

Using scale–area curves to quantify the distribution, abundance and range expansion potential of an invasive species

Ruan Veldtman^{1*}, Steven L. Chown¹ and Melodie A. McGeoch^{2†}

¹Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, and ²Department of Conservation Ecology and Entomology, Centre for Invasion Biology, Stellenbosch University, Stellenbosch, South Africa

ABSTRACT

Aim Invasive species distribution and abundance data are essential for management decisions on mitigating impacts but is seldom available. Here, we use scale–area curves to assess the distribution, abundance and consequent management implications of an invasive plant (*Acacia longifolia*) within selected occupancy grid cells, spread across regional ranges and representing the full national extent. We determine whether occupancy patterns are explained by climatic suitability or range structure and identify areas where *A. longifolia* can still be regarded as an important invasive based on contiguous occupancy.

Location South Africa including the Fynbos, Thicket, Savanna and Grassland biomes.

Methods The quarter degree occupancy of *A. longifolia* was used to select core, edge, and climatically unsuitable grid cells within different regions of the national range. Cells were surveyed across a linear resolution from 25 km to 2.5 m allowing the first multi-scales description of an invasive species' space-filling properties. Patterns from grid cells in turn were viewed regionally to describe regional variation in spatial structure.

Results In regions with contiguous areas of favourable habitat, scale–area curves indicated greater occupancy in core than edge areas, whereas patterns were reversed when suitable areas were more fragmented. Also, at times climatically suitable areas were unoccupied, while unsuitable areas were occupied. Within cells, occupancy was well explained by the presence of fynbos vegetation types, while nationally, contiguous occupancy was almost exclusive to the Fynbos Biome.

Main conclusions Scale–area curves can advance the understanding of biological invasions and invasive plant distributions. Here, we detected potential areas of invasive concern, plus differences in abundance and distribution patterns, and associated correlates, at landscape and national scales. As there was no general relationship between range position or climatic suitability and *A. longifolia*'s spatial structure, we propose habitat suitability as an alternative explanation which, in turn, suggests limited range expansion potential.

Keywords

Acacia longifolia, biological invasions, climatic suitability, niche-limited, occupancy, *Trichilogaster acaciaelongifoliae*

*Correspondence: South African National Biodiversity Institute, Applied Biodiversity Research, Kirstenbosch Research Centre, Private Bag X7, Claremont, 7735, South Africa. E-mail: r.veldtman@sanbi.org.za

†Present address: South African National Parks, Cape Research Centre, Cape Town, South Africa.

INTRODUCTION

Invasive alien species are one of the greatest threats to native biodiversity (Pimm *et al.*, 1995; Blackburn *et al.*, 2004; Hassan *et al.*, 2005). Managing the threat posed by invasive alien

species requires information on the occurrence, abundance and rate of spread in the introduced range of each species. One fundamental difference between the distributions of indigenous and invasive species is that the distribution of the latter may not have reached equilibrium (Rouget *et al.*, 2004), with

the geographic extent of alien species often being highly influenced by human activity, such as transport routes and habitat transformation (Shaughnessy, 1980; Thuiller *et al.*, 2006; Wilson *et al.*, 2007). Consequently, the range of a species with multiple points of introduction is likely to exhibit occupancy patterns influenced by factors such as time since introduction, size and distribution of potential habitat, propagule pressure and distance from founder population (Von Holle & Simberloff, 2005; Colautti *et al.*, 2006; Wilson *et al.*, 2007).

Nonetheless, species with high average local abundances tend to have extensive regional distributions (Brown, 1984; Gaston & Lawton, 1990; Hanski *et al.*, 1993; Gaston, 1999). For an invading species, this implies that if its abundance increases after establishment, so will its regional occupancy – the so-called ‘double trouble’ hypothesis (Gaston, 1999). Thus, high abundance observed at the current edge of an alien species’ range, suggests that further spread may be likely provided suitable habitat exists (Arim *et al.*, 2006). Conversely, low abundance at the edge suggests a comparatively small chance of further spread. Monitoring the abundance of invasive species thus provides information on likely range expansion and limitation. Unfortunately, abundance data are costly to collect and seldom available for invasive species (Gaston, 1999). Further, given the increasingly large number of introduced and potentially invasive species, monitoring of each species’ abundance is not practicable. Therefore, a major constraint in determining the current invasive potential (spread or stationary) of introduced species is the logistic difficulty of collecting local scale abundance data across regional species distributions (e.g. Foxcroft *et al.*, 2009).

Scale–area curves can be used to describe the space-filling properties of a species at multiple scales, thus representing a useful method to simultaneously collect abundance and distribution data from small to large scales (Hartley *et al.*, 2004). Specifically of interest is the rate (slope of the curve) at which the log area occupied decreases with log linear resolution (Kunin, 1998). When the curve is flat, it means that a species’ occupancy is continuous and aggregated (all cells nearly filled), whilst when steep, occupancy is scattered and fragmented (cells filled sparsely). Wilson *et al.* (2004) used this methodological approach to predict the spread and contraction of species ranges using regional occupancy data at only two spatial resolutions. Species with sparse, fragmented distributions (steep scale–area curves) are predicted to be experiencing population declines because of extinction processes (Brown *et al.*, 1995; Johnson, 1998), while contiguously, densely distributed species (shallow scale–area curves) are predicted to experience increases in population size locally as a result of distance-limited colonization (Shigesada & Kawasaki, 1997). British butterfly species with shallow scale–area curves were indeed found to increase their ranges over time, while species with steep curves experienced range reduction (Wilson *et al.*, 2004). The usefulness of scale–area curves to assess the extinction risk and conservation priority of rare species has also been demonstrated (Hartley & Kunin, 2003). As invasion

(range expansion) represents the converse of extinction threat (range contraction) (Gaston, 1999; van Kleunen & Richardson, 2007), scale–area curves can therefore also be used to assess the threat of invasion, and consequent management priorities, of an introduced species.

A basic scale–area curve can be produced from national occupancy data if of intermediate resolution, which is then aggregated to produce coarse resolution occupancy information (see Kunin, 1998). However, it is well known that species rarely exhibit the same population trends throughout their range (Hengeveld, 1990; Brown *et al.*, 1995; Sagarin & Gaines, 2002). Rather, population dynamics at extremes of the range may be more variable compared with those at the core of the range (Guo *et al.*, 2005), and many species ranges consist of high and low density zones throughout the range (Brewer & Gaston, 2002; McGeoch & Price, 2004). In such cases, a single scale–area curve will produce a prediction of range expansion or decline averaged across the species distribution, potentially missing significant regional differences in species population dynamics. Indeed, the scale–area curves have been shown to be sensitive to spatial clustering and position relative to the border of the range (Witte *et al.*, 2008). Given that the intra-specific abundance–occupancy relationship is scale independent (e.g. He & Gaston, 2003), scale–area curves could thus be used to predict population size trends for subsets of the distribution (i.e. landscape instead of regional ranges). Such an approach may improve predictions and better describe spatial variation in species population and range dynamics at various scales (see also With, 2002).

In South Africa (including Lesotho and Swaziland), the occupancy of more than 500 species of alien plants has been recorded at quarter degree grid (QDG) resolution in the South African Plant Invaders Atlas (SAPIA) database (Henderson, 2001). These data provide a baseline for alien and invasive alien plant distributions recorded from 1979 to 1998 (Henderson, 2001). One invasive alien plant species, *Acacia longifolia* (Andr.) Willd., is an aggressive invader of mountain fynbos, especially mesic mountain slopes and riverine valleys, as well as coastal fynbos in the Western and Eastern Cape provinces of South Africa (Macdonald & Jarman, 1984; Boucher & Stirton, 1987). Anecdotal evidence suggests that the weed is no longer as significant as it was previously owing to excellent biological control by a flower-bud galling wasp, *Trichilogaster acaciaelongifoliae* Froggatt, which causes substantial reductions in seed production (Dennill *et al.*, 1999). Nonetheless, the likely future range and therefore impacts of this species, given the control interventions already made, have not been comprehensively assessed across its local (South African) range (see discussion in van Wilgen *et al.*, 2004). One approach, involving climate envelope modelling (Rouget *et al.*, 2004) has demonstrated that *Acacia longifolia* currently occupies 4.7% (~95 or 60,000 km²) of South Africa’s QDG cells, whereas 11.5% (~232 or 145,000 km²) of these cells are climatically suitable for the species (see supplementary appendix 1 of Rouget *et al.*, 2004). In another estimate, based on expert opinion and estimating condensed cover, *A. longifolia* has a potential

distribution range of 78,000 km², versus a current estimated 1500 km² range in South Africa (van Wilgen *et al.*, 2004). In both assessments, this invasive plant is thus predicted to have the potential to more than double its distribution.

Here, we use scale–area curves as a basis for understanding spatial structure in the distribution and abundance of *A. longifolia* across its range in South Africa. Specifically, we construct scale–area curves for QDG cells representative of *A. longifolia*'s entire range by stratifying sampling into range position categories (i.e. core, edge and climatically unsuitable cells). This allows within-range variation in the space-filling properties of this invasive species to be determined at multiple scales for the first time. These patterns in turn indicate the parts of the national range where *A. longifolia* either still requires further control or, alternatively, is of little concern. In so doing, we provide a wholly different assessment approach to those used previously (see Rouget *et al.*, 2004; van Wilgen *et al.*, 2004).

METHODS

Patterns of occupancy within the range of *Acacia longifolia* and its introduced biocontrol agent, the pteromalid wasp *Trichilogaster acaciaelongifoliae*, in South Africa were determined across a range of nested spatial scales. The presence or absence of wasp-induced galls on *A. longifolia* within each sampling grid at each scale was also recorded. Existing coarse-scale *A. longifolia* occupancy data (from Henderson, 2001) were used, and then finer scale occupancy data were collected for selected occupied cells using a fractal sampling approach (Kunin, 1998; Hartley *et al.*, 2004).

The South African Plant Invaders Atlas (SAPIA) database was used as the basis to determine the current quarter degree grid (QDG) occupancy of *A. longifolia* in South Africa (Henderson, 2001). Additional occupied QDG cells were added by including known *T. acaciaelongifoliae* release sites (Dennill, 1987), extra records in the Fynbos Biome (Richardson *et al.*, 1992) and recent additions to the *A. longifolia* SAPIA database (L. Henderson, pers. comm.). Next, QDG cells were classified as climatically suitable or unsuitable for *A. longifolia* (more or < 50% suitable) based on the climate envelope probability of occurrence data from Rouget *et al.* (2004) (which describes the construction of the climate envelope in detail).

The national distribution of *A. longifolia* was divided into three zones: western, southern and north-eastern South Africa. Depending on the number of direct neighbouring cells (maximum of eight to four depending on position relative to coastline) and position within the climate envelope, QDG cells were classified as 'core' (more than 70% of potential neighbouring QDG cells occupied – expressed as a percentage to accommodate QDG cells bordering the coast), 'edge' (< 70% of potential neighbouring QDG cells occupied), 'climatically suitable' and 'unsuitable' (inside and outside the calculated climate envelope, respectively) (hereafter referred to as range-position categories). Using these criteria, three QDG cells per

range-position category were selected in western South Africa; two core, two suitable and one unsuitable edge QDG cells in southern South Africa; and one suitable and two unsuitable edge QDG cells in north-eastern South Africa (no core QDG cells available) with a total of 17 QDG cells sampled. The distance between QDG cells of different categories within zones was minimized as far as possible.

Field surveys

Surveys were conducted in the selected QDG cells from May 2005 to April 2006. Only, QDG cells with good road access and < 5% alien clearing (according to local land owner or GIS information on national Working for Water alien clearing operations) were used. The fractal sampling approach used by Hartley *et al.* (2004) was employed (slightly modified for geographically referenced occupancy, see later) to determine the within-QDG occupancy of *Acacia longifolia* and *Trichilogaster acaciaelongifoliae*. Each selected QDG cell (15' latitude by 15' longitude) was divided into 100 cells of 1.5' by 1.5' (Fig. 1a), in each of which the occupancy of the weed and wasp was recorded by systematically searching the area using a vehicle and on foot, with a global positioning system receiver (GPS, Garmin GPSMap C60; Garmin International, Olathe, KS, USA). Simultaneously, an assessment of *A. longifolia* abundance was made to assign cells to low, medium or high density groups (< 10, > 10 but < 50 or more than 100 *A. longifolia* trees estimated in a 50-m radius, respectively) (see also Hartley *et al.*, 2004). Next, one representative high and one representative low density 1.5' by 1.5' cell of each QDG cell were further subdivided into 100 cells of 0.15' by 0.15' to determine occupancy at this scale (Fig. 1b). Hereafter, the density assessment procedure was repeated, and one high and one low density 0.15' by 0.15' cell further subdivided into 100 cells of 0.015' by 0.015' and occupancy recorded on foot with a GPS (Fig. 1c). Finally, the occupancy and abundance of *A. longifolia* in each 0.015' by 0.015' cell were classified as < 10 (low), between 20 and 50 (medium) or more than 50 trees (high). Subject to availability, two 0.015' by 0.015' cells of each abundance category were haphazardly selected (Fig. 1c). From one corner of each selected cell, 25 m was sequentially measured off in all four cardinal compass directions with a marked steel chain. At every five metre increment, a rope was used to connect opposite sides of the cell to produce a 5 × 5 grid after clearing vegetation from these paths. Each cell of this grid was then further subdivided into four 2.5 by 2.5 m cells in each of which the number of *A. longifolia* trees (basal circumference > 150 mm) was counted (Fig. 1d).

Analyses

Scale–area curves were constructed to investigate the relationship between log area of occupancy (km²) and log linear dimension (km). For southern QDG cells (between 33°S and 34°S) and northern QDG cells (between 25°S and 26°S), 17

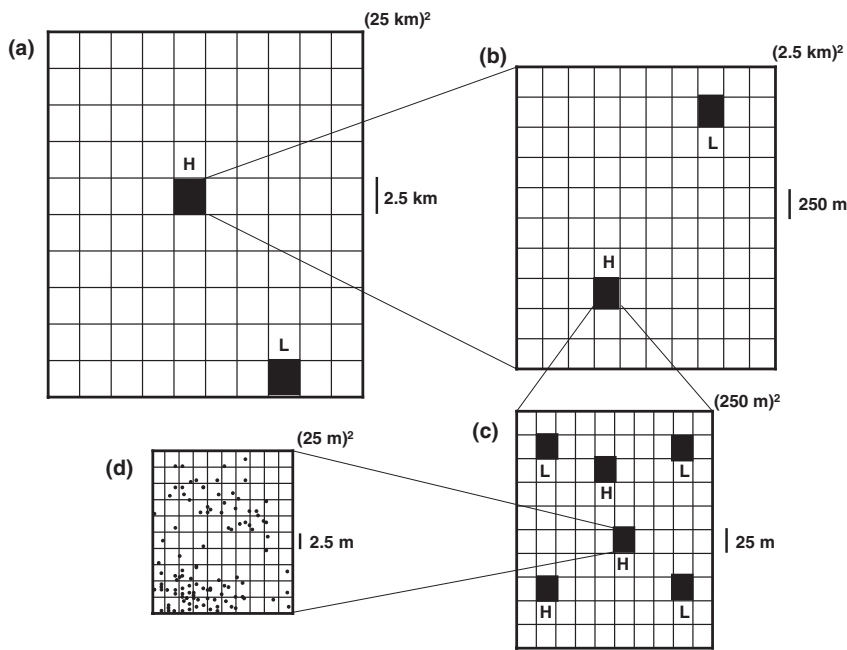


Figure 1 Fractal sampling design for determining occupancy at the (a) quarter degree grid (15' latitude by 15' longitude $\sim 25 \times 25$ km), (b) intermediate (1.5' by 1.5' $\sim 2.5 \times 2.5$ km), (c) fine (0.15' by 0.15' $\sim 250 \times 250$ m) and (d) micro (0.015' by 0.015' $\sim 25 \times 25$ m) scales.

longitude was converted to 22.8 and 24.9 km, respectively. For all QDG cells, 15' latitude was converted to 27.6 km. Consequently the mean length of the linear dimension was 25.2 and 26.25 km for southern and northern QDG cells, respectively. A similar procedure was adopted for the scale–area curve calculations for the intermediate and fine scales. However, at the micro scale limitations in GPS accuracy (3–8 m) meant that 0.015' latitude (27.6 m) and longitude (22.8 or 24.9 m) were approximated to 25 m. The effect of this approximation on log area and log linear dimension values was negligible.

Occupancy sampled at each of the four scales was expressed at four resolutions, by aggregating fine resolution occupancy data (100 cells) to intermediate resolutions (25 and 4 cells, with one QDS cell as the coarsest scale) (Hartley *et al.*, 2004). This study thus investigated occupancy across 12 scale-specific fractal dimensions (*sensu* Hartley *et al.*, 2004; Wilson *et al.*, 2004) (scales i – j in approximate km: micro scale, 0.0025–0.005, 0.005–0.0125, 0.0125–0.025; fine scale, 0.025–0.05, 0.05–0.125, 0.125–0.25; intermediate scale 0.25–0.5, 0.5–1.25, 1.25–2.5; and QDG-scale, 2.5–5, 5–12.5, 12.5–25).

The relationship between the box-counting fractal dimension (D_{ij}) and scale (i – j km) was determined separately for core, climatically suitable and climatically unsuitable edge QDG cells. This allowed a comparison between QDG categories in the change of absolute D_{ij} -values across the entire scale range (25 km to 2.5 m). When an occupied coarse scale cell is completely filled by occupied finer scale cells $D_{ij} = 2$, and if only one finer scale cell is occupied $D_{ij} = 0$ (Kunin, 1998). D_{ij} was calculated with the equation, $D_{ij} = 2 - b_{ij}$, where b_{ij} is the regression coefficient (or slope) of the linear regression of log area of occupancy (km^2) and log linear dimension (km) between scales i (fine resolution) and j (coarse resolution) (Hartley *et al.*, 2004). When $D_{ij} > 1$ occupancy becomes more contiguous with an increase in resolution, whereas $D_{ij} < 1$

indicates that occupancy becomes more fragmented as resolution increases (see also Wilson *et al.*, 2004).

To determine whether vegetation type influenced the occupancy of *A. longifolia* within a QDG cell, each focal cell was divided into ten rows by ten columns (100 cells). A minimum of ten occupied cells per QDG cell was required for analysis. The general vegetation type (e.g. sandstone fynbos, and based on Mucina *et al.*, 2005) present in each of these smaller cells was then determined using GIS tools (ArcGIS® 9.2; ESRI, Redlands, CA, USA). When more than one vegetation type was present in the vegetation covering, the largest area was selected to represent the small cell (maximum was 6.3504 km^2). Each vegetation type was assumed to have an equal probability of *A. longifolia* being present or absent. To determine whether potential differences in frequencies were significant, Chi-square goodness of fit analyses were performed (Zar, 1984). Only vegetation types with more than 10 occupied cells were formally analysed. Alpha level corrections for multiple testing were performed using the step-up false discovery rate (FDR) correction procedure, which has been shown to be the least over-corrective of current alpha-level correction methods (García, 2004).

RESULTS

Of the 17 QDG cells surveyed for *A. longifolia*, all core cells ($n = 5$) were found to contain the species, while five of six edge cells and two of five unsuitable edge cells contained trees (Fig. 2a). The wasp, *T. acaciaelongifoliae*, was present within all cells where *A. longifolia* occurred, irrespective of scale, tree density or climatic suitability. Consequently, the scaling curves of *T. acaciaelongifoliae* and *A. longifolia* will be identical.

Scale–area curves were markedly different between QDG cells (Fig. 3). For example, in the Western Cape, core cells had

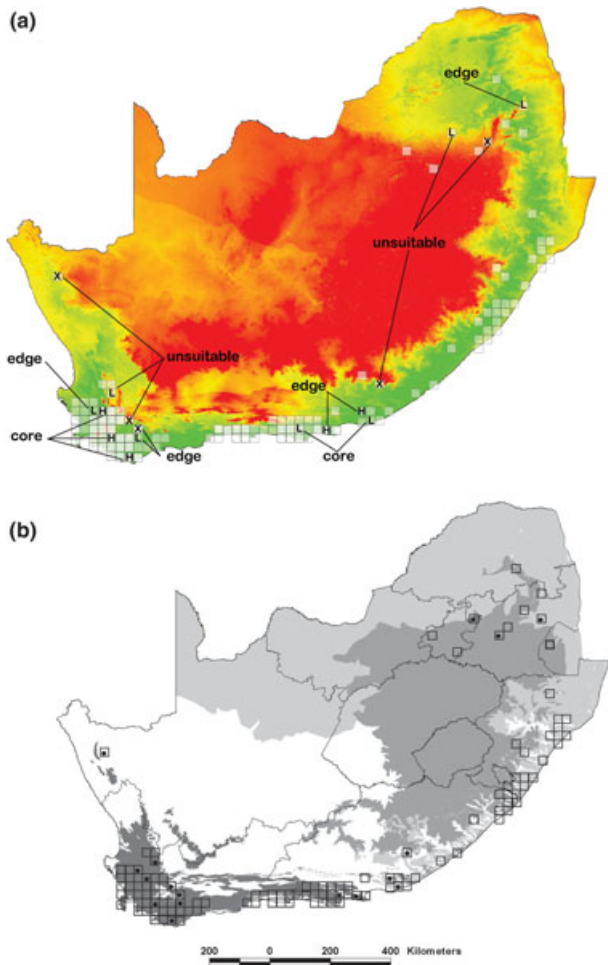


Figure 2 (a) Quarter degree grid (QDG) distribution of *Acacia longifolia* in South Africa (squares), climate envelope prediction (green = favourable, red = unfavourable), plus quarter degree grids sampled and subjective density assessments. X, L and H refer to absent, low and high density, respectively. (b) *Acacia longifolia* QDG distribution overlaid with Fynbos, Savanna and Grassland biomes.

much flatter curves than edge cells, with the sole occupied unsuitable cell having a scale-area curve with intermediate slope (Fig. 3). However, these differences were reversed in the Eastern Cape, with edge cells having shallow slopes and core cells having steep slopes. In fact, curves for QDG cells with high, intermediate and low occupancy had respective mean b_{ij} values of approximately 0.5, 1.0 and 1.5 across all 12 distance classes, irrespective of their range category (Table 1). This suggests that the Elim, Tulbagh, Caledon, Salem and Uitenhage populations are of concern in terms of requiring control attention, whereas the Porterville, Stormsvlei, Kenton and Sokuhlumi populations are not.

Plots of D_{ij} values across all scales sampled also highlighted the marked differences in distribution and abundance of *A. longifolia* (i.e. its space-filling properties) between range-position categories of different zones (Fig. 4). For example, in the Western Cape, core QDG cells typically had $D_{ij} > 1$

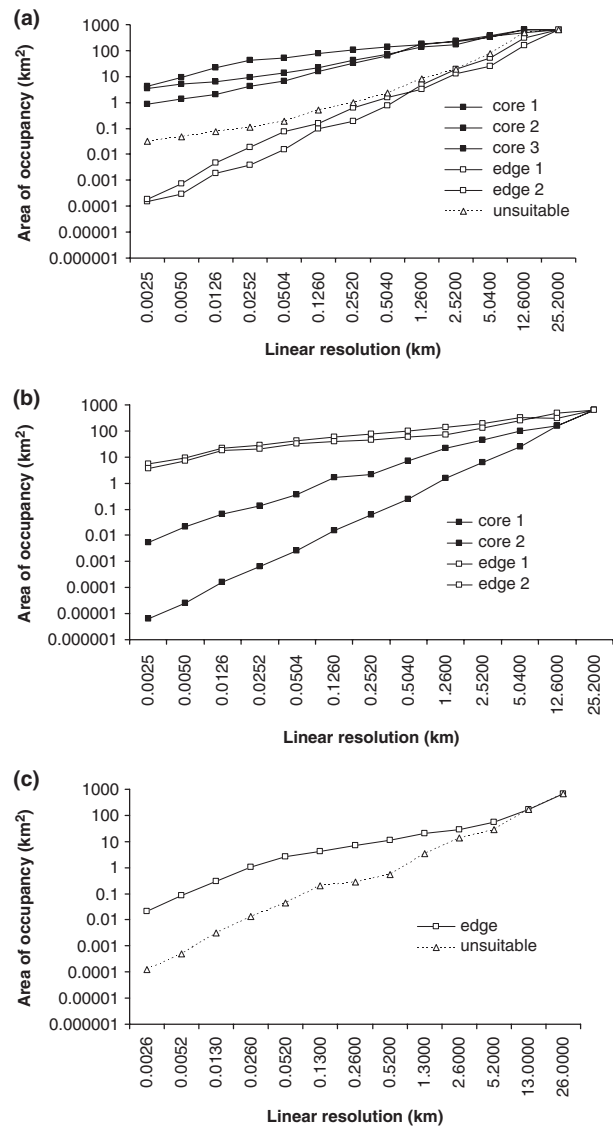


Figure 3 *Acacia longifolia* scale-area curves for quarter degree grid (QDG) cells that were surveyed at finer resolutions (linear resolution from ~25 km to 2.5 m) in (a) western, (b) southern and (c) north eastern South Africa. Lines with steep slopes indicate declining populations, while gentle slopes are typical of increasing populations.

(Fig. 4a), and edge cells had $D_{ij} < 1$ (Fig. 4b), whereas the exact opposite was observed for Eastern Cape QDG cells (Fig. 4c,d). The sole occupied unsuitable edge cell in western South Africa showed a decrease in D_{ij} from 1.5 to 0 with an increase in scale, except at the largest scale range where $D_{ij} > 1.5$ (Fig. 4e). Finally, in north-eastern South Africa, an edge cell had $D_{ij} > 1$ at intermediate scales, but $D_{ij} < 1$ at small and large scales (Fig. 4f), while D_{ij} for an unsuitable cell was generally less than one.

Three core and two edge QDG cells had sufficient *A. longifolia* occupancy to allow Chi-square analysis (Table 2). In all cases, fynbos vegetation types did not deviate significantly from the null hypotheses, that a particular vegetation

Table 1 Slopes (b_{ij}) of scale–area curves (log area of occupancy over log linear resolution). Maximum occupancy has a slope of 0, while minimum occupancy has the slope equals 2.

QDG cell	Range category	Scales $i-j$ (km)															Mean b_{ij}	CV
		0.0025–0.005	0.005–0.0125	0.0125–0.025	0.025–0.05	0.05–0.125	0.125–0.25	0.25–0.5	0.5–1.25	1.25–2.5	2.5–5	5–12.5	12.5–25					
Elim	Core	1.09	0.94	0.98	0.33	0.41	0.50	0.35	0.21	0.51	0.66	0.56	0.00	0.54	0.57			
Caledon	Core	0.60	0.22	0.59	0.56	0.51	0.91	0.75	0.71	0.26	1.11	0.32	0.42	0.58	0.44			
Tulbagh	Core	0.70	0.44	1.06	0.63	0.97	0.99	0.97	1.16	0.29	0.57	0.71	0.00	0.71	0.47			
Stormsvlei	Edge	1.00	2.00	1.01	2.00	2.00	1.00	2.00	2.00	2.00	1.42	2.00	1.00	1.62	0.29			
Porterville	Edge	2.00	2.00	2.01	2.00	0.80	2.00	1.26	0.80	2.00	1.00	2.00	2.00	1.66	0.30			
De Meul	Unsuitable	0.58	0.51	0.53	0.79	1.10	0.96	1.17	1.36	1.26	2.00	2.00	0.42	1.06	0.49			
Hankey	Core	2.00	1.24	1.01	1.42	1.69	0.42	1.68	1.24	1.00	1.19	0.49	2.00	1.28	0.38			
Kenton	Core	2.00	2.00	2.01	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	0.00			
Uitenhage	Edge	0.75	0.93	0.41	0.49	0.40	0.39	0.32	0.36	0.50	0.79	-0.04	1.00	0.52	0.54			
Salem	Edge	0.90	1.01	0.24	0.59	0.28	0.15	0.41	0.22	0.85	0.93	0.69	0.42	0.56	0.54			
Kaapsehoop	Edge	2.00	1.36	1.82	1.34	0.54	0.68	0.68	0.69	0.42	1.00	1.24	2.00	1.15	0.48			
Sokuhlumi	Unsuitable	2.00	2.00	2.14	1.68	1.69	0.42	1.00	2.00	2.00	1.00	2.00	2.00	1.66	0.32			

type would have an equal number of cells with *A. longifolia* present or absent. In contrast, other vegetation types such as shale renosterveld, thicket and thornveld had significantly fewer cells occupied than expected (only one exception, but sample size was small, see Table 2). Similarly, across all QDG cells, subdivided cells with sandstone, shale or quartzite fynbos, the percentage of cells with *A. longifolia* recorded as belonging to the densest subjective density category ranged between 6.7% and 35.7%, while all other vegetation types were < 2.7%.

At a national scale, vegetation type also seems to influence *A. longifolia*'s occupancy (Fig. 2). Extensive, apparently climatically suitable areas (e.g. $\sim 3 \times 3$ QDG cells on the West Coast of the Western Cape) were not occupied by the weed. Overlaying the national occupancy of *A. longifolia* on the major biomes of South Africa (Low & Rebelo, 1998) revealed that the majority of occupied QDG cells were found in the Fynbos Biome and were clustered together. Savanna and Grassland were the only other biomes with more than a single occupied QDG cell (Fig. 2b).

DISCUSSION

Overall, the scale–area curve approach proved useful for quantifying the spatial structure of an invasive plant species and assessing its invasive potential across its introduced range. Prior to this study, the fine and intermediate scale distribution and abundance of *A. longifolia* populations' across South Africa were unknown, with only course scale (QDG) occupancy information being available (Henderson, 2001). Furthermore, the information gathered here covers a range of scales from an individual plot to the entire landscape. Consequently, curve shape was expressed from large to small spatial scales, making it possible to describe complex multi-scale patterns in the occupancy and abundance of an invasive species, and consequently, its ecological importance as an invasive in a given landscape (i.e. QDG cell) (see also With, 2002). For example, a steep section of the scale–area curve, indicated by large b_{ij} values (1.5–2.0; or $D_{ij} < 1$), at large scales (2.5–25.0 km) means the invasive species is not widely distributed across the landscape. In turn, a shallow curve ($b_{ij} = 0-0.5$; or $D_{ij} > 1$) at small scales (2.5–25.0 m) indicates the species is contiguously distributed and abundant within plots where it does occur. Control efforts would thus be limited to specific areas within the landscape but could still mean substantial numbers of trees that need to be removed from occupied plots. In contrast, a consistently shallow curve across scales would indicate simultaneous high local abundances and an extensive regional distribution or 'double trouble' (Gaston, 1999).

Constructing scale–area curves for QDG cells representing different range categories across the national range was also informative. Marked variation in the occupancy and abundance of *A. longifolia* recorded within QDG cells sampled was not well explained by range category position, with opposite patterns being documented in different zones of the national distribution. For the Western Cape, flat curves in the core of

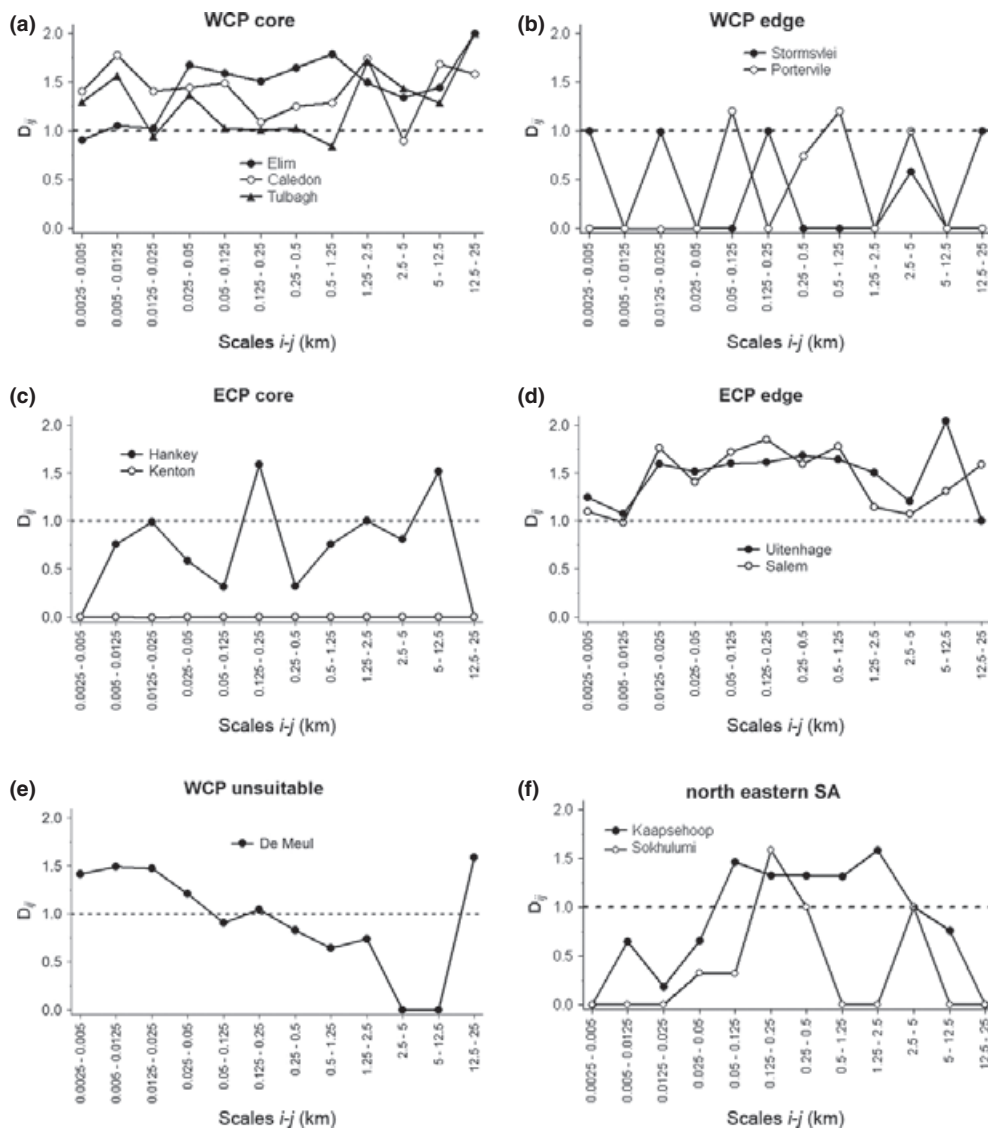


Figure 4 *Acacia longifolia* scale specific box-counting fractal dimensions (D_{ij}) for all quarter degree grid surveyed (linear resolution from ~ 25 km to 2.5 m). D_{ij} values > 1 indicate high occupancy across scale, while values < 1 indicate low occupancy.

the range versus steep curves at the edge suggest that *A. longifolia*'s regional range has reached an equilibrium and is unlikely to spread (see Brown, 1984; Brussard, 1984; Gaston, 2003; Guo *et al.*, 2005). Although the Western Cape regional range does support the idea of an abundant centre distribution (see e.g. Sagarin & Gaines, 2002; Sagarin *et al.*, 2006), this pattern did not hold for any other regional range surveyed in this study. Clearly, there is no general relationship between range position category and slope of the scale-area curve for *A. longifolia*. This means that national occupancy patterns cannot be used to predict landscape spatial structure when QDG cells are classified by range category.

Climatic suitability of sampled QDG cells also failed to explain all spatial structure patterns recorded. Given that some cells, predicted to be suitable on the basis of the climate envelope model (Rouget *et al.*, 2004), were found to be

unoccupied, while others, deemed climatically unsuitable, were in fact occupied, indicates that alternative explanations need to be sought for those patterns not adequately explained by climatic envelopes. The sole occupied unsuitable edge cell in the Western Cape that had unexpectedly high occupancy and abundance at the fine and micro scales was confined to a distinct highly suitable riverine-site. This supports the idea that although *A. longifolia*'s occupancy is strongly limited in unsuitable QDG cells, if it reaches favourable habitat (that is per definition scarce at the landscape scale outside a species' range; Holt & Keitt, 2000), occupancy or abundance can be high at local scales. Nonetheless, the importance of climatic suitability is evident from the majority (3 of 5) of recorded unsuitable (previously occupied) QDG cells that contained no *A. longifolia* individuals during resurveying in this study. Also, consistent with predictions, unsuitable edge cells, where

Table 2 Presence–absence and subjective density estimate of *Acacia longifolia* after dividing quarter degree grids into 10 rows by 10 columns (100 cells).

QDG cell Vegetation type	<i>n</i>	None	L	M	H	% cells occupied	χ^2	% occupied cells with H
Elim								
Ferricrete Fynbos	44	27	5	5	7	38.6	2.27	15.9
Inland Salt Pan	7	7	0	0	0	0.0	7.00**	0.0
Limestone Fynbos	9	9	0	0	0	0.0	9.00**	0.0
Sandstone Fynbos	24	6	1	8	9	75.0	6.00*	37.5
Shale Renosterveld	11	9	1	1	0	18.2	<u>4.45*</u>	0.0
Caledon								
Sandstone Fynbos	27	13	6	4	4	51.9	0.04	14.8
Shale Fynbos	13	10	0	2	1	23.1	3.77	7.7
Shale Renosterveld	60	51	8	0	1	15.0	29.40***	1.7
Tulbagh								
Alluvium Fynbos	24	17	6	1	0	29.2	<u>4.17*</u>	0.0
Sandstone Fynbos	28	13	8	4	3	53.6	0.14	10.7
Shale Fynbos	11	6	3	0	2	45.5	0.09	18.2
Shale Renosterveld	37	29	5	2	1	21.6	11.92***	2.7
Uitenhage								
Alluvial Vegetation	6	6	0	0	0	0.0	6.00*	0.0
Sandstone Fynbos	45	20	11	11	3	55.6	0.56	6.7
Shale Renosterveld	6	6	0	0	0	0.0	6.00*	0.0
Thicket	35	35	0	0	0	0.0	35.00***	0.0
Salem								
Quartzite Fynbos	28	17	3	2	6	39.3	1.29	21.4
Thicket	7	5	2	0	0	28.6	1.29	0.0
Thornveld	63	55	6	1	1	12.7	35.06***	1.6

L, M and H refer to low, medium and high *A. longifolia* density, respectively (see text).

A χ^2 analysis on the presence and absence of the weed for each vegetation type was performed to determine any possible vegetation type preference. *, ** and *** indicate significance between categories at $P < 0.05$, 0.01 and 0.001. Underlined values were non-significant after column wide step-up false discovery rate (FDR) correction at the 0.05 level.

A. longifolia was still present, had low occupancy at the landscape scale.

Here, we propose habitat suitability as an alternative explanation for the observed spatial structure of *A. longifolia*. At the QDG scale, the occupancy of *A. longifolia* was clearly influenced by the vegetation type present in a cell. If sandstone fynbos was present, *A. longifolia* had a better than 50% chance of being present. This was also true for most other fynbos vegetation types, although patterns were less marked. In stark contrast, other vegetation types such as Shale Renosterveld, Thicket and Thornveld had a very low occurrence of *A. longifolia*. Our findings suggest that within a landscape, vegetation type present will influence spatial structure patterns independently from climatic suitability. In many cases, especially in the climatically suitable areas of the western zone, despite QDG cells being homogenous with respect to climatic suitability, heterogeneity in vegetation type and *A. longifolia* occupancy were observed, the latter being well correlated (see Table 1). For the sole suitable edge cell sampled in north-eastern zone, both climatic suitability and suitable vegetation were severely limiting. Finally, high occupancy and abundance observed within the two southern zone edge cells (comparable to western zone core cells) are possibly because of suitable

vegetation (sandstone fynbos or quartzite fynbos) being surrounded by unsuitable vegetation (e.g. thicket or thornveld) (see Table 1).

Patterns observed at a national scale provide further support that vegetation type, in addition to climate, is important in determining *A. longifolia*'s distribution. The Fynbos Biome overlapped well with *A. longifolia*'s national occupancy, areas of contiguous occupancy almost exclusively being limited to this biome. In contrast, nowhere in north eastern South Africa was occupied QDG cells bordered by more than one occupied neighbouring cell. Furthermore, QDG cells sampled in the Western Cape all fell within the Fynbos Biome, whereas cells sampled in the southern region lay on the boundary between the highly suitable Fynbos Biome and other less suitable biomes, such as Albany Thicket (Low & Rebelo, 1998). Here, the fragmented availability of suitable habitat explains the contrast between western and southern South Africa as seen in the scale–area curves described for sampled core and edge QDG cells. In fact, the apparent continuous QDG occupancy in southern South Africa (Fig. 2) may be an artefact of spatial resolution (i.e. Levin, 1992), with QDG cells being far larger than the small portion of suitable habitat they incorporate (see also Witte *et al.*, 2008). The close correspondence between

A. longifolia's occupancy and the Fynbos Biome, rather than core or edge QDG-category, suggests that both climate and geology, the primary determinants of vegetation type in South Africa (e.g. Mucina *et al.*, 2005), are important factors in determining its distribution.

One caveat to the regional range patterns documented here is that the QDG cells were not randomly selected, and the cells surveyed are thus not necessarily representative of other QDG cells in the same range categories. Rather, cells with adequate road access (more than 80% of intermediate scale cells could be surveyed directly) were selected to allow more accurate surveying of occupancy at the within QDG scale. However, from observations, it was clear that *A. longifolia* growing in drier areas was strictly limited to permanent water courses. If during surveying these favourable areas could not be accessed, occupancy would be greatly under estimated. Also, because this bias applies equally to all surveyed QDG cells, the non-random selection of cells does not invalidate range-position category comparisons. Finally, since the aim was to use occupancy data of a QDG cell surveyed at several scales to predict the state of invasion within that cell, the non-random selection procedure used was a more appropriate method to allow comparison of equal-sized areas with different range positions.

Simultaneously recording the range structure of *A. longifolia*'s biological control agent provides some insight into the wasp's reported efficacy in reducing the spread of its host. The complete overlap in occurrence between *T. acaciaelongifoliae* and *A. longifolia* at least partly reflects the large number of original introductions of the control agent by Dennill (1987) and subsequent re-distribution by state organizations (Plant Protection Research Institute) and members of the public from original release sites (Hoffman, 2001). However, this agent appears to be highly vagile (see McGeoch & Wossler, 2000) as indicated by its presence on isolated trees in QDG cells neighbouring original release sites (> 25 km away). What is astounding was that during more than 100 days of field surveys, 99.9% of *A. longifolia* trees (circumference > 15 cm) encountered had *T. acaciaelongifoliae* galls present, irrespective of tree density.

Thus, assessing the value of biological control provided by *T. acaciaelongifoliae* based on the distribution patterns of its host plant is difficult. The high occupancy at all fractal dimensions within the range core in the Western Cape and range edge in the Eastern Cape, suggests that *T. acaciaelongifoliae* is not successfully reducing locally dense populations of the *A. longifolia* or at least has not performed so over the past c. 20 years. The absence of high density populations of *A. longifolia* from north-eastern South Africa also suggests that climate and habitat suitability limit the geographic range of this invasive tree species, and that its biological control agent may have a secondary role.

In conclusion, the use of the scale–area curve technique to assess the distribution, abundance, as well as likelihood of further invasion of alien species, is significant. If combined with remote sensing techniques (Richardson & Pyšek, 2008), the scale–area curve technique could be an easier method to assess variation in the distribution and abundance of an

invasive species, and consequent control effort required, at least for species easily distinguished from the landscape matrix. In addition, scale–area curves can describe patterns indicative of invasion risk (continuous occupancy at the scale in question) of alien species before they become naturalized, one of the fundamental problems with monitoring the early spread of invasive species (Gaston, 1999).

ACKNOWLEDGEMENTS

Farmers, landowners and residents from the Western Cape, Eastern Cape, Mpumalanga and Gauteng are thanked for allowing or assisting with surveys; CapeNature and Eastern Cape Department of Economic Affairs, Environment and Tourism for supplying collection permits; T.F. Lado and S. Kritzingner for integral assistance during field work, L. Henderson for *A. longifolia* quarter degree grid data, Working for Water for providing geographic information on alien plant clearing in South Africa, M. Rouget for providing *A. longifolia* climate envelope data, Ş. Procheş for providing biome GIS data, H. Terrapon for assistance with extracting GIS vegetation data, and J.R.U. Wilson for stimulating discussion; C.L. Seymour, J.F. Colville and three anonymous referees are thanked for useful comments on previous drafts of the article. The Claude Leon Foundation is thanked for funding the Post-doctoral fellowship of RV.

REFERENCES

- Arim, M., Abades, S.R., Neill, P.E., Lima, M. & Marquet, P.A. (2006) Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences of the USA*, **103**, 374–378.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.
- Boucher, C. & Stirton, C.H. (1987) *Acacia longifolia* (Andr.) Willd. *Plant Invaders, Beautiful but Dangerous* (ed. by C.H. Stirton), pp. 44–47. Department of Nature and Environmental Conservation of the Cape Provincial Administration, Cape Town.
- Brewer, A. & Gaston, K.J. (2002) The geographical range structure of the holly leaf-miner. I. Population density. *Journal of Animal Ecology*, **71**, 99–111.
- Brown, J.H. (1984) On the relationship between abundance and distribution of a species. *American Naturalist*, **124**, 255–279.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.
- Brussard, P.F. (1984) Geographic patterns and environmental gradients: the central-marginal models in *Drosophila* revisited. *Annual Review of Ecology and Systematics*, **15**, 25–64.
- Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Dennill, G.B. (1987) *The biological control of the weed Acacia longifolia* by the gall wasp *Trichilogaster acaciaelongifoliae*: a

- study of plant insect interaction. Ph.D. Thesis, University of Cape Town, Cape Town.
- Dennill, G.B., Donnelly, D., Stewart, K. & Impson, F.A.C. (1999) Insect agents used for biological control of *Acacia* species and *Paraserianthes lophantha* (Willd) Nielsen (Fabaceae) in South Africa. *African Entomology, Memoir*, **1**, 45–54.
- Foxcroft, L.C., Richardson, D.M., Rouget, M. & MacFadyen, S. (2009) Patterns of alien plant distribution at multiple spatial scales in a large national park: implications for ecology, management and monitoring. *Diversity and Distributions*, **15**, 367–378.
- García, L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos*, **105**, 657–663.
- Gaston, K.J. (1999) Implications of interspecific and intraspecific abundance–occupancy relationships. *Oikos*, **86**, 195–207.
- Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Gaston, K.J. & Lawton, J.H. (1990) Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos*, **75**, 211–220.
- Guo, Q., Taper, M., Schoenberger, M. & Brandle, J. (2005) Spatial-temporal population dynamics across species range: from centre to margin. *Oikos*, **108**, 47–57.
- Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of a species. *Historical and Geographical Determinants of Community Diversity* (ed. by R. Ricklefs and D. Schluter), pp. 108–116. University of Chicago Press, Chicago.
- Hartley, S. & Kunin, W.E. (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, **17**, 1559–1570.
- Hartley, S., Kunin, W.E., Lennon, J.J. & Pockock, M.J.O. (2004) Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society of London B*, **271**, 81–88.
- Hassan R., Scholes R. and Ash N. (Eds) (2005) *Ecosystems and Human Well-Being: Current State and Trends*, Vol. 1. Findings of the Conditions and Trends Working Group of the Millennium Ecosystem Assessment. Island Press, Washington, DC.
- He, F. & Gaston, K.J. (2003) Occupancy, spatial variance, and the abundance of species. *American Naturalist*, **162**, 366–375.
- Henderson, L. (2001) *Alien Weeds and Invasive Plants: A Complete Guide to Declared Weeds and Invaders in South Africa*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, South Africa, Pretoria.
- Hengeveld, R. (1990) *Dynamic Biogeography*. Cambridge University Press, Cambridge.
- Hoffman, J.H. (2001) *The Long-Leaved Wattle Bud Galling Wasp*. Available at: <http://www.arc.agric.za/home.asp?PID=2901&ToolID=65&ItemID=2475> (accessed 30 Sept 2009).
- Holt, R.D. & Keitt, T.H. (2000) Alternative causes for range limits: a metapopulation perspective. *Ecology Letters*, **3**, 41–47.
- Johnson, C.N. (1998) Species extinction and the relationships between distribution and abundance. *Nature*, **394**, 272–274.
- van Kleunen, M. & Richardson, D.M. (2007) Invasion biology and conservation biology: time to join forces to explore the links between species traits and extinction risk and invasiveness. *Progress in Physical Geography*, **31**, 447–450.
- Kunin, W.E. (1998) Extrapolating species abundance across spatial scales. *Science*, **281**, 1513–1515.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Low, A.B. & Rebelo, A.G. (1998) *Vegetation of South Africa, Lesotho and Swaziland*. South African Department of Environmental Affairs and Tourism, Pretoria.
- Macdonald, I.A.W. & Jarman, M.L. (1984) *Invasive Alien Organisms in the Terrestrial Ecosystems of the Fynbos Biome, South Africa*. South African National Science Progress Report, No. 85, CSIR, Pretoria.
- McGeoch, M.A. & Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, **73**, 506–516.
- McGeoch, M.A. & Wossler, T.C. (2000) Range expansion and success of the weed biocontrol agent *Trichilogaster acaciaelongifoliae* (Froggatt) (Hymenoptera: Pteromalidae) in South Africa. *African Entomology*, **8**, 273–280.
- Mucina, L., Rutherford, M.C. & Powrie, L.W. (2005) *Vegetation Map of South Africa, Lesotho and Swaziland, 1–1,000,000 Scale Sheet Maps*. South African Biodiversity Institute, Pretoria.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brookes, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.
- Richardson, D.M. & Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, **14**, 161–168.
- Richardson, D.M., Macdonald, I.A.W., Holmes, P.M. & Cowling, R.M. (1992) Plant and animal invasions. *The Ecology of Fynbos: Nutrients, Fire and Diversity* (ed. by R.M. Cowling), pp. 271–308. Oxford University Press, Cape Town.
- Rouget, M., Richardson, D.M., Nel, J.L., Maitre, D.C., Ego, B. & Mgidi, T. (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. *Diversity and Distributions*, **10**, 475–484.
- Sagarin, R.D. & Gaines, S.D. (2002) The “abundant center” distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, **21**, 524–530.
- Shaughnessy, G.L. (1980) *Historical ecology of alien woody plants in the vicinity of Cape Town, South Africa*. Ph.D. Thesis, School of Environmental Studies, University of Cape Town, Cape Town.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Thuiller, W., Richardson, D.M., Rouget, M., Procheş, Ş. & Wilson, J.R.U. (2006) Interactions between environment,

- species traits and human uses describe patterns of plant invasion. *Ecology*, **87**, 1755–1769.
- Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.
- van Wilgen, B.W., de Wit, M.P., Anderson, H.J., Le Maitre, D.C., Kotze, I.M., Ndala, S., Brown, B. & Rapholo, M.P. (2004) Costs and benefits of biological control of invasive alien plants: case studies from South Africa. *South African Journal of Science*, **100**, 113–122.
- Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.
- Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11–22.
- With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**, 1192–1203.
- Witte, J.-P.M., He, F. & Groen, C.L.G. (2008) Grid origin affects scaling of species across spatial scales. *Global Ecology and Biogeography*, **17**, 448–456.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice-Hall, New Jersey.

BIOSKETCHES

Ruan Veldtman works in the field of applied biodiversity research. His particular interests include ecological entomology, plant–insect interactions, pollination ecosystem services and biological control of plant invasions.

Steven L. Chown works in the fields of macroecology, macrophysiology and community ecology. He has a long-standing interest in the ecology, physiology and evolution of the biotas of the islands of the Southern Ocean.

Melodie A. McGeoch works in the field of spatial ecology and conservation. Her particular interests include bioindication and the impacts of global environmental change on protected areas.

Author contributions: R.V., S.L.C. and M.A.M. conceived the ideas; R.V. collected and analysed the data and led the writing.

Editor: Mark Robertson