Richardson *et al*. (2000). This evidence implies that the artificial selection in this global natural experiment of the movement of Australian acacias around the world is not random but favours those species that have particular types of native geographic distributions, which are tied with species invasiveness, functions and spatial scales. Further work is needed to elucidate the potential implications of these range features and to link them to biological traits and ecological characteristics of the species (e.g., see Gallagher *et al*., 2011). Distinguishing the narrow- and broad-sense of invasiveness is especially necessary for teasing apart the environmental and biological factors that determine invasion success at different stages. We suspect that the results presented here are just the tip of an iceberg, and that further work and deeper collaboration between related fields on species distributions will reveal strong links between macroecology and invasion ecology, with far-reaching implications for management (Richardson & Whittaker, 2010; Procheş *et al*., 2011).

Acknowledgments

Data on Australian *Acacia* species records are used with permission of the Council of Heads of Australian Herbaria, the custodian of Australia's Virtual Herbarium. We acknowledge financial support from the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme, and funding from the Oppenheimer Memorial Trust and Stellenbosch University in support of the October 2010 *Acacia* workshop in Stellenbosch at which a preliminary version of this paper was presented. C.H. is supported by the NRF Blue Sky Programme and Subcommittee B fund at Stellenbosch University. We are grateful to Rachael Gallagher, Carla Harris, Michelle Leishman, Dan Murphy and Jaco le Roux for their advice on the native distribution of invasive acacias in Australia.

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Biosketch

Cang Hui is currently a researcher at the DST-NRF Centre of Excellence for Invasion Biology, Stellenbosch University. His particular interests include mathematical and spatial modelling in macroecology and biogeography, as well as theoretical models in evolutionary ecology. All authors are interested in the ecology of biological invasions and management opportunities for controlling their spread.

Author contributions: C.H., D.M.R. and J.R.U.W. developed the idea, M.P.R. and C.J.Y. undertook data transformation, C.H. did the analyses and writing, and all authors assisted with the writing.

Figure captions

Figure 1. Distribution records for *Acacia* subgenus *Phyllodineae* records from Australia's Virtual Herbarium for (**a**) all species and (**b**) the 23 invasive Australian acacias (Richardson & Rejmánek, 2011). Different colours represent the number of records per half-degree cell (white: no records; yellow: <10; green: 10~100; blue: 100~1000; red: >1000).

Figure 2. Illustrations of the geographical range of *Acacia maitlandii* (Maitland's Wattle) in Australia: (**a**) convex hull, (**b, c, d**) α-hull at d=512, 256 and 128 km.

Figure 3. Frequency distributions of (**a**) the percolation intercept (ln(a)), (**b**) the percolation exponent (ln(b)) and (**c**) the logarithms of range size (P_{128}). Dark lines indicate the values for the 23 invasive species (Richardson & Rejmánek, 2011).

Figure 4. Box plots of **a)** the percolation intercept (ln(a)); **b)** the percolation exponent (ln(b)); and **c)** the logarithms of range size (log(P_{128}) for the 23 invasive Australian acacias (Richardson & Rejmánek, 2011), demonstrating the discrepancy between observed values and expected values from the randomization tests. Species are ranked according to their observed values; hinges of the boxes are set to indicate the 2.5% and 97.5% quantiles, with the whiskers and asterisks indicting data range and outliers. The zero line is expected to cross through hinges of the box for 95% of species. Given there are 23 invasive species, there should be three or fewer species outside the zero line ~97.5% of the time, suggesting four or more such outlying species represents a significant bias).

Figure 5. A dendrogram from a cluster analysis of Australian acacias based on the percolation exponent (ln(b)) and the logarithms of range size (P_{128}), using Ward linkage and Squared Euclidean distance. Numbers in the boxes indicate the number of species in each of the 10 clusters. The 23 invasive Australian acacias (Richardson & Rejmánek, 2011) are distributed among only four of the clusters. See Table S2 for the full membership of the most invasive cluster.

Figure 6. A schematic illustration of the selection bias at different invasion stages for three cascaded tests: seed exportation (introduced: ATSC; naturalised: ATSC∩GCW; invasive: ATSC∩GCW∩R&R; where '∩' stands for the intersection of two species lists), species in the global transplanting (introduced: GBIF; naturalised: GBIF∩GCW; invasive: GBIF∩GCW∩R&R), and species in the South Africa regional experiment. ATSC: records of seeds sent from Australian Tree Seed Centre; GCW: species listed in Rod Randall's Global Compendium of Weeds; R&R: Richardson & Rejmánek's (2011) list of invasive species; GBIF: recorded species outside Australia in the Global Biodiversity Information Facility. Only significant selection bias was presented; random draw represents no significant selection bias. Numbers in the box indicate the number of species. See Table S3 and Richardson et al. 2011 for more details of the lists used, and Table S4 for the detailed statistics.

Online supplementary material

Table S1: Range sizes of Australian acacias estimated from the revised α-hull at different scales and convex hull, as well as the nonlinear regression results for the percolation intercept and slope.

Table S2: Species in the cluster with the highest proportion of invasive acacias.

Table S3: A description of the 30 species lists as well as the median and 95% confidence interval of the discrepancy of three macroecological variables.

Table S4: Statistic results of the cascaded comparison for seed exportation, global and South Africa experiments. See Fig. 6 for a schematic illustration of this table and the meaning of the acronyms. For details of the species lists used see Richardson *et al.* (2011).

Animation S1: Relationships between the percolation intercept ln(a), exponent ln(b) and the logarithms of range size (P_{128}) for Australian acacias, forming a cone shape in the 3D space. Each green dot indicates a species; red dots indicate the 23 invasive species (Richardson & Rejmánek, 2011).

Figure S1: (A) The frequency distribution of the number of records for 1012 acacia species, and (B) the relationship between the number of records and the convex hull estimates of the geographic range sizes. The frequency distribution of the number of records is highly skewed (lognormal shape, D = 0.04, p = 0.1, Kolmogorov-Smirnov test), with a mean of 133.5, a median of 49, the maximum of 2402 records for one species (*Acacia ligulata*, non-invasive; high weediness potential according to biological characteristics, florabank.org.au), 105 species having less than 10 records and 684 species having less than 100 records.

Figure S2: The discrepancy (prediction - observation) from the randomization tests for species lists at different geographical scales (South Africa: SAPIA; southern Africa and rest of Africa: Richardson & Rejmánek, 2011) (**a**), for different functions (forestry, dune stabilisation and ornamental; Richardson & Rejmánek, 2011) (**b)** and for different geographical regions; Richardson & Rejmánek, 2011) (**c**). Open boxes indicate the discrepancy of ln(P_{128}) and grey boxes indicate the discrepancy of ln(b). The discrepancies also declined for invasive species lists from continental to regional scales (Fig. S2a) and species introduced for forestry to ornamental purpose (Fig. S2b). The discrepancies for the invasive species in different geographical regions further showed that invasive acacias in the Middle East and Atlantic islands had the highest discrepancy of range size (Fig. S2c), whereas invasive acacias from the Atlantic, Indian Ocean and Pacific islands, as well as from North and South America had the highest discrepancy of the percolation exponent. Cluster analysis using Ward’s method can group these regions into four clusters: {Atlantic islands, Middle East}, {North America, Europe, rest of Africa, Australia, New Zealand}, {southern Africa, Asia, South America} and {Indian Ocean islands, Pacific islands}.

Fig.1

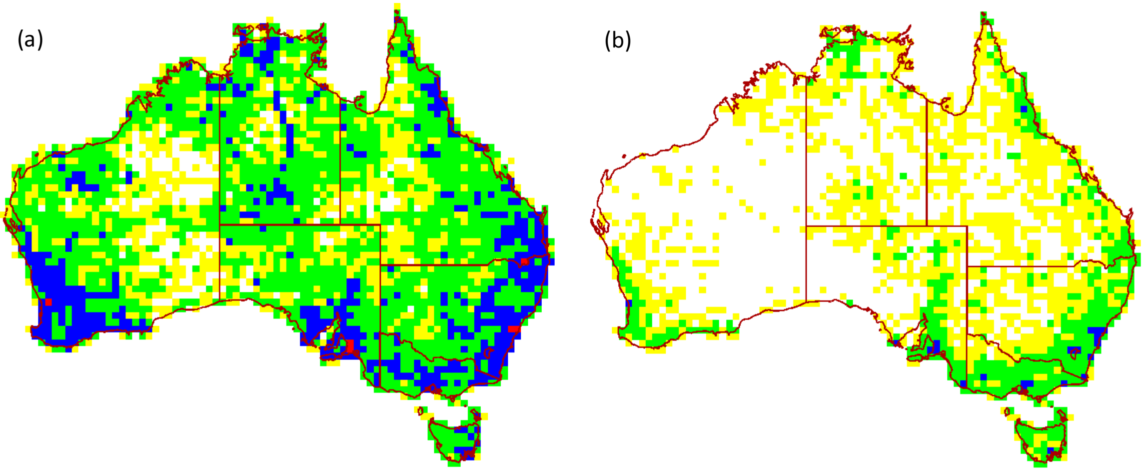


Fig.2

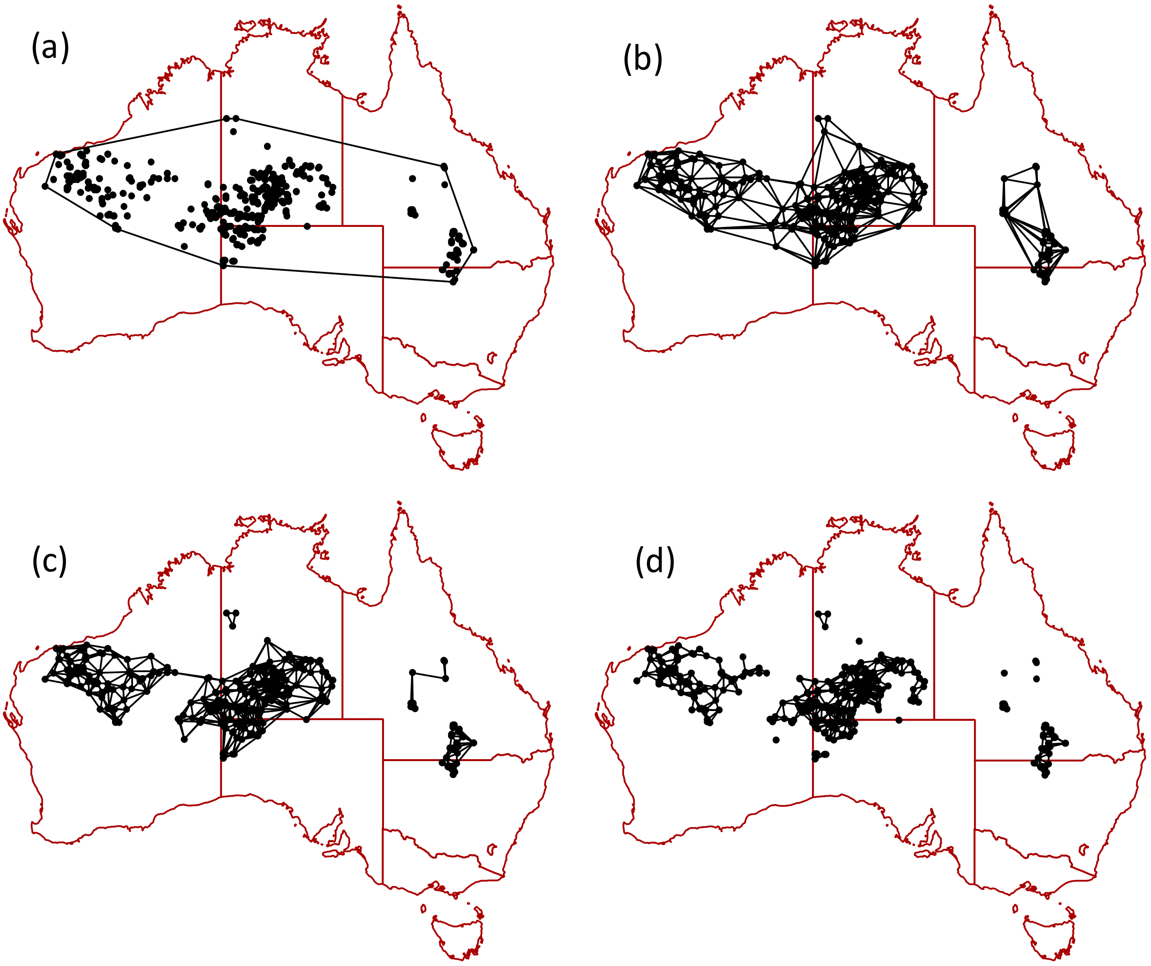


Fig.3

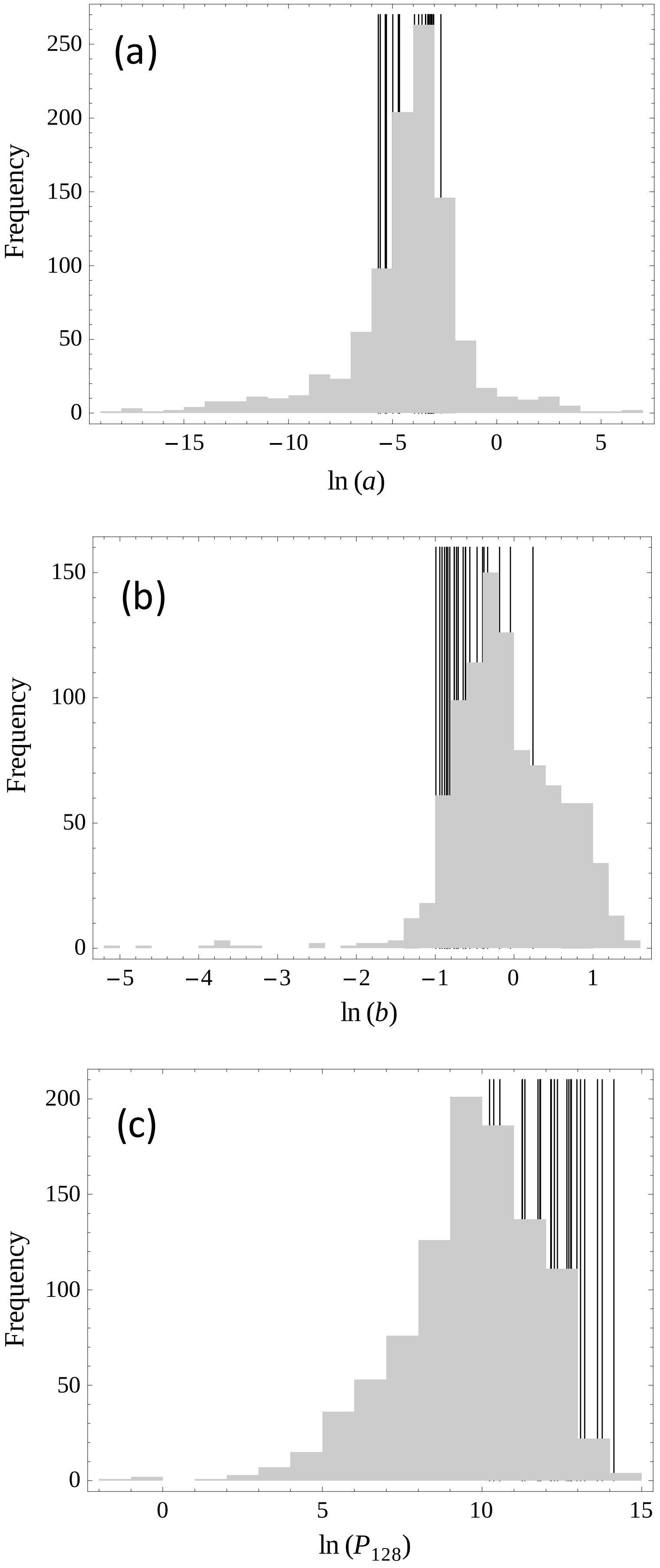
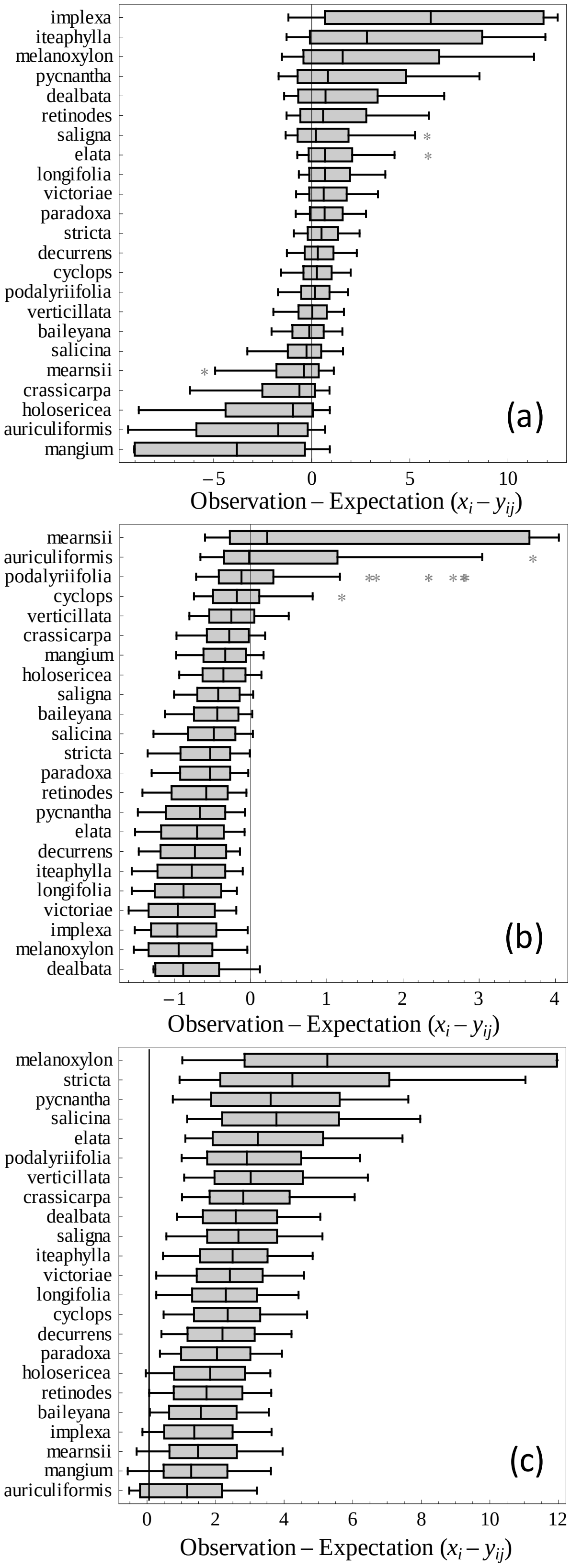

(a)
Frequency
0
50
100
150
200
250
−15
−10
−5
0
5
ln (*a*)
(b)
Frequency
0
50
100
150
−5
−4
−3
−2
−1
0
1
ln (*b*)
(c)
Frequency
0
50
100
150
200
0
5
10
15
ln (P_{128})

Fig. 4


implexa
iteaphylla
melanoxylon
pycnantha
dealbata
retinodes
saligna
elata
longifolia
victoriae
paradoxa
stricta
decurrens
cyclops
podalyriifolia
verticillata
baileyana
salicina
mearnsii
crassicarpa
holosericea
auriculiformis
mangium
(a)
−5
0
5
10
Observation – Expectation ($x_i - y_{ij}$)
mearnsii
auriculiformis
podalyriifolia
cyclops
verticillata
crassicarpa
mangium
holosericea
saligna
baileyana
salicina
stricta
paradoxa
retinodes
pycnantha
elata
decurrens
iteaphylla
longifolia
victoriae
implexa
melanoxylon
dealbata
(b)
−1
0
1
2
3
4
Observation – Expectation ($x_i - y_{ij}$)
melanoxylon
stricta
pycnantha
salicina
elata
podalyriifolia
verticillata
crassicarpa
dealbata
saligna
iteaphylla
victoriae
longifolia
cyclops
decurrens
paradoxa
holosericea
retinodes
baileyana
implexa
mearnsii
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(c)
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10
12
Observation – Expectation ($x_i - y_{ij}$)

Fig. 5

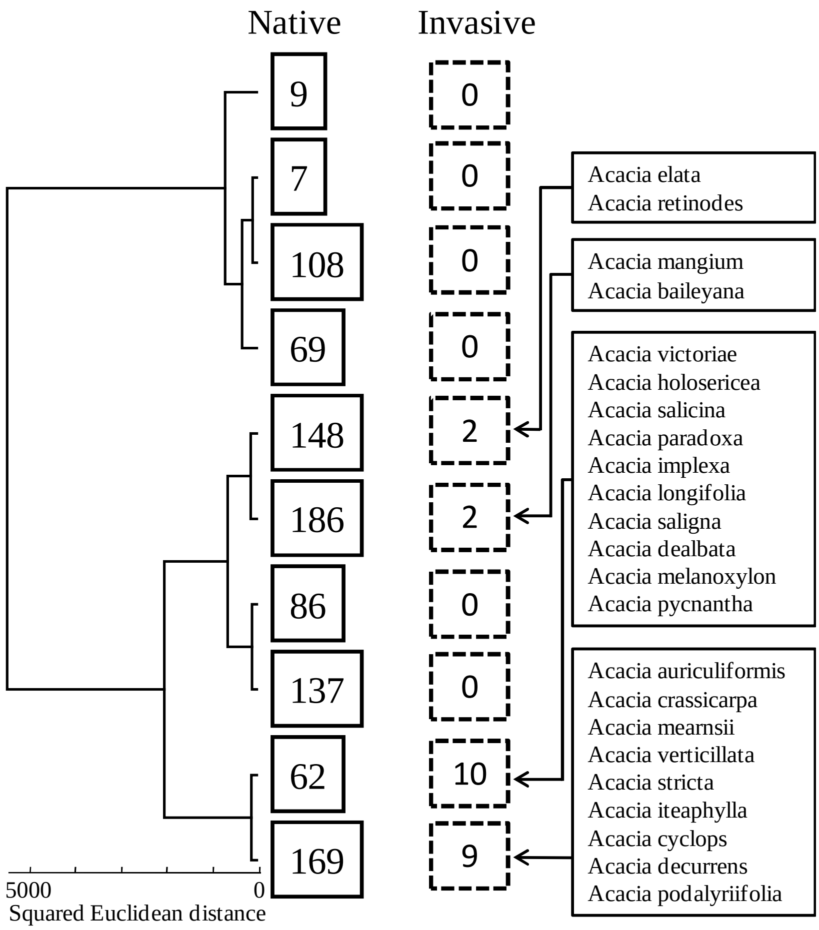
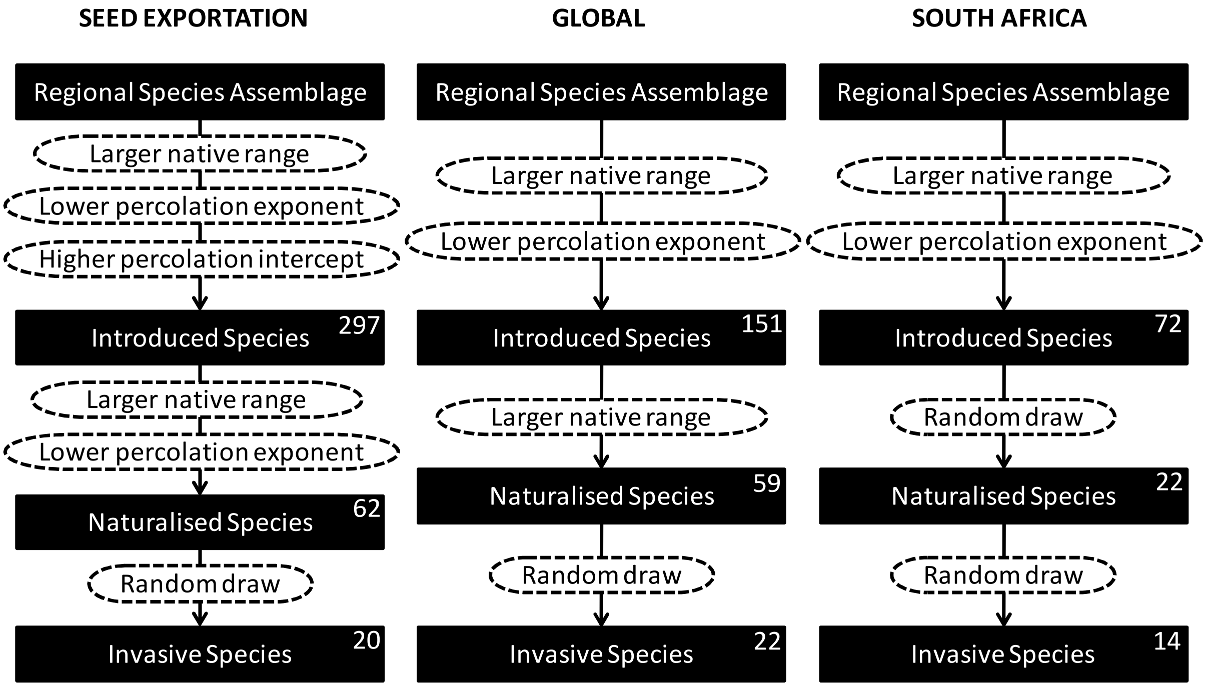

Native
Invasive
9
0
7
0
108
0
69
0
148
2
186
2
86
0
137
0
62
10
169
9
Acacia elata
Acacia retinodes
Acacia mangium
Acacia baileyana
Acacia victoriae
Acacia holosericea
Acacia salicina
Acacia paradoxa
Acacia implexa
Acacia longifolia
Acacia saligna
Acacia dealbata
Acacia melanoxylon
Acacia pycnantha
Acacia auriculiformis
Acacia crassicarpa
Acacia mearnsii
Acacia verticillata
Acacia stricta
Acacia iteaphylla
Acacia cyclops
Acacia decurrens
Acacia podalyriifolia
5000
0
Squared Euclidean distance

Fig. 6


SEED EXPORTATION
GLOBAL
SOUTH AFRICA
Regional Species Assemblage
Larger native range
Lower percolation exponent
Higher percolation intercept
Introduced Species
297
Larger native range
Lower percolation exponent
Naturalised Species
62
Random draw
Invasive Species
20
Regional Species Assemblage
Larger native range
Lower percolation exponent
Introduced Species
151
Larger native range
Naturalised Species
59
Random draw
Invasive Species
22
Regional Species Assemblage
Larger native range
Lower percolation exponent
Introduced Species
72
Random draw
Naturalised Species
22
Random draw
Invasive Species
14