Scale-area curves: a tool for understanding the ecology and distribution of invasive tree species

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Abstract Scale-area curves are increasingly used in ecology to predict population trajectories, based on the assumption that observed patterns are indicative of population dynamics. However, for introduced species, scale-area curves might be strongly influenced by introduction history. We examined the spatial structure of an invasive tree species (*Acacia elata*; Fabaceae) introduced to South Africa as an ornamental plant and compared our findings with previous work done on a species introduced for dune stabilization (*A. longifolia*). A fractal sampling method was used to map the occupancy of *A. elata* at twelve spatial scales for ten quarter-degree grid cells throughout South Africa. Based on the fractal dimension (D_{ij}) calculated at different spatial scales we found that populations were more contiguous at plot (2.5–25 m) and regional scales (2.5–25 km) than at local and landscape scales (0.025–2.5 km). We argue that the lack of contiguous *A. elata* populations over 250 m to 2.5 km is not indicative of a low risk, but the result of the spatial

structure of available land in suburban environments. When working with introduced species, scale-area curves representing fragmented populations at the edge of invasions should not be considered to indicate a lack of invasive spread/threat. Rather they can be used to identify “missing links” in the invasive introduction-naturalization-invasion continuum, but only if the life-history traits, introduction history, and area suitable for invasion are well understood and are used in interpreting the results. We suggest that their greatest value will lie in their use as a method for long-term monitoring of introduced species.

Keywords *Acacia elata* · Biological invasions · Australian acacias · Invasive distributions · Tree invasions · Scale-area curves · Human use

Introduction

The spatial distribution of invasive tree species has important implications for their management. Invasive populations that are aggregated and confined to small patches will require different strategies to those that are spread over large areas, even if they consist of similar numbers of individuals with a similar condensed canopy area (Wilson et al. 2013). Management of invasive species could be substantially improved by better understanding aspects of their distribution and

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spatial structure. Unfortunately the collection of distribution data of the quality required to be useful for detailed management planning is expensive and is usually not available (Gaston 1999, 2008 though see Caplat et al. 2013; Kaplan et al. 2013). One solution is to collect data on a subsample of quadrats at multiple resolutions and use scale-area curves to describe the spatial structure of populations and their potential for future spread (Wilson RJ et al. 2004; Wilson JRU et al. 2013; Veldtman et al. 2010). Scale-area curves are generated by comparing the log-area occupied with log-linear resolution (Kunin 1998). The slope provides information on the space-filling properties of populations over a given range of scales; steep slopes indicate fragmented populations whereas flatter gradients denote more contiguous populations (Kunin 1998; Wilson et al. 2004; Veldtman et al. 2010). Thus, scale-area curves can be used to analyse the distribution and occurrence patterns of invasive species to elucidate options for management (Veldtman et al. 2010).

Scale-area curves are an elegant way of extracting important information from available data; they involve predicting species abundance by projecting the occupancy–scale relationship across multiple scales down to a ‘micro’ scale which incorporates single individuals (Hartley and Kunin 2003; Hartley et al. 2004; Hui et al. 2009; Hui 2011). The use of scale-area curves to estimate the abundance of a populations at different scales (Kunin 1998; Hui et al. 2009) enables predictions of the probability of range expansion and contraction in species—those with steep scale-area curves (low abundance) may be expected to be in decline while those with flat curves (high abundance) are expected to expand (Wilson et al. 2004).

Veldtman et al. (2010) suggested that scale-area curves can be used to analyse the potential of invasive spread of populations as well as in the analysis of occurrence patterns. They suggested that further spread is likely for invasive species with flat scale-area curves at the current edge of their invasive range, whereas species with steep curves have a much smaller chance of further spread. While this approach is suitable for populations that have long residence times (enough time to reach all potentially invisable sites and to spread), special problems exist when applying such methods to invasive species with shorter residence times, for which dimensions of spatial structure may be more influenced by peculiarities of the particular introduction and early human-mediated

dissemination than by any innate feature of the species and its capacity to establish and spread. In general, species distributions are defined by a mixture of physical limitations (e.g. climate and geography) and biological interactions (e.g. predation and dispersal limitations) that act over a range of spatial and temporal and scales (Brown et al. 1996). In the case of species introduced to new regions by humans many of the conditions governing their natural range size will have been severely altered or negated by movement to new areas where populations are not at equilibrium (Rouget et al. 2004). It has thus been suggested that the spatial structure of invasive populations may be better described by features related to their introduction conditions than to any intrinsic species traits (Lonsdale 1999; Lockwood et al. 2005, 2009; Thuiller et al. 2006; Wilson et al. 2007, 2009; Castro-Díez et al. 2011; Procheş et al. 2012). As introduction conditions are inherently linked to the human use of a species, species introduced in similar ways (i.e. for similar human uses) should, at least initially, have similarities in their spatial patterns (Castro-Díez et al. 2011). Ignoring the influence of human history in shaping the early spatial patterns of invasive populations could lead to inappropriate management decisions. For example, species planted recently may be experiencing local-scale processes highly conducive to spread. However, being in the early phase of invasion, the signature of human-dictated placement at scattered localities may suggest that the distribution of the species’ population is fragmented, in decline and/or of minor importance (cf. Wilson et al. 2004) resulting in management decisions that are not suited to a spreading species. As the early stages of invasion are the most sensitive to management and represent the greatest opportunity for control, the development of a method for the use of scale-area curves in invasive risk management would be of great value to land managers if used appropriately. In this paper we demonstrate how scale-area curves in conjunction with knowledge of both the life-history traits and introduction history of invasive species can be used to inform the management of an invasive species that occupies a small proportion of its suitable range, and compare our findings to previous work on an invasion closer to broad-scale equilibrium.

Plants selected for use as ornamentals are often planted in small numbers, as individual trees or small populations (Mack 2005), with most plantings around

human settlements (Deutschewitz et al. 2003; Foxcroft et al. 2008). Invasive populations stemming from these introductions will occur predominately within these same conurbations. Therefore ornamental plantings will likely appear fragmented at the broad scale, at least in the early phases of an invasion. Moreover, while the urban landscape may provide areas of disturbance and protection from stochasticity as a result of human activity (Deutschewitz et al. 2003; Chytrý et al. 2008), the fragmented nature of available land within urban landscapes might further impose a spatial structure on any invasive populations. This is in contrast to other methods of introduction such as the introduction of trees for silviculture where continuous broad-scale stands are typically planted over large areas with numerous introduction sites in regions of close proximity to one another (Richardson 1998; Richardson and Blanchard 2011). Invasions stemming from such introductions may be expected to have a contiguous spatial structure at the landscape scale (e.g. Richardson and Brown 1986). Human-usage factors at an individual stand would therefore play a reduced role and thus the spatial structure of specific stands should be a representation of natural spread rather than an artefact of human introduction.

Previous research on the distribution of invasive *Acacia* species in South Africa used scale-area curves at multiple scales to facilitate the assessment of the invasive risk of species in different habitats (Veldtman et al. 2010). However, this work focused on a species introduced and widely disseminated (mainly for dune stabilisation), that is common throughout its climatically suitable non-native range in South Africa. Here we identify and analyse the spatial pattern of an invasive *Acacia* species disseminated as an ornamental tree that is likely to still exhibit spatial patterns in its distribution related to the method of introduction.

Australian *Acacia* species were disseminated globally for a multitude of purposes for a period greater than 150 years (Richardson et al. 2011). Many of these introduction events resulted in the establishment and spread of introduced *Acacia*, resulting in a number of species becoming amongst the most widespread invasive woody plants globally (Richardson and Rejmánek 2011). Australian *Acacia* invasions in South Africa have received a substantial amount of focus in the literature, resulting in a wealth of information on their introduction histories, life history traits and current distribution (Henderson 2006;

Poynton 2009; Gibson et al. 2011; Le Roux et al. 2011). The variety of reasons why humans introduced Australian *Acacia* species to South Africa, and the frequency and extent of invasions resulting from these introductions makes this system ideal for exploring the degree to which introduction history shapes current invasion patterns.

Acacia longifolia was brought to South Africa for use in the stabilization of mobile dune systems in coastal areas (Avis 1989). Historical attempts at dune stabilization were characterized by the planting of large numbers of trees into open landscapes over large areas of coast (Avis 1989). In contrast *Acacia elata* was disseminated in South Africa as a garden ornamental tree (Poynton 2009). Low numbers of trees were therefore introduced into conurbations haphazardly scattered throughout the country. The reproductive history of both species is characterized by gravity dispersed, high dormancy seeds that form substantial soil stored seed banks under their respective canopies. Similarities in seed dispersal mechanisms and life-history traits combined with the well documented differences in introduction history make these species ideal for developing an understanding of how human use influences the invasive distributions of tree species. Here we describe the spatial structure of invasive populations of *A. elata* in South Africa using scale-area curves and compare our findings to those of Veldtman et al. (2010) who focused on *A. longifolia*.

In this paper we aim to identify differences in the spatial structure of invasive populations of *A. elata* and *A. longifolia* that can be linked back to their reason for introduction using scale-area curves. In so doing we also aim to highlight the potential for scale-area curves to be used to prioritize the management of invasive species.

Materials and methods

Study species

Acacia elata (A. Cunn. Ex Benth.), one of at least 80 Australian *Acacia* species introduced to South Africa (Richardson et al. 2011), was initially used in trial plantings for silviculture in the early twentieth century (Poynton 2009). However, the species failed to impress for its original intended use, and instead became widely distributed as a popular ornamental

tree. Consequently, *Acacia elata* was planted in small numbers at many sites of human habitation across the country (Poynton 2009). It has since become naturalized and invasive in a number of regions but to date has received little direct management attention, although indications are that it has a similar potential impact to many other invasive Australian acacias. Invasive populations develop substantial seed-banks of hard coated seeds that respond to disturbance. Dispersal is mostly through gravity with some evidence of secondary movement by ants (O'Dowd and Gill 1986; Donaldson 2013) and so seeds do not naturally disperse particularly far (99.9 % < 20 m).

Acacia longifolia was brought to South Africa during the nineteenth century for use in the stabilization of mobile dune systems in coastal areas (Avis 1989). Native to the south-eastern coastal belt of Australia it was selected for its ability to grow in sandy soils (Avis 1989). Dune stabilization plantings were carried out extensively along the southern coast of South Africa with substantial effort put into aiding the establishment of populations both in terms of numbers and cultivation effort (Avis 1989). Although some plantings of *A. longifolia* are linked to the ornamental trade, the majority of established populations have resulted from larger introduction events into natural and/or disturbed landscapes adjacent to suitable areas for spread associated with dune stabilization. The reproductive biology of *A. longifolia* is similar to that of *A. elata* with a high proportion of the seeds being dormant and dispersed via gravity and secondary ant dispersal, resulting in large soil stored seed banks under the dense canopies but with little long-distance seed movement (Milton and Hall 1981; Marchante et al. 2010).

Study area

We followed the methodology of Veldtman et al. (2010). All quarter-degree grid cells (QDGC, 15' latitude by 15' longitude) recorded as occupied by *A. elata* were extracted from the Southern African Plant Invaders Atlas (SAPIA; details in Richardson et al. 2005). A subsample of these 48 QDGCs was selected for fractal sampling. Cells that incorporated populations from the entire distribution of the species in South Africa were selected. Cells were selected to cover populations from the northern, southern and western regions of the country similar to those worked

on by Veldtman et al. (2010) to allow comparison with populations of *A. longifolia*. QDGCs sampled were named after the largest major town incorporated in or close to each cell (Elgin, Somerset West, Hermanus, Springbok, Knysna, Storms River, George, Hankey, Carletonville and Johannesburg).

For fractal sampling and scale-area curves to become a practical management tool at the national scale they need to be feasible both economically and temporally. To limit expenses while still sampling a reasonable portion of occupied cells we selected ten QDGCs for analysis (Fig. 1). This number was based on an average driving distance of 200 km per QDGC cell and 3 working days with two surveyors per cell for fractal sampling field surveys. Four cells were selected from each of the two most heavily invaded regions (western and southern) and two cells from the less densely occupied northern region of South Africa (Fig. 1). Cells selected were those with the greatest road access to maximize sampling efficiency (Kunin 1998; Hartley et al. 2004; Veldtman et al. 2010).

Fractal sampling

Field surveys to collect abundance and occupancy data took place from January to March 2013 when adult trees were in flower and easy to identify in the landscape. Each selected QDGC was visited and divided into 100 equally sized cells (1.5' by 1.5') which were systematically surveyed by driving all available roads and mapping populations with a global positioning system receiver (Garmin GPSmap 62 s; Garmin International, Olathe, KS, USA) containing the predefined grids setup for field surveys. In areas where trees were densely populated, visibility was poor, or road access was restricted, the area was searched further on foot. Within each cell the presence or absence of *A. elata* was noted and the abundance within the cell estimated as low (<10 mature individuals), medium (between 10 and 100 individuals) or high (more than 100 individuals). Of the 100 cells assessed, two cells (one 1.5' by 1.5' cell with high and one 1.5' by 1.5' cell with low abundance) were selected and split into a further 100 cells (0.15' by 0.15') and these cells surveyed more intensively on foot with the abundance and occupancy recording process repeated. Again, from the 100 smaller cells, two cells were selected (one high and one low density) and divided into a further 100 cells (0.015' by 0.015').

Fig. 1 Quarter-degree grid cells occupied by *Acacia elata* (black dots) in South Africa. The ten cells sampled in this study are shaded completely black. An example of the fractal sampling design used to determine occupancy at four different

scales is indicated on the right with one low and one high occupancy cell selected at each resolution where possible: Regional (15' latitude by 15' longitude), landscape (1.5' by 1.5'), local (0.15' by 0.15') and plot (0.015' by 0.015')

The abundance in these cells was identified as low (<10), medium ($10 < x < 50$) or high (>50) on foot by walking transects and, where possible, two cells of each category randomly selected. The six randomly selected 0.015' by 0.015' cells were then split into 100 cells each. All the trees with a circumference of greater than 150 mm in the selected 0.015' by 0.015' grids cells were mapped (Fig. 1). Abundance estimates at the smallest scale were averaged between cells of the same category to estimate relative abundances for larger resolution cells.

Generating scale-area curves

We constructed scale-area curves by comparing the linear occupancy (km^2) and linear resolution (km). Longitude was converted to the appropriate distance in kilometres using the equation: longitude (km) = $(\pi/180) * R * \cos(A)$, where R represents the radius of the earth and A represents latitude. Across the study area (26°S–35°S) the longitudinal length of cells varies only slightly 25.2–26.1 km, with a constant latitudinal length of 27.6 km. Occupancy was determined at each

scale by multiplying the number of occupied grid cells by the size of the cell (Hartley et al. 2004). Occupancy was estimated at four different resolutions by aggregating the finest resolution data (100 cells) into three levels of coarser resolution (25 cells, 4 cells and 1QDGC; also see Veldtman et al. 2010). As a result we analysed occupancy at 12 fractal dimensions (sensu Veldtman et al. 2010; Hartley et al. 2004; Wilson et al. 2004) (scales $i-j$ in approximate km: plot scale, 0.0025–0.005, 0.005–0.0125, 0.0125–0.025; local scale, 0.025–0.05, 0.05–0.125, 0.125–0.25; landscape scale 0.25–0.5, 0.5–1.25, 1.25–2.5; and regional scale, 2.5–5, 5–12.5, 12.5–25).

For each of the 10QDGCs sampled during field work we computed the relationship between the box-counting fractal dimension (D_{ij}) and scale ($i-j$ km). The fractal dimension (D_{ij}) was calculated using the equation $D_{ij} = 2 - b_{ij}$, where b_{ij} represents the slope of the regression between log area of occupancy (km^2) and log linear dimension (km) (Hartley et al. 2004). D_{ij} is used to describe the spatial makeup of a species between scales $i-j$ with the maximum value of 2 indicating coarse cells are completely filled with

occupied fine scale cells, while a minimum value of 0 indicates the occupancy of a coarse scale cell by a single occupied fine scale cell (Kunin 1998).

Statistical analysis

All analyses were done in R3.0.1 (R Core Team 2013). Differences between population structure at four different scales (plot, local, landscape, regional) were assessed by comparing all QDGC D_{ij} scores at different scales using the Friedmans Rank Sum Test (Hollander and Wolfe 1999). As post hoc analyses on Friedmans Rank Sum Test are considered weak (Baguley 2012), we therefore rank transformed data before testing for interactions between different scales using a one-way repeated measures ANOVA with scale the within-subjects-factor grouped by QDGC. A post hoc Tukey HSD test was then run to assess where differences in spatial structure between scales occurred (Canover and Iman 1981; Baguley 2012).

To compare the spatial structure of *A. elata* with that of *A. longifolia* we used data for the 8 occupied *A. elata* QDGCs with the 12 QDGCs occupied by *A. longifolia* (data from Veldtman et al. 2010). We compared D_{ij} values at each scale between the two species using a Wilcoxon Signed Rank Test (Hollander and Wolfe 1999).

Results

Spatial Structure of *Acacia elata*

Occupancy levels varied markedly between cells (Fig. 2). Despite this, there was a consistent relationship across all assessed QDGC containing invasive populations with high D_{ij} scores at the finest and coarsest scales [(i.e. plot (0.0025–0.025 km) and regional (2.5–25 km)] compared to the intermediate scales [(i.e. local (0.025–0.25 km) and landscape (0.25–2.5 km); see Table 1, Fig. 3)]. This suggests that at the very localized and broad levels the spatial distribution of *A. elata* in South Africa shows greater continuity than the relatively fragmented state of the distribution at the local and landscape scale.

The Friedmans Rank Sum Test ($p < 0.001$) and one-way repeated measures ANOVA ($p < 0.001$) indicated that there were differences in D_{ij} scores between scales. The post hoc analysis showed that

Fig. 2 Scale–area curves for *Acacia elata* for quarter-degree grid cells surveyed at multiple scales in South Africa. Steeper slopes indicate fragmented populations, whereas more gradual gradients are typical of more contiguous populations

(a) populations at the plot scale were more contiguous than those at the both local and landscape scales ($p < 0.001$); (b) local and landscape scales did not differ significantly; and (c) populations appear more contiguous at the regional scale than the landscape scale ($p < 0.01$) but are not significantly different in structure to those at the plot and local scale.

Comparison between *A. elata* and *A. longifolia*

The Wilcoxon Signed Rank Test indicated that populations of *A. longifolia* were found to be significantly more contiguous ($p < 0.05$) than *A. elata* across most scales, in particular between 125 m and 5 km (Fig. 3).

Discussion

The relatively low D_{ij} scores for *Acacia elata* at the local and landscape scale when compared with the plot and regional scales suggest that spatial distribution is scattered between 250 m and 2.5 km. Hui et al. (2006) suggest that low D_{ij} are indicative of weak spatial autocorrelation resulting from the absence of strong ecological processes at the scale analysed. In the case of *A. elata* it appears that ecological processes acting over distances between 250 and 2.5 km seem to be the reason for the limited distribution of *A. elata* in South Africa. One potential reason for the observed pattern is that ornamental trees cultivated in gardens may act as source populations for small invasive patches. These

Table 1 Scale-specific box-counting fractal dimensions (D_{ij}) for quarter-degree grids cells occupied by *Acacia elata* in South Africa (linear resolution from 25 km to 2.5 m)

QDGC	Latitude	Longitude	Scale (i-j)			
			2.5–25 m plot	25–250 m local	250 m–2.5 km landscape	2.5–25 km regional
Elgin	–34° 15' S	19°00'E	0.92	0.88	0.66	0.92
Somerset West	–34° 15' S	18°45'E	1.00	0.70	0.71	0.91
Hermanus	–34° 30' S	19°15'E	0.76	0.33	0.10	0.40
Knysna	–34° 15' S	23°00'E	0.58	0.51	0.33	0.33
Storms River	–34° 00' S	23°45'E	1.13	0.63	0.55	0.88
George	–34° 00' S	23°15'E	0.60	0.57	0.00	0.62
Carletonville	–26° 30' S	27°15'E	0.23	0.00	0.00	0.25
Johannesburg	–26° 15' S	27°45'E	0.64	0.38	0.65	0.78

D_{ij} explains the spatial makeup of a species between scales i – j ; the maximum value of 2 indicates that coarse cells are completely filled with occupied small-scale cells, while a minimum value of 0 indicates the occupancy of a coarse-scale cell by a single occupied smaller scale cell

Fig. 3 Comparison of mean box-counting fractal dimensions (D_{ij}) for *Acacia elata* ($n = 8$; this study) and *A. longifolia* ($n = 12$; Veldtman et al. 2010) for quarter-degree grid cells surveyed at multiple scales in South Africa. Maximum values of 2 indicate that coarse cells are completely filled with occupied fine scale cells; a minimum value of 0 indicates the occupancy of a coarse scale cell by a single occupied fine-scale cell (Wilcoxon signed rank test, $*p < 0.05$, $**p < 0.01$)

patches may occur in uncultivated areas with broader conditions that do not support sustainable populations. As a result small pockets of invasive trees will be interspersed by large areas where trees are absent. This cannot be fully discounted and will undoubtedly play a role in the observed spatial structure of certain naturalized populations. However, the presence of multiple generations of trees in invasive stands, and presence of invasive stands far from cultivated trees suggests other factors are limiting spread over the intermediate scale. We suggest that the failure of processes operating over distances of 250 m to 2.5 km

is linked to interactions between life-history trait limitations and the human-mediated method of introduction as ornamental trees. Ornamental trees are introduced into suburban habitats, a habitat that is often highly fragmented at scales between 250 m and 2.5 km. The combination of the fragmented landscape and the inability of *A. elata* to disperse over large distances will mean that populations may establish in suitable pockets in urban space but that further spread will be limited by a lack of suitable land (Minor et al. 2009). Thus despite suitable conditions that allow initial establishment and naturalization, the

Fig. 4 Position of invasive *Acacia elata* trees spreading in a suburban area of Knysna, Western Cape, South Africa

combination of dispersal limitations and placement into heavily human altered landscapes with large areas of unsuitable land will limit expansion of populations beyond the plot scale. Roads, properties, and intensive management of human-dominated areas create large unsuitable areas with large distances between patches of suitable habitat (Fig. 4; Minor et al. 2009). In such cases, secondary dispersal (in the form of a mutualism with birds, passive dispersal in water, or through the deliberate or unintended movement of seed by humans) is required (Minor et al. 2009). As *A. elata* is not adapted for dispersal by birds (O'Dowd and Gill 1986), medium-distance movements of propagules will rely heavily on dispersal by humans and with deliberate introductions limited to personal preference, plantings of long-lived trees into gardens is likely to be infrequent resulting in low numbers of deliberately moved propagules over medium to long distances. Thus the most likely movement of seeds will be through unintentional human movement. Support for this notion is provided by the relatively continuous spatial structure at landscape scales of two sites where forestry is the dominant land use type (Storms River and Elgin sites). Heavy machinery used in silvicultural operations has been shown to be a key dispersal vector for many invasive species (Watkins et al. 2003; Christen and Matlack 2009), including other *Acacia* species (Kaplan et al. 2013). It is likely that at these two sites the increased accidental

movement of seeds by machinery is acting to override the natural dispersal limitations of *A. elata* being experienced at other sites.

If populations are dispersal limited, we would predict that the scale-area curves would be steep and that the gradient would only become shallow when dispersal barriers are overcome or where trees are introduced or seeds are dispersed to areas with large tracts of connected suitable land as the invasion progresses (with increased residence time), and so D_{ij} scores would become more consistent across spatial scales. Species with a longer residence time, larger initial propagule pressure, efficient long-distance dispersal, placement into areas with large, connected areas susceptible to invasion, or large extent of initial distribution would likely have scale-area curves more indicative of observed population dynamics. This seems to be the case for *A. longifolia* which experienced substantially more planting effort than *A. elata*, with larger numbers of trees introduced over large areas with large tracts of connected suitable habitat. Thus, despite the similarly limited dispersal capabilities of *A. longifolia*, occupied cells consistently showed greater continuity in population structure than *A. elata* across all scales assessed (Fig. 2). Furthermore, the most heavily occupied *A. elata* cells assessed in this study had steeper scale-area curves than for the most occupied *A. longifolia* cells, indicating that *A. elata* populations are not (yet) as

dense as *A. longifolia* at landscape and local scales. This is expected to change over time and we would suggest that, if left unmanaged, *A. elata* populations will eventually reach sites with more connected suitable land which will favour spread and could result in invasions of a similar scale to more notorious and currently damaging *Acacia* species such as *A. mearnsii* and *A. saligna*. A more definitive test of these assumptions would be to assess species with similar human introduction pathways but different natural dispersal mechanisms. Research analysing the spatial structure of bird-dispersed species such as *A. cyclops* may provide more definitive comparisons regarding the influence of human use on the spatial structure of invasive plants. Alternatively, patterns in QDGCs that differ in known aspects of planting effort could be compared, though detailed data on planting effort (i.e. dates and localities) are often not available for ornamental species.

We argue that the lack of contiguous *A. elata* populations over 250 m to 2.5 km is not indicative of a low risk, but the result of the spatial structure of available land. Contrary to the suggestions of Veldtman et al. (2010) that fragmented populations are unlikely to spread we would argue that these populations in urban environments may represent substantial invasive debt (Essl et al. 2011) that if afforded the opportunity to “escape” fragmented environments and reach open landscapes could result in an increased rate of invasion. This could explain to some extent the lag phases observed for certain species initially introduced to urban landscapes (Aikio et al. 2010). We suggest that in cases such as that of *A. elata*, management should focus on maintaining the current “missing links” in the invasive chain by limiting the movement of trees and seed over distances between 250 m and 2.5 km and ensuring that populations remain restricted to urban areas that do not allow further spread i.e. ensure populations near green belts and open land are removed and new introductions to areas away from conurbations are completely limited. In this capacity the control of *A. elata* seems relatively straight forward with containment and localized eradications the most feasible option (Moore et al. 2011). Effective containment could be greatly improved through the introduction of biological control of seed production which would reduce the likelihood of accidental seed movement (Impson et al. 2011). Areas where urban environments are in close

proximity to forestry stations should receive the greatest attention with Somerset West, Elgin, and Storms River representing the greatest threat according to this study.

We argue that, when working with introduced species, scale-area curves representing fragmented populations should not be considered to indicate a lack of invasive spread/threat. Rather D_{ij} scores at the plot scale will give the greatest representation of a population’s ability to establish as anything larger may simply be representative of the fragmented landscape into which species are introduced. Scale-area curves can provide a useful management tool, however care should be taken to understand the area into which subject species have been introduced and the time since introduction when assessing invasive threat. Species that show dense populations at the plot scale after short periods since introduction should be identified as threatening. In particular species introduced initially as ornamentals to urban environments that appear in contiguous populations outside conurbations a short period after introduction should be considered a substantial threat as these would be species that display the ability to disperse beyond the ‘restrictive’ urban environment and thus display widespread dispersal capacities indicative of major invasive species such as Brazilian peppertree (*Schinus terebinthifolius*) in Florida and Hawaii and miconia (*Miconia calvescens*) on islands in the South Pacific (Meyer 1996, 1998; Williams et al. 2007).

Scale-area curves can thus be used to identify “missing links” in the invasive introduction-naturalization-invasion continuum if they are used in an appropriate manner. Of particular use is the ability to identify sections where weak processes are limiting invasive spread, which with appropriate knowledge of species life-history traits, introduction history and area affected can aid management in developing management protocols that will be the most fruitful. Perhaps a more powerful use of scale-area curves is their potential for monitoring. One interesting area is the increasing trend in horticulture to match species to the surrounding habitat in an attempt to reduce cultivation expenses (eco-gardening) and as a result threatens to introduce an entirely new suite of invasive species (Bradley et al. 2011). With the large number of species involved in the trade and diversity of stake holders identifying and monitoring potential threats is set to become an increasingly expensive challenge to

managers looking to limit invasive costs. Scale-area curves could be used as a standard means to monitor such species. Naturalized populations that have high D_{ij} values at the plot scale would be considered indicative of potentially threatening species. More definitively plots could be set up for similar assessments at the edge of urban landscapes where large tracts of potentially invisible land are present. In these areas species that appear and develop flattened curves over multiple scales and short periods should be highlighted as species that need immediate consideration.

In summary, we believe that scale-area curves can provide useful insights for invasive species management, but only if the life-history traits, introduction history and potential area suitable for invasion are well understood and are used in interpreting the results. We suggest that their greatest value will lie in their use as a feasible method for the long-term monitoring of introduced species.

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References

- Aikio S, Duncan RP, Hulme PE (2010) Lag-phases in alien plant invasions: separating the facts from the artifacts. *Oikos* 119:370–378
- Avis AM (1989) A review of coastal dune stabilization in the Cape Province of South Africa. *Landscape Urban Plan* 18:55–68
- Baguley T (2012) *Serious stats: A guide to advanced statistics for behavioural sciences*. Palgrave
- Bradley BA, Blumenthal DM, Early R (2011) Global change, global trade, and the next wave of plant invasions. *Front Ecol Environ* 10:20–28
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. *Annu Rev Ecol Syst* 27:597–623
- Canover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *Am Stat* 35:124–129
- Caplat P, Hui C, Maxwell B, Peltzer DA (2013) Cross-scale management strategies for optimal control of trees invading from source plantations. *Biol Invasions*. doi:10.1007/s10530-013-0608-7
- Castro-Díez P, Langendoen T, Poorter L, Saldaña-López A (2011) Predicting invasiveness of Australian *Acacia* species on the basis of their native climatic affinities, life-history traits and human use. *Divers Distrib* 17:934–945
- Christen DC, Matlack GR (2009) The habitat and conduit functions of roads in the spread of three invasive plant species. *Biol Invasions* 11:453–465
- Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541–1553
- Deuschewitz K, Lausch A, Klotz S, Kühns K (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecol Biogeogr* 12:299–311
- Donaldson JE (2013) The invasion ecology of *Acacia elata* (A. Cunn. Ex Benth.) with implications for the management of ornamental wattles. MSc Dissertation, Stellenbosch University, pp 13–34
- Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K, Jarošík V, Kleinbauer I, Krausmann F, Kühn I, Nentwig W, Vilà M, Genovesi P, Gherardi F, Desprez-Loustau M, Roques A, Pyšek P (2011) Socioeconomic legacy yields an invasion debt. *Proc Natl Acad Sci USA* 108:203–207
- Foxcroft LC, Richardson DM, Wilson JR (2008) Ornamental plants as invasive aliens: problems and solutions in the Kruger National Park, South Africa. *Environ Manage* 41:32–51
- Gaston KJ (1999) Implications of interspecific and intraspecific abundance-occupancy relationships. *Oikos* 105:657–663
- Gaston KJ (2008) Biodiversity and extinction: the importance of being common. *Prog Phys Geog* 32:73–79
- Gibson MR, Richardson DM, Marchante E, Marchante H, Rodger JG, Stone GN, Bryne M, Fuentes-Ramírez A, George N, Harris C, Johnson SD, Le Roux JJ, Miller JT, Murphy DJ, Pauw A, Prescott MN, Wandrag EM, Wilson JR (2011) Reproductive biology of Australian acacias: important mediator of invasiveness. *Divers Distrib* 17:911–933
- Hartley S, Kunin WE (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conserv Biol* 17:1559–1570
- Hartley S, Kunin WE, Lennon JJ, Pocock MJO (2004) Coherence and discontinuity in the scaling of species' distribution patterns. *Proc R Soc Lond B* 271:81–88
- Henderson L (2006) Comparisons of invasive plants in South Africa originating from southern temperate, northern temperate and tropical regions. *Bothalia* 36:201–222
- Hollander M, Wolfe DA (1999) *Nonparametric statistical methods*, 2nd edn. Wiley, New York
- Hui C (2011) Forecasting population trend from the scaling pattern of occupancy. *Ecol Model* 222:442–446
- Hui C, McGeoch MA, Warren M (2006) A spatially explicit approach to estimating species occupancy and spatial correlation. *J Anim Ecol* 75:140–147
- Hui C, McGeoch MA, Reyers B, Le Roux PC, Greve M, Chown SL (2009) Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecol Appl* 19:2038–2048

- Impson FAC, Kleinjan CA, Hoffmann JH, Post JA, Wood AR (2011) Biological control of Australian *Acacia* species *Paraserianthes lophantha* (Willd.) Nielsen (Mimosaceae) in South Africa. *Afr Entomol* 19:186–207
- Kaplan H, van Niekerk A, Le Roux JJ, Richardson DM, Wilson JR (2013) Incorporating risk mapping at multiple spatial scales into eradication management plans. *Biol Invasions*. doi:10.1007/s10530-013-0611-z
- Kunin WE (1998) Extrapolating species abundance across spatial scales. *Science* 281:1513–1515
- Le Roux JJ, Brown GK, Byrne M, Ndlovu J, Richardson DM, Thompson GD, Wilson JR (2011) Phylogeographic consequences of different introduction histories of invasive Australian *Acacia* species and *Paraserianthes lophantha* (Fabaceae) in South Africa. *Divers Distrib* 17:861–871
- Lockwood JL, Cassey P, Blackburn TM (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* 20:223–227
- Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers Distrib* 15:904–910
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Mack RN (2005) Predicting the identity of plant invaders: future contributions from horticulture. *Hort Sci* 40:1168–1174
- Marchante H, Freitas H, Hoffmann JH (2010) Seed ecology of an invasive alien species, *Acacia longifolia* (Fabaceae), in Portuguese dune ecosystems. *Am J Bot* 11:1780–1790
- Meyer J-Y (1996) Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). *Pac Sci* 50:66–76
- Meyer J-Y (1998) Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). *Biotropica* 30:609–624
- Milton SJ, Hall AV (1981) Reproductive biology of Australian *Acacias* in the south-western Cape province, South Africa. *T Roy Soc S Afr* 44:465–487
- Minor ES, Tessel SM, Engelhardt AM, Lookingbill TR (2009) The role of landscape connectivity in assembling exotic plant communities: a network analysis. *Ecology* 90:1802–1809
- Moore JL, Runge MC, Webber BL, Wilson JR (2011) Contain or eradicate? Optimizing the management goal for Australian *acacia* invasions in the face of uncertainty. *Divers Distrib* 17:1047–1059
- O'Dowd DJ, Gill AM (1986) Seed dispersal syndromes in Australian *Acacia*. In: Murray DM (ed) *Seed dispersal*. Academic Press, Australia, pp 87–121
- Poynton RJ (2009) Tree planting in southern Africa, Volume 3: Other genera. Department of Agriculture, Forestry and Fisheries, South Africa
- Procheş Ş, Wilson JR, Richardson DM, Rejmánek M (2012) Native and naturalised range size in *Pinus*: relative importance of biogeography, introduction effort and species traits. *Global Ecol Biogeogr* 21:513–523
- Richardson DM (1998) Forestry trees as invasive aliens. *Conserv Biol* 12:18–26
- Richardson DM, Blanchard R (2011) Learning from our mistakes: minimizing problems with invasive biofuel plants. *Curr Opin Environ Sust* 3:36–42
- Richardson DM, Brown PJ (1986) Invasion of mesic mountain fynbos by *Pinus radiata*. *S Afr J Bot* 52:529–536
- Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species—a global review. *Divers Distrib* 17:788–809
- Richardson DM, Rouget M, Ralston SJ, Cowling RM, van Rensburg BJ, Thuiller W (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *EcoScience* 12:391–402
- Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JR (2011) Human-mediated introductions of Australian *acacias*—a global experiment in biogeography. *Divers Distrib* 17:771–787
- Rouget M, Richardson DM, Nel JL, Le Maitre DC, Egoh B, Mgid T (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. *Divers Distrib* 10:475–484
- R Core Team (2013) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Thuiller W, Richardson DM, Rouget M, Procheş S, Wilson JR (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology* 87:1755–1769
- Veldtman R, Chown SL, McGeoch MA (2010) Using scale-area curves to quantify the distribution, abundance and range expansion potential of an invasive species. *Divers Distrib* 16:159–169
- Watkins RZ, Chen J, Pickens J, Brososke KD (2003) Effects of forest roads on understory plants in a managed hardwood landscape. *Conserv Biol* 17:411–419
- Williams DA, Muchugu E, Overholt WA, Cuda JP (2007) Colonization patterns of the invasive Brazilian peppertree, *Schinus terebinthifolius*, in Florida. *Heredity* 98:284–293
- Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature* 432:393–396
- Wilson JR, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L, Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Divers Distrib* 13:11–22
- Wilson JR, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol Evol* 24:136–144
- Wilson JR, Caplat P, Dickie IA, Hui C, Maxwell BD, Nuñez MA, Pauchard A, Rejmánek M, Richardson DM, Robertson MP, Spear D, Webber BL, van Wilgen BW, Zenni RD (2013) A standardized set of metrics to assess and monitor tree invasions. *Biol Invasions*. doi:10.1007/s10530-013-0605-x