RESEARCH ARTICLE

Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem

Jesse M. Kalwij · Suzanne J. Milton · Melodie A. McGeoch

Abstract Disturbed habitats are often swiftly colonized by alien plant species. Human inhabited areas may act as sources from which such aliens disperse, while road verges have been suggested as corridors facilitating their dispersal. We therefore hypothesized that (i) houses and urban areas are propagule sources from which aliens disperse, and that (ii) road verges act as corridors for their dispersal. We sampled presence and cover of aliens in 20 plots (6 × 25 m) per road at 5-km intervals for four roads, nested within three localities around cities ($n = 240$). Plots consisted of three adjacent nested transects. Houses ($n = 3,349$) were mapped within a 5-km radius from plots using topographical maps. Environmental processes as predictors of alien composition differed across spatial levels. At the broadest scale road-surface type, soil type, and competition from indigenous plants were the strongest predictors of alien composition. Within localities disturbance-related variables such as distance from dwellings and urban areas were associated with alien composition, but their effect differed between localities. Within roads, density and proximity of houses was related to higher alien species richness. Plot distance from urban areas, however, was not a significant predictor of alien richness or cover at any of the spatial levels, refuting the corridor hypothesis. Verges hosted but did not facilitate the spread of alien species. The scale dependence and multiplicity of mechanisms explaining alien plant communities found here highlight the importance of considering regional climatic gradients, landscape context and road-verge properties themselves when managing verges.

Keywords Anthropogenic disturbance · Exotics · Invasion · Invasive species · Karoo · Habitat conduits · Road ecology · Seed dispersal · South Africa

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Introduction

Habitat corridors may improve population persistence by facilitating the exchange between populations and the colonization of suitable habitat (Beier and Noss 1998; Gonzalez et al. 1998), and by directing the movement of propagules to habitats with a relatively high survival probability (Wenny 2001). Conservation measures, therefore, often aim at connecting isolated populations through habitats corridors, reducing the effect of local extinctions (e.g., Hazell

and Gustafsson 1999). However alien plants, such as invasive and alien species or noxious weeds, may also profit from such corridors. This potentially compromises the conservation value of these habitats and the adjacent matrix (Procheş et al. 2005). The most widely available linear habitats in human-influenced ecosystems are roadside verges, i.e., strips of habitat situated between the road surface and adjacent land. The corridor function of road verges is thus of growing interest to ecologists and conservation practitioners (Spellerberg 1998; Saarinen et al. 2005; Sýkora et al. 2002).

Road verges may play a constructive role as habitat reserves for native species (Esler and Milton 2006; Forman 2003), particularly if less affected by anthropogenic disturbance than adjacent land (Spooner and Lunt 2004). They may also act as effective habitat corridors, as has been shown for various mobile species in observational studies (e.g., Ries et al. 2001; Saarinen et al. 2005). However, verges are commonly affected by various anthropogenic disturbances and edge effects. This may result in colonization and eventually dominance of verges by disturbance-adapted alien species, which establish readily in disturbed habitats and have high seed production (Pauchard and Alaback 2004; Hansen and Clevenger 2005). Once established, populations of alien species may spread rapidly along the continuous habitat provided by the road verge, particularly along those verges that are disturbed as a result of road construction and management practices (Christen and Matlack 2006). High propagule pressure from alien-dominated verges may also lead to invasion of adjacent land, and spread of alien plant species across the landscape (Richardson et al. 2000; Von Holle and Simberloff 2005).

The role of road verges as either habitat reserve or invasive species reservoir and conduit is likely to be ecosystem and management dependent (Von Holle and Simberloff 2005). In arid ecosystems, where water resources are limited and plants have a relatively low growth and reproduction rate, verges are especially susceptible to invasion due to road construction and verge management related disturbances (Spellerberg 1998), to increased fire frequency and intensity (Milberg and Lamont 1995), and to increased water and nutrient input as a result of road surface run-off (Milton and Dean 1998; O'Farrell and Milton 2005). While it has been

well documented that verges in arid to semi-arid ecosystems are commonly colonized by alien species (e.g., Gelbard and Belnap 2003; Pauchard and Alaback 2004), the demographic processes of road-verge invasion are still little studied (Christen and Matlack 2006).

Urban, agricultural, and other areas with high levels of human activity often serve as sources of alien and invasive species propagules (Pauchard and Alaback 2004; Milton and Dean 1998; Larson 2003; Qian and Ricklefs 2006). The invasion process may thus result in a spatial distribution of alien species with highest occurrences and abundances near urban centers (Arévalo et al. 2005; Grapow and Blasi 1998), farm houses (Dauer et al. 2007), or adjacent to agroecosystems (Gelbard and Belnap 2003; O'Farrell and Milton 2005; Johnston and Johnston 2004; Wester and Juvik 1983; Rentch et al. 2005). The process of dispersal and colonization is likely to follow a Poisson or negative binomial distribution from source to sink, reflected by an advancing wave of high to low richness and abundance of alien species (Levin et al. 2003; Christen and Matlack 2006). However, both the pattern of richness and abundance and the processes underlying them are difficult to observe directly or to quantify in field experiments as they have various distinct spatial and temporal components (Christen and Matlack 2006; Nathan 2006). Bullock and Clarke (2000), for example, showed that seed dispersal of *Erica* species was best described as a combination of two functions: one describing a short distance seed rain and the other describing the long distance dispersal. Although long distance dispersal events are rare and difficult to quantify in field experiments, their effect on species dispersal rate may be disproportionally important (Nathan 2006; Von der Lippe and Kowarik 2007). Spatially explicit analysis of colonization patterns is therefore required to control for the spatiotemporal limitations of observational and experimental studies on long distance seed dispersal (Crawley and Brown 2004; Spooner et al. 2004).

Here we test the hypothesis that road verges in an arid ecosystem act as conduits for the dispersal of alien plant species originating from human-inhabited areas. To determine if human population density affects the distribution pattern of alien species communities we distinguished between potential propagule dispersal from urban areas (highly

transformed, densely human populated urban centers) and single anthropogenic structures (sparsely distributed houses along roadways between urban centers). We hypothesized that alien plant richness and cover were negatively related to (i) distance from urban areas, (ii) distance from anthropogenic structures, and (iii) distance from road edge. We adopted a spatially hierarchical sample design to examine correlates of alien plant community patterns, i.e., across the region (Nama-Karoo), within localities (around urban centers), and within individual roads.

Methods

Study area

The study area was located between 28°56′–32°33′S and 21°32′–25°56′E in the Upper and Lower Karoo bioregion of the Nama-Karoo biome of South Africa (Mucina and Rutherford 2006), with annual precipitation varying between 125–410 mm (Lynch 2003). The Nama-Karoo's arid ecosystem is dominated by drought-adapted shrubs and herbs, with drought-tolerant indigenous grass species. The main land usage is low-intensity sheep grazing. Three localities were selected, around the towns of Beaufort West, Prieska, and Middelburg, in such a way that each urban area (>10,000 inhabitants) was centrally located with no other urban areas present within a 200-km radius (Fig. 1). Within each locality four road stretches of 100 km (two tarred and two graveled roads with assumed different disturbance regimes) were selected that each originated from the urban area.

Sampling

Plots (6 × 25 m) were sampled at 5-km intervals on road verges along 12 stretches of 100 km of road. Plots were sampled on alternate sides of roads in September 2005 or May 2006. Each plot ($n = 240$) consisted of three adjacent, nested transects of 2 × 25 m at 0, 2, and 4-m distance from the road surface edge respectively (Fig. 1, bottom). The list, definition, and taxonomic nomenclature of alien plant species followed Germishuizen and Meyer (2003). Alien species presence and cover was recorded
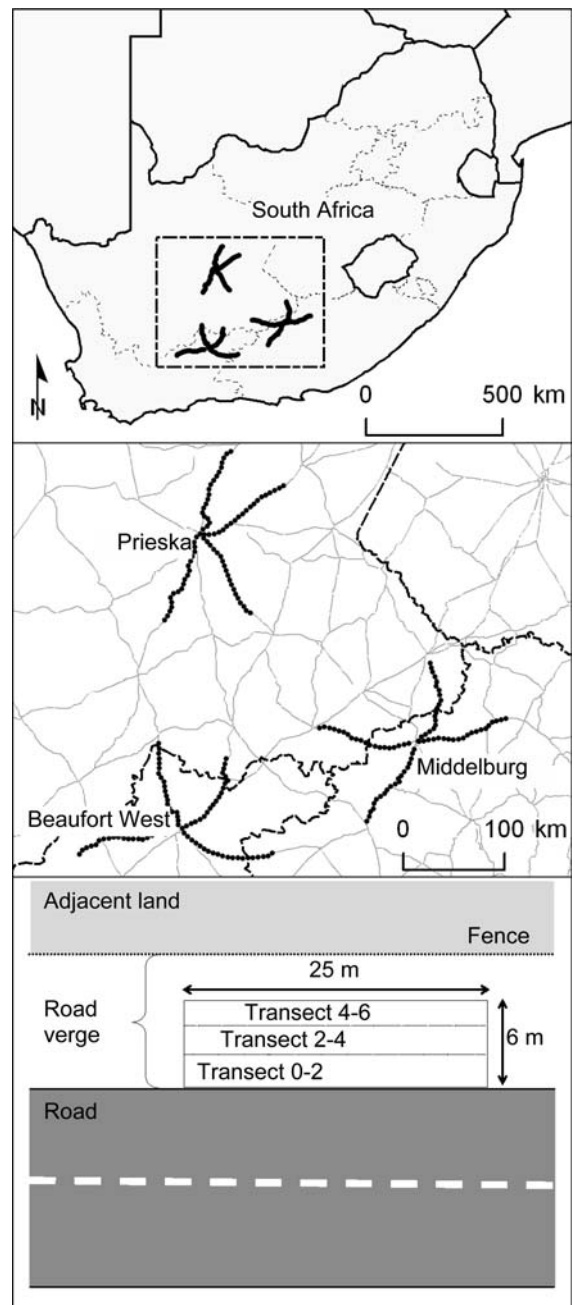

Fig. 1 Study area in the Nama-Karoo biome of South Africa (top). This area contained three localities within which four roads were nested (center). Each road included 20 plots at 5-km intervals and consisted of three 2 × 25 m adjacent nested transects (below)

for each nested transect and for the entire plot following the Braun-Blanquet approach of visual cover estimation (Mueller-Dombois and Ellenberg

1974). As many indigenous species are geophytes or only sprout in favorable, specific conditions, we chose not to record cover for each indigenous species separately as this would have required several revisits to approach a reliable indigenous species richness estimate (Kraaij and Milton 2006). In contrast, alien species are usually vigorous growers, able to withstand unfavorable conditions. Sampling accuracy of such species can, therefore, be regarded as seasonally independent. We did not sample beyond 6 m from the road edge as our pilot study indicated that road verge management in the study area was restricted to within the 0–3 m zone.

Variables were recorded for plots as a whole and for each nested transect separately. We recorded the total percentage cover of alien plants, indigenous plants, and bare soil; assessment of the plot's soil type (fine soil (i.e., silt, clay, loam), sand, or rock); verge slope (−5–0% (verge higher than road), 0–2%, 2–5%, and >5%), and verge width (in meters) for the side of the road where the plot was located. In addition we did a qualitative assessment of anthropogenic disturbance of soil and vegetation. This included mowing, crushing or compaction by vehicles, or road construction related digging during the last growing season. These types of disturbances were classified into three disturbance categories at plot and transect level: (i) soil and vegetation disturbed, (ii) vegetation disturbed, and (iii) no clear disturbance. In addition, we classified land-use of the adjacent hinterland into the categories (i) intensive land-use, or (ii) extensive rangeland. Intensive landuse of adjacent areas comprised cattle aggregating around water points or of non-commercial small-scale cropland. Such intensively used areas are often infested by alien plants (Milton and Dean 1998). Extensive land-use comprised low-intensity grazing by sheep and cows. The plots' distance from urban area was determined using governmental road markers; permanent posts placed at a distance interval of one kilometer along roads throughout South Africa. All plots were photographed and their geographical position recorded with a handheld GPS (Garmin 12XL).

Data on annual precipitation and elevation were determined for each plot from existing data sets using ArcGIS 9.1. Spatial resolution of these data was 1 arc minute ($\sim 1{,}600 \times 1{,}850$ m) for precipitation data (Lynch 2003), and 3 arc seconds ($\sim 80 \times 92.5$ m) for elevation data (USGS 2004) respectively. All

permanent structures (including houses, barns, cottages and train stations) were digitized in a 5-km radius around each plot from 1:50,000 topographical maps (Chief Directorate of Surveys and Mapping, Topographical Maps, c1998) to determine the distance to anthropogenic structures as a measure of potential seed source proximity for alien species. The number of permanent structures was then counted per buffer area i, where $i = 0$–100, 0–200,…, 0–5,000 m ($houses_i$, hereafter referred to as house density). The Euclidean distance to the k-nearest permanent structure was determined for $k = 1, 2,\ldots, 10$ for each k-nearest permanent structure within a 5-km radius.

Data analysis

To determine which variables were related to cover and species richness of aliens we used multivariate analysis on plots as the sample unit at the regional level (including all three localities; $n = 240$ plots), and transects as sample units at the locality levels (each locality separately; $n = 240$ transects per locality). Detrended Correspondence Analysis (DCA) was used on the entire alien species dataset to assess the degree of sample heterogeneity and to identify outliers (Lepš and Šmilauer 1999). The DCA showed no evident environmental gradient or distinct clusters of transects, justifying a Canonical Correspondence Analyses (CCA) (Lepš and Šmilauer 1999). The DCA ordination also identified one alien species (*Trifolium angustifolium*) as an outlier. This species had a low frequency and did not co-occur with any other aliens in transects, and was thus omitted from multivariate analyses.

We used CCA to quantify the contribution of each environmental variable to overall variation in alien species community structure using CANOCO 4.5. We restricted the regional level CCA to environmental variables that contributed significantly to overall variation in alien species community structure using a step-wise constructed model (Lepš and Šmilauer 1999; Monte Carlo test, 1,000 permutations, $P < 0.05$), with variance inflation factors <10 (Gross 2003). Results of this CCA were interpreted using a samples-by-environmental-variables biplot in which the length of each arrow represents the proportional contribution of that particular variable to the overall CCA model (Lepš and Šmilauer 1999).

To examine the relationship between house density and alien species composition, we performed CCAs to obtain lambda-1 for all distance categories. Lambda-1 is a quantification of overall variation in community structure explained by each variable independently (Lepš and Šmilauer 1999), and was used here to examine the variation explained by house density. This was done with and without downweighting of rare species. Downweighting of rare alien species effectively weights species observations according to their relative cover rather than excluding rare alien species entirely (Lepš and Šmilauer 1999). To determine how house density was related to alien plant community structure, a CCA biplot was constructed (using no downweighting of rare species) showing how house density in each distance class was related to community structure.

To determine if alien species richness within plots ($n = 240$) could be attributed to road-specific habitat conditions or to the distance from urban areas, we fitted three-level nested Generalized Linear Models (GLM) assuming a Poisson distribution and using a logistic link function in S-Plus 6.0. We adjusted for overdispersion of errors by adopting the quasi-likelihood method to estimate the dispersion parameter from the data (Morton 1987). This method estimates the dispersion of errors as a scale parameter while fitting the model instead of assuming dispersion a priori (Myers et al. 2002). The GLMs included the variables locality, road surface type and road. The variable road was nested within road surface type, in turn nested within locality. Likewise, a GLM was fitted to test for the effect of distance from urban area on number and cover of alien plants whereby distance from urban area was nested within road surface type and road surface type was nested within locality. An F-test was used to determine which variables contributed significantly to each model and to test the statistical differences in model fit (McCullagh and Nelder 1989).

To determine if density of, and proximity to, anthropogenic structures affected cover and richness of alien species, we conducted Pearson correlations between the number of alien species per plot ($n = 240$; normally distributed) and house density (log-transformed). These correlations were calculated for increasing buffer sizes of 100-m intervals, up to a buffer of 5,000 m around each sampled plot. Likewise we calculated Pearson correlation coefficients to examine the relationship between farmhouse density and cover of alien species per plot.

To examine the relationship between proximity of anthropogenic structures (hereafter 'houses', as most structures were houses) and alien species richness, we calculated the Pearson correlation coefficients, C_p, between alien species richness per plot and distance to k-nearest house. These correlations were calculated for increasing k up to the 10th-nearest neighboring house ($n_1 = 238$, $n_2 = 237$,…, $n_{10} = 178$). Subsequently, a linear regression model was fitted to estimate the relationship between C_p and k (Quinn and Keough 2002).

To determine at the verge level if alien species richness was explained by the distance of transects from road surface edge, four-level nested GLMs were used to test the effect of distance of transects from road surface edge on alien species richness and cover ($n = 720$ transects). The same assumptions and adjustments were applied as for the three-level nested GLMs.

Results

Regional patterns

A total of 26 alien plant species were found in 225 transects (Appendix S1) nested in 48% of the plots. Of these 26 species, nine are considered invasive in South Africa (Henderson 2001). By virtue of their national status, their comparatively wide range occurrence, high frequency and cover in this study, the most important invasive species along road verges were *Salsola kali*, *Atriplex lindleyi inflata*, *Cynodon dactylon,* and *Argemone ochroleuca* (Fig. 2; Appendix S1). All recorded alien species had very patchy distributions, occurring in maximum continuous stretches of 20 km or less (out of the total 100 km possible). Only one alien species, *Sonchus oleraceus*, was as important (based on the same occurrence and frequency criteria) as the above invasive species.

The regional-level CCA separated the three localities along the first two canonical axes, although there was overlap between Prieska and Middelburg (Fig. 3). The significant environmental variables road surface type, soil type, and cover of indigenous plants (Monte Carlo test; $P < 0.05$) were most strongly

Fig. 2 Frequency
distributions for the number
of observations at 5-km
intervals from urban centers
along roads ($n = 12$) for
Salsola kali, *Atriplex
lindleyi inflata*, *Cynodon
dactylon*, and *Argemone
ochroleuca*; the four most
common invasive alien
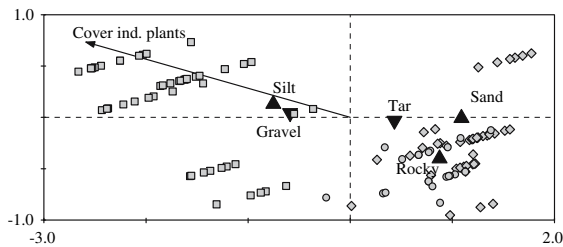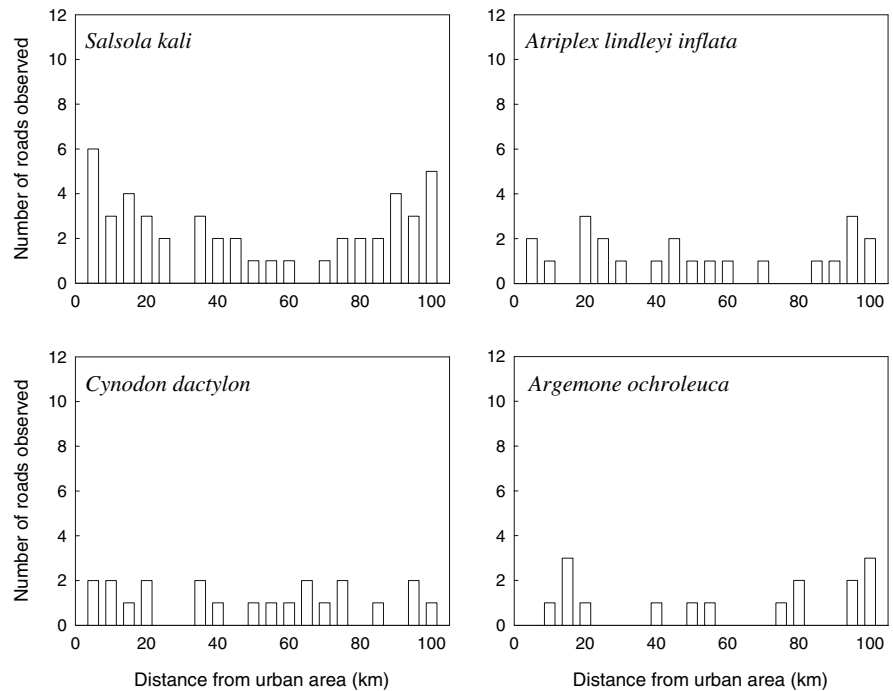species found in the Nama
Karoo

Fig. 3 Regional-level CCA biplot of alien species community
structure for sampled plots and the significant environmental
variables cover indigenous plants, soil type (silt, sand, rocky),
and road surface type (tar, gravel). Samples are displayed
according to locality (squares, Beaufort West; circles, Prieska;
triangles, Middelburg)

correlated with the first two canonical axes of the
regional-level ordination. In contrast, plot disturbance
categories, distance from urban area, and distance
from road edge did not contribute significantly to
explaining alien plant community structure across
localities. Alien species richness and cover also
differed significantly between localities (Table 1).

The relationship between alien species community
structure along road verges and house density
declined strongly with the increase in distance
category from sample plots (Fig. 4, left panel). This
relationship was strongest within the 500-m radius

around sample plots, decreased strongly with increasing distance up to 2 km, and then increased slightly
up to the observation limit of 5 km (Fig. 4, left
panel). The pattern was similar with rare species
down-weighted.

The CCA ordination of house density per distance
category showed that the contribution of house
density to alien species community structure also
depended strongly on the distance category considered (Fig. 4, right panel). While distant house
densities were mainly correlated with the first
canonical axis, nearby house densities were mainly
correlated with the second canonical axis. The arrows
of the nearby and distant house densities were nearly
orthogonal, with relatively little correlation with
housing density at middle-distances (2,000–2,600 m).

Local patterns

Since alien plant communities differed between
localities, localities were also examined separately.
At each locality a different set of environmental
variables explained alien plant community structure
best (Fig. 5). The most important environmental
variables around Beaufort West (locality with lowest
number of houses and lowest annual precipitation)

Table 1 The effects of predictor variables locality and road surface type on exotic plant species richness and cover within plots (nested analysis of deviance; $n = 240$) and within transects (nested analysis of deviance tables; $n = 720$)

| Response variable	Res. deviance/df	Res. df	F	P	Terms included	df	% deviance explained	F	P
Plot level									
Alien species richness	1.46	234	7.96	<0.0001	Locality	2	8.51	11.30	<0.0001
					Surface (locality)	3	6.48	5.73	<0.0001
Cover of alien species	2.46	234	2.49	<0.0001	Locality	2	9.10	5.18	0.0063
					Surface (locality)	3	1.83	0.69	0.5570
Transect level									
Alien species richness	1.20	714	15.09	<0.0001	Locality	2	6.83	22.61	<0.0001
					Surface (locality)	3	4.56	10.07	<0.0001
Cover of alien species	2.94	714	7.54	<0.0001	Locality	2	7.37	11.56	<0.0001
					Surface (locality)	3	4.65	4.87	0.0023
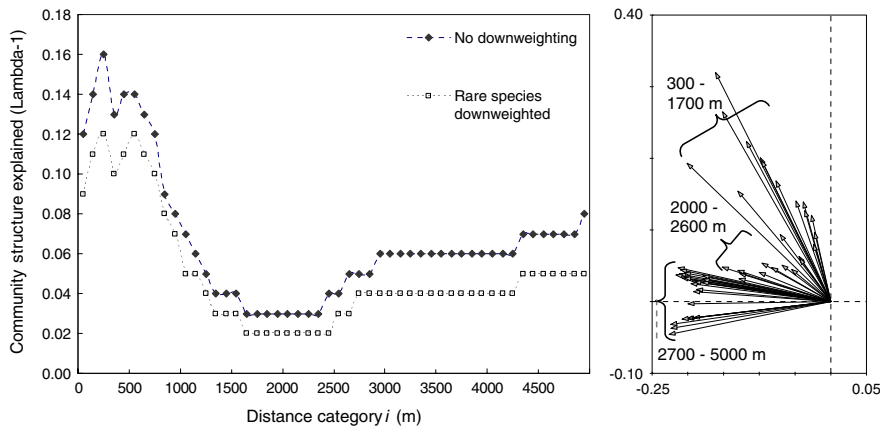
Fig. 4 Regional level alien species community structure (lambda-1) explained by housing density. The left side panel shows how downweighting of infrequent species affects the species composition within plots explained by house density. The right side panel shows the ordination scatterplot of housing density within increasing distance bands (m) under a full-model CCA of exotic species composition
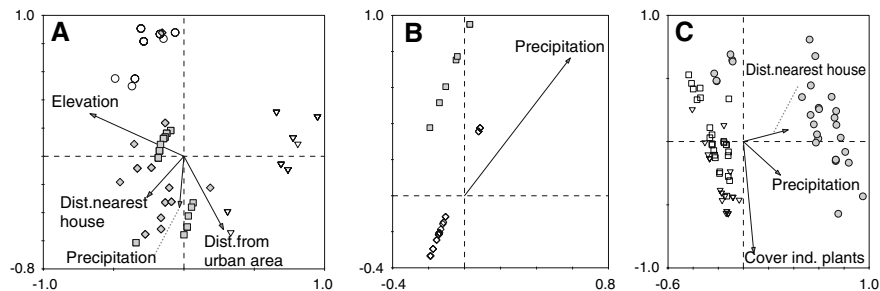

Fig. 5 Locality-level CCA biplots of transects and environmental variables for Beaufort West, Prieska, and Middelburg. Variables include annual precipitation, elevation, distance from urban area, and distance from nearest house around Beaufort West (least-populated locality), annual precipitation around Prieska (only locality near the grassland biome), and elevation, distance from nearest house, and cover indigenous species around Middelburg (only location with an elevation gradient). Open symbols are tarred and closed symbols graveled roads

were annual precipitation, elevation, distance from urban area, and distance to nearest house. Around Prieska (locality encompassing the strongest precipitation gradient) annual precipitation was the only important explanatory variable, whereas around Middelburg (locality with strongest relief and highest annual precipitation) annual precipitation, distance to nearest house, and cover of indigenous plants were important explanatory variables (Fig. 5).

There were significant differences in alien plant richness between localities and between road surface types, whereas only the locality effect was significant for cover (Table 1). The distance from urban area (nested within surface and within locality), however, never improved the model fit for alien plant richness (three-level nested GLM; $P > 0.05$) or cover ($P > 0.05$). The frequencies of the most important alien species recorded also demonstrate the absence of a relationship between distance to urban area and alien plant incidence at 5-km intervals from urban centers (Fig. 2). In addition, road (nested within surface and within locality) did not improve the model fit for alien plant richness (three-level nested

GLM $P > 0.05$) or cover ($P > 0.05$). The difference in alien species richness and cover between gravel and tar varied between localities (Fig. 6).

Density of houses in a 5-km radius around plots was more than twice as high along tarred roads as along graveled roads (Fig. 7a). The Pearson's correlation coefficients C_p between house density and alien species richness per plot also differed considerably between tarred and graveled roads, particularly at distances greater than 1 km from sample plots (Fig. 7b). Along graveled roads, alien species richness was significantly correlated ($P < 0.05$) with house density for all distance categories from sampling plots, but only between 500–1,400 m along tarred roads (Fig. 7b). Along graveled roads this relationship was strongest between 200–900 m from sample plots (Fig. 7b). No significant coefficients, C_p, were found between house density and alien plant cover (data not presented).

In addition, all Pearson's correlation coefficients C_k between alien plant richness and distance to the kth nearest house (for each $k = 1, 2,…,10$) were negative and significant (linear regression model:

Fig. 6 Alien species richness (a) and cover (b) at plot level, and alien species richness (c) and cover (d) at transect level. Each error bars ($n = 40$) represent means ± s.e.
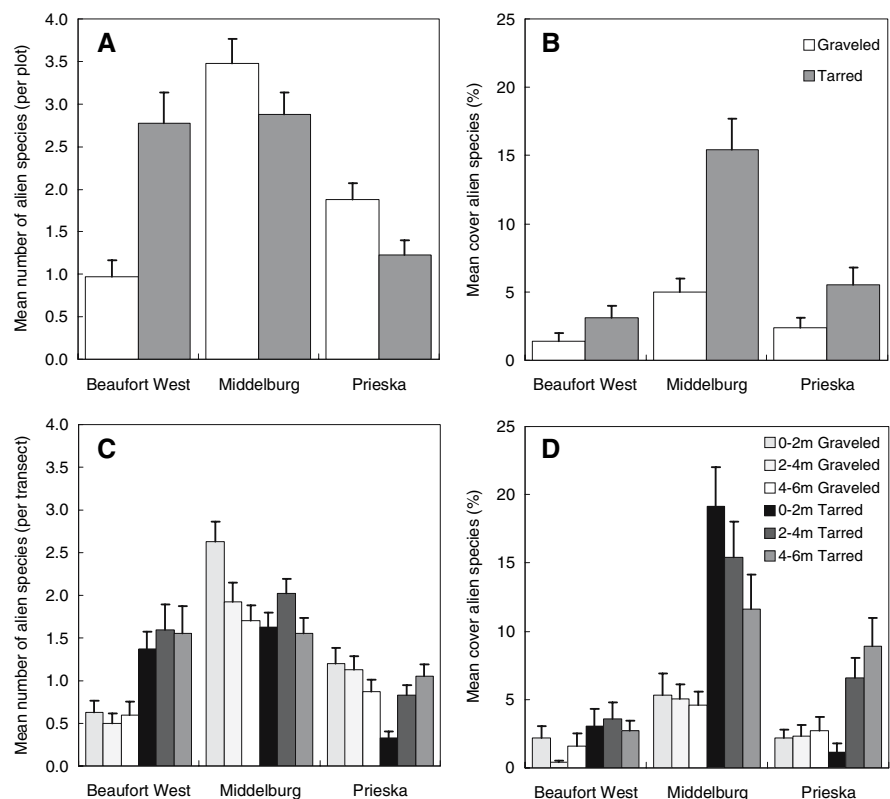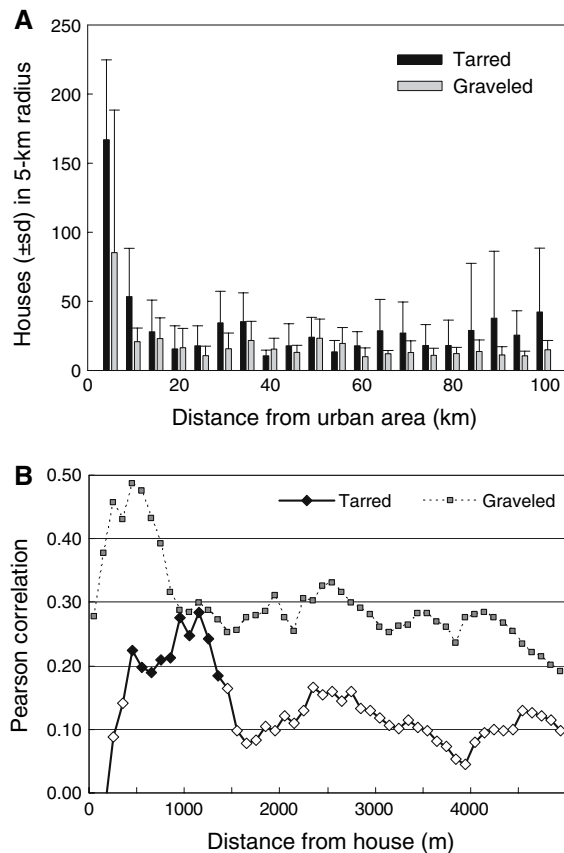
Fig. 7 (**a**) Mean number of houses (±s.d.) within a 5-km radius of plots along graveled ($n = 6$) and tarred roads ($n = 6$) against the distance of plots from urban areas, and (**b**) Pearson's correlation coefficients of the relationship between number of houses ($\log(\chi + 0.5)$ transformed) and alien species richness at the plot level ($n = 240$) with increasing distance intervals ($n = 50$) of 100 m (tarred: $n = 129$; graveled $n = 111$). Closed symbols (◆ and ■) represent Pearson's correlation coefficients with a significance level of $P < 0.05$, whereas coefficients with open symbols (◇ and □) have a significance level of $P > 0.05$

$r^2_{adj} = 0.633$, $n = 10$, $P = 0.0036$; $C_k = -0.218 - 0.010\ k$). Alien plant richness per plot thus decreased with distance from nearest house. No correlation was found between alien plant cover and kth-nearest house (data not presented).

Within road verges

At the road verge level, alien species richness and cover within transects also depended mostly on locality and road surface (Table 1; Fig. 6c, d). In agreement with the plot level analysis, variation

between roads did not contribute significantly to the model fit of either alien species richness (three-level nested GLM; $P > 0.05$) or cover ($P > 0.05$). Also, the distance of transects from urban areas or from road edge did not improve the model fit of either alien plant richness (three-level nested GLM; $P > 0.05$) or cover ($P > 0.05$). Alien plant richness was generally higher near road edges along graveled roads, whereas there was no clear pattern along tarred roads (Fig. 6c, d).

Discussion

We hypothesized that alien plant richness and cover were negatively related to (i) distance from urban areas, (ii) distance from anthropogenic structures, and (iii) distance from road edge. Our findings have led to the rejection of the first hypothesis, and acceptance of the other two. This suggests that alien species richness is influenced as much by disturbance regimes as by propagule pressure.

Distance from urban areas

The distribution of alien species in this arid ecosystem clearly demonstrates that alien propagules seldom originate and disperse from a single source (Sax and Brown 2000; Petit 2004). This finding calls into question the generality of the concept of road verges as corridors for alien plant dispersal (see also Christen and Matlack 2006). The corridor hypothesis posits that habitat corridors facilitate the movement of propagules between suitable habitat patches by directing dispersal along conduits (Levey et al. 2005; Levin et al. 2003). Such directed dispersal *sensu lato* would be evidenced by declining alien plant richness and cover, and frequency and cover of individual species, away from the primary source (Levin et al. 2003; Christen and Matlack 2006). Here we found that alien species were generally infrequent, with discontinuous distributions, and that richness and cover were not related to distance from urban centers. Instead, the findings of this study suggest that road verges in the Nama-Karoo act as suitable recipients of alien plant propagules from multidirectional sources. Because the large majority of species were infrequent, occurred at low densities and were

patchily distributed within and across roads, this provides further evidence against the conduit function of road verges in this biome for alien plant species. In contrast, our results strongly support the habitat function of road verges (*sensu* Christen and Matlack 2006) for alien plant species.

The absence of spatially continuous distributions (or 'wave fronts' in which the abundance of a species declines away from the center of its range) for alien species may merely imply that the period of opportunity for spread along verges has been too short (Christen and Matlack 2006). The function of road verges as a suitable habitat is a precursor to its function as a potential conduit, i.e., where the availability of suitable habitat followed by colonization and establishment of the alien plant species are necessary before populations begin to spread (Richardson et al. 2000). The sampling resolution of this study (plots every 5 km) may also have been too coarse to detect early development of such wave fronts. The absence of a relationship between distance from urban center and alien plant richness, cover and community structure may also be a consequence of the fact that the decline in the density of dwellings away from urban centers was not sufficiently strong (but see Fig. 7), as even a relatively low housing density along roads was significantly related with the local richness of alien plants. Nonetheless, our results do demonstrate that there is no relationship between the alien plant community along road verges and distance beyond 5 km from urban centers in this arid ecosystem.

There are few comparable road verge studies on the spatial distribution of alien plant species around urban areas (Christen and Matlack 2006). Although Cilliers and Bredenkamp (2000) found urban–rural transient vegetation types within a 10-km area around urban centers, they did not sample beyond this zone. Barton et al. (2004) showed alien species to be clustered up to 10 km around a single urban area, but did also not sample beyond this distance. Arévalo et al. (2005) found alien plants along two roads in the Canary Islands to be related to distance from urban areas, but this variable was strongly confounded by altitude because urban areas were located at or near sea level. However, we found that distance from urban centers did not explain patterns in alien plant community structure, richness or cover. The absence of a decline in alien species number or cover with

distance from urban areas could thus have been a consequence of the spatial grain of the sample design, and low sampling resolution within the 10-km radius of urban areas. Habitat edge, or ecotone, effects have commonly been shown to occur over short distances with sharp declines in the effect away from the edge (Fagan et al. 1999; McGeoch and Gaston 2000). It is possible that this general pattern may also apply to urban center—rural transitions for some alien plants.

Distance from anthropogenic structures

Although distance from urban center was not significant, local density of dwellings and distance of sampling plots from the closest houses did significantly explain patterns in alien plant community structure and species richness. This relationship was particularly strong and significant for house density and distance variables within a 1.5-km radius of the road verge. Cultivated areas such as gardens or croplands are often sources from which alien species escape (Wilson et al. 1992; Flory and Clay 2006; Milton 2004). In the arid Nama-Karoo biome, such potential sources occur virtually exclusively in the immediate vicinity of houses. Houses (and associated human activity) distributed along major roads, particularly tar roads, thus appear to act as alien plant propagule sources (see also Gelbard and Belnap 2003). Combined with the discontinuous, low frequency and low cover of the majority of species recorded, this result suggests that patterns in the alien plant community are generated predominantly by short-distance dispersal events with local human settlements as the source (although the possible contribution of long-distance dispersal events cannot be estimated here). The spatial relationship between density of man-made structures and local alien species richness therefore suggests that human-inhabited areas were indeed important sources from which alien species originated (Pauchard and Alaback 2004; Arévalo et al. 2005). Once established, an alien species population is unlikely to disappear from a verge due to the combination of a persistent seed bank and ongoing anthropogenic disturbance that favors the establishment and persistence of alien plant species (Milton 2004; Milton and Dean 1998).

Road surface type and distance from road edge

Housing density in this study was higher along tarred than along graveled roads. Gelbard and Belnap (2003) also found that invasive plant species richness and cover were higher along paved than unpaved roads, although they did not examine local housing density as a possible explanatory variable because the study was conducted in an area with apparently few houses and little development. These authors further suggest that the difference found between paved and unpaved roads results from road construction, maintenance and traffic characteristics. Indeed, tarred roads do carry more traffic than gravel roads (at least partly as a consequence of higher housing density along these roads) and the intensity of vehicle movement may also have contributed to the differences found in alien plant richness in this study between tar and gravel roads. Vehicles have been shown to collect and transfer alien species propagules along roads (Schmidt 1989; Zwaenepoel et al. 2006; Lonsdale and Lane 1994). However, the effect of road surface type on the relationship between housing density and alien species richness suggests that the spatial effect of houses reached much further along graveled than tarred roads. Differences in disturbance regimes and dispersal potential between gravel and tarred roads offer possible explanations for increased diversity of alien plant species along gravel roads. Gravel roads are graded at annual intervals in the Karoo (O'Farrell and Milton 2005). This grading involves frequent disturbance of the soil in the road reserve. Furthermore, maintenance of gravel roads involves the construction of shoulders and drains to lead water off the road surface into the road reserve, thereby generating a heterogeneous drainage pattern in roadside habitats. In contrast, drainage from tarred roads is generally channeled into storm water drains and led into drainage line rather than into the road reserve. This difference in disturbance regime and habitat heterogeneity may explain the greater diversity of alien plant species along gravel roads. Alternatively or additionally, propagule-containing mud from the surface of wet gravel roads would become attached to cars or agricultural vehicles, and for this reason more propagules are likely to be transported and shed along gravel than along tar roads (Von der Lippe and Kowarik 2007).

Conclusion

Alien plant community patterns in this arid ecosystem clearly demonstrate the scale dependence of mechanisms underlying alien plant community structure, richness and cover. Regionally, broad scale variables such as soil type were found to be important correlates of community structure (Wilson et al. 1992), as well as cover of indigenous plants (a surrogate for the degree of local disturbance; Hansen and Clevenger 2005). Correlations between alien richness or local alien composition and regional-level climatic conditions such as annual precipitation or elevation are characteristic for arid to semi-arid regions (Rouget et al. 2004; Pauchard and Alaback 2004; Wester and Juvik 1983). The explanatory value of indigenous plant cover, however, suggests that in addition to disturbance, competition may be an important factor affecting alien plant composition (Gelbard and Belnap 2003). Whereas factors explaining community structure differed between localities, within localities richness and cover differed significantly between road surface types. Finally, at the finer scale within roads, local housing density and house distance played a role in explaining alien plant species richness (Pauchard and Alaback 2004). These findings demonstrate the role of multiple mechanisms operating at several scales as determinants of alien plant communities.

Therefore, over stretches of 100 km and 5-km intervals, this study supports the habitat function of road verges in an arid ecosystem, and not the corridor function. Because verges were not found to be functioning as conduits at this scale, and to prevent their potential to do so, alien plant species in this ecosystem should be monitored at fine scales, over distances of less than 5 km. This would facilitate early detection of alien species spread along verges. The scale dependence and multiplicity of mechanisms found to explain alien plant community patterns in this study highlights the importance of considering regional and local environmental variables, the landscape context and road verge properties themselves when managing verges to minimize their role as alien plant habitats.

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